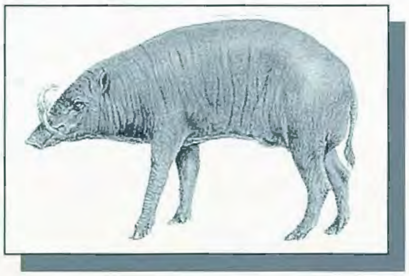
Babirusa
(Babyrousa babyrussa)



Population and Habitat Viability Assessment

Taman Safari Indonesia
Bogor, Java Barat, Indonesia
July, 1996

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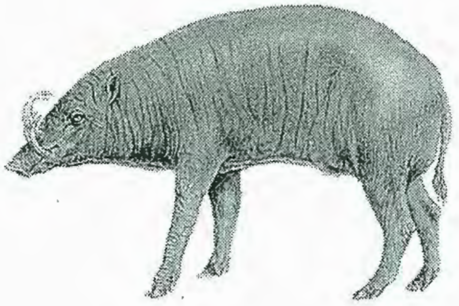
BABIRUSA

(Babyrousa babyrussa)

Population and Habitat Viability Assessment

22 - 26 July 1996

Taman Safari Indonesia
Cisarua, Java Barat, Indonesia



Jansen Manansang, Alastair Macdonald, Dwiatmo Siswomartono,
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The sponsors of the PHVA workshop were the Indonesian Directorate of Forest Protection and Nature Conservation (PHPA), Taman Safari Indonesia (TSI/PKBSI), the Singapore Zoo, the St. Louis Zoo, the Jersey Wildlife Preservation Trust, the Copenhagen Zoo, the Antwerp Zoo and Howletts & Port Lympne Wild Animal Parks.

Cover Illustration: Photo of Babirusa (*Babyrousa babyrussa*), Marisa study site, northern Sulawesi courtesy of Maurice Patry. Babirusa artwork by William L.R. Oliver.

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BABIRUSA

(*Babyrousa babyrussa*)

Population and Habitat Viability Assessment

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  Leus, K.Y.G. 1996. The habitat and diet of the Sulawesi babirusa (*Babyrousa babyrussa celebensis*). 121
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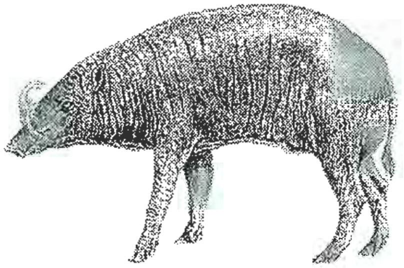
POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996



Section 1
Executive Summary And Recommendations

EXECUTIVE SUMMARY

Too few data exist to quantify the status of the babirusa but they still appear to be widely distributed on Sulawesi. However, there is little doubt that they have been in decline since the beginning of the twentieth century; and no doubt that they have declined over the 1970-1995 period, precipitously in some areas. Hunting and habitat loss have been, and continue to be, the major causes of the decline with hunting the more serious factor in most areas. The current status of the babirusa is thus a matter for serious concern with populations in small reserves and threatened with local extinction. Even the populations in large protected areas and other large forest blocks are reported to be in decline as a result of heavy hunting pressure.

This species is vulnerable due to its restricted range and the possibility of extinction from several threats including hunting, habitat loss, and possible natural catastrophes. The management and conservation objective is to maintain genetically viable, self-sustaining, free-living babirusa population(s). In order to achieve this goal, it is necessary to understand the risk factors that affect survival of the babirusa. Risk characterization is a major concern in endangered species management and a goal is to reduce the risk of extinction to an acceptable level by risk management. A set of software tools to assist simulation and quantitative evaluation of risk of extinction is available and was used as part of the Population and Habitat Viability Assessment Workshop. This technique can improve identification and ranking of risks and can assist assessment of management options.

Thirty-seven biologists, managers, and decision makers attended a Population and Habitat Viability Assessment (PHVA) Workshop in Cisarua, Indonesia at the Safari Garden Hotel on July 22-26, 1996 to apply the recently developed procedures for risk assessment and formulation and testing of management scenarios to the babirusa. The workshop was proposed by the PHPA and was a collaborative effort of the PHPA, TSI/PKBSI, and the Conservation Breeding Specialist Group (CBSG) and the Pigs and Peccaries Specialist Group of the Species Survival Commission/World Conservation Union (SSC/IUCN). The purpose was to review data from the wild and captive populations as a basis for assessing extinction risks, assessing different management scenarios, evaluating the effects of removals by hunting from the populations, evaluating available information on the taxonomy, and developing stochastic population simulation models. These models estimate risk of extinction and rates of genetic loss from the interactions of demographic, genetic, and environmental factors as a tool for ongoing management of the subspecies. Other goals included determination of habitat and capacity requirements, role of captive propagation, and prioritized research needs.

The first day consisted of a series of presentations summarizing data from the wild and captive populations. After a presentation on the PHVA process the participants formed three working groups (wild population, captive population, and population biology and modelling) to review in detail current information, to hear all ideas, and to develop management scenarios and recommendations. Stochastic population simulation models were developed and initialized with ranges of values for the key variables to estimate the viability of the wild population using the VORTEX software modelling package. Using data compiled from the literature and by consultation with workshop participants, a series of concensus baseline population values for the parameters required by the VORTEX program were developed. These were then used to model populations of several sizes.

This workshop report includes a set of recommendations for management and critical genetic and survey research on the wild and captive populations as well as sections on the history of the population, the population biology and simulation modelling of the population, and presentations made at the workshop.

RECOMMENDATIONS

Wild Population Priorities

1. The most important priority is to stop the indiscriminate and excessive hunting for Babirusa meat in Northern Sulawesi. On the long term this must be combined with a community development program by extending the existing program from the protected areas to the local people.

2. More survey work is needed in the areas for which we have insufficient data: S. E. Sulawesi, Butung and Muna, Rawa Aopa and the rest of South Sulawesi, and the Sula islands (Taliabu and Mangole).

3. There is insufficient information on babirusa population density and trends. Census work needs to be done in all areas.

4. We fully endorse the creation of a protected area around the Nantu forest (North Sulawesi).

5. Establish protected areas for the 2 subspecies that do not have a protected refuge: ***Babyrousa babyrussa togeanensis*** on the Togian islands and ***Babyrousa babyrussa babyrussa*** on Taliabu, Mangole and Buru.

6. Create a Sulawesi Endemic Wildlife Information and Study Center. The creation of this center can be based on the experience gained with a similar center (WARSI) on Sumatera

Captive Population Priorities

1. Only *Babyrousa babyrussa celebensis* should be considered for captive management.

2. A management group needs to be formed within one year to manage the captive population.

3. All institutions keeping babirusa should be required to positively identify each individual babirusa and maintain rigorous record-keeping standards.

4. Collect enough animals to achieve an effective founder base to maintain 90% heterozygosity over 100 years. The methods of collection must be up to the highest welfare standards making full use of the available expertise.

5. Holders of wild-caught babirusa must meet minimum requirements for facilities and management experience. Space for new founders needs to be created in Indonesia.

6. All wild-caught stock should remain in Indonesia. Only F1 or later generations should go to the rest of the world population.

7. Animals should only go to those world institutions that agree to join the management committee.

Modeling Group Priorities

1. Current life-table parameter estimates give a baseline babirusa population model with a growth rate potential of about 21% annually. Sensitivity analyses indicate that the proportion of adult females breeding each year may be the most important aspect of babirusa population dynamics in regards to population viability. Parameters requiring better estimation are annual female breeding success, adult mortality, and first year mortality.

2. Estimates of babirusa density and monitoring of changes in density are needed in protected areas and across Sulawesi.

3. Babirusa populations need to be managed to reduce losses from hunting to a rate of less than 15% annually. Estimates of animals killed by hunting in Central and North Sulawesi indicate that 30% of babirusa are being removed annually from these populations (equivalent to removing about 450 animals from a population of 1500). This produces simulated population declines of about 24% annually. The probability of extinction at this rate is nearly 100% within 30 years. Reducing the annual hunting rate to 20% produces a 6% annual rate of decline and a 50% probability of extinction within 85 years (See Figure 1-1). If removel of babirusa is reduced to 15% annually, the simulated population shows an average rate of increase of 2-3% per year. Adult female mortality is the most sensitive mortality parameter since this is a polygynous species. The proportion of females producing litters annually and the mean litter size are the most sensitive reproductive parameters.

Figure 1-1.
Babirusa Population Viability: Effects of Hunting on Population Persistence

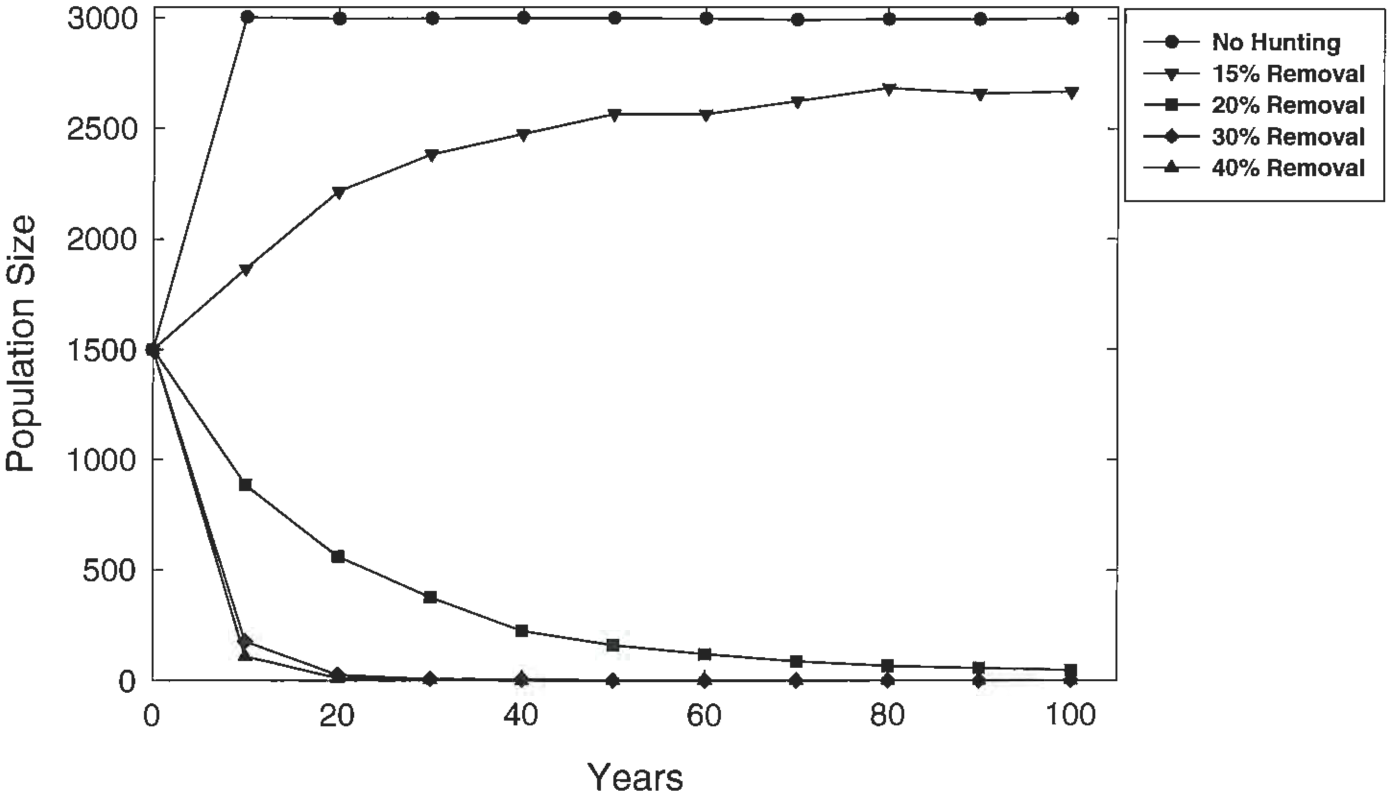
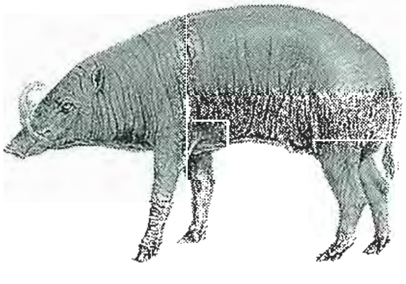


Figure 1-1. Impact of increasing levels of hunting on babirusa population viability. Time series plots of population size as a function of time (years) for simulated babirusa populations subjected to increasing levels of hunting. For these models, hunting was simulated by increasing age-specific mortality rates above the baseline values according to estimates of proportional removals of individuals from wild populations. In each model, a carrying capacity of 3000 was imposed, above which population size was truncated.

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 2
Babyrousa babyrussa: An Introduction



MINISTRY OF FORESTRY OF THE REPUBLIC OF INDONESIA
DIRECTORATE GENERAL OF FOREST PROTECTION AND NATURE CONSERVATION
Gedung Pusat Kehutanan Manggala Wanabhakti Blok IV Lt. 8, Jl. Jend. Gatot Subroto Jakarta Pusat (10270)
Telp. (021) 5730312, 5730313, Fax. (62-21) 5734818 Telex : 45996 DEPHUT IA

Jakarta, 29 March 1996

TELEFAX

No : 218/ VI-Sek / BKff /96

To : ULLYSES SEAL,
IUCN/SSC Conservation Breeding Specialist Group (CBSG)
Johnny Cake Road , Apple Valley , MN 55124, U S A

Fax : 1-612-432-2757

From : Ir Soekadji
for Director General of PHPA
Ministry of Forestry Indonesia

Subject : Babirusa/ Anoa PHVA Workshop

We would like to request the assistance of CBSG to coordinate a PHVA Workshop for the Babirusa and the Anoa in Sulawesi , Indonesia.
The best time would be sometimes in July 1996. Please contact Mr Jansen Manangsang at Taman Safari Indonesia about the details of the workshop as he might be able to organize the venue of the workshop.

As for the last workshops, we would appreciate the support of about 20 PHPA staff to attend the Babirusa and Anoa Workshop so that we can learn from the experience and be part of the process in developing a conservation action plan for Babirusa and Anoa.

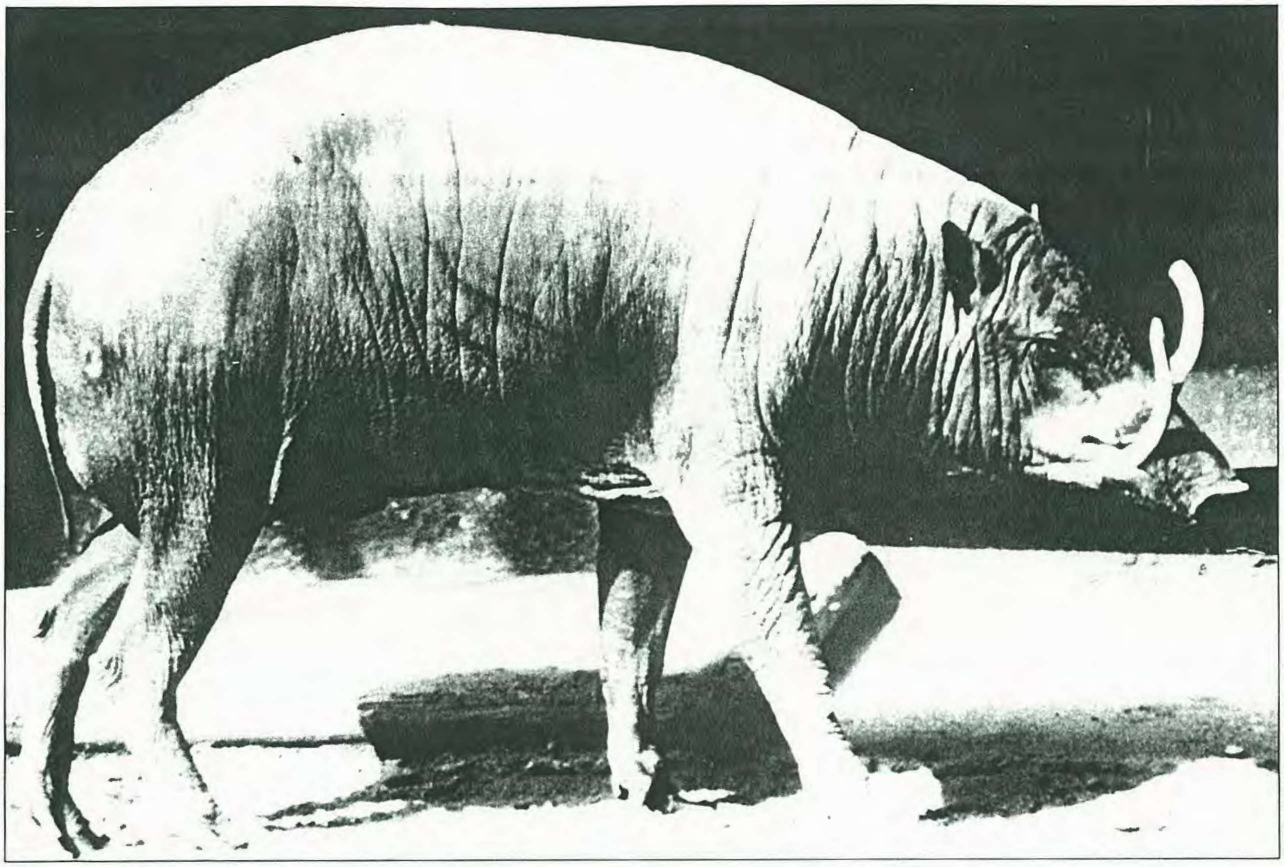
Your assistance in this very important issue in Indonesia is very much appreciated, and we look forward to hearing your reply.

Yours sincerely,

Soekadji
Secretary of the Directorate General of PHPA

cc:
Mr Jansen Manangsang,
Director of Taman Safari Indonesia.

Pages 161-171 in: Oliver, W.L.R., ed. 1993. Status Survey and Conservation Action Plan: Pigs, Peccaries, and Hippos. IUCN: Gland, Switzerland.



Phillip Coffey

An old male babirusa (*B. b. celebensis*).

5.8
The Babirusa (*Babyrousa babyrussa*)

Alastair A. Macdonald

Status and Action Plan Summary

Status categories 4-5 (vulnerable or endangered) according to subspecies.

The babirusa is known only from Sulawesi (*B. b. celebensis*), some of the Togian Islands (*B. b. togeanensis*), the Sula Islands and Buru (*B. b. babyrussa*). Two extinct forms, one fossil and one recent (*B. b. bolabatuensis*), have been found in south Sulawesi. The species is therefore presumed to have been more widely distributed on Sulawesi in earlier times, but by the middle of the last century they were reported to occur only in the east and northeast parts of the island and to have disappeared from the whole of the southwestern peninsula. Currently, babirusa are known only from the northern peninsula, central and southeastern parts of the Sulawesi mainland, and from three of the larger Togian Islands. Reports obtained in 1990 indicate that babirusa also survive on Buru and two of the Sula islands, Mangole and Taliabu, but that they may now be extinct on Sulabesi (formerly Sanana). However, there is no doubt but that babirusa are seriously threatened over most of their remaining range by deforestation and hunting pressure; the latter is particularly intense in parts of northern Sulawesi where there is commercial trade in the meat of these animals (Blouch 1990; Budiarso *et al.* 1991).

Much of the available information on the natural history and biology of this species is anecdotal or derived from the study of captive specimens. Distribution and status surveys in all parts of its range are required as a matter of high priority, with a view to the development of management plans for its enhanced future protection and the establishment of additional reserves in key areas, such as

Buru, Mangole and the Togians. The possibility of relic populations of *B. b. bolabatuensis* surviving in remote locations in south Sulawesi should be investigated, and the taxonomic relationships of the central and southeastern Sulawesi populations, which are unknown at present, need to be assessed. The first longer-term field study of the species' behavior and ecology has been initiated recently in northern Sulawesi, and such studies should be continued and extended to other parts of the species' range in the near future. Particular emphasis should be placed on obtaining a proper understanding of its habitat preferences, population sizes and densities in different habitats, and the nature and extent of factors, such as hunting pressure, deforestation and agricultural encroachment, which are negatively influencing the distribution and numbers of surviving populations. Although there are large numbers of *B. b. celebensis* being maintained and bred in zoological collections at present, the captive population is extremely inbred. Priority should therefore be given to the acquisition of additional, wild-caught founders of this subspecies, and to the development of properly structured breeding programs for the more threatened Togian subspecies, *B. b. togeanensis,* and, especially, the golden or hairy subspecies, *B. b. babyrussa.*

Introduction

B. babyrussa is the sole living representative of the subfamily Babyrousinae, and is generally considered to be in an isolated position with regard to the other living suids. Being endemic to Sulawesi, it also has a very limited geographical distribution. This island has long been isolated by water from mainland Asia, the strait never having been narrower than about 40 kilometers during Pleistocene times. Since the fossil record is confined to Pleistocene material from Sulawesi and from Buru, the hypothesis has been put forward that *Babyrousa* has developed since Oligocene times along a separate evolutionary line (Thenius 1970; Groves and Grubb, this vol., section 5.1). This concept is fully supported by chromosome data; although the babirusa has a diploid chromosome number of 38, as in most other suids, five pairs of babirusa autosomes (Nos. 6,12,14,15, and 17) have no direct equivalents in *Sus* species (Bosma 1980; Bosma and de Haan 1981; Bosma *et al.* 1991).

In any event, there is no doubt that the babirusa is one of the world's most bizarre mammals, and is certainly one of the most extraordinary suids. Among its many peculiarities are that the upper canines of the male emerge vertically from the maxillary alveoli, penetrate through the skin of the nose and then curve posteriorly over the front of the face towards the forehead; this is a unique feature in mammals. The mandibular canines of the male also grow over the front of the face. The peculiar appearance of the adult male (the canines of the female are either absent or markedly reduced) has led local people to liken its appearance to deer (i.e. *"babi"* = pig and *"rusa"* = deer) and, on some islands, to confer mythical properties to it. The function of these tusks remains unknown. They are quite brittle and therefore easily broken, and they are rarely used in combat between males (see below).

Subspecific Taxonomy

Following Groves (1980) and Groves and Grubb (this vol., section 5.1), three extant subspecies are currently recognized. However, it is possible that some central or southern Sulawesi populations are of a fourth subspecies, *B. bolabatuensis* (Hooijer 1950), which is known only from Tolian deposits collected from caves and rock shelters in southwestern Sulawesi. The (three) living forms are described as follows:

1. *B. b. babyrussa* (Linnaeus, 1758), the "hairy" or "golden" babirusa is known only from the islands of Buru and Taliabu, Sulabesi (where it is now extinct) and, probably, Mangole in the Sula Islands. This is the smallest subspecies, and is otherwise characterized by its long and thick body hair, which is colored white, creamy gold, black or gold with a black rump. The upper canines of the males are usually short and slender, with the alveolus forwardly rotated, so that lower canine crosses the upper in lateral view.

2. *B. b. togeanensis* (Sody 1949), the Togian Islands' babirusa is, as its name suggests, confined to the Togian Archipelago, between the northern peninsula and central Sulawesi. This is the largest subspecies. It is also characterized by the possession of body hair, though this is shorter and less dense than in the nominate form. The pelage of the upper parts is also darker than that of the underparts and fawn, brown or black in color. The upper canines of the males are usually short, slender and somewhat rotated forward, and always converge.

3. *B. b. celebensis* (Deninger 1910) is certainly known only from the northern peninsula and the northeastern part of mainland Sulawesi, including the offshore island of Lembeh. This is the only subspecies to be maintained in captivity at the present time and is therefore the most familiar. The adult male body size is fairly large (though smaller than that of the preceding subspecies), ranging from 60 to 100 kg . The female is approximately 30% smaller. It is usually considered to be naked, though in reality its body hair is merely short (0.5-1.0 cm), sparse and dark brown in color over

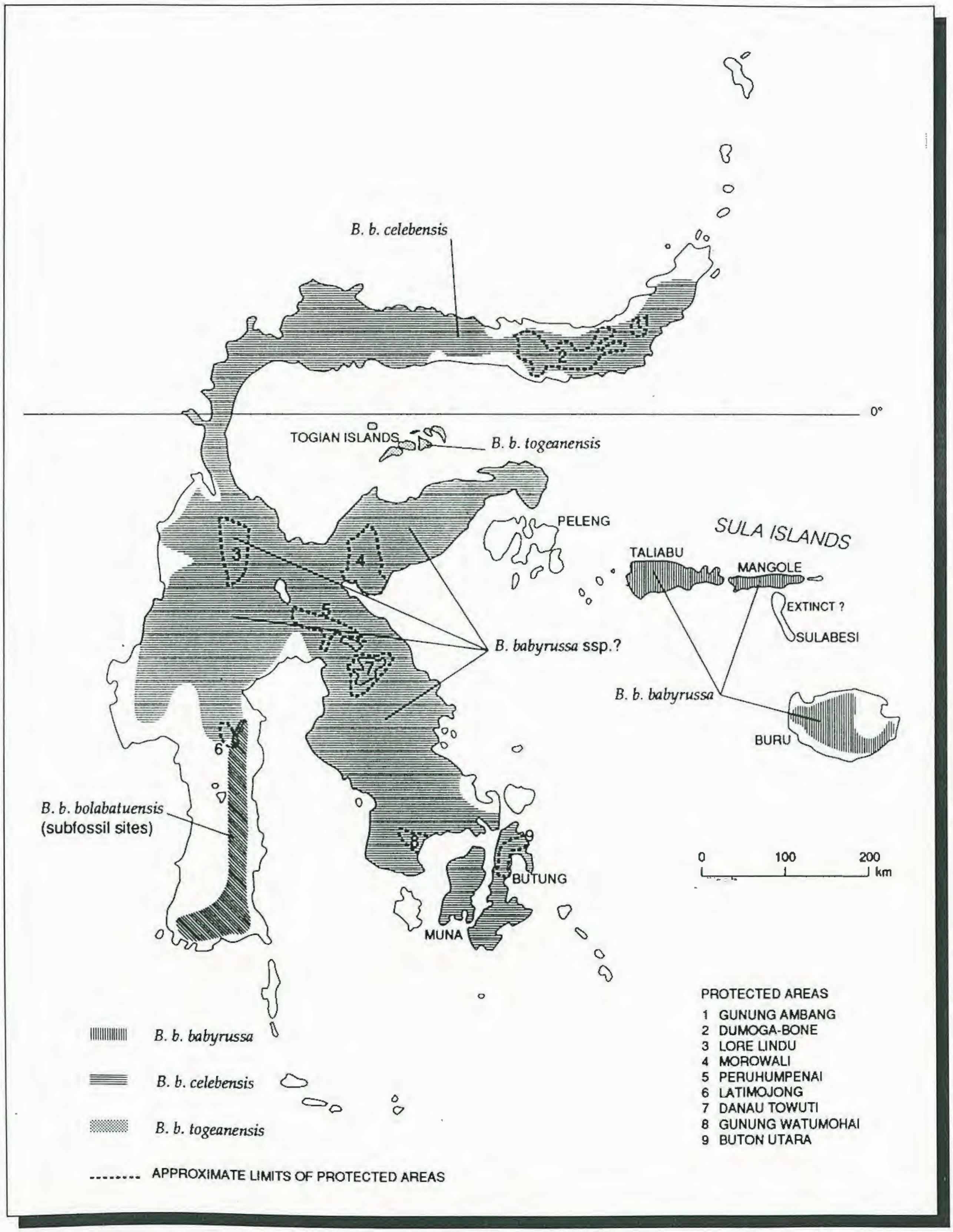


Figure 16. Approximate known range of native and introduced populations of babirusa (*Babyrousa babyrussa* ssp.). Modified after Groves (1980), MacKinnon (1981), Kyari, Tjiu, and Macdonald (unpubl.).

grey skin. The upper canines of the males are generally long and thick, and the alveoli vertically implanted, so that upper canine emerges vertically and is not crossed by the lower canine, converging in almost all cases (Groves 1980).

Former and Present Distribution

The species appears to have been more widely distributed over the island of Sulawesi in former times than it is now. Two extinct forms, a Pleistocene fossil (*B. b. beruensis*) and one Holocene subfossil (*B. b. bolabatuensis*), described from remains found in caves and rock shelters on the east side of the southwest peninsula (Sarasin and Sarasin 1905; Dammerman 1939; Hooijer 1948, 1950), also indicate that babirusa were the principal large prey species of prehistoric man in some localities in the island (Franssen 1949; Heekeren, 1949). By the middle of the last century the species was reported to survive in the east and northeast parts of Sulawesi but to have vanished from the whole of the southwestern peninsula (Temminck 1849; Sarasin and Sarasin 1905), and by the 1930's it was said to be: "being squeezed slowly into the hinterland of Sulawesi" (Heynsius-Viruly and Heurn 1935).

Babirusa are now definitely known only from the northern peninsula (*B. b. celebensis*), and central and southeastern Sulawesi, though various recent reports indicate that populations also occur at intervals along the length of the southwestern peninsula (H. B. Hasanuddin, J. Clark and A. Kyari, pers. comm.). However, the taxonomic status of the central and the southern Sulawesi populations is not known, i.e. these may represent the otherwise believed extinct form *B. b. bolabatuensis*. The subspecies *B. b. togeanensis* is known only from the Togian islands of Batudaka, Togian and Talatakoh, where Selmier (1983) estimated that the total population was in the region of 500 to 1,000 individuals in 1978. The nominate subspecies, *B. b. babyrussa*, is now known only from Buru and from the Sula islands of Mangoli and Taliabu. It also occurred on Sulabesi (formerly Sanana), the only other large island in the Sula Group, but this population is now thought to be extinct (A. Sol and M. Patry, pers. comm.) (Fig. 16).

Habitat, Ecology, and Behavior

The babirusa inhabits tropical rainforest on the banks of rivers and ponds abounding in water plants. Whereas in the past the animal has tended to occur in low lying areas near coasts, recent anecdotal and survey reports indicate that it is now confined mostly to the interior, on higher and less accessible ground.

Maurice Patry

Part of a wild social family group in north-central Sulawesi.

In common with most of the other suids, babirusa are omnivorous. The species' intestinal tract is similar to that of the domestic and wild pig (*Sus scrofa*) in many ways (Flower 1872; Mitchell 1905, 1916; Langer 1973, 1988), although its enlarged stomach diverticulum has led to the spurious suggestion that this may be involved in rumination. However, all the available evidence shows that this is not the case (Macdonald 1991). Whether the diverticulum is actually a food storage chamber or an enlarged "acid bath" is now being investigated, along with other studies of the species' digestive physiology. Except in mud and swampy ground, babirusa do not exhibit the rooting behavior typical of other suids, but this is associated with its lack of a rostral bone in the nose. From observations of both wild and captive individuals they are known to consume a wide variety of leaf, root, fruit and animal material, though detailed studies of their diet in the wild still need to be carried out. Their jaws and teeth are reported to be strong enough to crack very hard nuts with ease (Peters 1985), and adult babirusa have been observed to catch and eat small mammals. In captivity, adults of both sexes will also sometimes attack and cannibalize infants born to other individuals.

The available information suggests that babirusas are social, with groups or troops of up to eight individuals having been observed in rainforest, especially around water, communal wallowing areas and salt licks (Valentijn 1726;

Desmarest 1820; Selmier 1983; Macdonald *et al.* 1989; Patry and Capois 1989; M. Patry, pers. comm.). No detailed accounts of group structure have been published, though field studies currently underway in Sulawesi are expected to shed light on this, and whether the species is territorial (M. Patry and L. Clayton, pers. comm.). Recent video film of wild animals has shown that they may associate with the sympatric warty pigs (*Sus celebensis*) and that, contrary to Jennison (1927), they are active during daylight hours (Selmier 1983; Patry and Capois 1989).

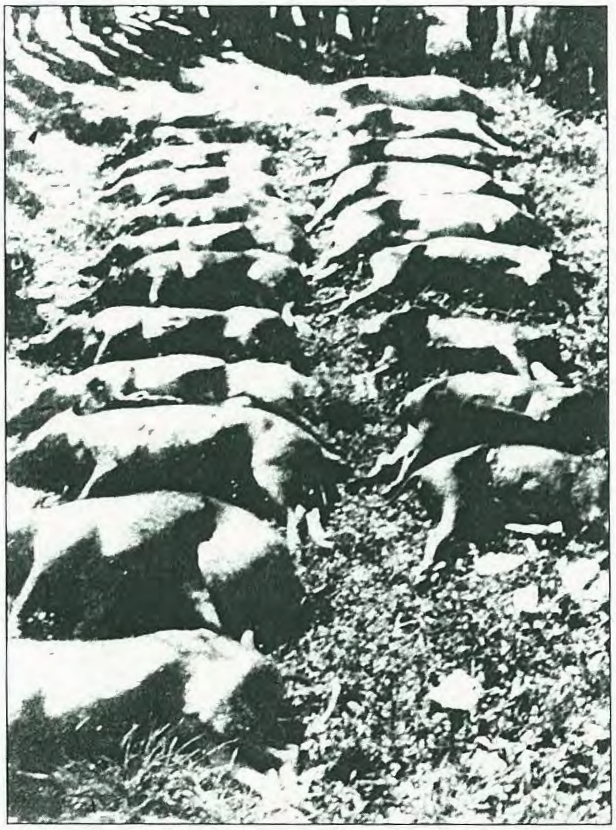
Nests built in the wild are reported to be similar to those of the other wild pigs (Deninger 1910). Babirusas shelter from the rain under bitten off branches of leaves, though nests have also been found in volcanic rock caves (Selmier 1978). Sleeping nests tend to have little or no padding on the ground, being essentially "babirusa-sized depressions", and all babirusa flushed out of such nests were solitary (Selmier 1983). Nests built by sows for farrowing are up to 3 m long and 25 cm deep, and are layered with branches torn from trees and bushes (Guillemard 1886; Selmier 1978).

Captive babirusa may become sexually mature as early as five to ten months of age (National Research Council 1983), and have lived as long as 24 years (Mohr 1960). However, it is likely that the age of sexual maturity in the wild is influenced by the level of nutrition and that animals are unlikely to breed until they are more than one year old. Oestrus cycle lengths of between 28 and 42 days have been recorded, and captive females generally re-cycle within 3 months post-partum (Chaudhuri *et al.* 1990; P. Vercammen and P. Immens, pers. comm.). Oestrus lasts 2-3 days, and the female is not receptive to males at other times (Macdonald, Leus and Vercammen, unpubl. data). Gestation length is usually 155-158 days, though up to 171 days has been reported (Heinroth 1908; Reinhard and Frädrich 1983; Bowles 1986; Vercammen 1991). The normal litter size is one or two, but a low incidence of triplet births has been recorded both in captivity and in the wild, and four fetuses have been reported in utero in a wild female (Patry 1990). Although the gestation is six weeks longer than that of *S. scrofa* (±114 days), neonate babirusa are smaller in size and seem to be no more developed as a consequence of the longer time spent in the uterus. The young are uniformly brown in color, rather than striped, as in all other wild suids with the exception of the warthog, *Phacochoerus* spp..

In captivity, sows produce young at all times of the year (Plasa 1990), and may produce two litters within a 12 month period. However, since it seems likely that diet or other seasonal factors would normally influence inter-birth intervals, wild litters may be produced less frequently. Females which are normally quite docile in captivity, become exceedingly aggressive to their keepers and other babirusas from shortly before parturition to about two weeks after the young are born (Dittoe 1945; Reinhard and Frädrich 1983; Peters 1985; Anggawijaya *et al.* 1985).

Threats to Survival

Adult babirusa have few, if any, natural predators, though pythons (*Python reticulatus* and *P. molurus*) and Sulawesi civet (*Macrogalidea musschenbroeckii*) may predate younger animals (Whitten *et al.* 1987). Indeed, given the small litter size, babirusa appear unadapted to a high rate of predation; a consideration evidently supported by MacKinnon (1979) who suggested that, having evolved in a more or less predator-free environment, babirusa were especially vulnerable to hunting pressure. However, hunting by humans with nets, spears and dogs has undoubtedly been an important factor since prehistoric times (Guillemard 1886; Franssen 1949) and continued hunting pressure now constitutes an increasing threat to the remaining populations of these animals in some areas (Blouch 1990; Budiarso *et al.* 1991; L. Clayton, pers. comm. and unpubl.; M. Patry, pers. comm.). The market hunting practiced by the Christian community in north



Dick Watling

Results from a day's hunting in north Sulawesi; Sulawesi warty pigs *Sus celebensis* (left) and babirusa *B. b. celebensis* (right).

Table 10
Existing and proposed national parks and other protected areas known to contain babirusa populations

Location/name	Existing area (sq. km)	Proposed area (sq. km)
Sulawesi		
Dumoga-Bone NP	3,000	
Lore Lindu NP	2,300	
Bulusaraung NR	57	
Gunung Ambang NR	86	
Lasolo-Sampara NR		450
Pegunungan Peruhumpenai NR	900	
Tangkoko-Dua Saudara NR	89	
Buton Utara GR	820	
Gunung Manembo-Nembo GR	65	
Lambu Sango GR		200
Pegunungan Morowali/Pelantak GR		5,000
Rangkong GR		590
Rawa Opa GR		1,500
Tanjung Peropa GR	380	
Gunung Watumoha HR	500	
Danau Towuti RP	650	
Gunung Lompobatang PR	200	
Pegunungan Latimojong PR	580	
Sula Islands		
Taliabu NR		700
Buru		
Gunung Kelapa Muda GR		1,450
Togian Islands		All Islands

Key:
NP = national park; NR = nature reserve; GR = game reserve;
HR = hunting reserve; RP = recreation park; PR = protected forest

Sulawesi is concentrated on the warty pig, *S. celebensis*, but some babirusa are also taken. Budiarso *et al.* (1991) counted 295 babirusa among 2,612 wild suids they recorded in a survey of hunters and markets in four areas of north Sulawesi. This relatively small proportion (11.3%) of the total wild pig harvest is caused, at least in part, because babirusa reportedly now live further from human habitations than the warty pigs. Additionally, they fetch no more in the market place, giving hunters little incentive to go after them (Blouch 1990 and pers. comm.). Nonetheless, babirusa skulls are openly sold in tourist areas south of the Lore Lindu National Park and in large department stores in Jakarta.

In recent years large-scale commercial logging operations have also posed a major and increasingly serious threat to this species (Smiet 1982). The loss and degradation of habitat has already resulted in the dramatic diminution in the known range of this species and the recent extirpation of some populations, e.g. in parts of north Sulawesi and on Sulabesi (Selmeir 1978; Clayton, in prep.; M. Patry, pers. comm.). Babirusa are one of the first animals to become locally extinct after logging or land opening, which not only deprives them of their moist forest habitat but may also increase their exposure to hunting pressure by immigrant settlers and their dogs (Whitten *et al.* 1987).

Little is known about the susceptibility of this species to natural or introduced diseases (Munro *et al.* 1990), though many babirusa on the Togian islands reportedly died during an epidemic skin disease in the early 1970s (Selmier 1983). The increased likelihood of babirusa in formerly remote and inaccessible areas being exposed to virulent (insect- or livestock- borne) diseases to which they have no natural resistance may, therefore, pose a potentially serious threat to this species, as it does to some other threatened suids (Oliver *et al.* this vol., section 5.2).

Conservation Measures Taken

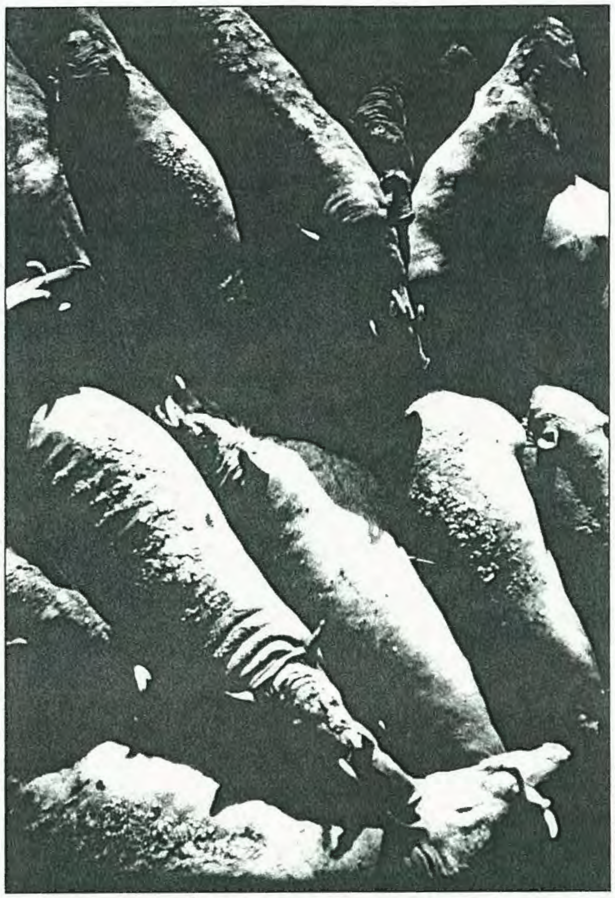
The babirusa was accorded full protection under Indonesian law in 1931, and the legislation relating to babirusa and nature conservation in general in Indonesia was summarized by Dammerman (1950) and by Setyodirwiryo (1959). Since 1978, *B. babyrussa* has been categorized as "vulnerable" in the IUCN Red Data Book (IUCN 1978), and listed as "endangered" by the United States Department of the Interior since 1980 (United States Department of the Interior 1980). The species has also been included on Appendix I of CITES since 1982, although international trade in this species is not thought to be have been an important issue in recent times.

To date, approximately 12,000 sq. km of land on Sulawesi have been formally declared as wildlife protection areas, and a further 20,000 sq. km within the distribution of this species have been proposed as wildlife reserves of one form or another, but await formal gazetting. Populations of mainland babirusa occur in a number of these national parks, nature reserves, hunting reserves and protected forests in Sulawesi (Table 10 and Fig.16), some of which have been designated specifically for their protection. However, babirusa are patchily distributed and/or still subject to hunting pressure in many of these areas (e.g. Dumoga-Bone). Efforts are being made by the parks service to educate local people and to control animal poaching and timber cutting within the existing protected areas, but chronic lack of financial resources, pressure from an expanding human population and insufficient up-to-date information seem to combine with other factors to make much of the protective legislation ineffective at a local level (Blouch 1990; Clayton, in prep.). In some cases, the amount of suitable habitat remaining within these areas is also considerably less than the designated size of the reserves (Basjarudin 1971; Olivier and Watling 1977; Wind 1984; MacKinnon and MacKinnon 1986). As yet there are no national parks or other wildlife reserves within the range of *B. b. babyrussa,* though relatively large areas have been designated for protection in north-central Taliabu (700 sq. km) and west Buru (1,450 sq. km), but these have yet to be formally gazetted. Similarly, there are as yet no wildlife reserves in the Togian Islands, though the whole archipelago has been proposed for future protection.

Captive Breeding

Babirusa have been maintained and bred in captivity at intervals since the early 19th century, and perhaps for much longer. Quoy and Gaimard (1830), for example, recorded that the Rajahs of Celebes often kept and raised babirusa to present them as diplomatic gifts. In 1820, the first pair of animals to arrive in Europe were maintained at the Menagerie du Jardin des Plantes in Paris, where a male piglet was produced in March 1821 (Boitard 1851). During the ensuing 150 years the small captive zoo population fluctuated in number but never exceeded 20 individuals. These included three *B. b. babyrussa*—2 from the Sula Is. and 1 from Buru—being maintained at Amsterdam Zoo from 1915 to 1925 (Mohr 1960). However, as a result of the extremely successful breeding of this species at Surabaya Zoo, Java, since the early 1970s, there has been a dramatic increase in the captive population which, by the end of 1989, stood at 68 (36 males, 29 females + 3 unsexed) in four Indonesian zoos, 50 (25 males, 25 females) in eleven European collections and 13 (7 males, 6 females) in 3 zoos in the U. S. (Plasa 1990). The latter author states that these animals were derived from 13 (7 males, 6 females) wild-caught founders, though this is almost certainly incorrect. Unpublished Indonesian sources describe the stock as descended from a wild-caught pair obtained in 1968 (Matur 1989), while other reports suggest that this stock is entirely derived from 4 (2 males, 2 females) of 5 wild-caught individuals from the vicinity of Poso, north-central Sulawesi, acquired by Surabaya Zoo in 1975 (S. Soebakir, pers. comm. to W. Oliver). There is also a possibility of a contribution to the world zoo population from 11 animals said to have been brought from Sulawesi to Jakarta in 1977.

In any event the present stock is highly, perhaps chronically, in-bred. In addition, there is increasing concern about the difficulties relating to the useful dispersal of surplus stock in some collections, particularly in Surabaya which was maintaining 49 babirusas (37% of the total captive population) on 31.12.89. Fortunately, these animals are evidently able to live amicably in large groups, though overcrowding has resulted in high levels of infant mortality and, hence, a greatly reduced rate of recruitment (pers. obs.; Plasa 1990).



Alastair Macdonald

Captive *babirusa* at Surabaya Zoo, Java.

Additional Remarks

The babirusa is considered by the Indonesian authorities and a proportion of the general public to be a species of particular patrimonial interest and especially worthy of protection. Evidence for this is found in various unpublished reports in Indonesia, which have suggested that it is second only to the rhinos as the most important wild mammal in the country, and in observations that it has potential as a "flagship species" for conservation interests. The babirusa has been selected as the emblem of the Lore Lindu National Park, and the species is frequently referred to in staff training and conservation materials produced by the PPA (Forestry Department) and PHPA (Forestry and Nature Conservation Department). In recent years, it has also been increasingly featured in children's text and coloring books in Indonesia.

Conservation Measures Proposed: An Action Plan

The bizarre appearance of this species, coupled with its high degree of taxonomic uniqueness, has attracted comment in the scientific community for 500 years; it has been a treasured resource to local people for much longer. Recent and current research is rapidly adding to our understanding of its biology (Macdonald 1991), though basic information on many aspects of its ecology and behavior is still lacking. The species' shyness and the relative remoteness of its distribution has limited earlier academic studies, but anthropological research has indicated that there is also an extensive local knowledge of these animals which is almost entirely unreported. Its potential importance as a classic indicator of forest disturbance has also been recognized only very recently and this factor, together with the need for recent and more detailed information about its present distribution, threats to its survival, and various aspects of its biology, must be reflected in the structure and priorities of any future management and research initiatives.

Objectives

1. To determine the present distribution and relative population sizes of the species throughout its known range.

2. To assist the establishment of a network of protected areas to safeguard the survival of representative populations of all subspecies of babirusa and, where necessary, promote the establishment of captive populations of these subspecies as a safeguard to their survival.

3. To promote further research into the systematics, biology, conservation status and future management needs of the species in order to better ensure its long-term survival.

4. To promote interest and awareness among local people and visitors of the need to conserve this unique natural resource.

Priority Projects

1. Conduct field status surveys in selected priority areas, including the Togian Islands, the Sula Islands and Buru, with a view to the development of management recommendations/plans for the enhanced protection of two or more representative populations of the least known, but potentially most threatened subspecies, *B. b. togeanensis* and *B. b. babyrussa.*

2. Assist the relevant governmental authorities in their efforts to establish national parks in the Togian Islands,

the Sula Islands (Taliabu and Mangole) and Buru, and such other of those islands where the animals occur and require further protection.

3. Conduct surveys in selected areas of central, southern and southeastern Sulawesi to assess the distribution, conservation and taxonomic status of relic populations of animals which may represent extant examples of *B. b. bolabatuensis* (Hooijer 1950).

4. Assess and implement options for the development of properly structured captive breeding programs for the most threatened subspecies, *B. b. babyrussa* and *B. b. togeanensis*.

5. Promote efforts to introduce fresh blood-stock from the wild into the captive population of *B. b. celebensis*, assist the useful placement of surplus, captive-bred stock in Indonesian collections (including the possibility of reintroducing some of these animals), and promote development of integrated, in-country management and conservation-education projects with the support of the international zoo community and other relevant bodies.

6. Investigate subsistence hunting methods and levels of utilization of this species throughout its range, in order to determine its cultural and economic importance to local people and to enhance future monitoring and regulation.

7. Investigate current methods and levels of commercial trade (intra- and inter-island) in the flesh and other products of these animals within Indonesia, with a view to the enhanced future monitoring, regulation and/or prohibition of this trade.

8. Investigate the species' ecology in representative habitats, its habitat preferences, and the reasons for its apparent inability to survive in disturbed areas.

9. Conduct further research into the social and reproductive behavior and physiology of the babirusa, with particular reference to group size and composition, and factors relating to age of puberty, reproductive cycles and litter size.

10. Investigate the species' natural diet and its digestive physiology, with a view to an understanding of its dietary requirements, the function of the gastric diverticulum and the animal's ability to digest cellulose and other fibrous material.

Acknowledgements

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References

Anggawijaya, M. D. A., Pertamawati, F., Engeline, M., and Sunarjo, V. O. 1985. Kehidupan *Babyrousa babyrussa* di Kebun binatang Surabaya. *SMAK Santa Maria, Surabaya.*

Basjarudin, H. 1971. *Nature reserves and national parks in Indonesia—present situation and problems.* IUCN Publications (N.S.), 19: 27-33.

Blouch, R. 1990. Report from the field: Indonesia. *Smithsonian Instit. Conserv. & Res. Center Newsletter, National Zoo, Washington D.C.*, 1: 6-8.

Boitard, P. 1851. *Le Jardin des Plantes.* G. Barba, Paris: 273 pp.

Bosma, A. A. 1980. The karyotype of the babirusa (*Babyrousa babyrussa*): karyotype evolution in the suidae. *Proc. 4th European Colloquium of Cytogenetics in Domestic Animals:* 238-241.

Bosma, A. A. and de Haan, N. A. 1981. The karyotype of *Babyrousa babyrussa* (Suidae, Mammalia). *Acta Zoologica et Pathologica Antwerpiensia,* 76: 17-27.

Bosma, A. A., de Haan, N. A., and Macdonald, A. A. 1991. The current status of cytogenetics of the Suidae: a review. *Bongo, Berlin* 18: 258-272.

Bowles, D. 1986. Social behavior and breeding of babirusa. *Dodo, J. Jersey Wildl. Preserv. Trust* 23: 86-94.

Budiarso, Wilar, A. F., Tulung, B., Kaligis, D., and Kaligis, W. A. A. 1991. The importance of Sulawesi wild pig (*Sus celebensis*) as a source of meat in North Sulawesi. (Unpubl.) rep, Universitas Sam Ratulangi and World Wide Fund for Nature Indonesia Program: 19 pp.

Chaudhuri, M., Carrasco, E., Kalk, P., and Thau, R. B. 1990. Urinary oestrogen excretion during oestrus and pregnancy in the babirusa. *Int. Zoo Yb.* 29: 188-192.

Dammerman, K. W. 1939. On prehistoric mammals from south Celebes. *Treubia,* 17: 63-72.

—. 1950. Gescheidenis van de natuurbescherming in Indonesie. *Chronica Naturae,* 106: 216-228.

Deninger, K. 1910. Uber Babyrusa. *Berichte der Naturforschen den Gesellschaft zu Freiburg i. Br.,* 18: 1-22.

Desmarest, A. G. 1820. *Mammalogie.* Veuve Agasse, Paris: 391-392.

Dittoe, G. B. 1945. A pig by another name. *The San Diego Zoonooz,* 18: 3-4.

Flower, W. H. 1872. Lectures on the comparative anatomy of the organs of digestion of the Mammalia (Lecture IX). *Medical Times & Gazette,* 1872, (2): 319-322.

Frädrich, H. 1975. Varkens und Pekaris. In: B. Grzimek (ed.): *Grzimek's Het Leven der Dieren- Zoogdieren IV, 13.* van Nostrand Reinhold, Amsterdam: 78-110.

Franssen, C. J. H. 1949. Bijdrage tot de kennis van het Toaliaan op Zuid-Celebes. *Tijdschrift voor Indische Toal, Land en Volkenkunde,* 83: 331-339.

Groves, C. P. 1980. Notes on the systematics of *Babyrousa* (Artiodactyla, Suidae). *Zoologische Mededelingen,* 55: 29-46.

Guillemard, F. H. H. 1886. *The Cruise of the Marchesa to Kamchatka and New Guinea,* Vol. 2. J. Murray: London: 190-191 & 200-205.

IUCN. 1978. *Red Data Book. 1 Mammalia,* Morges, Switzerland 19.120.5.1.

Heekeren, H. R. van. 1949. Early man and fossil vertebrates on the island of Celebes. *Nature,* 163: 492.

Heinroth, O. 1908. Trachtigkeits-und Brutdauern. Zoologischer Beobachter. *Der Zoologische Garten, 49:* 14-25.

Heynsius-Viruly, A. and Heurn, F. C. van. 1935. Overzicht van de uit Nederlandsch-Indie ontvangen gegevens. *Mededeelingen [van de] Nederlandsche Commissie voor Internationale Natuurbescherming,* 10: 25-77.

Hooijer, D. A. 1948. Pleistocene Vertebrates from Celebes; III. *Anoa depressicornis* (Smith) subsp., and *Babyroussa babirussa beruensis* nov. subsp.. *Proc. of the Section of Sciences [of the] Koninklijke Nederlandische Akademie van Wetenschappen,* 51: 1322-1330.

—. 1950. Man and other mammals from Toalian sites in southwestern Celebes. *Verhandelingen der Koninklijke Nederlandische Akademie van Wetenschappen,* 46: 164 pp.

Jennison, G. 1927. *Natural History, Animals.* A. & C. Black, London: pp. 313-314.

Langer, P. 1973. Vergleichend-anatumische untersuchungen am magen der Artiodactyla (Owen, 1848). 1, Untersuchungen am magen der non-ruminata (Suiformes). *Gegenbauers Morphologisches Jahrbuch, Leipzig* 119: 514-561.

—. 1988. The Mammalian Herbivore Stomach. G. Fischer, Stuttgart: 557 pp.

Macdonald, A. A., Bell, J., Munro, S. A., Kaspe, L., Harwood Gepak, V., Sasmita, R., and Bowles, D. 1989. Observations on the behavior and health of captive babirusa. *Prosiding Simposium Nasional Penyakit Satwa Liar, Surabaya:* 244-253.

Macdonald, A. A. 1991. Monographie des hirschebers (*Babyrousa babyrussa*). *Bongo, Berlin* 18: 69-84.

MacKinnon, J. 1979. A glimmer of hope for Salawesi. *Oryx* XV(1): 55-59.

—. 1981. The distribution and status of wild pigs in Indonesia. (Unpubl.) rep. to IUCN/SSC Pigs and Peccaries Specialist Group: 9 pp.

MacKinnon, J. and MacKinnon, K. 1986. *Review of the Protected Areas System in the Indo-Malayan Realm.* IUCN Gland and Cambridge: 284 pp.

Matur, H P. 1989. Usaha penangkaran dan pelestarian babirusa (*Babirousa babyrussa*) di kebun binatang Surabaya. (Unpubl.) Proceedings of the Indonesian Zoo Association Meeting, Jakarta Zoo, Nov. 1989.

Mitchell, P. C. 1905. On the intestinal tract of mammals. *Trans. Zool. Soc. Lond.* 17: 437-531.

—. 1916. Further observations on the intestinal tract of mammals. *Proc. General Meetings for Scien. Business of Zool. Soc. Lond. 1916:* 183-251.

Mohr, E. 1960. *Wilde Schweine. Neue Brehm-BHcherei no. 247.* Ziemsen Verlag, Wittenberg-Lutherstadt.

Munro, S. A., Kaspe, L., Sasmita, R., and Macdonald, A. A. 1990. Gastrointestinal helminthosis in the babirusa (*Babyrousa babyrussa*) and response to "Albendazole". *Veterinary Record,* 126: 16.

National Research Council. 1983. *Little Known Asian Animals with a Promising Economic Future.* National Academy Press. Washington D. C..

Olivier, R. C. D. and Watling, R. J. 1977. Lore Kalamanta, Sulawesi: ecological survey and preparation of a management masterplan. (Unpubl.) IUCN/WWF project proposal, 1526: 24 pp.

Patry, M. 1990. *Babiroussa: une Vie Jusqu'au Bout du Reve.* Fixot, Paris: 221 pp.

Patry, M. and Capois, J. 1989. Pour la premier fois le *Babiroussa* a l'etat naturel. *Connaissance de la Chasse,* 156: 45-46.

Peters, C. T. M. 1985. De babiroesa: het hertzwijn. *Dieren,* 5: 135-139.

Plasa, L. 1990. *Internationales Zuchtbuch fur den Hirscheber (International studbook for the babirusa), Babyrousa babyrussa, 1989.* Wilhelma Zoologisch-botanischer Garten: Stuttgart. 24 pp.

Quoy, J. R. C. and Gaimard, J. P. 1830. *Voyage de decouvertes de l'Astrolabe, Zoologie,* I. J. Tastu, Paris: 125-132.

Reinhard, R. and Frädrich, H. 1983. Bemerkungen zur Zucht Hirschebern (*Babyrousa babyrussa* L.) im Zoo *Bongo, Berlin,* 7: 65-70.

Sarasin, P. and Sarasin, F. 1905. *Materialien zur Naturgeschichte der Insel Celebes.* C. W. Kreidels, Wiesbaden, 5: pp. 4-5, 36-43 & 52-54.

Selmier, V. J. 1978. Only in Indonesia—the babirusa. (Unpubl.) report to LIPI and PPA, Indonesia: 40 pp.

—. 1983. Bestandsgrosse und verhalten des hirschebers (*Babyrousa babyrussa*) auf den Togian Inseln. *Bongo, Berlin,* 7: 51-64.

Setyodirwiryo, K. 1959. Nature protection in Indonesia. *Proc. of the Ninth Pacific Science Congress of the Pacific Science Association,* 7: 18-20.

Smiet, F. 1982. Threats to the spice islands. *Oryx,* 14: 323-328.

Sody, H. J. V. 1949. Notes on some primates, carnivora, and the babirusa from the Indo-Malayan and Indo-Australian regions (with descriptions of 10 new species and subspecies). *Treubia,* 20: 121-190.

Temminck, C. J. 1849. *Coup d'oeil general sur les possessions Neelandaises dans L'Inde archipelagique.* Arnz, Leiden; 3: pp 113-114 & 249.

Thenius, E. 1970. Zur Evolution und Verbreitungsgeschicht der Suidae (Artiodactyla, Mammalia.). *Zeitschrift fur Saugetierkunde,* 35: 321-342.

United States Department of the Interior. 1980. *Republication of the lists of endangered and threatened species and correction of technical errors in final rules.* Federal Register, 45: 33768-33781.

Valentijn, F. 1726. *Oud en neiuw Oost-Indien.* J van Braam, Dordrecht, Amsterdam; 5: 268-269.

Vercammen, P. 1991. Ubersicht uber die haltung von hirscheben (*Babirousa babyrussa celebensis* L.) im Zoo Antwerpen. *Bongo, Berlin* 18: 244-249.

Whitten, A. J. Mustafa, M. and Henderson, G. S. 1987. *The Ecology of Sulawesi.* Gadjah Mada Univ. Press, Yogyakarta: 779 pp.

Wind, J. 1984. Management plan 1984-1989: Dumoga-Bone National Park. (Unpubl.) ms, W.W.F.- Bogor.

5.9

Origins of Domestication and the Pig Culture

William L. R. Oliver, Colin P. Groves, C. Roger Cox, and Raleigh A. Blouch

Abstract and Action Plan Summary


L. Cipriani

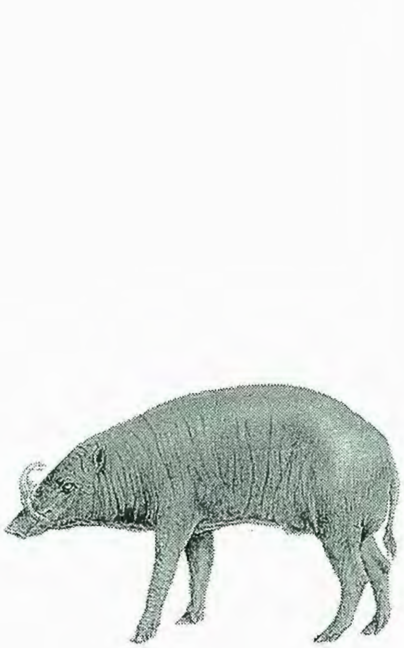
An Onge tribal with a wild pig (long-snouted form), Little Andaman Island.

The long and close association between people and pigs has crossed many biogeographic and ethnic boundaries. It is an association which, on archaeozoological evidence, dates back at least 40,000 years, and one which has subsequently involved the independent domestication of at least two species of *Sus,* and the carriage of these animals, or their domestic, feral and bybrid derivatives, to all continental land masses and a great many oceanic islands. The resulting diversity of native and introduced forms has produced patterns of distribution and interrelationships of great confusion. Some of these forms are of potential importance in terms of genetic resources for the further domestication of one of man's major sources of animal protein, and some are of considerable anthropological interest in terms of the ethnic origins and the cultural integrity of many surviving tribal societies. However, many formerly important cultural and economic relationships between people and their pigs are breaking down as other economic options become available or religious prejudice fosters change in values. Nonetheless, pigs are still among the most important of all domestic animals, particularly in Asia where the annual consumption of pork

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 3
Wild Population Status and Management



BABIRUSA WILD POPULATION STATUS AND MANAGEMENT

The single remaining member of the subfamily Babyrousinae, the babirusa (*Babyrousa babyrussa*) is one of the more interesting endemic mammals on the island of Sulawesi. The species was given full protection under Indonesian law in 1931 but its very survival continues to be under severe threat, primarily through hunting for food and trade by the local human populations.

The Indo-Pacific is a tectonically active area with many volcanoes situated near the tectonic plate margins. Quite a number of volcanoes are found in North Sulawesi, the main ones being Tangkoko, Dua Saudara, Batuangus, Manadotua, Lokon, Klabat and Una Una on Una Una island of the Togian island group.

In the wild, the juvenile age class (0-1) is likely to be the class where predation plays the largest role. The only natural predators of the babirusa in Sulawesi are the reticulated python (*Python reticularis*) and possibly the three civet species: Sulawesi palm civet (*Macrogalidia musschenbroekii*), Malayan civet (*Viverra tangalunga*), common palm civet (*Paradoxurus hermaphroditus*). The civets are only likely to take the juvenile animals, whereas the python is capable of taking babirusa of all ages.

I. Recent information on the distribution of the Babirusa

Area	Year	Evidence
1. *Babyrousa babyrussa babyrussa*		
Buru	1991, 1993	Tiju reports (North and eastern areas)
	1995	Grimes and Grimes (Central and southern areas)
	06/96	Persulessy and (Western area) Poulsen report (Birdlife Int. Indonesia Program).
Taliabu	1991	University of East Anglia
Mangole	1992	From obs. bird survey.
2. *Babyrousa babyrussa togeanensis*		
Malenge	09/93	Pers observation: 15 - 20 females and juveniles, adult white male

Area	Year	Evidence
Ketupat	01/94	Skull : male
Wakai	01/94	Skull : male, captive animal.

3. *Babyrousa babyrussa celebensis*

Area	Year	Evidence
Donggala	1995	Observation
Lore Lindu	1995	Observation
Morowali	1987	Observation
Toli-toli	1991 - 1992	Local people
Adudu (Nantu)	1983 - 1995	Local people + Forest survey
Matana Lake	1995	Environmental Management Analysis report (environmental impact).
Faruhumpenai	1992	Research survey
Panua	1995	PHPA Report
Butung	1995	Personal observation. No babirusa found.

II. Threats to survival

Area	Threat
1. *Babyrousa babyrussa babyrussa*	
Buru	Hunting by coast-based individuals to supply merchant
2. *Babyrousa babyrussa togeanensis*	
Malenge	Hunting by fisherman
Ketupat	???
Wakai	hunting

Area	Year	Evidence
3. *Babyrousa babyrussa celebensis*		
Donggala	hunting	
Lore Lindu	hunting	
Morowali	???	
Toli-toli	hunting, habitat loss	
Adudu Nantu Forest	habitat loss	
Matana Lake	???	
Faruhumpenai	habitat loss	
Panua	hunting	
Mangole	habitat loss	

<u>Conclusion: Hunting poses the greatest immediate threat to the survival of the Babirusa.</u>

Bogor, 20 July 1996

III. Population Size Estimates

Buru	500	(estimate)
Taliabu	500	(guess)
Mangole	200	(guess)
Togians	400-600	(estimate)
North Sulawesi	1500-2500	(estimate)
Central Sulawesi	3000	(guess)
Southeast Sulawesi	1500	(guess)
South islands	0	

Requirements:
Survey data from Central and South Sulawesi, Buru and the Sula islands, and the Togian islands. Age make-up of the population: of 586, 327 adult, 165 sub-adult, 94 juveniles (i.e. 249 are less than 2 years old) so average adult age may be 4 years (from Patry et al. 1995).

IV. Recommended Priorities for Babirusa Conservation

1. The most important priority is to stop the indiscriminate and excessive hunting for Babirusa meat in Northern Sulawesi. We believe that the most effective way to reach this goal is to target the dealers that supply the markets. Road blocks and better law enforcement offer the fastest solution to achieve this goal (removal of all snares in protected areas and law enforcement after arrest). In the long term this must be combined with a community development program by extending the existing program from the protected areas to the local people.

2. More survey work is needed in the areas for which we have insufficient data: S. E. Sulawesi, Butung and Muna, Rawa Aopa and the rest of South Sulawesi, the Sula islands (Taliabu and Mangole)

3. With the present data, we have insufficient information on population density and trends. Census work needs to be done in all areas.

4. We fully endorse the creation of a protected area around the Nantu forest (North Sulawesi).

5. We call for the establishment of protected areas for the 2 subspecies that do not yet have a protected refuge: ***Babyrousa babyrussa togeanensis*** on the Togian islands and ***Babyrousa babyrussa babyrussa*** on Taliabu, Mangole and Buru. Preferably the creation of such areas should be based on local recognition of areas which have already some kind of protection through local customs and beliefs for instance the Baran area on Buru.

6. We call for the creation of a Sulawesi Endemic Wildlife Information and Study Center. The creation of this center can be based on the experience gained with a similar center (WARSI) on Sumatera

IV. Captive Breeding

We shall not rely on captive breeding alone to conserve this species for the future. Better protection in the field remains the most important conservation measure. However, a captive population can serve as a kind of safety measure should disaster strike the wild population. Captive animals also allow the collection of supporting data on the biology and behavior of the species. Captive animals can offer us the possibility to collect information that is impossible to obtain in the wild because the techniques are too invasive or create too much disturbance for the wild population.

The present captive population is not suitable for reintroduction. These animals are probably too inbred to survive in the wild, and their origins are not exactly known. There exists a risk of spreading diseases from the captive population to the wild. At present, hunting pressures are too high to offer any reintroduced animal a good chance of survival.

Wild group recommendations and conditions for capture of new founders in order to establish a new captive breeding population:

- All new founders should go to Indonesian breeding centers only and all offspring must be well managed.

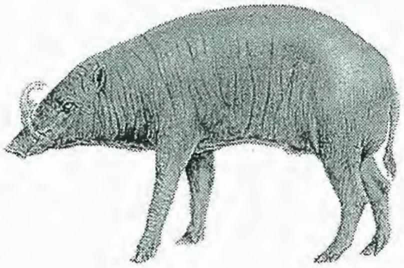
- A survey is needed to determine a capture location. We do recommend not to capture in S. E. Sulawesi because it is not clear what subspecies occurs there. No animals should be captured in protected areas in order not to disturb the local babirusa population

- No animals should be reintroduced to the wild until there is clear evidence that hunting pressure has been reduced. Any animal scheduled for inclusion in potential reintroduction schemes should be carefully screened. We do not recommend reintroduction from the captive population unless **all** existing internationally recognized guidelines for this procedure are followed.

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 4
Population Biology and Modeling



POPULATION BIOLOGY AND MODELLING OF THE BABIRUSA

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Introduction

The single remaining member of the subfamily Babyrousinae, the babirusa (*Babyrousa babyrussa*) is one of the more interesting endemic mammals on the island of Sulawesi. The species was given full protection under Indonesian law in 1931 but its very survival continues to be under severe threat, primarily through hunting for food and trade by the local human populations.

The need for and consequences of intensive management strategies can be modeled in order to estimate which practices may be the most effective in conserving the babirusa. VORTEX, a simulation software package written for population viability analysis, was used as a tool to study the interaction of a number of life history and population parameters treated stochastically, to explore which demographic parameters may be the most sensitive to alternative management practices, and to test the effects of a suite of possible management scenarios.

The VORTEX package is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild populations. VORTEX models population dynamics as discrete sequential events (e.g., births, deaths, sex ratios among offspring, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or as random variables that follow specified distributions. The package simulates a population by stepping through the series of events that describe the typical life cycles of sexually reproducing, diploid organisms.

VORTEX is not intended to give absolute answers, since it is projecting stochastically the interactions of the many parameters which are entered into the model and because of the random processes involved in nature. Interpretation of the output depends upon our knowledge of the biology of the babirusa, the conditions affecting the population as well as possible changes in the future. What little data exists on the population biology of the babirusa were utilized for this analysis.

Input Parameters for Simulations

Mating System: Polygynous: Observations on groups of babirusa in captivity revealed a hierarchy among the males resulting in the largest proportion of matings being carried out by the dominant male (Leus et al. 1992; Macdonald et al. 1993). Furthermore, analyses of video recordings of sightings of 586 babirusa at two salt licks in Northern Sulawesi (Patry et al. 1995) revealed that almost half of the sightings were of single animals. Of these single individuals, 84% were solitary adult males. In contrast, females usually occurred in groups together with other females and their offspring. These results suggest that adult male babirusa are normally solitary and will only associate with female groups for breeding. Disputes between a small number of males in the vicinity of what is presumed to be an oestrus female have also been observed on the films. These results suggest that the mating system for babirusa is polygynous rather than monogamous.

Age of First Reproduction: VORTEX precisely defines breeding as the time at which offspring are born, not simply the age of sexual maturity. In addition, the program uses the mean (or median) age rather than the earliest recorded age of offspring production. In captivity, babirusa males and females can reach sexual maturity as young as 5 months of age. Most captive babirusa approach the age of one year before reaching sexual maturity. However, the animals are still quite small at this age and it is considered unlikely that they will reproduce until they are more than one year of age (Macdonald 1993). Taking into account the gestation length of about 5 months (usually 155-158 days) we believe female babirusa in the wild will have their first litter at the age of 2 years. The males on the other hand will have to deal with mating competition by older and stronger males. We estimate that a male's first offspring will be born at the later age of 4 years.

Age of Reproductive Senescence: VORTEX assumes that animals can breed (at the normal rate) throughout their adult life. Based on information from the captive population, this indeed appears to be the case for the babirusa. The maximum age ever obtained by a babirusa in captivity was 24 years. However, the studbook data show that most animals die at the age of 14-15 (Plasa 1996). Since most animals generally live longer in captivity than in the wild, the age of reproductive senescence for babirusa was set at 12 years of age.

Sex Ratio at Birth: Assumed to be even in the absence of data to the contrary.

Maximum Number of Offspring: Most females have litters of one or two piglets but a low incidence of triplets has been observed in captivity. The maximum number of offspring is therefore 3.

Offspring Production: For the purposes of modeling babirusa population dynamics, we defined "reproduction" for a given female as the successful birth of a piglet. With a gestation length of about 5 months we believe that babirusa females are able to give birth once per year. This is readily obtained in captivity. Based on the proportion of females at reproductive age believed to be without young in the filmed population in Northern Sulawesi, and given some undefined level of infertility and failed gestations we set the limit to reproduction at 80% of the adult females having a successful birth per year.

Annual variation in female reproduction is modeled in VORTEX by entering a standard deviation (SD) for the proportion of females that do not reproduce in a given year. Since no appropriate data were available for this species, we set this variation to approximately 25% of the mean value. VORTEX then determines the proportion of females breeding each year of the simulation by sampling from a binomial distribution with the specified mean (e.g., 20%) and standard deviation (e.g., 5%). The sex ratio of piglets (proportion of males) produced in a given year was set at 0.500 based on sex ratio at birth obtained in captivity (Plasa 1996).

In captivity most babirusa females have one or two piglets with a slightly higher occurrence of singletons. Triplets are born only sporadically (Plasa 1996). We therefore assume the litter size distribution in a given year to be the following:

Litter size	% of females at breeding age in a given year
0	20
1	46
2	31
3	3

Male Breeding Pool: Although no data are available for this parameter, we do know that some competition occurs between the males for the access to oestrous females in captivity (Leus et al. 1992; Macdonald et al. 1993). It is therefore unlikely that all adult males will have the opportunity to breed in a given year in the wild. For the purpose of this model it was assumed that only 50% of the males at breeding age will sire an offspring annually.

Mortality: Again, data are lacking on the mortality of specific age-sex classes of babirusa but we have made the following assumptions.

In the wild, the juvenile age class (0-1) is likely to be the class where predation plays the largest role. The only natural predators of the babirusa in Sulawesi are the pythons (*Python reticularis* and *Python molurus*) and possibly the three civet species: Sulawesi palm civet (*Macrogalidia musschenbroekii*), Malayan civet (*Viverra tangalunga*), and Common palm civet (*Paradoxurus hermaphroditus*). These predators, especially the civets, are more likely to take the juvenile animals rather than the large ones. We have therefore estimated the juvenile mortality in the wild to be 30%. There is no reason to assume a difference in survival rate for juvenile males and females. Predator pressure is likely to drop significantly from the age of one onwards because of the larger size of the individuals. We estimate the mortality of the subadult animals (males and females) to be only 5% with the exception of the males in age class 2-3. It is likely that at this age, the males will leave the maternal group to either become solitary or join the company of other adult males. It was assumed that this would be a period of higher risk for these animals causing the mortality to rise from 5 to 10%. Full grown adult animals are likely to have a very low mortality which may be slightly higher for the females than the males because of the inherent risks of gestation, parturition and lactation. Values of 3% mortality for males and 4% for females were taken.

As with the environmental variation set for female reproduction, we set the annual variation in mortality to be approximately 25% of the mean rates.

Catastrophes: Catastrophes are singular environmental events that are outside the bounds of normal environmental variation affecting reproduction and/or survival. Natural catastrophes can be tornadoes, floods, droughts, disease, or similar events. These events are modeled in VORTEX by assigning a probability of occurrence and a severity factor ranging from 0.0 (maximum or absolute effect) to 1.0 (no effect).

The Indo-Pacific is a tectonically active area with many volcanoes situated near the tectonic plate margins. Quite a number of volcanoes are found in North Sulawesi, the main ones being Tangkoko, Dua Saudara, Batuangus, Manadotua, Lokon, Klabat and Una Una on Una Una island of the Togian island group. Colleagues at the workshop with knowledge on Sulawesi estimated that a significant volcanic eruption in the immediate region of Sulawesi would take place every 50 years which gives a probability of occurrence of 2% annually. It was assumed that falling ash and toxic gases that accompany these events would take a toll on the babirusa. In addition, the alteration of the landscape following an eruption would also result in a lowered frequency of successful reproduction in the year an eruption occurred. We estimated a 15% decrease in female reproduction and 15% extra female mortality.

The tectonic activity also causes earthquakes. It was estimated that a fairly large earthquake takes place every 5 years giving a probability of occurrence of 20% annually. We estimated 15% extra female mortality as a result of the earthquake. We assumed that earthquakes would not take such a large toll on the environment as a volcanic eruption. Therefore, if a female survives the eruption she is likely to still reproduce that year.

Initial Population Size: Current estimates of babirusa distribution indicate that the species is still occurring in the forested regions of Northern, Central and South-eastern Sulawesi, Taliabu, Mangole, Buru and most of the Togian islands. No solid data is available on the densities and population sizes in these various regions. However, we made the following assumptions:

Northern Sulawesi: 1500-2500 babirusa based on the number of babirusa filmed during the study in the Gorontalo region northern Sulawesi (Patry et al. 1995). It was estimated that this population of babirusa was present in the valley system incorporating the salt licks where the observations were made. Based on the surface area of this valley system and the remaining forest cover in Northern Sulawesi it was estimated how many babirusa could be present in Northern Sulawesi.

Central Sulawesi: 3000; guess based on a conservative estimate of the numbers that might be there in relation to forest cover.

South East Sulawesi: 1500; guess based on a conservative estimate of the numbers that might be there in relation to forest cover.

Taliabu: 500; guess based on a conservative estimate of the numbers that might be there in relation to forest cover.

Mangole: 200; guess based on a conservative estimate of the numbers that might be there in relation to forest cover.

Buru: 500; guess based on a preliminary survey by Bing Tjiu in 1993 + the amount of inaccessible forested areas + the experience with Northern Sulawesi.
Togian islands: 400-600; guess based on a conservative estimate of the numbers that might be there in relation to forest cover.

To cover this range of possible population sizes the VORTEX models were run with a selection of initial population sizes equal to 500, 1500 and 2500.

Carrying Capacity: The carrying capacity, K, for a given habitat patch defines an upper limit for the population size, above which additional mortality is imposed across all age classes in order to return the population to the value set for K. VORTEX, therefore, uses K to impose density-dependence on survival rates. The program also has the capability of imposing density-dependent effects on reproduction that change as a function of K, but since no such data are available for babirusa populations, we chose not to include density-dependent reproduction in our models.

No information is available on the carrying capacities of the different regions of Sulawesi where babirusa occur. Considering the high hunting pressure on the species, especially in northern Sulawesi, we can assume the initial population size to be below carrying capacity. We have therefore arbitrarily set the carrying capacity at twice the initial population size so that it could be graphically shown whether or not the population has a potential for growth

Iterations and Years of Projection: All scenarios were simulated 100 times, with population projections extending for 100 years. Output results were summarized at 10-year intervals for use in some of the figures that follow. All simulations were conducted using VORTEX version 7.2 (June 1996).

Results from Simulation Modeling

The Baseline Model

The demographic and environmental parameters discussed were assembled in the VORTEX model to assess the status of a babirusa population free from any human-mediated threats to its persistence. This is considered the baseline babirusa population model.

The results from the baseline model for a babirusa population of 1500 initial individuals are shown in the first row of Table 4-1. Under the conditions simulated in the baseline model, a babirusa population can realize as much as 21% growth per year. This conclusion is based on a stochastic rate of increase, r_s, of 0.212 calculated from the model. Under these conditions of stochastic population growth, an undisturbed population can be expected to double in size in less than 5 years. As a result, the simulated population reaches the habitat carrying capacity rapidly and remains at that size throughout the duration of the simulation. Because of the large population size maintained during the 100 years, the loss of heterozygosity is negligible as shown by a population mean heterozygosity of 0.993. Based on these results, therefore, we can conclude that babirusa populations have the capacity for fairly dramatic growth if left undisturbed.

The first rows of Tables 4-2 and 4-3 show the results from the baseline model but with different initial population size conditions. Even when populations are small (as in Table 4-3), the risk of extinction is negligible and retention of population heterozygosity is high.

Alternative Models and Sensitivity Analysis

Since many of the demographic parameters for the simulated babirusa populations are based on educated guesses from limited field data, it is instructive to use the simulation modelling approach in an investigation of the relative sensitivities of the populations to changes in different demographic parameters. In other words, we can determine which parameters are more influential in determining the future viability of babirusa populations and utilize this information to help prioritize the collection of additional population data.

For the babirusa populations modelled here, three demographic parameters were chosen for investigation: the maximum age of reproduction, proportional female breeding success, and the extent of polygyny (an explicit investigation of the effect of additional mortality is discussed in detail below). The maximum age was increased to 15 years based on observations made in zoo populations. Additionally, the proportional female breeding success was decreased from the baseline value of 80% (20% of adult females failing to reproduce in a given year) to 70% and 60%. Finally, the extent of polygyny was likewise varied from the baseline value of 50% of the adult males in the pool of available breeders to 30% and 70%.

Table 1 shows the results of this type of sensitivity analysis with $N_0 = 1500$. Within a given extent of polygyny, an increase in the maximum age of reproduction results in even greater potential for population growth (age=12: $r_s = 0.212$; age=15: $r_s = 0.218$), although this increase is quite modest, only 3%. If proportional female breeding success is decreased below the baseline value, the growth rate of the population is likewise decreased. For example, under the baseline model with proportional female breeding success set at 80%, r_s is 0.212. However, when only 60% of adult females are expected to reproduce in a given year, the growth rate is reduced almost 28% to 0.153. Finally, the data indicate that changing the extent of polygyny does not measurably alter the dynamics of babirusa populations. This can be seen by the fact that changing the extent of polygyny from, for example, 50% to 70% does not change the stochastic growth rate r_s by more than 0.5%.

Tables 4-2 and 4-3, which differ from Table 4-1 only by the initial population size and corresponding carrying capacity, show almost identical results from this sensitivity analysis. In other words, the initial size of simulated babirusa populations does not influence the sensitivity of these populations to changes in demographic characteristics. This is almost certain to change, however, if babirusa populations decline to very small numbers, for example, just a few tens of individuals. Figure 4-1 summarizes the results of the sensitivity analysis and shows the enhanced sensitivity of simulated babirusa populations to changes in the proportional breeding success of females.

In summary, the simple sensitivity analyses presented here suggest that the degree of female reproductive success is an important factor in influencing the growth dynamics of babirusa populations. Specific considerations of the role played by age-specific mortality rates on babirusa population viability is explored in detail in the following section.

The Effects of Hunting on Babirusa Population Viability

Numerous discussions at this workshop indicated that hunting of babirusa by local human populations for subsistence as well as the meat trade is perhaps the primary threat facing the species. To explore the impact that various levels of hunting may have on the future characteristics of babirusa populations on Sulawesi, VORTEX models were developed that simulated additional babirusa mortality brought about by hunting pressure. Instead of simulating hunting through the harvest of a constant number of animals annually, using the Harvest module in VORTEX, we simulated this pressure by increasing age-specific mortalities to more closely mimic the density-dependent nature of this type of population threat.

More specifically, hunting pressures were quantified based on broad estimates of proportional off-takes from babirusa populations in Central and Northern Sulawesi (L. Clayton, pers. comm.). For example, if approximately 300 babirusa are removed in a year from a population of 1500 animals, this translates into a 20% removal rate and is simulated in the VORTEX models by adding 20% mortality to all age-sex classes (because of the predominance of snare hunting, which is quite non-selective, all age-sex classes were assumed to be equally impacted by this hunting). Initial levels of hunting pressure studied were 20%, 30% and 40% additional annual mortality. Discussions by workshop participants indicated that 40% annual hunting removal on particular populations is not unrealistic.

Table 4-4 and Figures 4-2 and 4-3 show the results of these analyses on simulated populations of 1500 individuals and a carrying capacity of 3000. Under 20% hunting pressure, the population decreases at a rate of about 6% annually. This rate of decline results in a probability of extinction for a population such as this of almost 50% (P(E) = 0.49) within 100 years and a mean time to extinction of 83 years. The picture is made considerably worse, however, by noting that the size of those surviving populations after 100 years is only 45 animals, with nearly 25% of the original population heterozygosity lost during the simulation. Babirusa populations are driven very rapidly to certain extinction if the removal rates are increased to 30-40% (P(E) = 1.0; T(E) = 23-29 years). Additional models utilizing removal rates of 10 - 15% demonstrate that babirusa populations cannot survive if removal rates exceed 15% annually. Furthermore, hunting models were constructed that removed either males or females exclusively to investigate the sensitivity of this species to sex-biased hunting practices. The results in Table 4-4 dramatically indicate that removal of females carries much greater consequences for population viability than does removal of males only. This is explained by the polygynous nature of the babirusa breeding system, where females are the limiting sex in terms of overall population dynamics.

Conclusions and Recommendations

1. Current life-table parameter estimates give a baseline babirusa population model with a growth rate potential of about 21% annually. This represents a substantial growth potential given the small litter sizes characteristic of this species, and is perhaps best explained by the ability of adult females to reproduce annually. In fact, simple sensitivity analyses indicate that the proportion of adult females breeding each year, obtained from data on inter-birth intervals, may be the most important aspect of babirusa population dynamics with regard to the prediction of future population viability. A greater effort is needed to determine the demographic parameters governing the growth dynamics of babirusa populations on Sulawesi. This can be accomplished through the conduct of long-term longitudinal studies of wild babirusa populations. Particular parameters requiring better estimation are: annual female breeding success, age-specific mortality, and reproductive lifespan.

2. Further field work is necessary in order to more firmly establish concensus estimates of babirusa density across Sulawesi. Concensus must be reached as to the preferred methods to be used in such work.

3. Models were developed that explored the effects of hunting of babirusa for food on the viability of populations subjected to this pressure. Proportional additions to mortality were used to simulate this pressure, based on estimates of animals killed by these activities in Central and North Sulawesi. Results from these models suggest that, if hunting removes an additional 30% of babirusa annually from these populations (equivalent to removing about 450 animals from a population of 1500), the simulated populations decline at a rate of almost 24% annually. As a result, the extinction of this population is virtually assured within 30 years. Twenty percent additional mortality above the baseline levels results in a population exhibiting nearly a 6% annual rate of decline and a 50% probability of extinction, likely to occur within 85 years. In fact, with the current life table parameter estimates, babirusa populations can only sustain a hunting rate of less than 15% annually. The models also demonstrate that removal of females is much more damaging to the populations than is the removal of an equivalent proportion of males. Hunting of babirusa, therefore, appears to be a primary factor in determining the future viability of babirusa populations across Sulawesi. Studies must continue in their attempts to quantify the extent of hunting of babirusa across the island.

References

Leus, K., D. Bowles, J. Bell, and A.A. Macdonald. 1992. Behaviour of the babirusa (*Babyrousa babyrussa*) with suggestions for husbandry. Acta Zoologica et Pathologica Antverpiensia **82**:9-27.

Macdonald, A.A. 1993. The Babirusa (*Babyrousa babyrussa*). Pages 161-171 In: Oliver, W.L.R. (Ed.). Status Survey and Conservation Action Plan: Pigs, Peccaries and Hippos. IUCN: Gland, Switzerland.

Macdonald, A.A., D. Bowles, J. Bell, and K. Leus. 1993. Agonistic behaviour in captive babirusa (*Babyrousa babyrussa*). Zeitschrift für Säugetierkunde **58**:18-30.

Patry, M., Leus, K. & Macdonald, A.A. (1995) Group structure and behaviour of babirusa (*Babyrousa babyrussa*) in northern Sulawesi. Australian Journal of Zoology, **43**, 643-655.

Plasa, L. 1996. *Babyrousa babyrussa* 1994/95. Internationales Zuchtbuch für den Hirscheber / International Studbook for the Babirusa 1994/95. Wilhelma Zoologisch Botanischer Garten: Stuttgart.

Table 4-1. Babirusa Population Viability. Initial population size is 1500 and the carrying capacity, K, is 3000. r_s is the stochastic population growth rate calculated from the simulation, P(E) is the probability of population extinction within 100 years, N_{100} is the size of the simulated population at the end of the 100-year simulation, and H_{100} is the population heterozygosity at 100 years.

Max. Age	Breeding Success	r_s	P(E)	N_{100}	H_{100}
50% Polygyny					
12	80	0.212	0.0	3000	0.993
15	80	0.218	0.0	2996	0.993
12	70	0.182	0.0	2996	0.993
15	70	0.191	0.0	2996	0.994
12	60	0.153	0.0	2997	0.994
15	60	0.162	0.0	2998	0.992
30% Polygyny					
12	80	0.212	0.0	3000	0.992
15	80	0.218	0.0	2997	0.992
12	70	0.182	0.0	2997	0.993
15	70	0.191	0.0	2998	0.993
12	60	0.151	0.0	2999	0.993
15	60	0.161	0.0	2993	0.993
70% Polygyny					
12	80	0.211	0.0	2995	0.993
15	80	0.218	0.0	3000	0.993
12	70	0.182	0.0	2999	0.994
15	70	0.190	0.0	3000	0.994
12	60	0.151	0.0	2995	0.994
15	60	0.162	0.0	3000	0.994

Table 4-2. Babirusa Population Viability. Initial population size is 2500 and the carrying capacity, K, is 5000. See Table 1 legend for table definitions.

Max. Age	Breeding Success	r_s	P(E)	N_{100}	H_{100}
50% Polygyny					
12	80	0.212	0.0	5000	0.996
15	80	0.217	0.0	4995	0.996
12	70	0.183	0.0	5000	0.996
15	70	0.189	0.0	4997	0.996
12	60	0.152	0.0	4990	0.996
15	60	0.161	0.0	4994	0.997
30% Polygyny					
12	80	0.210	0.0	5000	0.997
15	80	0.218	0.0	4998	0.996
12	70	0.182	0.0	4999	0.996
15	70	0.190	0.0	5000	0.995
12	60	0.151	0.0	4990	0.996
15	60	0.160	0.0	4991	0.997
70% Polygyny					
12	80	0.211	0.0	5000	0.996
15	80	0.217	0.0	4997	0.996
12	70	0.183	0.0	4993	0.997
15	70	0.191	0.0	4997	0.997
12	60	0.151	0.0	4993	0.996
15	60	0.161	0.0	5000	0.996

Table 4-3. Babirusa Population Viability. Initial population size is 500 and the carrying capacity, K, is 1000. See Table 1 legend for table definitions.

Max. Age	Breeding Success	r_s	P(E)	N_{100}	H_{100}
50% Polygyny					
12	80	0.211	0.0	998	0.979
15	80	0.217	0.0	1000	0.980
12	70	0.182	0.0	997	0.980
15	70	0.189	0.0	1000	0.981
12	60	0.152	0.0	999	0.981
15	60	0.161	0.0	1000	0.982
30% Polygyny					
12	80	0.211	0.0	1000	0.976
15	80	0.218	0.0	1000	0.977
12	70	0.183	0.0	996	0.978
15	70	0.191	0.0	1000	0.979
12	60	0.150	0.0	998	0.979
15	60	0.162	0.0	999	0.980
70% Polygyny					
12	80	0.212	0.0	999	0.980
15	80	0.218	0.0	998	0.980
12	70	0.183	0.0	999	0.980
15	70	0.191	0.0	998	0.981
12	60	0.153	0.0	997	0.983
15	60	0.160	0.0	998	0.982

Table 4-4. The effects of hunting on babirusa population viability. Initial population size is 1500 and the carrying capacity, K, is 3000. See Table 1 legend for table definitions, and see text for further discussion of the quantification of population hunting pressure.

Hunting Pressure	r_s	P(E)	T(E)	N_{100}	H_{100}
20%	-0.058	0.49	83	45	0.749
30%	-0.237	1.0	29	—	—
40%	-0.292	1.0	23	—	—
20%, ♀♀ only	-0.050	0.53	75	45	0.843
20%, ♂♂ only	0.212	0.0	—	3000	0.985
10%	0.090	0.0	—	2976	0.992
15%	0.025	0.0	—	2667	0.991

Figure Legends

Figure 4-1. Effects of changes in babirusa population demographic parameters on the stochastic population growth rate, r_s. Each bar represents the average growth rate across all simulation models using the specified demographic parameter. The parameters include the extent of polygyny, defined as the proportion of adult males in the available breeding pool in a given year; the maximum age of reproduction for both sexes; and the extent of female reproductive success, defined as the average proportion of adult females that produce offspring in a given year.

Figure 4-2. Impact of increasing levels of hunting on babirusa population viability. Time series plots of population size as a function of time (years) for simulated babirusa populations subjected to increasing levels of hunting. For these models, hunting was simulated by increasing age-specific mortality rates above the baseline values according to estimates of proportional removals of individuals from wild populations. In each model, a carrying capacity of 3000 was imposed, above which population size was truncated.

Figure 4-3. Impact of hunting on the probability of extinction of simulated babirusa populations.

Figure 4-1.
Babirusa Population Viability: Sensitivity Analysis

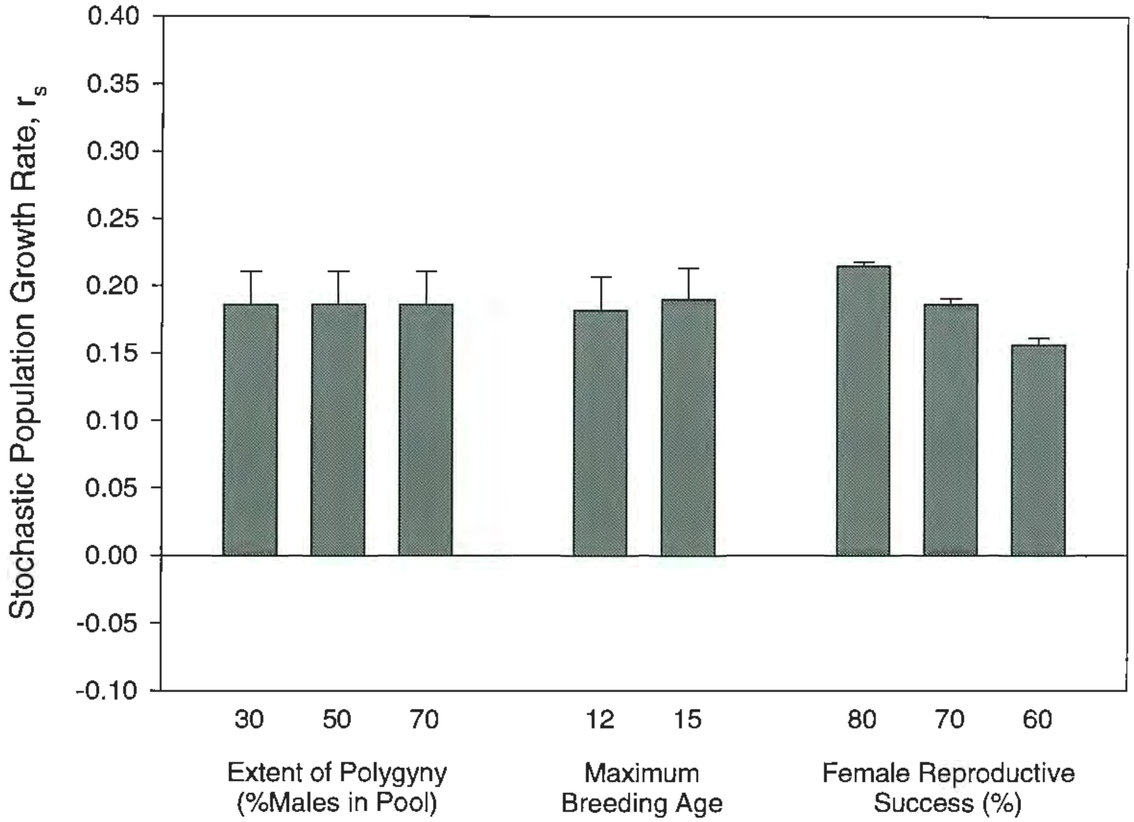


Figure 4-2.
Babirusa Population Viability:
Effects of Hunting on Population Persistence

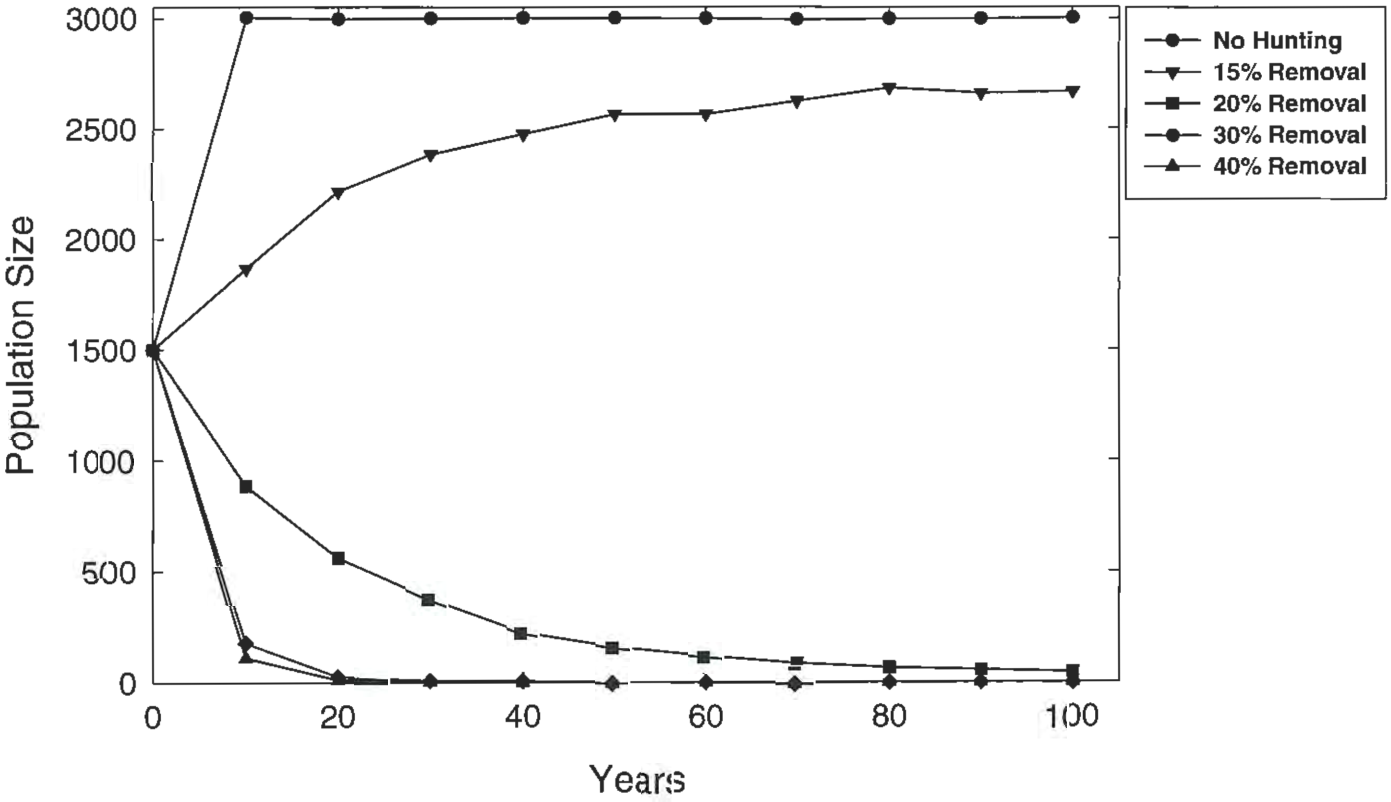
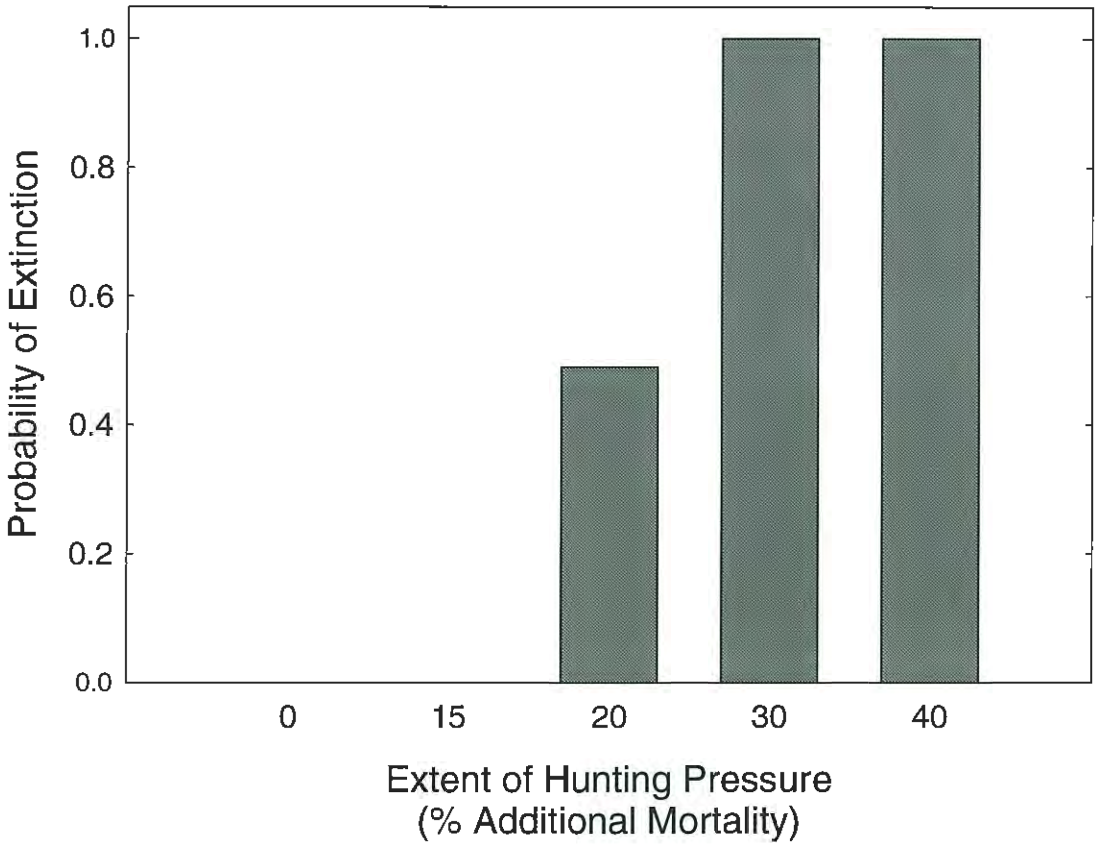


Figure 4-3.
Babirusa Population Viability:
Hunting Pressure and Extinction Probability



Sample VORTEX Input File

```
BAB_201.OUT     ***Output Filename***
Y      ***Graphing Files?***
N      ***Each Iteration?***
Y       ***Screen display of graphs?***
100      ***Simulations***
100      ***Years***
10      ***Reporting Interval***
1      ***Populations***
N      ***Inbreeding Depression?***
Y      ***EV correlation?***
2      ***Types Of Catastrophes***
P      ***Monogamous, Polygynous, or Hermaphroditic***
2      ***Female Breeding Age***
4      ***Male Breeding Age***
12      ***Maximum Age***
0.500000     ***Sex Ratio***
3      ***Maximum Litter Size***
N      ***Density Dependent Breeding?***
20.000000     ***Population 1: Percent Litter Size 0***
46.000000     ***Population 1: Percent Litter Size 1***
31.500000     ***Population 1: Percent Litter Size 2***
2.500000     ***Population 1: Percent Litter Size 3***
5.000000     ***EV--Reproduction***
50.000000     ***Female Mortality At Age 0***
10.000000     ***EV--FemaleMortality***
25.000000     ***Female Mortality At Age 1***
5.000000     ***EV--FemaleMortality***
24.000000     ***Adult Female Mortality***
5.000000     ***EV--AdultFemaleMortality***
50.000000     ***Male Mortality At Age 0***
10.0000000     ***EV--MaleMortality***
25.000000     ***Male Mortality At Age 1***
5.000000     ***EV--MaleMortality***
30.000000     ***Male Mortality At Age 2***
6.000000     ***EV--MaleMortality***
25.000000     ***Male Mortality At Age 3***
5.000000     ***EV--MaleMortality***
23.000000     ***Adult Male Mortality***
5.000000     ***EV--AdultMaleMortality***
2.000000     ***Probability Of Catastrophe 1***
0.850000     ***Severity--Reproduction***
0.850000     ***Severity--Survival***
20.000000     ***Probability Of Catastrophe 2***
1.000000     ***Severity--Reproduction***
0.950000     ***Severity--Survival***
N      ***All Males Breeders?***
Y      ***Answer--A--Known?***
50.000000     ***Percent Males In Breeding Pool***
Y      ***Start At Stable Age Distribution?***
1500      ***Initial Population Size***
3000      ***K***
0.000000     ***EV--K***
N      ***Trend In K?***
N       ***Harvest?***
N      ***Supplement?***
N      ***AnotherSimulation?***
```

Sample VORTEX Output File

```
VORTEX -- simulation of genetic and demographic stochasticity
BAB_201.OUT
Wed Jul 24 23:16:46 1996

  1 population(s) simulated for 100 years, 100 iterations

  No inbreeding depression

  First age of reproduction for females: 2   for males: 4
  Age of senescence (death): 12
  Sex ratio at birth (proportion males): 0.50000

Population 1:
  Polygynous mating;
 50.00 percent of adult males in the breeding pool.

  Reproduction is assumed to be density independent.

    20.00 (EV = 5.00 SD) percent of adult females produce litters of size 0
    46.00 percent of adult females produce litters of size 1
    31.50 percent of adult females produce litters of size 2
     2.50 percent of adult females produce litters of size 3

   50.00 (EV = 10.00 SD) percent mortality of females between ages 0 and 1
   25.00 (EV = 6.00 SD) percent mortality of females between ages 1 and 2
   24.00 (EV = 6.00 SD) percent annual mortality of adult females (2<=age<=12)
   50.00 (EV = 10.00 SD) percent mortality of males between ages 0 and 1
   25.00 (EV = 6.00 SD) percent mortality of males between ages 1 and 2
   30.00 (EV = 7.00 SD) percent mortality of males between ages 2 and 3
   25.00 (EV = 6.00 SD) percent mortality of males between ages 3 and 4
   23.00 (EV = 6.00 SD) percent annual mortality of adult males (4<=age<=12)
    EVs may have been adjusted to closest values
        possible for binomial distribution.
    EV in reproduction and mortality will be correlated.

  Frequency of type 1 catastrophes: 2.000 percent
    with 0.850 multiplicative effect on reproduction
     and 0.850 multiplicative effect on survival

  Frequency of type 2 catastrophes: 20.000 percent
    with 1.000 multiplicative effect on reproduction
     and 0.950 multiplicative effect on survival

  Initial size of Population 1:
    (set to reflect stable age distribution)
 Age   1   2   3   4   5   6   7   8   9  10  11  12    Total
     176 137  98  76  61  48  38  31  24  19  15  12    735  Males
     176 137 107  84  65  52  40  32  25  19  16  12    765  Females

  Carrying capacity = 3000 (EV = 0.00 SD)

Deterministic population growth rate (based on females, with assumptions of
  no limitation of mates, no density dependence, and no inbreeding
depression):

     r =  -0.044     lambda = 0.957     R0 =     0.813
   Generation time for:  females = 4.66    males = 6.45
```

Sample VORTEX Output File (Contd)

```
Stable age distribution:  Age class    females    males
                              0        0.156      0.156
                              1        0.081      0.081
                              2        0.062      0.062
                              3        0.049      0.045
                              4        0.038      0.035
                              5        0.030      0.028
                              6        0.024      0.022
                              7        0.019      0.018
                              8        0.015      0.014
                              9        0.011      0.011
                             10        0.009      0.009
                             11        0.007      0.007
                             12        0.005      0.006
Ratio of adult (>= 4) males to adult (>= 2) females: 0.551

Population 1

Year 10
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          886.46 (  33.08 SE,  330.83 SD)
     Expected heterozygosity =    0.998 (  0.000 SE,    0.001 SD)
     Observed heterozygosity =    0.999 (  0.000 SE,    0.001 SD)
     Number of extant alleles =  654.42 (  16.63 SE,  166.35 SD)
Year 20
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          562.45 (  31.13 SE,  311.26 SD)
     Expected heterozygosity =    0.994 (  0.000 SE,    0.002 SD)
     Observed heterozygosity =    0.997 (  0.000 SE,    0.003 SD)
     Number of extant alleles =  293.32 (  10.84 SE,  108.39 SD)
Year 30
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          378.39 (  23.44 SE,  234.40 SD)
     Expected heterozygosity =    0.987 (  0.001 SE,    0.006 SD)
     Observed heterozygosity =    0.992 (  0.001 SE,    0.007 SD)
     Number of extant alleles =  159.41 (   7.01 SE,   70.14 SD)
Year 40
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          224.64 (  15.43 SE,  154.32 SD)
     Expected heterozygosity =    0.976 (  0.001 SE,    0.013 SD)
     Observed heterozygosity =    0.986 (  0.001 SE,    0.012 SD)
     Number of extant alleles =   90.78 (   4.56 SE,   45.55 SD)
Year 50
     N[Extinct] =       0, P[E] = 0.000
     N[Surviving] =   100, P[S] = 1.000
     Population size =          160.39 (  16.48 SE,  164.81 SD)
     Expected heterozygosity =    0.954 (  0.003 SE,    0.032 SD)
     Observed heterozygosity =    0.972 (  0.002 SE,    0.023 SD)
     Number of extant alleles =   54.23 (   3.54 SE,   35.36 SD)
```

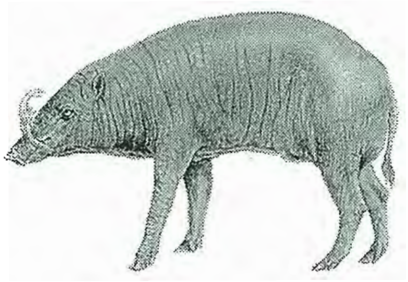
Sample VORTEX Output File (Contd)

```
Year 60
     N[Extinct] =       3, P[E] = 0.030
     N[Surviving] =    97, P[S] = 0.970
     Population size =          118.42 (  16.52 SE,  162.66 SD)
     Expected heterozygosity =    0.923 (  0.006 SE,    0.057 SD)
     Observed heterozygosity =    0.948 (  0.006 SE,    0.059 SD)
     Number of extant alleles =   35.45 (   2.87 SE,   28.23 SD)
Year 70
     N[Extinct] =       7, P[E] = 0.070
     N[Surviving] =    93, P[S] = 0.930
     Population size =           85.12 (  13.26 SE,  127.92 SD)
     Expected heterozygosity =    0.876 (  0.010 SE,    0.099 SD)
     Observed heterozygosity =    0.923 (  0.010 SE,    0.094 SD)
     Number of extant alleles =   24.34 (   2.40 SE,   23.14 SD)
Year 80
     N[Extinct] =      17, P[E] = 0.170
     N[Surviving] =    83, P[S] = 0.830
     Population size =           65.13 (  11.73 SE,  106.84 SD)
     Expected heterozygosity =    0.827 (  0.015 SE,    0.141 SD)
     Observed heterozygosity =    0.887 (  0.015 SE,    0.139 SD)
     Number of extant alleles =   17.64 (   2.00 SE,   18.19 SD)
Year 90
     N[Extinct] =      32, P[E] = 0.320
     N[Surviving] =    68, P[S] = 0.680
     Population size =           54.60 (  10.94 SE,   90.19 SD)
     Expected heterozygosity =    0.775 (  0.022 SE,    0.180 SD)
     Observed heterozygosity =    0.848 (  0.023 SE,    0.186 SD)
     Number of extant alleles =   13.75 (   1.73 SE,   14.24 SD)
Year 100
     N[Extinct] =      49, P[E] = 0.490
     N[Surviving] =    51, P[S] = 0.510
     Population size =           45.08 (   9.02 SE,   64.42 SD)
     Expected heterozygosity =    0.749 (  0.029 SE,    0.205 SD)
     Observed heterozygosity =    0.811 (  0.029 SE,    0.210 SD)
     Number of extant alleles =   11.86 (   1.76 SE,   12.55 SD)


In 100 simulations of Population 1 for 100 years:
  49 went extinct and 51 survived.

This gives a probability of extinction of 0.4900 (0.0500 SE),
  or a probability of success of          0.5100 (0.0500 SE).

Of those going extinct,
    mean time to first extinction was 83.29 years (1.69 SE, 11.82 SD).

Mean final population for successful cases was 45.08 (9.02 SE, 64.42 SD)

   Age 1       2       3   Adults    Total
    5.29    4.12    3.00    9.57     21.98  Males
    4.73                   18.37     23.10  Females

Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was -0.0584 (0.0017 SE, 0.1649 SD)

Final expected heterozygosity was      0.7487 ( 0.0287 SE,  0.2050 SD)
Final observed heterozygosity was      0.8115 ( 0.0294 SE,  0.2098 SD)
Final number of alleles was             11.86 (   1.76 SE,   12.55 SD)
```

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 5
Captive Population Management



CAPTIVE POPULATION MANAGEMENT

Working Group Members:

Djarot Harsojo	Surabaya zoo
Asep Heri	Bandung zoo
Budi Irawanto	Ragunan zoo
Penny Kalk	WCS/ New York
Alastair A Macdonald	The University of Edinburgh
Hari Palguna	Gembira Loko, Yogyakarta
Kumar Pillai (facilitator)	Singapore zoo
Bruno Van Puijenbroeck	Antwerp zoo
Rudi Reinhard	Berlin zoo
Endah Wahyuni	Surabaya zoo

Executive summary of recommendations: Babirusa captive management subgroup

1. Only B*abyrousa babyrussa celebensis* should be considered for captive management.

2. Animals should not be captured in South-east Sulawesi because it is unclear what subspecies may be represented there. No animals should be capured in protected areas in order to safeguard these populations.

3. Collect enough animals to achieve an effective founder base to maintain 90% heterozygosity over 100 years. The methods of collection must be up to the highest welfare standards making full use of the available expertise.

4. A management group needs to be formed within one year to manage the captive population. The group should appoint a Southeast Asian regional studbook keeper. It should develop a masterplan for the management of the captive population. A husbandry manual should be developed.

5. All institutions keeping babirusa should be required to positively identify EACH individual babirusa and maintain rigorous record-keeping standards.

6. Holders of wild-caught babirusa must meet minimum requirements for facilities and management experience. Holders of wild-caught babirusa who do not meet minimum requirements should hand over the animals to zoos which do meet these requirements. Spaces for new founders need to be created in Indonesia.

7. All wild-caught stock should remain in Indonesia. Only captive born descendants of wild-caught founders should go to the rest of the world population.

8. Animals should only go to those world institutions that agree to join the management committee and will be able to cooperate with the programme on a long-term basis.

History of the captive population

The group recognized that for sound captive management purposes it was essential to have as complete and accurate a record as possible of the history of the captive collection of the babirusa. Many of the details are present in the 1994-95 studbook (Plasa 1996). Additional material is being gathered by Paul Vercammen and Alastair Macdonald. The group worked to clarify some questions which related to the very early years of the studbook's founding stock.

- There were four visits made by staff from Surabaya zoo to Sulawesi to collect babirusa. All animals collected on the first three visits failed to survive.
- On the fourth visit (in 1972), 1.2 and 2 juvenile males were brought from Poso on the north coast of central Sulawesi to Surabaya.
- All three adults bred. However, there is no information available to indicate whether the two juvenile males ever bred. There is likewise no information to indicate whether the juveniles are related to the three adults collected. It is also unknown whether or not the three adults were related to one another.
- After 1972, no babirusa has come into Surabaya, from the wild or any other zoo. The conclusion reached by the group was that as the most conservative estimate, all the animals currently held in captivity contain the genetic material represented by 1.2 founders.

Written records in Surabaya indicate:	Records of zoos receiving animals indicate:
2.2 to Antwerp in 1975 (bred)	(Dec 1974, 1.1 arrived in Antwerp (bred), and in Mar 1975, 1.1 arrived in Stuttgart (bred))
	(Mar 1976, 1.1 arrived in Stuttgart (bred))
1.1 to Rotterdam in 1977	(Aug 1977, 1.1 arrived in Rotterdam (bred))
1.1 to Bandung	(Mar 1990, 1.1 arrived in Bandung (not bred)
	(Dec 1993, 1.0 arrived in Bandung (died next day) one female survives. There have been no offspring
3.5 to Singapore in 1992	(In Jul 1992, 3.5 arrived in Singapore (bred))
1.1 to Yogjakarta in Feb 1995	(which produced 1.0 in November 1995)

Written records in Ragunan indicate:	
2.3 from Surabaya in 1975.	This zoo has only had animals from Surabaya.
2.2 to Port Lympne in 1982.	(Port Lympne has no record of receipt of these animals)
2.2 to Antwerp in 1984.	(In April 1984 2.2 arrived in Antwerp (bred))

The group adopted the following framework for making its recommendations with respect to the future management of captive babirusa.

Goals

1. Prevent or reduce threat of extinction by the creation of a self sustaining population.
2. Provide the potential for reintroduction, ex situ by captive breeding and in situ by the legal protection of the biotope.
3. Research the biology of the species, ex situ and in situ.
4. Exhibit the animal and by public education programmes increase conservation awareness.

Objectives derived from the first two goals

1. Retain 90% heterozygosity for 100 years
2. Use the minimum number of wild caught founders necessary to achieve goal 1
3. Use some of the current captive stock as part of the new captive management programme
4. Minimise the risk of extinction of the captive population by good husbandry practices
5. Manage the smallest size of captive population necessary for the achievement of goal 1
6. Establish primary captive population of wild-caught founders in Indonesia

Summary of discussion by the subgroup, arranged according to the order of the executive summary

1)

The Togian islands have the subspecies of babirusa (*B.b. togeanensis*) with the smallest population size. The Buru and Sula group of islands contains the subspecies (*B. b. babyrussa*) with the next smallest population of babirusa. The island of Sulawesi has the subspecies of babirusa (*B.b. celebensis*) which occurs in the largest numbers. Although the first two subspecies are designated as endangered (Oliver 1993), the group decided that the *celebensis* subspecies is the only one for which captive propagation is merited and justifiable. The reasons for this decision are:

a. *B. b. celebensis* is the only subspecies which is numerous enough to tolerate removal of an adequate number for conservation breeding in captivity without the capture process contributing to the possible extinction of the race.
b. *B. b. celebensis* is also the only subspecies coming from a habitat with a large enough land mass to permit the potential for reintroduction in the future.
c. *B. b. celebensis* is the only subspecies currently in captivity.
d. It is likely that *B. b. celebensis* is suffering the highest rate of decline due to hunting pressure as indicated by the very large number of babirusa being sold weekly in the meat markets of North Sulawesi.
e. *B. b. celebensis* is the subspecies which has the best chance of long-term survival.

We felt that it was essential to carefully assess the potential harm to the species by the process of collecting animals from the wild for captive propagation. In our opinion, the potential harm caused by the relatively small collection of the *celebensis* subspecies for captive propagation should be measured against the very much larger damage currently being caused to this subspecies by the weekly cull of babirusa to supply city meat markets. Estimates were given of 5-20 animals per week (Budiarso et al, 1991; L. Clayton, pers. comm.)

In order to maintain 90% heterozygosity over 100 years, 20.20 babirusa need to be collected from the wild and brought into conservation management. This will result in approximately 10.10 effective founders.

Wild animals may need to be brought from near Poso, the region of origin of the original founders. However, we need to investigate the race from that region vis à vis the race from

North Sulawesi. For this purpose, there is a need to collect skulls (some are currently available at the museum in Bogor) and biochemical evidence from babirusa in Central Sulawesi and North Sulawesi to confirm that the animals there are *B. b. celebensis*. Additional skulls need to be gathered from zoo animals, and wild animals from the Poso region also need to be checked by Colin Groves, the taxonomist at the Australian National University, Canberra, Australia.

2)

Animals should not be captured in South-east Sulawesi because it is unclear what subspecies may be represented there. No animals should be captured in protected areas in order to safeguard these populations.

3)

Enough animals should be collected in order to achieve an effective founder base to maintain 90% heterozygosity over 100 years. The methods of collection must be up to the highest welfare standards making full use of the available expertise.

The methods needed to capture, acclimatise and transport babirusa from Sulawesi to the designated Indonesian zoos have yet to be developed adequately. For example, potential sites in North and North-central Sulawesi need to be identified to enable the holding of freshly caught wild founders. Both Surabaya zoo and Taman Safari have animal holding sites near Poso. Animal husbandry facilities at Universitas Sam Ratulangi may provide suitable animal holding pens in the Manado region. It is essential to the programme that the wild-caught animals be treated in a very special way because of the sensitivity to stress of animals from the forest. The animals will need a considerable amount of time to adjust to the presence of people. They will need a lot of time to overcome their natural instinct to flee from people. Somewhat younger animals adapt better than older adults. Wild-caught females must have separate housing from two weeks before birth (when the vulva starts to swell) until six weeks after delivery. The female is very agressive to others and protective of her young during this period. Some (dry vegetable) material should be provided to allow the female to construct a nest in which to have privacy and deliver her young. The aim will be to have an equal number of male and female offspring from every founder in order to equalise the founder representation in the captive population.

4)

A management group needs to be formed within one year to manage the captive population. The group suggests that the structure of this group follows the format of the Sumatran Tiger management group: for example, a representative from each SE Asian zoo with babirusa should be appointed to this group. People from outside the region may be invited to participate in the group. A co-ordinator for the programme is required.

The management group should appoint a Southeast Asian regional studbook keeper. Endah Wahyuni, was identified as the person who should begin immediately to facilitate the collection of appropriate records of the regional captive population. Correspondents in each SE Asian zoo currently holding babirusa were identified to supply her with the appropriate information. Births and deaths should be reported to the studbook keeper within 2 days.

A training course for record keeping will be held in Malaca in October, 1996. The group recommends that a representative and/or record keeper from each Indonesian zoo with babirusa should attend the course.

All babirusa holders should make and keep necropsy reports on all individuals that die. World zoos should send anaesthesia protocols for babirusa to Endah Wahyuni for local management purposes.

An interested veterinarian should be sought to undertake the long-term analyses of pathological and other veterinary reports on the babirusa gathered in the course of normal zoo routines, in order to detect disease and infirmity problems within the captive population, and to stimulate veterinary research to seek solutions to disease conditions which may arise in captivity or in the wild.

The management group should develop a masterplan for the management of the captive population.

A husbandry manual should be developed. Currently, global guidelines for the husbandry and management of babirusa are being developed under the coordination of Penny Kalk. 'Pak Djarot Harsojo has agreed to translate these into Bahasa Indonesia.

The management group is responsible for seeing that the masterplan is implemented.

5)

All institutions keeping babirusa should be required to positively identify **EACH** individual babirusa and maintain rigorous record-keeping standards. Zoo staff in Indonesia should micro-chip **AND** ear notch all babirusa, and until advised otherwise by the management group, should send the detailed records of individuals to Endah Wahyuni at Surabaya zoo.

The minimum requirements for conservation holding of wild-caught babirusa were defined as follows:

Adequate animal holding facilities, adequate management experience, and good animal breeding experience. It is very important that the facilities that receive wild-caught animals should meet the minimum housing and animal management requirements defined by this group:

Minimum housing requirements for babirusa were developed using the new Surabaya housing as a model. Indoor floor space was 2.25 x 3m, with an outside exercise area of 4 x 3m. The floor indoors should be made of concrete, whereas the outdoor area should be of sand. The minimum wall height should be 1.75m with the lower 1.5m solid and the area above that (to at least 1.75m) in wire mesh

* insert drawings of Surabaya facility and model developed by the group - Paul Vercammen has these as photographs.

The additional exhibition space can be as large or as small as space allows. Water and shelter are essential. An area to allow the animal to wallow in water or mud is recommended. Shade in the additional space is encouraged.

Possible improvements on the minimum housing requirements were suggested.

A) Gates connecting pens are located at the rear of the indoor enclosure
B) Sliding gates should connect all adjacent pens, and should be operated from outside the pens.
C) Roof sloped so that rain water falls outside the pen.

A tropical transport crate was designed by the subgroup. The important structural requirements were:

- The crate needs a large amount of air-flow through it.
- The animal needs privacy, therefore solid lower walls, and holes or thin wire mesh in the upper third of the box.
- Double skin roof to minimize radiant heating of animal.
- Crate height interior is 1.5x the shoulder height of animal.
- Crate width is same as shoulder height.
- Doors at both ends have holes/wire mesh in upper third of the doors.
- Both doors are sliding.
- Put low closing flap in the door to slide a basin of water in.
- Non slip flooring.

6)

Holders of wild-caught babirusa must meet minimum requirements for facilities and management experience. Holders of wild-caught babirusa who do not meet minimum requirements should hand over the animals to zoos which do meet these requirements. Spaces for new founders need to be created in Indonesia. The institutions which identified themselves as willing to collaborate in the wild-caught babirusa captive breeding programme were Bandung, Ragunan, Surabaya, Taman Safari and Yogyakarta.

7)

All wild-caught stock should remain in Indonesia. Only captive born descendants of wild caught founders should go to the rest of the world population.

The founder population should be managed to expand rapidly. We anticipate that 10 effective pairs will result in 7 living offspring each year. Losses due to neonatal mortality need to be kept as low as possible by careful management.

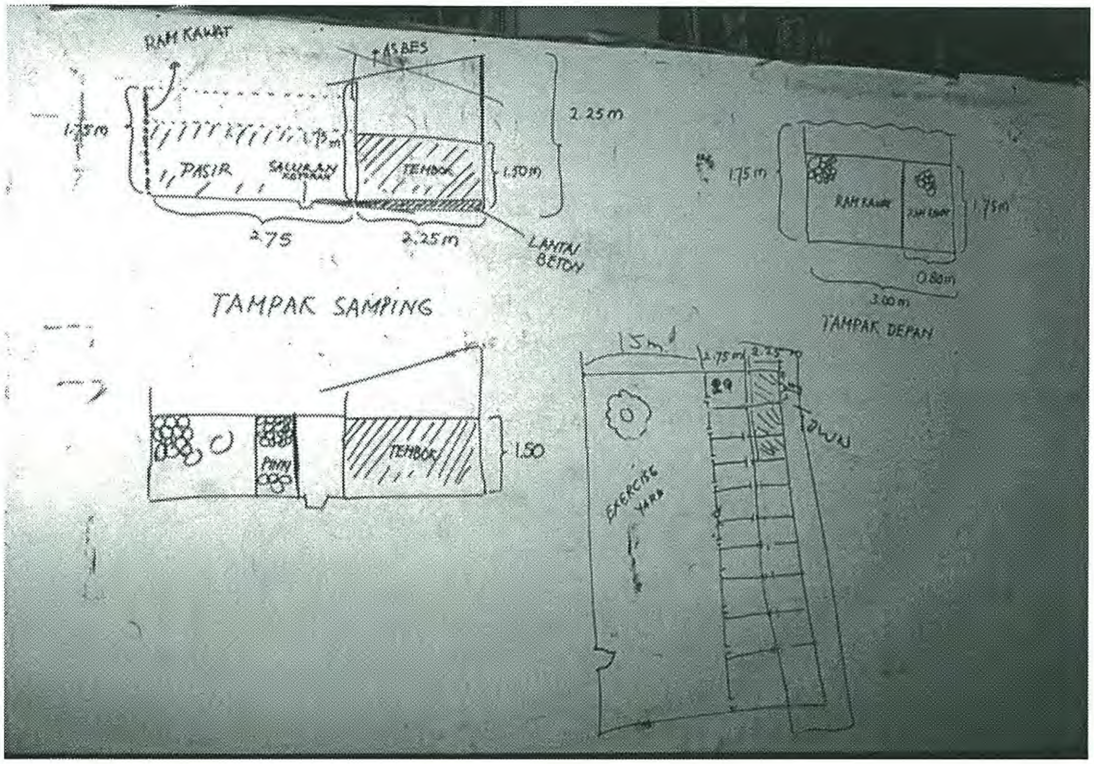
There should be consultation with the babirusa Endangered Species Program, babirusa Species Survival Plan, the Australian Species Management Programme, for the distribution to zoos within their areas of the captive born descendants of wild caught founders.

In order to produce F2 offspring it is important not to breed the F1 animals of common parents. The group recommended that zoos should plan to use SPARKS for studbook and breeding strategies.

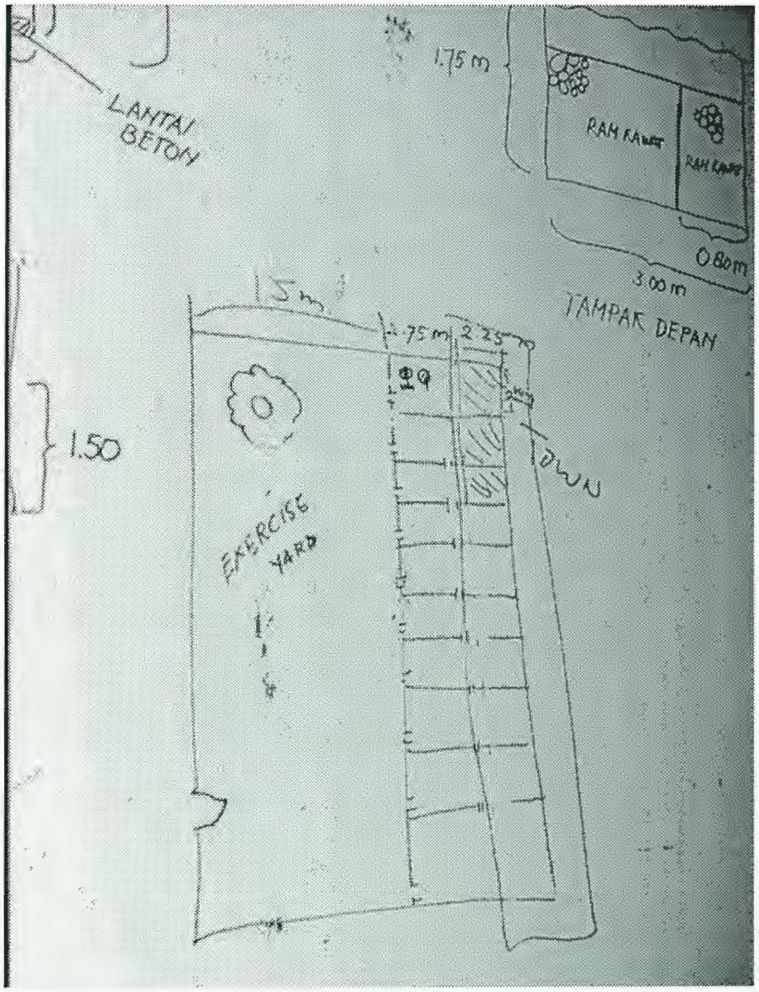
It was also proposed that 2-3 pairs of the current captive population of the lowest F generation should be identified to contribute to the captive breeding programme. It was recommended that faecal samples from the current captive stock in Indonesia should be collected for DNA analysis to assist with the identification of these animals. It was recommended that zoos should be warned to plan to stop breeding the current captive stock. However, it is very important that zoos do not castrate any animals until the 2.2 or 3.3 animals in the present collections which will contribute to the future captive population are identified.

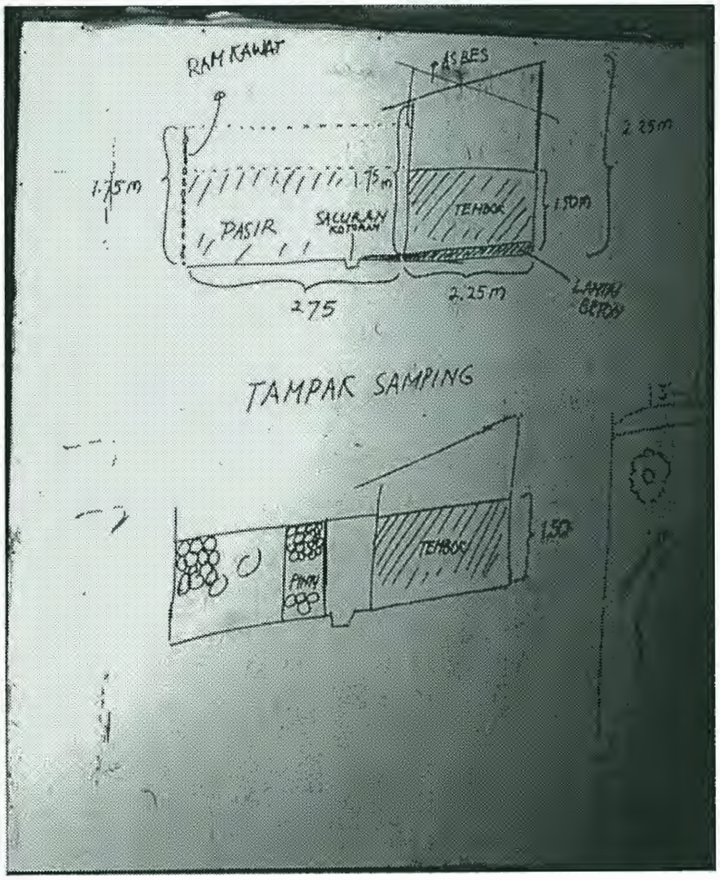
8)

Animals should only go to those world institutions that agree to join the management committee and will be able to cooperate with the programme on a long-term basis.
It is important that the zoos which are involved in the multiplication of babirusa to form the captive population are prepared to commit resources to this project for a number of generations in order to fascilitate the active management of the captive breeding programme.



Drawing depicting the Surabaya facility and model developed by the babirusa captive management group.



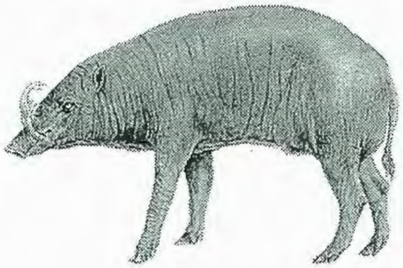


Details of drawings depicting the Surabaya facility and model developed by the babirusa captive management group.

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 6
Appendix I:
List of Participants



List of Workshop Participants

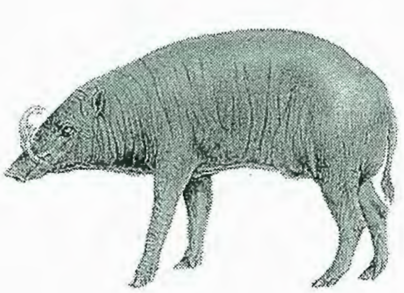
Name	Institution
Supeno AS	BKSDA VI PALU
Douglas Armstrong	Omaha's Henry Doorly Zoo
D. Ashari	PKBSI
Kuno Bleijenberg	Rotterdam Zoo
Boeadi	LIPI IPB
Andi P. Damayanti	PSL Untad Sulteng
Lukito Daryadi	PKBSI
Dedy Duryadi	FMIPA IPB
Dwiatmo	Direktur BKFF
Tumar Effendi	TN. Rawa Aopa
Endah	KBS
Firman	BscC
V. Harwono Gepak	KBS
Dr. Djarot Harsojo R.	KBS
Imam Hartadi	WWF
Simon Hedges	TN. Baluran
Faustina Ida	BKFF PHPA
Budi Irawanto	KBR
Ravi J.	The Singapore Zoo
Penny Kalk	Bronx Zoo
Margaret Kinnaird	Wildlife Conservation Society
Koesno	PHPA
Kristin Leus	The University of Edinburgh
Alastair Macdonald	The University of Edinburgh
Jansen Manansang	Taman Safari Indonesia
Ani Mardiastuti	Fahutan IPB
Endang Mashudi	Sub BKSDA Sulut
Ida Masnur	Taman Safari Indonesia
Philip Miller	CBSG
Abdul Haris Mustari	Fahutan IPB
Tim O'Brien	Wildlife Conservation Society
HM. Kamil Oesman	PKBSI
Hari Palguna	Gembira Loka
Kumar Pillai	The Singapore Zoo
Sharmy Prastiti	Taman Safari Indonesia
Bruno Van Puijenbroeck	Royal Zoological Society of Antwerp
Bambang Purwantara	FKH IPB
Rudolf Reinhard	Berlin Zoo
Rustandi	BKFF PHPA
Reny Sawatiri	P3H&KA Kehutanan
Marialice Seal	CBSG
Ulysses Seal	CBSG
Eri Setiadi	WWF
Soemarsono	Dirjen PHPA
Soetikno	Puslitbang Biologi

Nawangsari Sugiri	IPB Bogor
H. Sutarman	KBR
Abdullah Syam	P3H&KA Kehutanan
Paul Vercammen	Beekse Bergen Netherlands
Ratna Widuri	BKFF PHPA
Sri Winenang	TN Bogani Nani Wartabone

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 7
Appendix II:
Babirusa Bibliography and Selected Literature



Bibliography of references on the babirusa (*Babyrousa babyrussa*) pertaining to the PHVA held at Taman Safari Indonesia

compiled by

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2 Hendrik van Viandenstraat, Kampen, The Netherlands
3 Wildlife Conservation Society/ New York Zoological Society, New York, USA
4 Royal zoological Society of Antwerp, Antwerp, Belgium

Anggawijaya, A., Maya Dewi, F., Pertamawati, M., Engeline, & Sunarjo, V.O. (1985) Kahidupan *Babirousa babyrussa* di kibun binatang Surabaya. SMAK Santa Maria: Surabaya

Anonymous (1909) Zoogdieren. Vogels. Bepaling. Staatsblad van Nederlandsch-Indië, **594**, 1-3.

Anonymous (1909) Zoogdieren. Vogels. Verdaging der inwerkingtreding van de ordonnantie in Staatsblad 1909 No. 497. Staatsblad van Nederlandisch-Indië, **600**, 1.

Anonymous (1916) Natuurmonumenten. Maatregelen ter bescherming van de natuurrijkdommen van Nederlandsch-Indië. Staatsblad van Nederlandisch-Indië, **278**, 1-3.

Anonymous (1931) Onderwerp 23 "Nieuwe Jachtordonnantie en dieren-beschermingsordonnantie 1930." Handelingen van den Volksraad zittingsjaar 1930-1931, **23**, 340-351.

Anonymous (1931) Handelingen van het College van Gedelegeerden, 19de vergadering, vrijdag 20 maart 1931. Handelingen van den Volksraad zittingsjaar 1930-1931, p 342
(Abstract: There is fear expressed that the babirusa may be shot. They are very rare.)

Anonymous (1931) Nieuwe Jacht- en Dierenbeschermingsbepalingen. Mededeelingen [van de] Nederlandsche Commissie voor Internationale Natuurbescherming, **9**, 8-13.
(Abstract: A permit will be issued for up to two adult male babirusa. Only up to two babirusa permitted to be exported alive.)

Anonymous (1937) Brief Internationaal Bureau voor Natuurbescherming te Brussel. Mededeelingen [van de] Nederlandsche Commissie voor Internationale Natuurbescherming. **11**, 33-35, 118-119.
(Abstract: A request for: former range and numbers, present range and numbers, causes of depletion (or extinction), economic uses or importance, what measures are being taken for the preservation of the species concerned. List of vanishing mammals in the Malay archipelago. Suidae *Babirussa babyrussa* (babirusa))

Anonymous (1973) Convention on international trade in endangered species of wild fauna and flora. IUCN Bulletin, **4**, (3) Supplement, 1-11.
(Abstract: Appendix I. shall include all species threatened with extinction which are or may be affected by trade. ... Artiodactyla, Suidae, *Babyrousa babyrussa*)

Anonymous (1982) Family Suidae. In "Mammal species of the world. A taxonomic and geographic reference" (Eds: J.H. Honacki, K.E. Kinman & J.W. Koeppl) Allen Press, Inc. and the Association of Systematics Collections: Lawrence, U.S.A. pp. 315-317
(Abstract: *Babyrousa* Perry, 1811, Arcana, sig. C, Recto. ISIS NUMBER; 5301419001001000000.
Babyrousa babyrussa (Linnaeus, 1758) . Syst. Nat., 10th ed., 1;50. TYPE LOCALITY; "Borneo" (=Buru Isl., Indonesia). Distribution; N. and C. Sulawesi; Buru (N. Molucca Isls.); Sula Isls.; Malengi Isl. (Togean Isls.). Protected status; CITES - Appendix I and U.S.ESA - Endangered. ISIS number; 5301419001001001001.)

Anonymous (1986) Threatened species. Babirusa - *Babyrousa babyrussa*, The Dodo Dispatch, **18**, 3.

Appelman, F.J. (1930) Wat zullen de nieuwe Jacht-en Dieren beschermimgsOrdonnantie's ons brengen? Koloniale Studiën. Tijdschrift van de Vereeniging voor studie van Koloniaal-Maatschappelijke vraagstukken, **14**, 458-473.

Appelman, F.J. (1955) Natuurbescherming. Bosbouwkundig Tijdschrift, **43**, 219-235.

Appelman, F.J. (1956) Nature Protection. Mededelingen [van de] Nederlandsche Commissie voor Internationale Natuurbescherming, **17**, 24-41.

Balen, H. van (1914) De Dierenwereld van insulinde in woord en beeld. van den Burgh: Deventer pp 179-182.

Bartholinus, T. (1654) Historiarum anatomicarum rariorum, Centuria I et II. P. Hauboldt: Hafniae pp 342-345.

Basjarudin, H. (1971) Nature reserves and national parks in Indonesia - present situation and problems. IUCN publications (N.S.), **19**, 27-33.

Bemmel, A.C.V.van (1976) Zwijnen van de wereld. Artis, **21**, 183-187.

Bewick, T. (1790) A general history of quadrupeds. S. Hodgson, R. Beilby, & T. Bewick: Newcastle upon Tyne, pp 136-137.

Blouch, R. (1989) Report from the field. Conservation and Research Centre Newsletter, **1**, 6-8.

Blouch, R.A. & Oliver, W.L.R. (1993) Review of priorities for conservation action and future research on south and southeast Asian suids. In "Status survey and conservation action plan; pigs, peccaries and hippos" (ed. Oliver, W.L.R.), IUCN: Gland, Switzerland, pp 191-195.

Blower, J. (1979) New look in Indonesia. Oryx, **15**, 50-54.

Boitard, P. (1842) Le Jardin des plantes description et moeurs des mammifères de la Menagerie et du Museum d'Histoire Naturelle. J.J. Dubochet: Paris, pp 411.

Bosma, A.A. (1980) The karyotype of the babirusa (*Babyrousa babyrussa*); karyotype evolution in the suidae. 4th European Colloquium of Cytogenetics in Domestic Animals. Utrecht, pp 238-241.

Bosma, A.A. & de Haan, N.A. (1981) The karyotype of *Babyrousa babyrussa* (Suidae, Mammalia). Acta Zoologica et Pathologica Antverpiensia, **76**, 17-27.

Bosma, A.A., de Haan, N.A. & Macdonald, A.A. (1991) The current status of cytogenetics of the suidae; a review. Bongo, Berlin. **18**, 258-272.

Bowles, D. (1986) Social behaviour and breeding of babirusa. Dodo, Journal of the Jersey Wildlife Preservaion Trust, **23**, 86-94.

Budiarso, Wilar, A.F., Tulung, B., Kaligis, D. & Kaligis, W.A.A. (1991) The importance of Sulawesi wild pig (*Sus celebensis*) as a source of meat in north Sulawesi. Fakultas Peternakan Universitas Sam Ratulangi and World Wide Fund for Nature (WWF) Indonesia Programme: Manado, Sulawesi

Chaudhuri, M., Carrasco, E., Kalk, P. & Thau, R.B. (1990) Urinary oestrogen excretion during oestrus and pregnancy in the Babirusa. International Zoo Yearbook, **29**, 188-192.

Clayton, L. (1994) Conservation biology of the babirusa, *Babyrousa babyrussa*, in Sulawesi, Indonesia. Unpublished reports.

Clayton L.M. & Macdonald, D.W. (1992) Conservation biology of the babirusa, *Babyrousa babyrussa*, in Sulawesi, Indonesia. Unpublished proposal.

Clayton, L.M., Muskita, Y., Lagarusu, Z.H., Tuturong, R. & Wode, T. (1991) A survey of the flora and fauna of the upper Paguyaman/Nantu forest area, North Sulawesi. Unpublished report, Universitas Sam Ratulangi, Manado, Indonesia.

Conklin, N.L., Dierenfeld, E.S. & MacLaughlin, K.A. (1994) Digestibility and passage of a zoo diet fed to babirusa (*Babyrousa babyrussa*). Der Zoologische Garten N.F. **6**, 357-365.

Convention on International Trade in Endangered Species (1991) Appendices I, II and III to the Convention on International Trade in Endangered Species of Wild Fauna and Flora. September 1, 1991. U.S. Government Printing Office, Washington, D.C.

Coomans de Ruiter, L. (1928) Wildreservaten in Zuid-Sumatra en in de Minahassa, bijlage behoorende bij Mededeeling No 4. Medeelingen [van de] Nederlandsche Commissie voor Internationale Natuurbescherming, **4**, 32-39.
(Abstract: Babirusa were reported (in 1923) to be found in the area of the volcanoes Kalabat en Doea Saudara, in Minahassa, North Sulawesi. It is proposed that this area become an extension of the neighbouring nature conservation park.)

Coomans de Ruiter, L. (1948) Natuurbescherming in Nederlandisch-Indië. Indonesië, **2**, 140-162.

Crandall, L.S. (1964) Management of wild mammals in captivity. The University of Chicago press: Chicago and London.

Cubitt, G., Whitten, T. & Whitten, J. (1992) Wild Indonesia; the wildlife and scenery of the Indonesian archipelago. New Holland: London, pp 53-54, 58, 161.
(Abstract: Babirusa are rare. Dozens of carcasses are brought to the markets of north Sulawesi each month. Babirusa are uncommon or absent from the east end of the Dumoga Bone park probably as a result of hunting, but are still found in the west.)

Dammerman, K.W. (1926) Preservation of wildlife and nature reserves in the Dutch East-Indies. Proceedings of the Third Pan-Pacific Science Congress, Tokyo, **1**, 1103-1111.
(Abstract: Gunung Tongkoko Batoeangoes. Date of institution: February, 1919.
Location: Northeastern part of the Minahassa, opposite the island of Lembeh.
Characteristics: In this nature reserve two of Celebes' most remarkable mammals are still found, the hogdeer (*Babirussa babyrussa*) and the pigmy buffalo or anoang (*Anoa depressicornis*). It contains the volcanoes Gn. Tongkoko (1373 M.) and the Gn. Batoeangoes (1173 M.), an exceptionally fine preserve of the wild plant and animal life of North Celebes.)

Dammerman, K.W. (1929) Preservation of wildlife and nature reserves in the Netherlands Indies. The Proceedings of the Congress 4th Pacific Science Congress. Java. 1929 (99pp).
(Abstract: Gunong Tongkoko Batoeangoes. Reserved: February 1919.
Site: The area bounded on the north and the east by the Molluccan Sea, on the south by the imaginary line which connects the summit of the Mt. Tongkoko with Tanjoeng Batoeangoes, and on the west by the river Batoe Poetih and the imaginary line which connects the source of this river with the summit of the Tongkoko. Area: 446 hectares. Reason for protection: In the reserved areas two kinds of mammals, characteristic of Celebes, the hog-deer (Babirussa) and the dwarf buffalo (Anoa) still occur. Moreover this area with its interesting volcanoes, the still active Gn. Tongkoko (1373 m) and the Gn. Batoeangoes (1173 m), reaching down to the sea, is

exceptionally suitable for the preservation of the plant and animal life of the extreme north of Celebes.)

Dammerman, K.W. (1939) On prehistoric mammals from south Celebes. Treubia, **17**, 63-72.

Dammerman, K.W. (1941) Natuurbescherming in Nederlandsch-Indië. Tijdschrift van het Nederlandsch Aardrijkskundig Genootschap, **58**, 627-640.

Dammerman, K.W. (1950) Geschiedenis van de natuurbescherming in Indonesië. Chronica Naturae. Djakarta Jubileum-Aflaevering, **106**, 216-228.
(Abstract: This is a detailed account of the history of nature protection during the Dutch colonial period. It points out which act took care to mention the babirusa, which referred to wild pigs, and which commented on the area of ground to be protected.)

Davis, D.D. (1940) Notes on the anatomy of the babirusa. Field Museum of Natural History, Chicago, **22**, 363-411

De Graeff, (1931) Dierenbescherming. Jachtordonnantie. Staatsblad van Nederlandsch-Indië, **133**, 1-6.

De Graeff, (1931) Dierenbescherming. Staatsblad van Nederlandsch-Indië, **134**, 1-4.
(Abstract: The law permits "named species of animals" to be collected for research or teaching purposes.)

De Graeff, (1931) Dierenbescherming. Staatsblad van Nederlandsch-Indië, **265**, 1-7.
(Abstract: Babirusa named as one of the "large game animals" which are protected, and pigs other than the babirusa named as suitable as general game animals, babyrussa are only allowed "up to two adult males".)

De Graeff, (1931) Dierenbescherming. Staatsblad van Nederlandsch-Indië, **266**, 1-4.
(Abstract: It is forbidden to hunt, trap, kill, deal in living or dead parts of ...babirusa (*Babirussa*). Export of up to two babirusa may be permitted. Skins of wild pigs with the exception of babirusa may be exported. The hunting regulations can be extended to babirusa beyond the area of enforcement under the 1931 ruling.)

De Jonge, (1935) Dierenbescherming. Straatsblad van Nederlandsch-Indië, **513**, 1-3.
(Abstract: It is forbidden to hunt, trap, kill or deal in the animal parts of the babirusa)

Deninger, K. (1910) Über Babyrusa. Berichte der Naturforschenden Gesellschaft zu Freiburg i. Br. **18**, 1-22.

Dufay, P. (1989) Pour ces photos, le "cochon-cerf" a quittée sa legende. Le Figaro, 15 July, 70-75.

Dumont d'Urville, J.S.C. (1830) Voyage de découvertes de l'Astrolabe. J. Tastu: Paris, **1**, 125-133.

Durden, L.A. & Watts, C.H.S. (1988) A collection of ticks (Ixodidae) from Sulawesi Utara, Indonesia. Biotropica, **2**, 32-37.

Erdbrink, G.R. (1919) Natuurmonumenten. Aanwijzing van terreinen als Natuurmonumenten. Staatsblad van Nederlandsch-Indië, **90**, 1-6.
(Abstract: Establishment of nature reserves in north Sulawesi, at Goenoeng Lokon and Goenoeng Tongkoko (with Batoeangoes))

Fitzinger, L.J. (1864) Revision der bis jetzt bekannt geworden Arten der Familie der Borstenthiere oder Schweine (Setigera). Sitzungsberichte der Mathematisch-Naturwissensschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Wien, **50**, 383-434.
(Abstract: This is a bibliography with a description of the outward appearance of the babirusa)

Fock, D. Dierenbescherming. Zoogdieren. Vogels. Jachtordonnantie. Staatsblad van Nederlandsch-Indië, **234**, 1-9.
(Abstract: A listing of all the sorts of animals protected by law, including Anoa, together with the fines that would be incurred (50 guilders for Anoa))

Frädrich, H. (1972) Swine and peccaries. In "Grzimek's animal life encyclopedia. Mammals IV", (Ed. B. Grzimek), **13**, 76-108, van Nostrand Reinhold: London.

Franssen, C.J.H. (1949) Bijdrage tot de kennis van het Toaliaan op Zuid-Celebes. Tijdschrift voor Indische Taal-, Land- en Volkenkunde, **83**, 331-339.
(Abstract: According to Hooijer, all the animal remains sent by me are from babirusa, with the exception of a few human shoulder blades. The neighbouring Liang Karrassa is much richer in mammals, because Heekeren (1938) reported Sulawesi warty pigs, babirusa, the macaque, a large marsupial and a wild goat. Possibly it was so easy to catch the babirusa that people hunted this animal almost exclusively. The babirusa is now extinct in south Sulawesi.)

Geypen, M. (1990) Inleidend onderzoek naar het sociaal gedrag en de groei van Hertezwijnen, *Babyrousa babyrussa* L. in gevangenschap. Unpublished thesis, University of Antwerp. pp 44.

Giebel, C.G.A. (1855) Die Saugethiere in Zoologischer, Anatomischer und Palaeontologischer Beziehung. A. Abel: Leipzig, pp 231-232.
(Abstract: brief description of the babirusa, and that it prefers to eat fruit and leaves.)

Graafland, N. (1898) De Minahassa. G. Kolff: Batavia, ed. 2, vol. 2, appendix pp i-iv.
(Abstract: The babirusa is not so plentiful and widely distributed. It is found around the Amurang bay and round Kalabat.)

Groves, C.P. (1976) The origin of the mammalian fauna of Sulawesi (Celebes). Zeitschrift für Säugetierkunde, **41**, 201-216.
(Abstract: Strictly speaking, *Babyrousa* occupies a special position, as it is not restricted to Sulawesi but occurs also on the Sula islands and Buru; it might therefore better have been placed in group 4 (migrants from Sulawesi), but it is the only species of the genus and has doubtlessly originated on Sulawesi.

Groves, C.P. (1980) Notes on the systematics of *Babyrousa* (Artiodactyla, Suidae). Zoologische Mededelingen. **55**, 29-46.
(Abstract: Skins and skulls of *Babyrousa babyrussa* have been studied; the species is divisible into three living subspecies: *B. b. babyrussa* (syn. *frosti*) from Buru and Sula, *B. b. togeanensis* from Malenge, and *B. b. celebensis* from the northern arm of Celebes. A skull from near Kulawi, central Celebes, tends towards *babyrussa*, and may represent a surviving population of the inadequately characterised *B. b. bolabatuensis*, known as a subfossil from the southern arm of Celebes. Teeth of the latter form decreased in size through time. The possibility of the species having been introduced into Buru and Sula is discussed.)

Groves, C.P. (1981) Ancestors for the pigs: taxonomy and phylogeny of the genus Sus. Technical Bulletin No. **3** Department of Prehistory, Research School of Pacific Studies. Australian National University Press: Canberra, pp 1-6.

Groves, C.P. (1985) The Sulawesi "specials"; archaic, strange, endemic. Australian Natural History. **21**, 442-444.
(Abstract: Babirusa appear to be crepuscular, i.e. most active around dawn and dusk. They love to wallow in mud, and swim well. In the Togian islands they have been seen swimming a kilometre or more between small islands. Unlike true pigs, they are unable to dig deeply, because their snouts are not as strong and the rooting disc at the end is not as developed. They do not eat deep lying roots, but grasses, fallen fruit, mushrooms, and grubs which they gnaw from rotten wood.

Groves, C.P. & Grubb, P. (1993) The Eurasian suids *Sus* and *Babyrousa*; taxonomy and description. In "Status survey and conservation action plan; pigs, peccaries and hippos" (Ed: Oliver, W.L.R.), IUCN: Gland, Switzerland, pp 107-111.

Grubb. P. (1993) Order Artiodactyla. In "Mammal species of the world: a taxonomic and geographical reference" 2nd edition. (Eds. D.E. Wilson & D.M. Reder). Smithsonian Institution Press: Washington and London.

Guillemard, F.H.H. (1886) The cruise of the Marchesa to Kamschatka & New Guinea with notices of Formosa, Liu-Kiu, and various islands of the Malay archipelago. J. Murray: London, **2**, pp 190-191, 200-205.
(Abstract: (Maim bay, on Sulawesi) The Babirusa, according to the natives, generally has one or two young at birth; more often one, but sometimes, though rarely, three. They are born in the months of November, December, and January, and the sow makes a small underground hole for their reception, lining it with leaves - generally of the Livingstonia. The young, however, are

able to move about on the second day of their existence. We were told that they were of two colours - nearly black and light brown - and that the female can have young of both of these colours just as a sow has black and white pigs ... These colours were said to approximate with age, but the natives spoke of "white" and "black babirusas" even in the adult stage, and the one I have mentioned (young male) was certainly lighter in colour than others we afterwards killed on Limbe island. Our hunters also told us that, when assailed by dogs, the animal sometimes ascended the procumbent trunks of trees, and got out upon the larger lower branches. The natives told us that almost all the babirusa would come along the ridge. On Limbe island we caught four babirusa, the first being a female which had produced "a peculiar barking grunt".)

Hamerton, A.E. (1931) Report on the deaths occurring in the society's gardens during the year 1930. Proceedings of the Zoological Society, **1931**, 527-555.
(Abstract: A remarkable case of mass infestation of the lungs with the cysticeric of one of the Taeniidae (*Echinococcus*) occurred in a young Babirusa (*Babirussa babyrussa*) that died a few weeks after arrival from Celebes. The weight of the animal was 24lb., and the lungs weighed 2 lb. 5 oz. The connective tissue throughout the whole structure of the lungs was so closely infested with cysticerci that the organs bore a rough resemblance to bunches of grapes. The lung parenchyma between the cysts showed no pathological change except for emphysema at the apices and some congestion and oedema of the bases. The pleurae were adherent, and the lobes of the lungs were stuck together by adhesive pleuritis. The intercostal spaces were obliterated. The pressure effects of the mass of cysts on the heart and great vessels must have been considerable, and it was strange that the respiratory function could have been so long maintained. The liver and spleen were also infested with numerous large cysticerci containing hooked scolices.
Babirussa (*Babirussa babyrussa*) Class of parasite: Cestoda, Tissue affected: Lungs, liver and spleen, Lesion Pleurisy; cysticerci in lungs.)
Single infections *Microfilaria*, host *Babirussa babyrussa.*

Hamerton, A.E. (1941) Report on the deaths occurring in the society's gardens during the years 1939-1940. Proceedings of the Zoological Society, London, Series B, **111**, 151-185.
(Abstract: A female Babirusa (*Babirussa babyrusa*) that had been eight years in the Gardens and had reared several young, died from tuberculosis of the Bovine type - with deposits "pearles" in the parietal pleurae and sessile tubercles in the pericardium. Both lungs were consolidated by caseous masses of agglomerated tubercles. Secondary tuberculous lesions were found in the spleen, kidneys, cervical mediastinal and mesenteric lymph-glands.)

Hamerton, A.E. (1943) Report on the deaths occurring in the society's gardens during the year 1942. Proceedings of the Zoological Society of London. Series B, **113**, 149-160.
(Abstract: A male Babirusa (*Babirussa babyrussa*) that had been in the Gardens for 10.5 years died from senile atrophy of the intestinal mucosa and muscularis, causing the gut walls to be thin and diaphanous in texture. The jejunum and ileum in particular appeared to be denuded of all epithelial and glandular structures.

Hart, C. (1853) Reize rondom het eiland Celebes en naar eenige der Moluksche eilande. K. Fuhri: 's-Gravenhage, pp 72, 128, 134.
(Abstract: babirusa were found in the region of Taboenkoe of East Sulawesi, and Balank Manado in north Sulawesi. They are also found in the Ambon islands. They are also found on Buru)

Hartadi, I. (1996) Sekilas mengenai babirusa (*Babyrousa babirussa*) di Sulawesi. Informasi, WWF Indonesia 2pp.

Hasselt, J.C.van. (1880) De onderafdeeling Bangkala, geographisch en ethnologisch geschetst. Tijdschrift van het Aardrijkskundig Genootschap, **4**, 362-381.
(Abstract: There are no babirusa in the south-west point of south west Sulawesi)

Heekeren, H.R. van (1941) Over Toala's en de Toala-cultuur (Zuid-Celebes). Natuurwetenschappelijke Tijdschrift voor Nederlandsch Indië, **101**, 229-237

Heekeren, H.R. van (1950) Rock paintings and other prehistoric discoveries near Maros (Sout west Celebes). Laporan Tahunan Diras Purbakala Republik Indonesia 1950. 22-49.
(Abstract: Cave fauna; *Babyrousa babyrussa* (L) Now vanished from South west Celebes. Oldest example in caves larger than the *Babyrussa* still living in central Celebes. The type from the Bola Batu Cave was named *Babyrousa babyrussa bolabatuensis*. He describes the discovery of the cave painting of the ?babirusa?)

Heekeren, H.R. van (1966) Handen aan de wand. Verre naasten naderbij. (Rijksmuseum voor Volkenkunde te Leiden), **1**, 2-8.
(Abstract: A leaping pig was found in a cave at Leang Pattae. The thin legs and the thick body made him think immediately that it was a babirusa, but the tufts of hair on its back and neck made him unsure.)

Heekeren, H.R. van (1972) The stone age of Indonesia. Verhandelingen van het Koninklijke Instituut voor Taal-, Land-, en Volkenkunde. M. Nijhoff: The Hague, 2, **61**, 69-71, 116-122.

Heinroth, O. (1908) Trächtigkeits-und Brutdauern. Zoologischer Beobachter; Der Zoologische Garten, **49**, 14-25.
(Abstract: babirusa gestation length 158, 160 (Heinroth), 5 months and 5 days. The babirusa has at most two young, which are no larger than other pigs despite the month longer gestation. The lack of carnivores on Sulawesi may mean that the babirusa has retained the palaeontological gestation length.)

Herring, S.W. (1972) The facial musculature of the suoidea. Journal of Morphology, **137**, 49-62.

Herring, S.W. (1972) The role of canine morphology in the evolutionary divergence of pigs and peccaries. Journal of Mammology, **53**, 500-512.

Herring, S.W. (1972) Sutures- a tool in functional cranial analysis. Acta Anatomica, **83**, 222-247.

Heynsius-Viruly, A. & Heurn, F.C. van. (1935) Overzicht van de uit Nederlandsch-Indië ontvangen gegevens, gerangschikt door Mevrouw A. Heynsius-Viruly. Met biologische aanteekeningen omtrent de betreffende diersoorten door F.C. van Heurn. Nederlandsche Commissie Voor Internationale Natuurbescherming, Supplement op Mededeelingen. No 10, 25-77.
(Abstract: There is word from the region Mamoedjoe that the babirusa are in no danger of being exterminated in that area, however, there is more of a problem in the Minahassa region of Sulawesi. In the region around Laiwoei the babirusa are still found in Kendari, and sporadically on Buru behind Kajeli village. There is no word from the Sula islands or Lembeh.)

Hickson, S.J. (1889) A Naturalist in north Celebes. J Murray: London pp 18, 69, 353-354.
(Abstract: At the village of Koa, Talisse island, of the north coast of the northern peninsula of Sulawesi, Mr Cursham had a fine specimen of the babirusa in a bamboo kraal.)

Hodgden, R. (1985) Behaviour of Babirusa (*Babyrousa babirussa*) in captivity; a comparison of behaviour within the suborder Suiformes. Unpublished report, Jersey Wildlife Preservation Trust
(Abstract: A study of the behaviour of three captive babirusa).

Holland, J.S. (1994) North American regional studbook for babirusa (*Babyrousa babyrussa celebensis*). Los Angeles Zoo: Los Angeles, 51pp.

Holland, J.S. (1995) North American regional studbook for babirusa (*Babyrousa babyrussa celebensis*). Los Angeles Zoo: Los Angeles, 49pp.

Hooijer, D.A. (1948) Pleistocene Vertebrates from Celebes. III. *Anoa depressicornis* (Smith) subsp., and *Babyroussa babirussa beruensis* nov. subsp. Proceedings of the section of Sciences [of the] Koninklijke Nederlandsche Akademie van Wetenschappen, **51**, 1322-1330.
(Abstract: Neither the anoa nor the babirusa are living today in the region where their fossil remains were found. In the South-western peninsula of Celebes the anoa still only lives on the Peak of Bonthain in the extreme S. (Weber, 1890, p. 112; Sarasin, 1905, p. 32), while the babirusa has vanished from the whole of the South-western peninsula of the island (Sarasin, l.c., p. 41). The occurrence of both species in the prehistoric collections from caves near Lamontjong in S. Bone (ca. 60 km ENE of Macassar) and from the neighbourhood of Tjani (Lamontjong), Watampone (Central Bone, ca. 120 km N.E. of Macassar) and Bonthain on the S. coast, was described by Sarasin (1905) and Dammerman (1939) respectively. Sarasin (1905, p. 39/40) reported that the subfossil teeth of the babirusa agree well in size with the recent, but the subfossil teeth of the anoa (l.c., p. 30) average smaller than the recent.)

Hooijer, D.A. (1950) Man and other mammals from Toalian sites in south western Celebes. Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen, **46**, 1-164. (Abstract: In most of the Toalian sites the fauna of which I have studied the babirusa is present, while at this day the babirusa has vanished from the whole of the South-western peninsula of Celebes.
The babirusa is but one element to an interesting Pleistocene Vertebrate fauna which is now already known to contain extinct forms like a peculiar giant pig, *Celebochoerus heekereni* Hooijer (1948b).
The Pleistocene babirusa, then, is larger than the living races of babirusa from Celebes, Taliaboe, and Boeroe, and was baptized *Babyrousa babyrussa beruensis* Hooijer (1948d). This was the very first example I found for the island of Celebes of a living form averaging larger in former times than it does now.
Thus it is pretty evident that in South-western Celebes the babirusa has undergone a gradual diminution in size in the course of the Quaternary, thereby passing through the stage of size today represented by the Central and Northern Celebes babirusa, and this line came to an end while it was about of the size of the living insular races East of Celebes. The babirusa became extinct in South-western Celebes at the time of the formation of the Toalian caves, but if the species would have been in existence today in South-western Celebes it would certainly have been regarded by neozoologists as a separate subspecies peculiar to this region. *Babyrousa babyrussa bolabateunsis* nov. subsp. is the terminal form of one of the longest continuous clines of which we have now evidence in the island of Celebes, and the future finds of subfossil and Pleistocene babirusa teeth in other regions of Celebes, in the Soela Islands, and in Boeroe will show us how long the various lines leading to the extinct Toalian cave form and to the three subspecies we distinguish today have already been separate. The babirusa was smaller in the Toalian caves than it is nowadays in Northern Sulawesi, but about the size of the babirusa races now found on the islands of Buru and Taliabu, but in the Pleistocene of South-western Sulawesi it was definitely larger. All the material from caves north of Tjani are *Sus* and not babirusa as described by Dammerman 1939. p 69).

Hooijer, D.A. (1958) The pleistocene vertebrate fauna of Celebes. Archives Néerlandaises de Zoologie, **13**, supplement, 89-96.

Houston, E. (1992) Babirusa born at the St Louis Zoo. AAZPA Communique, March 1992, 11 (Abstract: A pair of babirusa on loan from the Los Angeles Zoo produced two female piglets at the St Louis Zoological Park on 16 December 1991. This represents the first ever birth of this species at the zoo. The piglets were up and walking within 15 minutes of the birth. Nursing was observed within 20 minutes. A neonatal exam was performed on one piglet at 48 hours post-partum; the other piglet was examined at 72 hours. Their weights were 901 grams and 811 grams, respectively. The sow readily accepted both piglets back after their exams and has proven to be an excellent mother. To date, both the piglets and their mother have been kept separate from the boar.)

International Union for the Conservation of Nature (1972) Red data book, Mammalia. (Eds. H.A. Goodwin & C.W. Holloway). IUCN: Morges, Switzerland, 2nd edition.

International Union for the Conservation of Nature (1990) 1990 IUCN Red list of threatened animals. IUCN, Gland, Switzerland, and Cambridge, UK, p 25.

Jardine, W. (1836) The naturalists library: Mammalia 5 The natural history of the pachydermes, or thick-skinned quadrupeds. W.H. Lizars: Edinburgh pp 216-217.
(Abstract: The figure is from F. Cuvier from live specimens brought back on the Astrolab. The male was aged and remarkably fat. The cold gradually produced diseased lungs, which killed them three years after they arrived. The male's short life (in Europe) was spent sleeping, eating and drinking. The female was younger, and more active; when the male retired to his litter (to sleep), she would cover him completely over, and afterwards herself slip under the straw, so that both were entirely concealed from sight. The skin was thinly furnished with hair; and that which grew upon them was long and hard.)

Kaspe, L. and Wahyuni, E. (1988) Panaritium. Prociding simposium nasional penyakit satwa liar. Fakultas kedokteran hewan Universitas Airlangga dan Kebun binatang Surabaya: Surabaya
(Abstract: Panaritium was found in babirusa in 1981 (4) , 1982 (3) , 1983 (1) , 1986 (2) , 1988 (10) and was treated.)

Kaudern, W. (1944) Ethnographical studies in Celebes. 6, Art in Central Celebes. Elanders Boktryckeri Aktiebolact: Gotenborg.

Keirans, J.E. & Robbins, R.G. (1987) *Amblyomma babirussae* Schulze (Acari: Ixodidae): redescription of the male, female, and nymph and description of the larva. Proceedings of the Entomological Society of Washington, **89**, (4), 646-659.
(Abstract: The male, female and nymph of *A. babirussae* are redescribed and the larvae is described for the first time. Adults and immatures are illustrated with black and white and colour drawings and with scanning electron photomicrographs of specimens collected primarily on artiodactyl mammals (wild and domestic pigs, domestic buffalo, cattle, *Bubalus depressicornis* and *Cervus timorensis*) and from vegetation on the island of Sulawesi, Indonesia.)

Kilveron, J.M. (1936) Natuurmonumenten. Dierenbescherming. Manado. Straatsblad van Nederlandsch-Indië, **521**, 1.
(Abstract: Establishment of nature reserve "Berbak")

Kilveron, J.M. (1938) Natuurmonumenten. Groote Oost. Staatsblad van Nederlandsch-Indië, **630**, 1-2.
(Abstract: The establishment of a nature reserve called "Panoea" near Gorontalo, North Sulawesi.)

Kilveron, J.M. (1939) Natuurmonumenten. Dierenbescherming. Groote Oost. Staatsbland van Nederlandsch-Indië, **626**, 1-2.
(Abstract: The establishment of three islands near Gorontalo as a nature reserve called "Mas-Popaja-Radja")

Kinnaird, M.F. (1996) North Sulawesi: a natural history guide. Wallacea Development Institute: Jakarta, 83pp.

Kinnaird, M.F. and O'Brien, T.G. (1996) Ecotourism in the Tangkoko DuaSudara Nature Reserve: opening Pandora's box? Oryx, **30**, 65-73.
(Abstract: Tourist brochures for Tangkoko state that it is possible to see babirusa *Babyrousa babyrussa*, which are extinct within the reserve.)

Kneepkens, A.F.L.M. Badoux, D.M. & Macdonald, A.A. (1990) Descriptive and comparative myology of the forelimb of the babirusa (*Babyrousa babyrussa* L. 1758). Anatomia Histologia Embryologia, **18**, 349-365.

Kooders, S.H. (1898) Verslag eener botanische dienstreis door de Minahassa. Mededeelingen van's Lands Plantentuin. G. Kolff: Batavia, pp 103.
(Abstract: Babirusa are very scarce in the Minahassa due to the increased hunting in the region. People are hunting them for food. Even the wild boar are shy.)

Kruyt, A.C. (1930) :De To Loinang van den Oostarm van Celebes. Bijdragen tot de Taal-, Land-en Volkenkunde (van Nederlandsch-Indië), **86**, 327-536.
(Abstract: The babirusa are largely caught by members of the Lingketeng clan when they go hunting for bamboo.)

Krumbiegel, I. (1954) Biologie der Säugethiere. Agis: Krefeld, pp 16, 39, 86, 181, 316, 323, 343, 367.
(Abstract: Babirusa can swim in the sea and reach islands. The babirusa does not make much sound. The babirusa had a gestation length of 158 days. Newborn babirusa are coloured black, those from *B. b. alfurus* are dark brown-red coloured.)

Kruska, D. (1970) Über die Evolution des Gehirns in der Ordnung Artiodactyla, Owen 1848, in besondere der Teilordnung suina, Gray 1868. Zeitschrift für Säugetierkunde, **35**, 214-238.

Kruyt, A.C. (1932) Balantaksche Studiën. Tijdschrift voor Indische Taal, Land en Volkenkunde, **72**, 328-390.
(Abstract: The babirusa (Balantak, east Sulawesi??) must have been here earlier, but it has been exterminated, or withdrawn, because you do not find it in the forest any more.)

Kuroda, N. (1933) Birds of the island of Java. Published by the author: Tokio, **1**, xiii
(Abstract: Babirusa are also regarded as natural monuments.).

Langer, P. (1973) Vergleichend-anatomische Untersuchungen am Magen der Artiodactyla (Owen 1848) 1. Untersuchungen am Magen der Nonruminantia (Suiformes). Gegenbauers morphologisches Jahrbuch, Leipzig, **119**, 514-561.

Langer, P. (1974) Stomach evolution in the artiodactyla. Mammalia, **38**, 295-314.

Langer, P. (1988) The Mammalian Herbivore Stomach: Comparative Anatomy, Function and Evolution. Gustav Fischer: Stuttgart, New York, pp 1-493.

Lesson, R.P. (1827) Manuel de mammalogie. Roret: Paris, pp 337-338.
(Abstract: He examined many individuals in Surabaya, males, females and many more young. In captivity, their character is not quiet but ferocious. They prefer to eat maize.)

Leus, K. (1990) Inleidende studie tot de voedings en verterings - karakteristieken van *Babyrousa babyrussa* L. (Hertezwijn); met vermelding van gastro-intestinale parasieten. Unpublished thesis, Universitaire Instelling Antwerpen.

Leus, K. (1993) La grande expédition des babiroussas dans la "presque-jungle" de St-Martin. Magazine trimestriel St Martin la Plaine Espace Zoologique, **30**, 4.

Leus, K. (1994) Foraging behaviour, food selection and diet digestion of *Babyrousa babyrussa* (Suidae, Mammalia). Unpublished PhD thesis, The University of Edinburgh.

Leus, K., Bland, K.P., Dhondt, A.A. and Macdonald, A.A. (1996) Ploughing behaviour of *Babyrousa babyrussa* (Suidae, Mammalia) suggests a scent-marking function. Journal of Zoology, London, **238**, 209-219.

Leus, K., Bowles, D., Bell, J. and Macdonald, A.A. (1992) Behaviour of the babirusa (*Babyrousa babyrussa*) with suggestions for husbandry. Acta Zoologica et Pathologica Antverpiensia, **82**, 9-27.

Leus, K and Macdonald, A.A. (1996) Gastrointestinal anatomy, diet selection and digestion in mammals: a brief overview. In "Research and captive propagation" (Eds. U. Ganslosser, J.K. Hodges & W. Kaumanns), Filander: Furth, Germany, pp 99-114.

Leus, K and Morgan, C.A. (1996) Analysis of diets fed to babirusa (*Babyrousa babyrussa*) in captivity with respect to their nutritional requirements. Ibex Journal of Mountain Ecology, **3**, 41-44.

Leus, K. and Vercammen, P. (1996) Behaviour of a male and female babirusa (*Babyrousa babyrussa* Suidae, Mammalia) during the first five days after their move to a semi-natural enclosure. Der Zoologische Garten N.F., **66** 133-155.

Lith, P.A. van der (1875) Nederlandisch Oost Indië. J. C. van Schenk: Doesbourgh, pp 30
(Abstract: Babirusa do not dig with their nose; they mostly eat fruit.).

Macdonald, A.A., Bell, J., Munro, S.A., Kaspe, L., Harwono Gepak, V., Sasmita, R. & Bowles, D. (1988) Observations on the behaviour and health of captive babirusa. Prociding Simposium Nasional Penyakit Satwa Liar. Universitas Airlangga dan Kebun Binatang Surabaya: Surabaya, Indonesia, pp 244-253.
(Abstract: The babirusa slept from just after nightfall to shortly before sunrise. They lay together in groups either inside the small sheds or outside on the concrete pads. In the morning animals rose and moved to an area near the centre of the pen where they excreted urine and faeces. Commonly male animals appeared to inspect freshly voided material by both smell and taste. Usually a large adult male inspected the vulva of each female when she moved to this part of the pen.
As the sun rose pairs of adult males were often seen to face each other with their heads elevated, and then began jousting. In many instances they would raise up onto their hind legs and "box" against the chest of their opponent. These competitions were of varied duration, and in all cases the animal whose head was lower than that of its opponent seemed to submit and lose the fight; in most instances the inferior animal emitted a shrieking vocalisation during the encounter. The tusks of the males did not appear to be used as weapons in these confrontations and infrequently caused damage. The incisor teeth were used by both male and female animals to nip other animals, particularly on the lower limb. There was rarely any fighting between male and female animals. The numbers of helminth eggs, protozoal and coccidial oocysts in 1g of freshly voided faecal material from male and female babirusa was measured.

Macdonald, A.A. (1990) Israel's kosher pig. Independent, 21 July, 17.

Macdonald, A.A. (1991) Monographie des Hirschebers (*Babyrousa babyrussa*). Bongo, Berlin, **18**, 69-84.

Macdonald, A.A. (1991) Comparative study of functional soft tissue anatomy in pigs and peccaries. Bongo, Berlin, **18**, 273-282.
(Abstract: The available information on the anatomy of tissues comprising the digestive tract, liver, scent glands, and male and female reproductive systems of the pigs and peccaries was reviewed together with new anatomical data on the pigmy hog (*Sus salvanius*), bush pig (*Potamocherus porcus*) and babirusa (*Babyrousa babyrussa*). The similarities between pigs in the anatomy of the stomach and intestinal tract was discussed and the different morphology of the peccary stomach indicated. The histology of the liver and distribution of the scent glands illustrated other differences between the pigs and peccaries, with inter-suid differences in scent gland distribution becoming apparent. The anatomy of the reproductive tracts followed the same basic pattern in all the animals considered; the functional significance of the differences in testicular and uterine structure which were not accounted for by relative body size remain a matter for future study.

Macdonald, A.A. and Frädrich, H. (1991) Les suidés: que sont-ils? Pigs and peccaries: what are they? In "Biology of Suidae, Biologie des Suidés" (Eds. R.H. Barrett & F. Spitz), IRGM, Imprimerie des Escartons: Briancon, France, pp 7-19.

Macdonald, A.A. and Oliver, W.L.R. (1992) Pigs and peccaries specialist group. Species, **19**, 56-57.

Macdonald, A.A. (1993) The Babirusa (*Babyrousa babyrussa*). In "Status survey and conservation action plan: Pigs, Peccaries and Hippos" (Ed. W.L.R. Oliver), IUCN: Gland, Switzerland, pp 161-171.

Macdonald, A.A. (1994) The placenta and cardiac foramen ovale of the babirusa (*Babyrousa babyrussa*). Anatomy and Embryology, **190**, 489-494.

Macdonald, A.A., Bowles, D., Bell, J. and Leus, K. (1993) Agonistic behaviour in captive Babirusa (*Babyrousa babyrussa*). Zeitschrift für Säugetierkunde, **58**, 18-30.

Macdonald, A.A. and Kneepkens, A.F.L.M. (1995) Descriptive and comparative myology of the hindlimb of the babirusa (*Babyrousa babyrussa* L. 1758). Anatomia, Histologia, Embryologia, **24**, 197-207.

Macdonald, A.A., Kneepkens, A.F.L.M., Bosma, A.A. (1984) Anatomical studies on the female and male reproductive tracts of wild pigs. In " Symposium International sur le Sanglier" (Eds. F. Spitz and D. Pepin), Les Colloques de l'INRA, 22, 93-104.

Macdonald, A.A., Kneepens, A.F.L.M., Kolfschoten, T. van Houtekamer, J.L., Sondaar, P.Y. & Badoux, D.M. (1985) Comparative anatomy of the limb musculature of some suina. In " Functional Morphology of Vertebrates" (Eds. H.R. Duncker and G. Fleischer), Fortschritte der Zoologie, 30, 95-97, Gustav Fischer: Stuttgart & New York
(Abstract: From the results of these studies on the soft tissues of these four members of the Suina we conclude that the babirusa and the pig are more closely related to one another than to either of the hippopotami.).

Macdonald, A.A. and Leus, K. (1994) A framework of ideas for research in zoos as illustrated by the study of babirusa (*Babyrousa babyrussa*) and other pig species. International Union of Directors of Zoological Gardens: Scientific sessions of the 48th annual conference, **48**, 37-49.

Macdonald, A.A. and Leus, K. (1995) Taxonomic hierarchy - *Babyrousa babyruss*a - The babirusa.
http://www.vet.ed.ac.uk/tol/chordata/mammalia/artiodac/suidae/babirusa/

Macdonald, A.A. and Leus, K. (1995) Babirusa at home and away. Ark File, Quarterly magazine of the Royal Zoological Society of Scotland, **4**, 4.

Macdonald, A.A. and Leus, K. (1996) Creating a public understanding of the biology of the babirusa (*Babyrousa babyrussa*) within a caring zoo environment. Ibex Journal of Mountain Ecology, **3**, 37-40.

Macdonald, A.A., Leus, K., Florence, A., Clare, J. & Patry, M. (1996) Notes on the behaviour of Sulawesi Warty pigs (*Sus celebensis*) in North Sulawesi, Indonesia. Malaysian Nature Journal, (in press)
(Abstract: Babirusa (*Babyrousa babyrussa*) and Sulawesi Warty pigs (*Sus celebensis*) use the same wallow and face rub on precisely the same flat spot).

MacKinnon, J. (1979) A glimmer of hope for Sulawesi. Oryx, **15**, 55-59.
(Abstract: Babirusa (*Babyrousa babyrussa*). Endangered. This extraordinary endemic pig has disappeared from large areas of its former range. Having evolved in a more or less predator-free environment, and because of its low recruitment rate (only two young at a time), it is highly vulnerable to all hunting pressures. Good populations still occur in remote forests where human activities are slight or recent, and also in Muslim pockets of this predominantly Christian region)

MacKinnon, J. (1981) The structure and function of the tusks of babirusa. Mammal Review, **11**, 37-40.
(Abstract: An examination of twenty-four male babirusa skulls indicates that the long tusks have an important function in intraspecific fighting. The upper tusks have developed a shielding, protective function whilst the lower tusks are offensive and daggerlike. As the upper tusks do not hone the lower canines as in other suids, the babirusa male actively sharpens his lower tusks on trees. Wear patterns on the tusks suggest that mainland babirusa use the upper tusks to interlock and hold their opponents' lower tusks during combat. In the Buru race this hooking function appears to have been lost and the upper tusks have a butting function instead.)

MacKinnon, J & Artha, B. (1981-1982) National conservation plan for Indonesia, FO/INS/78/061, FAO: Bogor.

MacKinnon, J. & MacKinnon, K. (1986) Review of the protected areas system in the Indo-Malayan Realm. IUCN: Gland, Switzerland, pp 180-186, 228, 231.

MacKinnon, K. (1985) Indonesië: Natuur en natuurbehoud. M & P Boeken: Weert.

MacLaughlin, K.A. and Thomas, P.R. (1991) The management of babirusa (*Babyrousa babyrussa*) at the New York Zoological Park. AAZPA regional proceedings, 650-657.

Martys, M. (1977) Das Flehmen der Schweine, Suidae. Zoologischer Anzeiger. **199**, 433-440.
(Abstract: babirusa did not appear to produce a flehmen response to the same test which was positive in *Sus scrofa*)

Matur, H.P. (1989) Usaha penangkaran dan pelestarian Babirusa (*Babyrousa babyrussa)* di kebun binatang Surabaya. Unpublished Proceedings of the Indonesian Zoo Association Meeting, Jakarta Zoo, 1-20.

Melisch, R. (1994) Observations of swimming Babirusa *Babyrousa babyrussa* in Lake Poso, Central Sulawesi, Indonesia. Malayan Nature Journal, **47**, 431-432.
(Abstract: At about 09.00 hours a single male babirusa was observed crossing Lake Poso from east to west. The babirusa dived and remained submerged for about 30 secs.)

Melisch, R. (1995) Babirusa skulls on sale in South Sulawesi. Traffic Bulletin, **15**, 99.
(Abstract: The tourist area in Rantepao, Tana Toraja, Sulawesi was surveyed in October 1993. 22 shops were visited, of which six (27%) sold babirusa skulls, and contained 3.5 on average. 20 skulls were of adult males, and one of a sub-adult male. They were said to come from the mountains around Nanggala, Quarles Mountains, Telondokalondo Mountain and the forest between Rantepao and Palopo. The prices asked were 60-90k rupiah. One of the traditional Toradja houses had tusks and a complete (skull?) attached to a beam.)

Mellink, C.H.M., Bosma, A.A., de Haan, N.A. and Macdonald, A.A. (1992) Numerical variation of nucleolar organizer regions after silver staining in domestic and wild suidae (Mammalia). Animal Genetics, **23**, 231-239.

Meyer, A.B. (1896) Säugethiere von Celebes und Philippinen Achipel. Abhandlungen und Berichte des Königlich zoologischen und antropologisch-ethnographischen Museum zu Dresden, **6**, 15-25.

Meyer, A.B. (1899) Säugethiere von Celebes- und Philippinen-Archipel. II. Celebes-Sammlungen der Herren Sarasin. Abhandlungen und Berichte des Königlich zoologischen und antropologisch-ethnographischen Museums zu Dresden, **7**, 28-29.

Miller, J.A. (1984) Kosher pig? Hold the bacon. (babirusa). Science News, **126** (Nov. 24 '84), 327.
(Abstract: The babirusa, an allegedly cud-chewing pig, has recently been touted as a breakthrough pork-producing animal with a potential appeal to those who don't eat pork. Several groups, including the U.S. Agency for International Development, have published enthusiastic support for cultivation of this ruminant-like creature. Rabbis at the Jewish Theological Seminary have reserved opinion until they view the animal's innards. Officials at the Los Angeles Zoo, where babirusas are housed, deny the validity of the claims, which rely on a 1940 autopsy report. They also note that babirusas breed slowly and would be poor food producers. American and Indonesian scientists will study a dozen of the animals to determine their suitability.

Mitchel, P.C. (1905) On the Intestinal Tract of Mammals. Transactions of the Zoological Society of London. **17**, 437-536.

Mitchell, P.C. (1916) Further observations on the intestinal tract of mammals. Proceedings of the general meetings for scientific business of the Zoological Society of London, **1916**, 183-251.

Moeffaert, N. Van (1994) Gedrag en vokalisatie bij de babirusa (*Babyrousa babyrussa* L.). Unpublished thesis, Universitaire Instelling Antwerpen.

Mohr, E. (1958) Zur Kenntnis des Hirschebers *Babirussa babyrussa*, Linne 1758. Der Zoologische Garten, **25**, 50-69.

Mohr, E. (1960) Wilde Schweine. Ziemsen: Wittenberg Lutherstadt, pp 12-18, 109-119.

Munro, S.A. Kaspe, L. Sasmita, R. & Macdonald, A.A. (1990) Gastrointestinal helminthosis in the babirusa (*Babyrousa babyrussa*) and response to albendazole. Veterinary Record, **126**, 16.

Muskita, Y. (1994) Babirusa di Cagar Alam Tangkoko Duasudara Sulawesi Tinggal Kenangan. WWF Radio Bulletin Indonesia Programme, **1**, (3), 9-10.

Musser, G.G. (1987) The mammals of Sulawesi. In "Biogeographical Evolution of the Malay Archipelago". (Ed. T.C. Whitmore), Clarendon Press: Oxford.

Muttaqin, I., Sinaga, D.W., Mustari, A.H., Clayton, L.M. & Lagurusu, Z.H. (1993) Laporan survey kehidupan babi rusa di kab. Gorontalo Sulawesi Utara. Tim Aphi - Dephut - IPB, Bogor, Indonesia.

National Research Council (1983) Little known Asian animals with a promising economic future. National Academy Press: Washington D.C, pp 89-94.

Nishihara, J. (1991) Endangered animals of Indonesia. Sahabat Satwa, Friends of the zoo: Jakarta, pp 22.

Nowak, R.M. (1991) Walker's mammals of the world. Johns Hopkins University Press: Baltimore and London, 5th edition.

Nowak, R.M. & Paradiso, J.L. (1983) Walker's mammals of the world. Johns Hopkins University Press: Baltimore, 4th edition, pp 1181-1182.

O'Brien, T.G. and Kinnaird, M.F. (1996) Changing populations of birds and mammals in north Sulawesi. Oryx, **30**, 150-156.

Oliver, W.L.R. and d'Huart, J.P. (1990) Pigs and peccaries specialist group. Species, **15**, 59-60. (Abstract: There is direct evidence of the continued existence of the 'hairy' babirusa known only from Buru and the Sula islands. A survey conducted in July 1990 yielded photos of skulls of recently caught males. There is a threat to the babirusa from logging and trans-migrants. The babirusa population in Sulawesi is also declining. The babirusa population in captivity (from Sulawesi) is now thought to have come from only four animals.)

Oliver, W.L.R. (1991) Pigs and peccaries specialist group. Species, **16**, 55-56.
(Abstract: The status of the hairy babirusa on Taliabu in the Sula islands will be investigated by a group from the University of East Anglia. There is the possibility of small numbers of babirusa in remnant patches of forest in the south west of Sulawesi.

Oliver, W.L.R. (1993-94) Pigs and peccaries specialist group. Species, **21-22**, 80-82.
(Abstract: Lynn Clayton started the first detailed study of wild populations of Sulawesi babirusa in Sulawesi, Alastair Macdonald and Paul Vercammen carried out studies on captive animals, assisted collection of data on wild babirusa on Buru and in the Togian islands and south-west Sulawesi.)

Oliver, W.L.R. (1994) Pigs and peccaries specialist group. Species, **23**, 75-76.
(Abstract: In October 1994, 4500 copies of a high-quality conservation-education poster featuring all seven species of pig wild to SE Asia was produced and distributed free. Paul Vercammen reported the status of babirusa in the Togian islands. They may only survive on four islands, Malenge (numbers low), Talataco (secure as long as forest remains intact), Togian (relatively secure, but coconuts have replaced much former forest), Patudoka (present but threatened by deforestation). Rowland Melish reports that trade in babirusa skulls continues at Tana Toradja, south central Sulawesi in 1933.)

Patry, M. (1990) Babiroussa; une vie jusqu'au bout du rêve. Fixot: Paris, 221pp.

Patry, M. & Capiod, J.A. (1989) Pour la première fois, le babiroussa. Connaissance de la Chasse, 156 (April 1989), 45-46.
(Abstract: Il observe le comportement d'une jeune femelle éjectant une autre jeune femelle du même rang, une femelle arrivant avec son petit qui se met a téter devant lui, puis c'est un cerf sambar qui vient se souiller, enfin un autre babiroussa en compagnie d'un babi hutan - ils se tolèrent mais ne fraterniscent pas. Ce sont enfin deux grands mâles aux dents profondement recorbées qui se rencontrent et s'affrontent. Mais, particularite de l'espèce, un animal paraissant, malgré l'absence d'ennemis naturels directs, constamment sur le qui-vive: il fait trois pas, redresse la tête, écoute, repart, refait trois pas, tend la tête. En fait, détail intéressant la encore, il ne fléchit pas l'avant-train - comme le font les sangliers et les phacochères par exemple - et surtout ne fouille pas le sol. Il mange des fruits, des larves trouvées dans des troncs pourris, de jeunes pousses de rotin, très abondants ici.)

Patry, M., Leus, K. & Macdonald, A.A. (1995) Group structure and behaviour of babirusa (*Babyrousa babyrussa*) in northern Sulawesi. Australian Journal of Zoology, **43**, 643-655.
(Abstract: The total number of babirusa sightings recorded on videotape was 586. These comprised 161 of adult males, 155 of adult females and 11 of adults of unknown sex; there were 78 of subadult males, 53 of subadult females and a further 34 cases where it was not possible to determine the sex of the subadult animal; juveniles were observed 94 times of which 19 could be identified as males and 12 as females, the sex of the other 63 remaining unclear. The babirusa were present in groups which ranged in size from one to eight animals, with 160 groups observed at the 'Marisa' site and 66 groups at the 'Lantolo' site (Table 1). The median group size (including solitary animals) was two babirusa for both 'Marisa' and 'Lantolo'. The adult males tended to be solitary whereas the adult females tended to be accompanied by young animals of one or two generations. Large bachelor groups were not seen. Groups rarely contained three or more adult females. The range of agonistic and ploughing behaviours observed were indistinguishable from those exhibited by babirusa in zoological collections.)

Persulessy, Y (1996) Babirusa (*Babyrousa babyrussa*) sebagai salah satu species babi liar Asia Tenggara. Unpublished report, BirdLife International, Ambon, Indonesia.

Persulessy, Y. and Poulsen, M.K. (1996) Notes on the distribution of babirusa *Babyrousa babyrussa* in Buru, Maluku province, Indonesia. In Manansang, J., A. Macdonald, D. Siswomartono, P. Miller and S. Seal (eds.). 1996. Population and Habitat Viability Assessment for the Babirusa (*Babyrousa babyrussa*). IUCN/SSC Conservation Breeding Specialist Group: Apple Valley, MN.

Peters, C.T.M. (1985) De babiroesa: het hertezwijn. Dieren, **1**, (5), 135-139.

Piso, W. (1658) Appendix. De Baby-Roussa. In "Bondt, J. De Indiae utriusque re naturali et medica libri quatuordecim ...annotationes & additiones. Apud Ludovicum et Danielem Elzevirios: Amstelaedami, 2nd edition, pp 61-62.

Plasa, L. (1990) *Babyrousa babyrussa* 1989: Internationales Zuchtbuch fur den Hirscheber/ International studbook for the babirusa. Wilhelma Zoologisch-Botanischer Garten: Stuttgart, 2nd edition.

Plasa, L. (1991) Das Hirscheber-Zuchtbuch. Bongo, Berlin, **18**, 258-253.
(Abstract: The first issue of the International Studbook for the babirusa was published in 1988 with data from all babirusas kept in captivity since 1820. From 1974 to 1977, 6.6 animals were imported to Europe from Indonesia. The present stock in Europe and North America are descendants of these animals. All of them belong to the subspecies *B.b. celebensis*. At the end of 1989 there were kept in Europe 25.25 babirusa in 11 zoos. 7.6 animals lived in the USA in 3 parks and 36.29.3 in Indonesia in 4 institutions so that the total world stock of babirusa in captivity on December 31st 1989 was 68.60.3 animals. Insufficient communication from the Indonesian zoological gardens seems to be the biggest problem for the stud-book keeper because more than 50% of the world stock are being kept there and it is very hard to get data from that country. Another difficulty is the lack of space. So it would be very important to find new keepers for this endangered species.)

Plasa, L. (1991) Babirusa (*Babyrousa babyrussa*) EEP Annual Report 1990. EEP Yearbook 1990, EEP executive office: Amsterdam, pp 131-133.
(Abstract: It would be worthwhile if we could import a number of wild-caught animals, as the founder stock of the babirusa in captivity is very small. Perhaps there is a possibility if all keepers of this species could work together in this regard.)

Plasa, L. (1991) *Babyrousa babyrussa* 1990: Internationales Zuchtbuch für den Hirscheber/ International studbook for the babirusa. Wilhelma Zoologisch-Botanischer Garten: Stuttgart, 3rd edition.

Plasa, L. (1992) Babirusa (*Babyrousa babyrussa*) EEP Annual Report 1991. EEP Yearbook 1991/92, EAZA/EEP executive office: Amsterdam, pp 147-149.

Plasa, L. (1992) *Babyrousa babyrussa* 1991: Internationales Zuchtbuch für den Hirscheber/ International studbook for the babirusa. Wilhelma Zoologisch-Botanischer Garten: Stuttgart, 4th edition.

Plasa, L. (1993) Babirusa (*Babyrousa babyrussa*) EEP Annual Report 1992. EEP Yearbook 1992/93. EAZA/EEP executive office: Amsterdam, pp 167-168.

Plasa, L. (1993) *Babyrousa babyrussa* 1992: Internationales Zuchtbuch für den Hirscheber/ International studbook for the babirusa. Wilhelma Zoologisch-Botanischer Garten: Stuttgart, 5th edition.

Plasa, L. (1994) Babirusa (*Babyrousa babyrussa*) EEP Annual Report 1993. EEP Yearbook 1993/94. EAZA/EEP executive office: Amsterdam, pp 196-197.

Plasa, L. (1994) *Babyrousa babyrussa* 1993: Internationales Zuchtbuch für den Hirscheber/ International studbook for the babirusa. Wilhelma Zoologisch-Botanischer Garten: Stuttgart, 6th edition.

Plasa, L. (1995) Babirusa (*Babyrousa babyrussa*) EEP Annual Report 1994. EEP Yearbook 1994/95. EAZA/EEP executive office: Amsterdam, pp 237-238.

Plasa, L. (1996) *Babyrousa babyrussa* 1994/95: Internationales Zuchtbuch für den Hirscheber/ International studbook for the babirusa 1994/95. Wilhelma Zoologisch-Botanischer Garten: Stuttgart, 7th Edition.

Pocock, R.I. (1943) The external characters of a forest hog (*Hylochoerus*) and a babirusa (*Babirussa*) that died in the society's gardens. Proceedings of the Zoological Society of London, **113**, 36-42.
(Abstract: The anatomy of the head, mouth, face, nose, ears, and feet of the young babirusa)

Poulard, J. (1990) Geheimnisvolle Hirsch-Eber. Das Tier, Jan 1990, 70-75.

Quoy, J.R.C. & Gaimard, J.P. (1830) Voyage de découvertes de l'Astrolabe. Zoologie. J. Tastu: Paris, **1**, 125-132.

Quoy, J.R.C. & Gaimard, J.P. (1833) Voyage de la Corvette l'Astrolabe. Atlas Zoologique. J. Tastu: Paris, 22-23.
(Abstract: adult male babirusa from Sulawesi viewed from the left side. Adult female babirusa from Sulawesi viewed from the right side and a juvenile male babirusa viewed from the left side.)

Ramaer, J. (1936) Natuurmonumenten. Dierenbescherming. Manado. Staatsblad van Nederlandsch-Indië, 122, 1-2.
(Abstract: Establishment of the nature reserve "Tanggala" near Gorontalo, north Sulawesi.)

Reinhard, R. and Frädrich, H. (1983) Bemerkungen zur Zucht von Hirscheber (*Babyrousa babyrussa*) im Zoo Berlin. Bongo, Berlin, **7**, 65-70.

Reksowardojo, D.H. (1995) Ringkasan disertasi studi kemampuan reproduksi dan produksi babirusa (*Babyrousa babyrussa celebensis* Deninger) melalui upaya budidaya. Unpublished PhD thesis, Bogor, Indonesia.

Rewell, R.E. (1948) Diseases of tropical origin in captive wild animals. Transactions of the Royal Society of Tropical Medicine and Hygiene, **42**, 17-25, 26-36.
(Abstract: In the list of animals in which microfilaria were found during the years 1925-1939 was babirusa.)

Rosenberg, H. von (1878) Der Malayische Archipel. G. Weigel: Leipzig, pp 269.
(Abstract: The babirusa is only to be found in the northern half of Sulawesi. At Tulabollo it was possible to see babirusa daily which were not particularly shy.)

Roulin, F.D. (1849) Dictionnaire universel d'histoire naturelle. Renard, Martinet, Langlios et Leclerc, Victor Masson: Paris, **2**, 397-408.

Rubenstein, S. (1984) Woman who ate 'kosher' pig says it's not tasty or kosher. San Francisco Chronicle, December 14.
(Abstract: Victoria Selmier ate the babirusa in 1978. She spent 2 years in the Indonesian jungle studying the animal. She never saw it chew the cud. She said that there were only 1000 of the animals left. The babirusa is a gentle and peaceful beast that settles its differences with its fellow babirusa in an unusual manner, worthy of preservation.)

Rumphius, G.E. (1743) Het Amboinsch Kruid-boek, Herbarium Amboinense. Meinard Uijtwerf: Amsterdam, **3**, 171.
(Abstract: He reports on the wonderful pigs from Buru and the Sula islands. Notes are given of their feeding habits and the rubbing of resin on their skin.)

Sanyal, R.B. (1892) A hand-book of the management of animals in captivity in lower Bengal. Natraj: Dehra Dun.
(Abstract: The length of life of the pair held in captivity in Calcutta was from April 1880-May 1884. The food they ate was fruits, roots, vegetables and grain. They showed no preference for a meat diet. Both died suddenly, the female undoubtedly from fat. They appeared to suffer from heat during the fierce hot days of May and June, probably more from radiated heat than from the effects of the temperature; at such a time they enjoyed a cold bath; though generally retiring (shy) they were less shy than even a wild Indian pig.)

Sarasin, P & Sarasin, F. (1905) Reisen in Celebes. C.W. Kriedel: Weisbaden, **2**, 6-48, 285
(Abstract: The babirusa can be found beside the Lindu lake.)

Schinz, H.R. (1824) Naturgeschichte und Abbildungen der Säugetheire. K.J. Brodtmann: Zurich, **1**, 284.
(Abstract: babirusa eat the leaves of banana and other trees, as well as fruit and roots.)

Schmidt, C.R. (1990) Pigs. In " Grzimek's encyclopedia of mammals". McGraw-Hill: New York, **5**, 20-55.

Schrader, R. (1941) Het Landschap Banggai. Nederlandsch-Indische Geographische Mededeelingen, **1**, 125-132.
(Abstract: babirusa are present in the Banggai countryside.)

Schwarze, E. S. (1934) Der Hirscheber von Sula. Zeitschrift für Säugetierkunde, **9**, 433-434.
(Abstract: The discoverer of the Sula babirusa, W.C.J. Frost has imported four babirusa from that island, three males and a female. They are not grey coloured, which is characteristic of the Buru babirusa, but have black hair. The ventral side is whitish, and one has whitish cheeks and anal region.)

Selmier,V.J. (1978) Only in Indonesia; the babirusa. Unpublished report to LIPI and PPA, Indonesia, 51-64.

Selmier,V.J. (1983) Bestandsgroße und Verhalten des Hirschebers (*Babyrousa babyrussa*) auf den Togian-Inseln. Bongo, Berlin, **7**, 51-64.
(Abstract: In the Togian islands there is an estimated babirusa population of 500-1000. The main threats are disease, native and feral dogs, trapping as pests by farmers, destruction of the habitat by logging. The prevalence of the Muslim faith protects the babirusa.)

Stevens, C.E. (1988) Comparative physiology of the vertebrate digestive system. Cambridge University Press: Cambridge.

Sody, H.J.V. (1949) Notes on some primates, carnivora, and the Babirusa from the Indo-Malayan and Indo-Australian regions. Treubia, **20**, 121-190.

Soebakah, R. (1988) Beberapa penyakit satwa liar didalam kebun binatang Surabaya dan usaha pengendaliannya. Prociding simposium nasional penyakit satwa liar. Fakultas kedokteran hewan Universitas Airlangga dan Kebun binatang Surabaya: Surabaya, pp 135-144.
(Abstract: anaplasmosis had been seen in babirusa, as had Panaritium.)

Stavorinus, J.S. (1798) Voyages to the East Indies. G.G. & J. Robinson: London, **2**, 350-351.
(Abstract: Among the wild animals, which inhabit the woods of the island Bouro, there is one which bears the name of babi-roussa, or the hog-deer; it has been fully described by Valentyn, who has given us a representation of it; but it appeared to me, when I compared the figure with one of the animals alive, that its legs were longer than they are there represented.
The translator, S H Wilcocke added: The babi-roussa .... are easily hunted down; but they frequently hurt the dogs with their lower tusks; the upper tusks are too far recurvated to admit of their defending them selves with them. Their flesh more resembles venison than pork; there is

little fat upon it, it being mostly solid meat. They do not live, like the other wild hogs, upon sago and canari, a sort of almonds, but chiefly upon grass and the leaves of trees. They never associate with the wild hogs, and when hunted, they generally take to the water, where they are very expert in swimming and in diving, and sometimes swim over from one island to the other.)

Teijsmann, J.E. (1861) Verslag van den honorair inspecteur van kultures J.E. Teysmann, over de door Z. ED. in 1860 gedane reize in de Molukken. Natuurkundig Tijdschrift voor Nederlandsch Indië, **23**, 290-369.
(Abstract: We did not see any babirusa in the wild though they are present in this area (Minahassa) Those that people had caught for us soon died. They seem to be more difficult to catch alive than the anoa. There are plenty *Sus celebensis*.)

Teysmann, J.E. (1879) Bekort verslag eener Botanische dienstreis naar het Gouvernement van Celebes en Onderhoorigheden. Natuurkundig Tijdschrift voor Nederlandisch Indië, **38**, 54-125.
(Abstract: babirusa can be found infrequently in the eastern part of Sulawesi and on Buru. *Sus celebensis* is all over Sulawesi like a plague for the population.)

Thenius, E. (1970) Zur Evolution und Verbreitungsgeschicht der Suidae. (Artiodactyla, Mammalia). Zeitschrift für Säugetierkunde, **35**, 321-342.

Thomsen, P.D., Høyheim, B & Christensen, K. (1996) Recent fusion events during evolution of pig chromosomes 3 and 6 identified by comparison with the babirusa karyotype. Cytogenetics and Cell Genetics, **73**, 203-208.

Urbain, A., Bullier, P. & Nouvel, J. (1938) Au sujet d'une petite épizootie de Fièvre aphteuse ayant sévi sur des animaux sauvages en captivité. Bulletin de l'Académie Vétérinaire de France, **11**, n.s., 59-73.
(Abstract: Animals of the Suidae family were very susceptible; the babiroussas (*Babirussa babyrussa*) were affected and, after inoculation with antiserum and virus, four wild boars contracted the infection. All recovered after treatment with antiserum; pigs had lesions confined mainly to the feet.)

Urbain, A, Dechambre, E. & Nouvel, J. (1939) Nouveau cas de tuberculose spontanée observée sur des mammifères sauvages vivant en captivité. Bulletin de l'Académie vétérinaire de France, **12**, n.s., 347-354.

U.S. [ESA] Fish and Wildlife Service (1991) Endangered and threatened wildlife and plants (those covered by the regulations for the U.S. Endangered Species Act), 50 CRF 17.11.12.12 July 15, 1991 U.S. Government Printing Office, Washington, D.C.

Valentijn, F. (1726) Oud en nieuw Oost-Indiën. J van Braam: Dordrecht, Amsterdam, **5**, 268-269.

Vercammen, P. (1991) Übersicht über die Haltung von Hirschebern (*Babyrousa babyrussa celebensis* L.) im Zoo Antwerpen. Bongo, Berlin, **18**, 244-249.

Vercammen, P. (1992) Le Babiroussa, un cochon pas comme les autres. Magazine trimestriel, Espace Zoologique, St-Martin la plaine, 28, hiver, 8-11.
(Abstract: Description. Habitat and habits. Babirusa in captivity. Scientific research and international cooperation. Distribution. Data file. Note erratum in text reported in Spring 1993 volume of same journal.)

Vietmeyer, N. (1984) Hog wild. (babirusa) International Wildlife, **14**, 35 il.

Vrolik, W. (1844) Recherches d'anatomie comparée sur le Babyrussa. Nieuwe verhandelinge der eerste klasse van het koninklijk-Nederlandsche instituut van wetenschappen, letterkunde en schoone kunsten te Amsterdam, **10**, 207-248.

Wadsworth, J.R. & Williamson, W.M. (1960) Neoplasms from captive wild species. Journal of the American Veterinary Medical Association, **137**, 424-425.
(Abstract: A female babiruoussa (*Babirussa alfurus*), 21 years old. Terminal pneumonia with secondary complications was believed to be the cause of death. Adenocarcinoma of the lung was diagnosed.)

Walker, E.P. (1964) Mammals of the World. Johns Hopkins University Press: Baltimore, 2nd edition, 1357-1358, 1364.

Walker, E.P. (1975) Mammals of the World. Johns Hopkins University Press: Baltimore, 3rd edition, 1364.

Wallace, A.R. (1869) The Malay archipelago. Macmillan: London.

Watling, R. (1982) Celebes: Wo Naturschutz noch eine Zukunft hat. Das Tier, **8**, 14-18.

Wemmer, C. & Watling, D. (1982) Eye colour polymorphism in the Babirusa pig. Malayan Nature Journal, **36**, 135-136.

Wemmer, C. & Watling, D. (1986) Ecology and status of the Sulawesi palm civet *Macrogalidia muschenbroekii* Schlegel. Biological Conservation, **35**, 1-17.

Whitten, A.J., Mustafa, M. and Henderson, G.S. (1987) The ecology of Sulawesi. Gadja Mada University Press: Yogyakarta, pp 34, 37, 41, 49, 412, 414-418, 447, 448.
(Abstract: Babirusa fight side by side, and lock teeth in contest. Babirusa is one of the first animals to become locally extinct after logging or land opening, possibly because village or feral dogs kill the piglets, a form of predation to which babirusa are poorly adapted.)

Wind, J. (1983) Dumoga Bone Nationaal Park Sulawesi - Indonesië. Panda, **19**, 99-101.

Wind, J. (1984) Management plan 1984-1989: Dumoga-Bone National Park. World Wildlife Fund: Bogor.

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NOTES ON THE SYSTEMATICS OF *BABYROUSA* (ARTIODACTYLA, SUIDAE)

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With 4 plates

SUMMARY

Skins and skulls of *Babyrousa babyrussa* have been studied; the species is divisible into three living subspecies: *B. b. babyrussa* (syn. *frosti*) from Buru and Sula, *B. b. togeanensis* from Malenge, and *B. b. celebensis* from the northern arm of Celebes. A skull from near Kulawi, central Celebes, tends towards *babyrussa*, and may represent a surviving population of the inadequately characterised *B. b. bolabatuensis*, known as a subfossil from the southern arm of Celebes. Teeth of the latter form decreased in size through time. The possibility of the species having been introduced into Buru and Sula is discussed.

INTRODUCTION

The remarkable babirusa (genus *Babirousa* Perry, 1811) attracted early notice in western scientific circles, despite its restricted distribution (see Mohr, 1958 for a brief pre-Linnaean history). It commanded attention because of the bizarre appearance of the male, not only for Europeans but also, perhaps, for Indonesians (see below). Modern zoology has confirmed that it is indeed no "ordinary pig", as shown by the anatomical study of Davis (1940): alone among the Suidae it retains four terminal tendons to M. plantaris; the arrangement of tendons to M. extensor digitorum communis resembles the peccaries; M. coracobrachialis has two heads, as is usual in ruminants; the stomach is complex, and the origin of M. omohyoideus again resembles the peccaries (Saban, 1968). While Deninger's (1909) claim that it had descended from a Miocene anthracothere can surely no longer be maintained, Thenius (1970) could see no common ancestor with the other Suidae more recent than the Oligocene, justifying its allocation to a separate subfamily, Babyrousinae.

HISTORY OF TAXONOMY

After a period when it was variously misassigned to Borneo, Sumatra, Amboina and other places (as noted by Sody, 1949) its occurrence in Celebes and Buru was finally confirmed, and authors set about elucidating its variation from place to place. First, Deninger (1909), on the basis of remarkably large samples for that period (16 from Buru, 10 from Celebes) distinguished the Celebes babirusa — taking Buru as type locality of *B. babyrussa* — as a separate species, *Babirusa* (sic) *celebensis*. The distinguishing characters of the Celebes species were the wrinkled, nearly hairless skin. contrasting markedly to the well-haired skin of the Buru species; the longer. narrower skull; the upper toothrow longer, above 73 mm, the nasals constricted between the canines of the males, and the longer, thicker upper canines with their alveoli upright instead of forwardly inclined. As a consequence of the difference in initial direction of the upper canines, in side view they are not overlapped by the backcurving lower canines as they are in the Buru form.

Later Dammerman (1929), comparing "a rather large series" (about seven?) of skulls from Buru with four from Celebes, found the following differences: the Buru skulls are shorter and broader, their profile less straight: the frontals have deep sharp-edged furrows, instead of shallower with rounded edges as in Celebes specimens; and the supraorbital foramen is more or less concealed from dorsal view. However, in only one of the four Celebes skulls were the nasals greatly constricted. The upper canines in the Buru skulls are parallel to each other, or diverge, whereas in two of the Celebes skulls they converge and nearly touch in the middle of their curve. Some of these characters, he notes, are similar to those which distinguish domesticated from wild pigs. Dammerman was aware of Deninger's paper but had "no access" to it.

As a matter of fact Lesson (1827), although referring to Buru, had in effect described Celebes babirusas under the name *Babirussa alfurus*; but Deninger, as well as Thomas (1920), Sody (1949), Laurie & Hill (1954) and others, showed that Lesson merely intended to rename Linnaeus's *Sus babyrussa* (even quoting the type locality as Buru) to avoid tautonymy.

Thomas (1920) reported on eleven skulls from Taliabu, in the Sula islands, comparing them with the Buru form after first noting that in Deninger's canine and nasal characters they followed the Buru, not the Celebes pattern. Retaining the division into two species, he described the Sula form as *B. b. frosti*, differing from *B. b. babyrussa* in its slightly smaller size, conspicuously smaller canines, narrower bullae, and more slender paroccipital processes. However, it is unclear how many skulls from Buru were available for comparison, only one being mentioned (this one, however, being the one figured by Seba and so the chief basis for Linnaeus's description, is the lectotype of the species): judging by the registration numbers, only one other Buru skull would seem to have been in the British Museum at that time.

Sody (1949) compared 10 skulls from Celebes, 4 from Malenge (Togean islands), 8 from Buru, and 4 from Sanana (Sula Islands). These last he referred to *frosti* with a query, as "judging on the description, there seem to exist differences" from the type series from Taliabu. He went on to describe the Malenge specimens (including 3 skins and one head-skin) as a new race, *B. b. togeanensis*. The new race was described as hairy like *babyrussa* (and also *frosti*, a fact not known to Thomas), with the underparts, as far as the sides of the upper lip and insides of the limbs, much lighter than the rest of the body. The toothrow was said to be much shorter than in *celebensis* but rather longer then in *frosti*, though about the same as in *babyrussa*; M^3 was narrower than in *celebensis*, perhaps a little smaller than in the other two; the nasals, pinched in like in *celebensis*. By implication, Sody included the Celebes form, too, in the single species *B. babyrussa*.

One further subspecific name has been applied to a babirusa. In 1964, F. de Beaufort, in a catalogue of type specimens of ungulates in the Paris museum, drew attention to a mounted babirusa skin from an animal brought back alive by Quoy and Gaimard and stated in the museum catalogue to be from Celebes. However, in the collector's manuscript catalogue the specimen is listed as from "Moluques". This, according to De Beaufort, makes the specimen a novelty, as the babirusa appears not to have been recorded from there since then; so it would have formed a geographic variety (now perhaps extinct), to be called *Babyrousa babyrussa Merkusi* (sic), after M. Merkus, governor of the Moluccas, who presented the animal to Quoy and Gaimard. Everything about this name is inexplicable; the Moluccas, then as now, included Buru, type locality of the species; the specimen was already in captivity in Merkus' residence, and could as easily have been presented to him from Celebes as from anywhere else; the capitalisation of the trinomial; and surely it was pointless to create a nomen nudum, which even if it represents a valid form will be displaced by any name (with description appended) which someone in the future cares to award.

Mohr (1958) reviewed the subspecies described up to that time, and presented photos of living *celebensis* and *frosti*, showing clearly the naked wrinkled skin of the former and the hairy covering of the latter. The snout of *frosti* is, as she notes, markedly more pointed than that of *celebensis*, and would seem to be more mobile in life. Other interesting photos include one of a female skull — perhaps the first published photo of the skull of the rather unspectacular, tuskless female — and one (Abb. 18) of a *frosti* skull said to be female, with small tusks in the upper jaw, and canines larger than usual for a female in the lower jaw. The specimen, evidently a young adult, is a wild-shot one, collected by Rosenberg; without supporting evidence, I would incline to consider it a male with rather short tusks, especially considering its evident youth.

Two extinct forms, one recent and one fossil, have been described by Hooijer (1948; 1950). Three M_3, one M^2 and one M^3 from Beru and Sompoh, near Cabenge in Sulawesi Selatan (South Celebes), associated with the Pleistocene giant suid *Celebochoerus heekereni*, were very much larger than most living homologues (than all, in the case of the M^2 and the two complete M_3), and were described as a subspecies *Babyrousa babyrussa beruensis* (Hooijer, 1948). Numerous teeth from the Holocene cave deposits at Bola Batu, also on the southern peninsula, were assigned to the subspecies *Babyrousa babyrussa bolabatuesis* by Hooijer (1950), as having "Teeth... of less average size (than Celebes specimens), comparable to that found in *Babyrousa babyrussa babyrussa* (L) of Boeroe and in *Babyrousa babyrussa frosti* (Thomas) of the Sula Is.". In other words, the new subspecies was distinguished from the other Celebes race but not from the Buru and Sula ones. But as the Bola Batu deposits seem fairly recent (they contain apparent dog remains, and 16th century Chinese sherds), the implication certainly is that if babirusa had survived on the southern peninsula up to the present they would be, in dental characters at least, more like *babirusa* than *celebensis*.

The present study

A study of babirusa taxonomy was begun in July 1975 at the Zoological Museum, Bogor, as a by-product of a study of southeast Asian Suidae. Further material was studied in various European museums in November and December 1976 and February 1977, and finally again in Bogor in July 1978. Standard measurements were taken on skulls and teeth, skin characters were recorded, and special attention was paid to those characters described in the literature (above) as diagnostic of one form or another. Dr. G. G. Musser kindly sent measurements and descriptions of specimens in the American Museum of Natural History (New York), and these have also been utilised in the present study.

Skin

The Bogor Museum (MZB) and American Museum of Natural History (AMNH) have good collections of babirusa skins; other museums little or none. Altogether I could study personally 3 (4?) from Celebes, 3 from Malenge, 5 from the Sula Is. (of which 4 were from Sanana), 2 (3?) from Buru, and the type of *merkusi*. In addition, I received descriptions of 9 skins from Celebes and 6 from Malenge in the AMNH.

All Buru and Sula skins have conspicuous long thick hair all over the head, body and legs. Of the 4 Sanana MZB specimens, 3293, a male, has hair that is mostly creamy gold with just a few black hairs intermingled, mostly towards the foreparts, and a dorsal stripe of unmixed golden hairs; but the rump hairs, in a triangle with its apex in the lumbar region, are entirely black, with the golden dorsal stripe continuing through it. The head is like the body, but round each eye is a ring of black and the hairs on the back of the ears are black. The cheeks and limbs are pale. MZB 3291, a female, is similar, but the hairs are sparser. MZB 3292, a female, has long dense hair of the same colour, but with no black hairs at all except a few sparse ones on the rump, round the eyes, and on the back of the ears. MZB 2014, a juvenile female, on the other hand has the fairly dense long hairs entirely black all over the body. Finally, a skin in the Amsterdam Museum, ZMA unreg., from "Sula Islands", has much sparser hair, especially on the hind parts, mainly white but with some black on the snout.

Of the Buru skins one (MZB 1871), a female, resembles MZB 3293 from Sanana, but has black hairs on the rump only and a few round the eyes. The other, ZMA unreg., female, has pale fawn hairs all over, rather sparser than the Bogor skin. Another skin, ZMA 9122, a juvenile said by Mohr (1958: 57) to be from Buru, but with "Celebes" on the present label, has thick black hairs all over.

All these skins, therefore, have a conspicuous hair-cover with both a light (fawn or gold) and a dark (black) hair type, varying in predominance, but tending to be differently distributed over the body. All skins, if complete in that region, show a well-developed tail tuft. The two unregistered ZMA skins (one from Sula, one from Buru) are noticeable paler on the underparts, a feature said by Sody to distinguish the Togean race.

The three *togeanensis* skins in Bogor, as Sody states, are variable in colour: mostly fawn, but some hairs in all skins are black, generally with fawn tips; they are paler fawn in the mid-dorsal region and black on the forehead, while the underparts are pale. The six AMNH Togean skins vary from "brown" to (in one case) black, which sounds in part similar to the Bogor skins and implies the same range of variation as in Buru and Sula. As in the latter, there is always a well-developed tail tuft. A difference, however — apparently the only consistent difference — is that the hairs, though still conspicuous, are much less long and dense.

The three Celebes skins in Bogor — two from Bumbulan, one from

G. Ile-Ile in the same region — are markedly different: the hair very sparse and short, dark brown but lighter in the median dorsal region; the overall effect is of complete nudity. Of the nine skins, all from Bumbulan, in the AMNH collection, Musser (pers. comm.) describes 5 as "sparse", 2 as "medium dense", 2 "dense" and either black or "brown", and in the substantial breeding group in the Surabaya zoo, evidently from Celebes, some animals are indeed much more conspicuously hairy than others. A skin in Amsterdam, ZMA 9121, from Celebes, also has a conspicuous hairy coat. Guillemard (1886: 205) describes a male from Lembeh island, off Bitung in Minahasa, as being "covered with a very fine yellowish down", and he also notes the colour polymorphism.

If there is less difference in hairy convering between the Celebes babirusa and the rest than has commonly been described, one substantial difference does remain: the small size and sparsity of the tail tuft, in which all specimens from Celebes — AMNH material included — differ consistently from all those from other islands.

Skull: a. non-metrical comparisons

Dammerman (1929) found that the dorsal profiles of his Buru series were less straight than those from Celebes. In the present study, two-thirds of the skulls from both Buru and Celebes have a profile that is noticeably concave at the nasal root (as have 40% from Taliabu and all from Malenge). This distinction therefore cannot be maintained.

The difference in degree of expression of the frontal furrows is much more diagnostic. The furrows are not sharp-edged in any skull from Minahasa or Malenge, nor in 16 out of 18 from the Bumbulan region, but they are in 12 out of 16 from the Sula Is. and in 23 out of 29 from Buru. Both males and females show this difference; in Buru and Sula they seem to become sharper-edged with maturity. The associated feature of the supraorbital foramen (which lies at the posterior end of the furrows) being overhung, concealed from dorsal view, in Buru but not in Celebes skulls, is not quite as good: it is visible from above in 16 out of 17 from Minahasa, 17 out of 18 from Bumbulan, and in all of 8 from Malenge, but also in 6 out of 15 from Sula and 17 out of 32 from Buru.

The canines of males differ markedly between the various geographical groups. As Deninger (1909) found, they tend to be much longer and thicker in Celebes than in Buru; Sula skulls align with Buru, and this time the Malenge skulls also tend to align with Buru. However, a Buru skull (Leiden, cat. ost. b) has the largest canines of any seen in this study. A difference that seems to differentiate in every case between males from northern Celebes and from Sula or Buru is the forward-rotated alveolus of the maxillary canine in the latter, such that, as Mohr (1958) stressed, the upper canine in Sula and Buru emerges much more closely behind the lower, and in side view the lower canine crosses lateral to the upper (pl. 1 fig. a, b). In Celebes male skulls the upper canine emerges vertically and the lower is always distinctly anterior of it (pl. 3 fig. a). In Malenge skulls the canine alveoli are rotated as in Buru, but less markedly in most cases (pl. 2 fig. b).

As Dammerman (1929) noted, the maxillary canines usually diverge or run parallel to each other in Buru skulls; they do slightly converge, however, in 10 out of 26 skulls, and even cross in one (Leiden, cat. ost. b). In Sula, somewhat by contrast, they converge in 9 out of 13, but in the restricted series from Taliabu they converge in 8 out of 10. They converge in all Malenge skulls, and in all but three of 22 skulls from northern Celebes (they cross in one of these).

The differences described by Thomas (1920) to distinguish *frosti* (Taliabu) from *babyrussa* (Buru) are not very convincing. The skulls do average slightly narrower, but not significantly. The canines are small in both as a general rule: it merely happens that in the lectotype of *babyrussa* they are rather large. Mohr (1958: 65) figures a Sula skull with unusually large canines. The bullae and paroccipital processes are not different.

Hooijer (1950) noted that, although most babirusa skulls lack P^2 or DM^2, this tooth is present on at least one side in 7 out of 13 skulls from Sula, compared to one out of 17 from Buru and two out of 15 from Celebes. Of the specimens not seen by Hooijer, one (MZB 2015) out of 14 from Buru has a P^2, making a full total of 2 out of 31, or 6.5%; 2 out of 4 from Sanana, making a full total of 9 out of 17, or 53% for Sula as a whole; none from Malenge; and one out of 9 from Celebes, giving a total of 3 out of 24, or 12.5%. Thus it is confirmed that the frequency of this anomaly is much higher in the Sula islands than elsewhere.

Skull: b. Metrical comparisons

A number of standard measurements were taken on skulls and teeth of all babirusa specimens studied, as well as two (distances between upper canines: (1) at their roots, (2) in the middle of their length) designed to bring out the convergent/divergent contrast. The results, population by population, are given for males in Table 1.

The two samples from the northern peninsula of Celebes, Minahasa and Bumbulan (the latter includes in addition one specimen each from Monano and Muton) are very alike metrically, as they are non-metrically. Bumbulan skulls are broader across the zygomata and canine roots and have a longer

TABLE 1

Skull measurements of geographical samples of male *Babyrousa*

(a) Groups

	Minahasa			Bumbulan			Malenge			Taliabu			Buru	
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean
Total length	16	293.9	9.90	13	296.9	14.78	5	309.0	6.75	10	280.2	11.91	26	281.8
Condylobasal	16	277.0	13.25	13	280.1	11.03	5	285.2	4.44	8	271.8	10.08	22	266.8
Bizygomatic	17	126.4	6.93	13	133.3	6.58	5	129.0	3.74	10	121.7	6.20	26	127.5
Palate l.	17	181.2	8.97	12	184.5	8.06	5	185.4	3.85	10	181.3	7.86	26	180.1
Toothrow l.	9	75.3	1.66	9	80.3	4.06	6	71.7	1.75	1	68.0	–	6	69.0
Occipital br.	8	70.6	9.90	13	67.7	7.16	5	68.4	3.85	10	64.3	3.86	26	69.5
Occipital ht.	7	66.6	5.02	13	66.0	4.03	5	62.8	3.96	9	57.8	5.33	24	61.9
Canine roots	9	57.8	1.92	12	62.3	6.43	6	61.0	2.35	10	50.1	2.69	26	56.1
Canine middle	6	24.7	11.52	10	15.4	16.30	5	0.0	0.00	10	27.8	20.25	18	53.7
M^3 length	7	24.4	1.60	13	25.4	1.98	6	20.8	0.75	10	22.1	1.10	15	22.6

(b) Single specimens

	Lembeh	Moa	Sanana
Total length	288	252	265
Condylobasal l.	(271)	(242)	254
Bizygomatic br.	134	128	121
Palate l.	183	(155)	169
Toothrow l.	(76)	69	67
Occipital br.	80	54	64
Occipital ht.	(73)	(46)	56
Canine roots	61	51	47
Canine middle	12	15	64
M^3 length	23	23.9	21

toothrow, but not one of the differences exceeds the traditional subspecific limits, with the coefficient of difference (C.D., i.e. difference between the means divided by sum of the standard deviations) greater than 1.28. The single specimen (Cambridge Zoology Museum, 13.002) from Lembeh, an island off the eastern coast of Minahasa, divided from it by a channel about half a kilometre wide, falls within two standard deviations of the Minahasa sample for all measurements; Deninger (1909) gives measurements, many of them comparable, for three more skulls from Lembeh, one of them (Dresden 2476) the type of *celebensis*.

The Malenge skulls average larger than those from Minahasa or Bumbulan, and have a shorter toothrow and shorter M^3, lower occiput, and the distance across the middle of the upper canines (a metrical expression of their invariable convergence) is zero. The third molar difference is beyond the traditional subspecific level of distinction from both the Minahasa (1.53) and Bumbulan (1.68) samples as is the toothrow length from the Bumbulan (1.48), though not from the Minahasa (1.06) sample. Taken in conjunction with the external differences, the Malenge form should be allotted to a different subspecies from the northern peninsula form.

The Taliabu skulls are smaller in almost every measurement than are the Celebes ones. The toothrow length and breadth across canine roots are significantly smaller than in the two mainland samples, and the latter and total skull length differ significantly from the Malenge material (C.D. above 1.28). Taken, again, in conjunction with the external differences, this confirms that the Taliabu form should be recognised as a subspecies distinct from the Celebes mainland and Malenge forms.

The single adult male skull from Sanana, the old name for the island of Sulabesi southeast of Taliabu in the Sula group, is smaller than all but one of the Taliabu skulls, but does not fall beyond the two standard deviation limits in any of its measurements.

Buru skulls are again small; they differ significantly from the Celebes mainland and Malenge samples in the smaller total length and condylobasal length, from the mainland samples also in the smaller toothrow length. But they do not differ significantly in any measurement from the Taliabu sample; and as it will be recalled that there are no external or visual skull differences either, there are no grounds for maintaining a subspecific distinction.

The female skulls are few in number. Thomas (1920) quotes Frost, the collector of the Taliabu sample, to the effect that the males defend the females so courageously that females are hard to kill. The female samples (Table 2) differ from one another in just the same manner as do the males, with the sole exception of the Malenge skulls, which are not larger than the Celebes mainland ones, unlike the corresponding males. Females are otherwise some 30 mm shorter in total and condylobasal length than are the respective males.

A most interesting specimen is the (slightly damaged) skull of a male from G. Malema, 1200 m, Moa, Kulawi district, central Celebes (MZB 12115, pl. 3 fig. a). The skull was purchased in 1977 from villages by WWF and PPA representatives, and is the first known specimen from Celebes that is not from the northern peninsula, although Dr. G. G. Musser (pers. comm.) saw live specimens several times in the same general area. The skull is

TABLE 2

Cranial and dental measurements of female *Babyrousa*

	Minahasa	Bumbulan		Malenge	Sanana	Buru	
	n = 1	n = 5		n = 2	n = 2	n = 3	
		mean	s.d.			mean	s.d.
Total length	257	262.6	5.22	257.5	246.5	253.0	11.36
Condylobasal	249	250.2	8.47	244.0	238.5	243.7	14.01
Bizygomatic	122	117.0	3.24	113.5	110.0	118.7	9.61
Palate l.	169	160.4	7.57	156.0	155.0	164.0	11.14
Toothrow l.	-	81.0	5.34	69.5	70.0	67.0 (1)	-
Occipital br.	70	52.4	5.18	50.5	54.0	60.7	7.09
Occipital ht.	55	50.8	5.31	47.5	48.5	52.3	3.21
Canine roots	52	-	-	36 (1)	35.0	40.7	4.73
P^3 length	-	11.0	0.71	10.5	10.5	9.0 (2)	-
P^4 l.	-	10.5	0.58 (4)	9.5	9.0	9.3	1.15
M^1 l.	-	13.8	0.84	13.0	12.5	11.5 (2)	-
M^2 l.	17.0	18.0	1.22	16.5	17.0	16.0	1.00
M^3 l.	-	23.8	1.79	21.0	21.0	20.3	0.58
P_3 l.	-	12.4	1.34	12.0	11.0 (1)	10.5	0.50
P_4 l.	-	12.4	1.14	12.0	10.5	11.0	0.00
M_1 l.	-	14.4	0.89	13.25	12.5	12.3	0.58
M_2 l.	-	17.0	0.71	15.75	16.0	15.7	1.04
M_3 l.	-	26.6	1.82	22.0	23.5	22.7	1.53

remarkably small — its total length being 11 mm less than the next smallest male skull — but it is fully adult. Total length is about four standard deviations from the Minahasa sample, three from Bumbulan, eight from Malenge, 2.4 from Taliabu and 2.3 from Buru. Toothrow length is more than two standard deviations from Celebes and 1.5 from Malenge; and canine roots more than two from the Malenge and Minahasa samples, but not quite (1.76) from Bumbulan. Occipital breadth is nearly two standard deviations, usually more, from all other samples.

The canines in the Moa skull are short, and in the upper jaw the alveoli are rotated forward to about the same degree as in some of the Malenge skulls. The frontal furrows are shallow with rounded edges, and the supraorbital foramen is visible from above, as is usual in Celebes and Malenge

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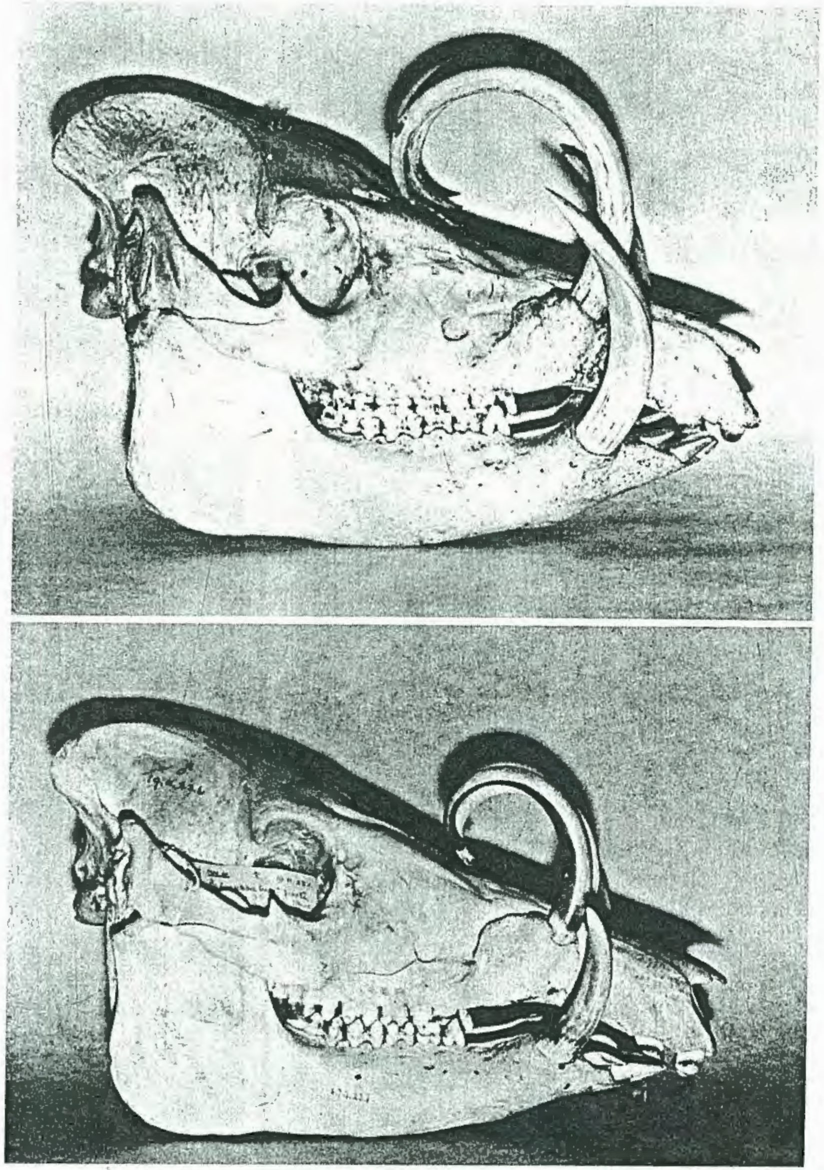

Fig. a (upper). BM (NH) 67.4.12.223, ad. ♂, Buru. Lectotype of *Sus babyrussa* Linnaeus, 1758. Formerly in the Seba collection. Fig. b (lower). BM (NH) 19.11.23.1, ad. ♂, Pulau Taliabu, Sula Islands. Holotype of *Babirousa babyrussa frosti* Thomas, 1920.

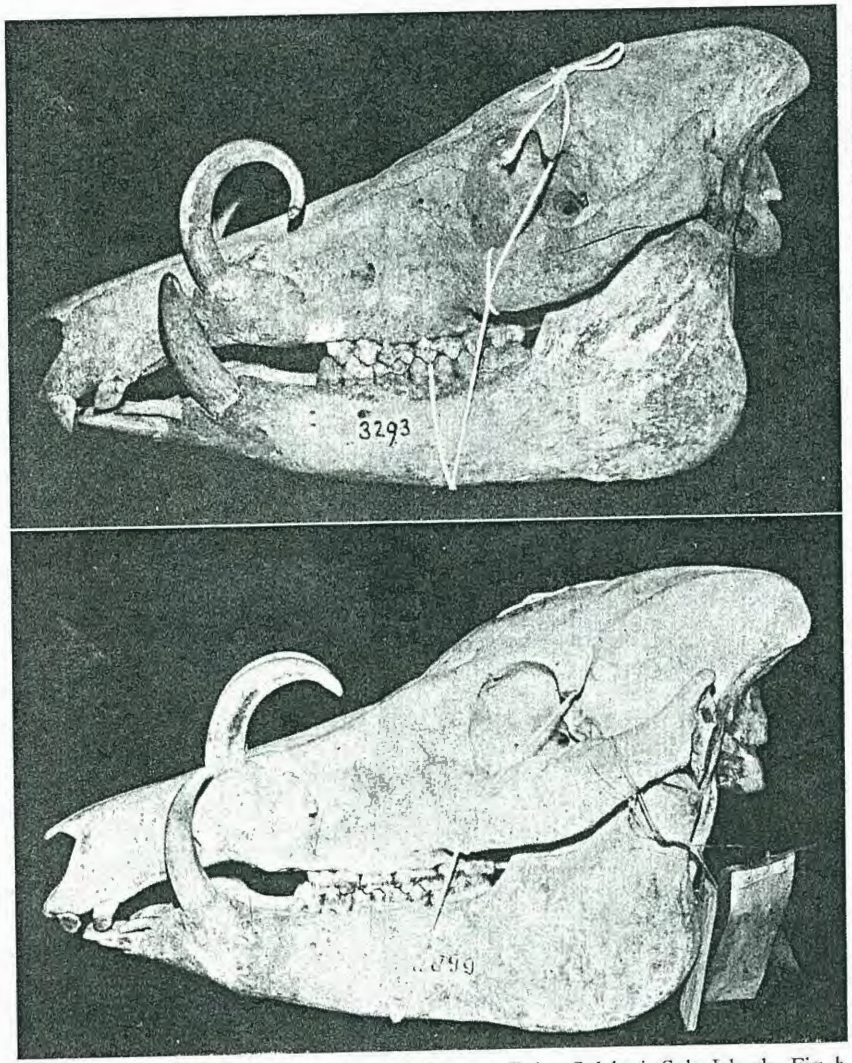

Fig. a. (upper). MZB 3293, young ad. ♂, Sanana, Pulau Sulabesi, Sula Islands. Fig. b (lower). MZB 6899, young ad. ♂, Pulau Malenge, Togian Islands. Holotype of *Babirousa babyrussa togeanensis* Sody, 1949.

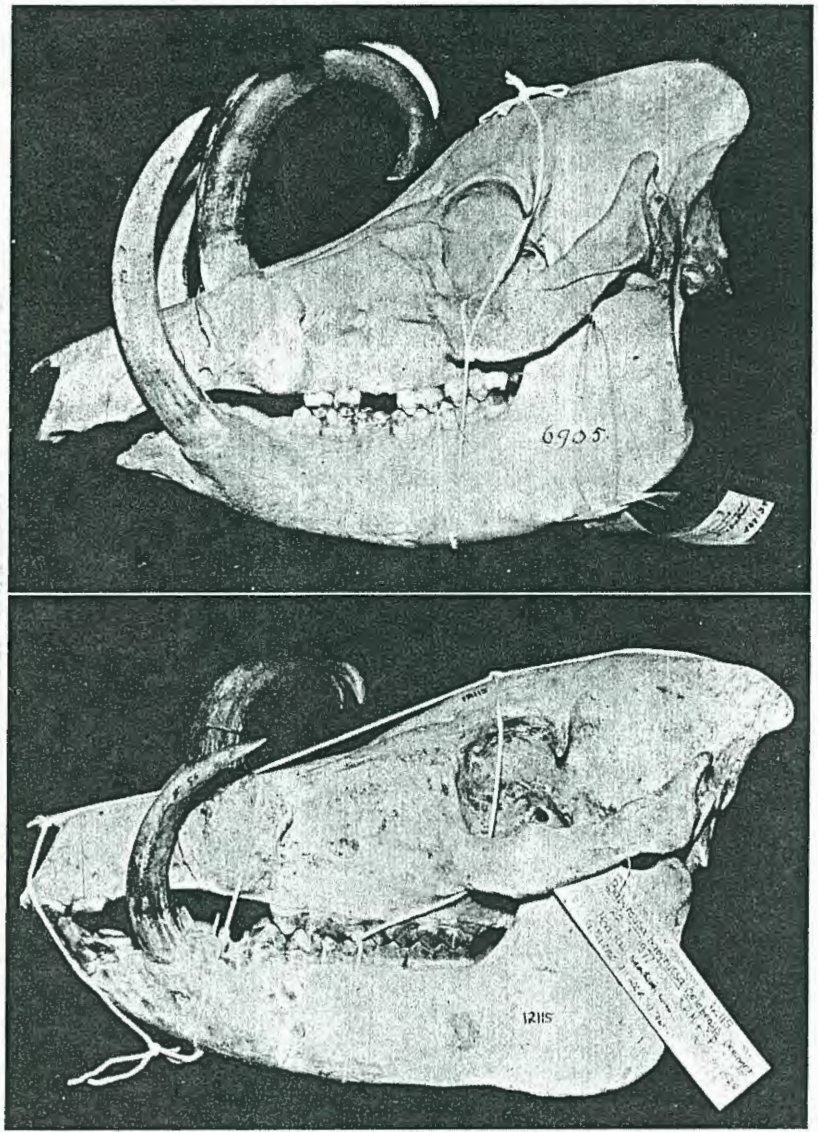

Fig. a (upper). MZB 6905, ad. ♂, Manado, Kab. Minahasa, N. Celebes. Fig. b (lower). MZB 12115, ad. ♂, Moa, Gunung Malema, 1200 m, Kulawi, central Celebes.

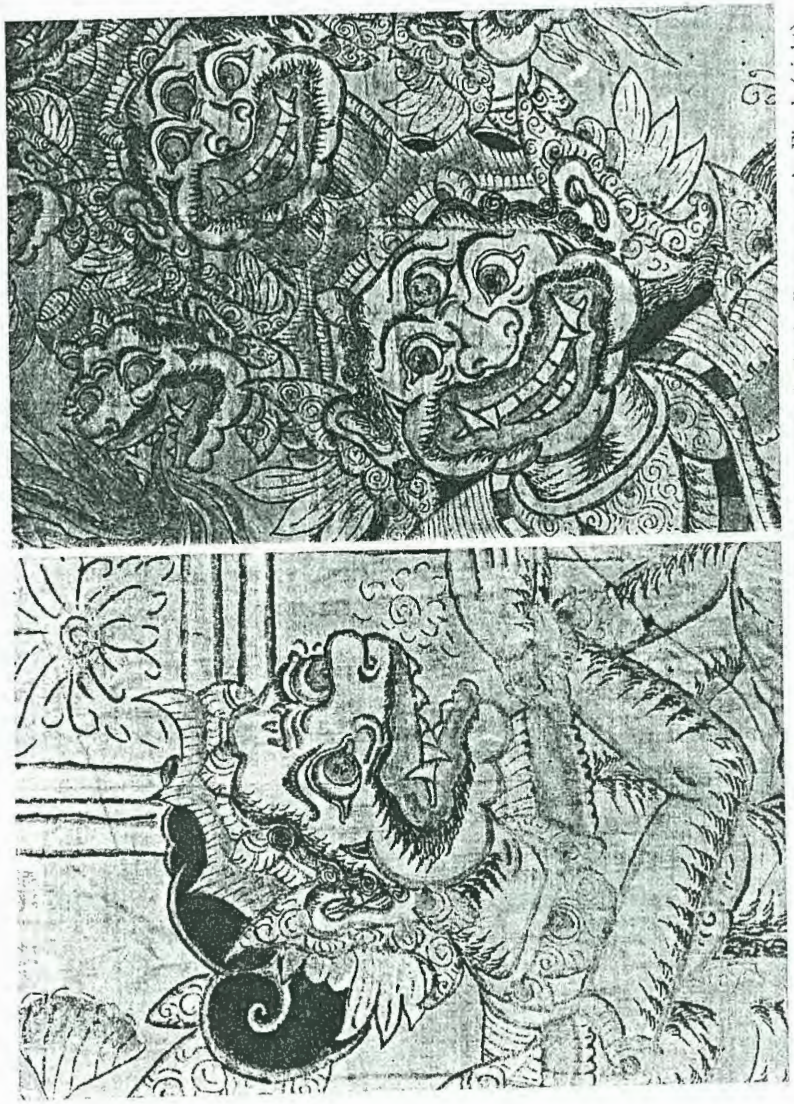

Fig. a (left). Head of a noble Raksasa, member of the kingdom of Lanka in the Ramayana epic. Fig. b (right). Penurtian form of a god; assumed by gods when enraged, this form has many arms and nine Raksasa-type heads, differing only in the presence of a third eye in each. Both from a traditional painting from Karangasem,

skulls; and the upper canines meet in the middle. There is no trace of P^2. From a general survey of its features, therefore, the Moa skull resembles a tiny version of a Malenge skull.

A simple way of comparing samples within a species is the Penrose multivariate statistic. This has the advantage that it can be calculated without the need for a computer, and that unlike the widely used Mahalanobis D^2 the size component of the distance is separated out and does not distort the final result, which should depend on shape alone. On the other hand it does not take allometry into account. It can be used, in any case, as a general guide to overall shape resemblances.

Table 3 shows the results of a Penrose statistic (on males only), calculated using a programme written for a Sharpe desk calculator by Dr R. V. S. Wright, of Sydney University. In Table 3(a) are the distances between the groups: size above the diagonals, shape below. The size statistics merely say what one already knew: Taliabu skulls (and those from Buru to a lesser extent) are very small compared to the rest. In the shape distances, Taliabu and Buru skulls are very close, Bumbulan and Minahasa are fairly close;

TABLE 3

Penrose size and shape statistics for *Babyrousa* skulls

(a) Groups

		Minahasa	Bumbulan	Malenge	Taliabu	Buru	
Minahasa		x	-0.10	0.03	0.69	0.12	SIZE
Bumbulan	SHAPE	0.30	x	0.25	1.32	0.45	
Malenge		0.65	0.81	x	0.44	0.03	
Taliabu		0.34	0.91	0.86	x	-0.23	
Buru		0.41	0.93	0.96	0.19	x	

(b) Single specimens

	SIZE			SHAPE		
	Lembeh	Moa	Sanana	Lembeh	Moa	Sanana
Minahasa	-0.08	1.90	1.19	0.57	1.50	0.96
Bumbulan	0.00	2.89	1.99	0.77	1.18	1.71
Malenge	-0.22	1.44	0.83	0.98	2.56	1.91
Taliabu	-1.28	0.29	0.07	1.19	1.22	0.33
Buru	-0.42	1.06	0.55	0.87	1.15	0.27

and these two pairs are closer to one another than either is to Malenge — a somewhat curious result. Three single specimens can now be brought in and compared to the groups. The Lembeh skull is, predictably, nearest to those from Minahasa in shape, and identical to Bumbulan in size. The Sanana skull is very close in size to Taliabu, and in shape even slightly closer to Buru. The Moa skull, though not far from Taliabu in overall size, is not like any other in shape.

Dentition

Table 4 gives the means and standard deviations for cheekteeth in different samples, both living and fossil. The samples for the living are based on males only; comparison with Table 2 shows that most of the cheekteeth in females are about the same size, only third molars being much smaller.

Applying the coefficient of difference test to the modern samples, the only cases where the values rise above 1.28 are M^3 for the Malenge sample in comparison with both Bumbalan and Minahasa — which was discovered previously — and M_3 for the Malenge/Bumbulan comparison, but only just. Compared to M^1 (Table 4(c)) the Taliabu and Buru samples have small P^3 but unreduced P^4, while M^3 is rather large in the North Celebes samples and very small in Malenge. Tooth sizes do differ between samples, but not at a level that bears on their taxonomic differentiation.

Mention has already been made that Hooijer's (1950) subfossil South Celebes subspecies *bolabatuensis* was distinguished from the living Celebes form but not from the Buru and Sula ones. In Table 4(b), the means and standard deviations, calculated from Hooijer's raw data, are presented. As Hooijer noted, the figures are in most cases very close to those for Buru and Sula, with the noteworthy exception of the first molars, both upper and lower, which are disproportionately large compared especially to the other molars. The means also seem close to the Moa skull, without such marked disproportion. Whether this can be interpreted to mean that the Moa individual represents a living population of *bolabatuensis* must await the discovery of more complete material of the latter.

Of the other fossil samples, Batu Ejaya teeth are mostly smaller than Bola Batu, as are some of those from the upper level (A-B) of Panganreang Tudea, though by a much smaller amount: it may be doubted whether, if larger samples were available, these latter would be any different at all from Bola Batu. On the other hand, the teeth from the lower levels (C-D) of Panganreang Tudea are uniformly larger than Bola Batu, and compare well with those from Minahasa.

Batu Ejaya has a C^{14} date reported as 920 ± 275 B.P. (Mulvaney &

TABLE 4

Dental measurements (n; X; s.d.) of recent and fossil *Babyrousa*
(Anteroposterior diameters only)

(a) Living

	Minahasa			Bumbulan			Malenge			Taliabu			Buru			Lembeh	Moa
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.	mean	s.d.
P^3	6	10.67	1.21	12	11.00	1.18	6	10.67	0.82	10	9.90	0.74	14	9.71	0.70	9.0	10.6
P^4	6	9.75	0.76	12	10.20	0.58	6	10.00	0.63	10	9.50	0.71	15	9.90	0.60	9.0	10.2
M^1	3	13.30	0.58	12	13.25	0.78	6	12.83	0.41	9	12.89	0.60	14	12.32	1.03	11.0	13.4
M^2	9	17.22	0.97	13	17.65	1.07	6	16.33	0.52	10	16.70	0.82	23	16.80	0.67	16.0	17.1
M^3	7	24.36	1.60	13	25.40	1.98	6	20.83	0.75	10	22.10	1.10	15	22.60	1.50	23.0	23.9
P_3	7	11.43	0.53	13	11.90	1.23	6	11.83	0.98	10	10.20	0.79	16	10.60	0.73	11.0	13.5
P_4	7	11.70	0.76	13	11.70	0.83	6	12.00	0.63	10	11.20	0.63	16	11.50	0.52	11.0	12.6
M_1	7	13.71	0.49	13	14.40	0.96	6	12.83	0.75	9	12.78	0.67	15	12.70	0.88	13.0	14.1
M_2	7	16.30	0.49	13	16.90	0.86	6	15.67	0.52	10	26.30	0.67	15	16.60	0.61	16.0	15.5
M_3	7	25.40	1.62	13	27.20	2.31	6	23.50	0.55	10	24.70	0.82	15	24.50	0.99	24.0	23.1

(b) Fossil and subfossil

	Bola Batu			Lompoa		Panganreang Tudea					Batu Ejaya		Beru & Sompoh	
						C - D		A - B						
P^3	22	9.95	0.51			1	10.5	2	9.60					
P^4	27	9.64	0.37			1	10.0	3	9.90	0.35				
M^1	27	13.33	0.52	1	13.4	1	13.6	1	13.4		1	12.8		
M^2	37	16.69	0.72	1	16.4	2	17.6	2	16.5		2	16.25	1	20.2
M^3	43	22.32	1.24			1	23.8	3	21.73	0.96	1	19.8	1	25.4
P_3	9	10.48	0.45											
P_4	12	11.55	0.48			1	11.9	1	10.9					
M_1	9	13.37	0.52					3	13.70	0.72				
M_2	15	16.27	0.81	1	16.8			1	16.8		1	17.8		
M_3	15	23.80	1.11					2	23.20				2	29.35

(c) Ratio of Maxillay Tooth Lengths
to length of M^1

	Minahasa	Bumbulan	Malenge	Taliabu	Buru	Lembeh	Moa	Bolabatu
P^3	.80	.83	.83	.77	.79	.82	.79	.75
P^4	.73	.77	.78	.74	.80	.82	.76	.72
M^2	1.29	1.33	1.27	1.30	1.36	1.46	1.28	1.25
M^3	1.83	1.92	1.62	1.72	1.83	2.09	1.78	1.67

Soejono, 1970), that is to say around A.D. 1030. In that Bola Batu has what are said to be dog remains (Hooijer, 1950), it may also be fairly late; but on the analogy of Timor (Glover, 1970) this could mean as much as 4000 B.P. Mulvaney & Soejono (1970) cast doubt on the reality of the claimed sequence at Panganreang Tudea, at least as far as the artefact associations are concerned, and mention Van Heekeren's opinion that the potsherds from there are intrusive. There are also no domestic or introduced animal remains at Panganreang Tudea, unlike Batu Ejaya. The implied sequence, Panganreang Tudea — Bola Batu — Batu Ejaya, is consistent with the hypothesis of a gradual dental size reduction in this species as in so many others in southeast Asia during the early Holocene (Hooijer, 1950).

The Pleistocene babirusa from the same region (Beru and Sompoh), *Babyrousa babyrussa beruensis* Hooijer, 1948, was noticeably larger in dental dimensions than any modern form. This makes the size-reduction hypothesis all the more plausible.

SUBSPECIES AND SYNONYMS

The following subspecific classification of the species is proposed:

Babyrousa babyrussa babyrussa (Linnaeus, 1758)

Sus babyrussa Linnaeus, 1758. "Borneo"; recte: Buru.
Aper orientalis Brisson, 1762. Name unavailable.
Babyrousa quadricornis Perry, 1811.
Babirussa alfurus Lesson, 1827. Buru.
Babirussa babyrussa frosti Thomas, 1920. Taliabu, Sula Islands.

Material studied from: — Sula Islands: Pulau Sulabesi, ca. 2.03 S, 125.59 E; Pulau Taliabu, 1.50 S, 124.40 E. Buru: S. Yalua, ca. 3.45 S, 126.50 E; Wa Kruma, NW. Buru; Lijotiking; Yuai Hi, NW. Buru; Lake Wakallo; Wai Hi. Localities mentioned in literature: Gunung Kapala Madang, 3.15 S, 126.15 E; Gunung Katina, ca. 3.21 S, 126.25 E; Wai-Hotton; Upper River Bilkofan, ca. 3.22 S, 126.25 E (Deninger, 1909). Upper (River) Wa Ha, ca. 3.22 S, 126.26 E; Kayeli, 3.25 S, 127.07 E; Wa'Kuma, SW. Buru; Wai Hi, NW. Buru (Dammerman, 1929).

Distribution: — Buru; Sula Islands (at least the islands of Taliabu and Sulabesi).

Characters: — Body hair always long and thick; tail tuft well-developed. Skull with frontal furrows mostly deep, sharp-edged. Upper canines of males usually short, slender, with alveolus forwardly rotated, so that lower canine crosses upper in lateral view; generally divergent or parallel to each other, or weekly convergent. Size small, with small teeth. Skulls from the Sula Islands have more convergent upper canines in the male than those from Buru, and more commonly retain P² (pl. 1 fig. a, b; pl. 2 fig. a).

Babyrousa babyrussa togeanensis Sody, 1949

Babirussa babyrussa togeanensis Sody, 1949. Malenge, Togean Islands.

Material studied from: — Pulau Malenge.

Distribution: — Known only from Malenge.

Characters: — Body hair less long and dense than in the previous subspecies, paler on underparts; tail tuft well-developed. Skull with frontal furrows always shallow, with sloping edges. Upper canines of males usually short, slender, somewhat rotated forward, always converging. The largest race, but teeth small, especially the third molars (pl. 2 fig. b).

Babyrousa babyrussa celebensis (Deninger, 1909)

Babirusa Celebensis Deninger, 1909. Pulau Lembeh, N. Celebes.
Babyrousa babyrussa Merkusi De Beaufort, 1964. Nomen nudum. "Les Moluques"; probably northern Celebes.

Material studied from: — Minahasa: Manado, 1.32 N, 124.55 E; Lumpias, 1.35 N, 124.59 E; Saludaa, 0.20 N, 123.27 E; Likupang, 1.40 N, 125.05 E; Kema, 1.23 N, 125.05 E; Pulau Lembeh, 1.25 N, 125.17 E. Bumbulan: Bumbulan, 0.31 N, 122.04 E; Gorontalo, 0.33 N, 123.05 E; Monano, 0.54 N, 122.42 E; Gunung Ile-Ile, 0.55 N, 121.45 E; Sumalata, 0.59 N, 122.31 E; Muton, 0.27 N, 121.13 E.

Distribution: — Northern peninsula of Celebes, at least as far west as Bumbulan, and including the offshore island of Lembeh.

Characters: — Body hair generally short and sparse; tail tuft small and sparse. Skull with frontal furrows mostly shallow, with sloping edges. Upper canines of males generally long and thick, the alveoli vertically implanted, so that upper canine emerges vertically and is not crossed by lower in lateral view; converging in almost all cases. Size fairly large. Skulls from the Bumbulan region are somewhat broader than those from Minahasa and have larger teeth (pl. 3 fig. a).

Babyrousa babyrussa beruensis Hooijer, 1948

Babyrousa babyrussa beruensis Hooijer, 1948. Beru, near Cabenge, S. Celebes; Pleistocene.

Distribution: — Known from Pleistocene deposits at Beru and Sompoh.

Characters: — Teeth as far as known noticeably larger than in any living form.

Incertae sedis:

Babyrousa babyrussa bolabatuensis Hooijer, 1950

Babyrousa babyrussa bolabatuensis Hooijer, 1950. Bola Batu caves near Watampone, early (?) Holocene.

Characters: — Known parts not certainly distinguishable from *B. b. babyrussa*, except perhaps by reduced size of first molars; but presumably distinct.

Skull from Gunung Malema, Moa, near Kulawi, central Celebes: — Size very small, with especially narrow occipital crest; otherwise mainly a diminutive version of *B. b. togeanensis*, though dental proportions like *bolabatuensis*. It is conceivable that this skull could represent a living population of *bolabatuensis* (pl. 3 fig. b).

DISCUSSION

The impoverished and unbalanced nature of the mammalian fauna of Buru led Dammerman (1929) to suggest that all mammals except the bats had probably been introduced by human agency, including the babirusa. The anatomical characters which he attributes to the Buru babirusa in distinguishing it from the Celebes form are, however, insubstantial, so that his claims that it has characters of domestication cannot be maintained. His statement that there is no Buruese name for the species would also seem to be in error, as Stresemann (1925) gives the names 'donit' (Maserete) and 'gonit' (Lisela), although in the Lumara dialect it is called simply 'bodi' (= white). Interestingly, Deninger (1909) says that the general name is the Malay/Indonesian 'babi putih' (= white pig), while in Masarete it is known in the local dialect as 'bodi'. Whether this can be taken to mean that in the interval between the visits of Deninger and Stresemann a simple descriptive term in Masarete had given place to a genuine name introduced from elsewhere can perhaps be solved by field work in that region among the older residents.

But Dammerman's hypothesis that the babirusa, along with other mammals, is a human introduction in Buru, seems plausible enough. At any rate, its near identity with the Sula Islands form indicates that it has spread very recently from the one to the other. It is even possible that it is not indigenous to the Sula Islands either, for it appears not to exist on Peleng, an island well-known from the collections of the Archbold Expeditions, and an essential stepping-stone from Celebes to the Sula group had babirusa extended their range without human help. The lack of material from east-central Celebes makes it impossible to confirm or refute this hypothesis at the moment, but it is worth noting that the subspecies *togeanensis* is intermediate between *celebensis* and *babyrussa*, while the Moa skull is a further step towards the Buru/Sula form.

Nor are linguistic studies much help here. The languages of the Sula group are entirely unknown (W. A. Foley, pers. comm.), while the names given by Mohr (1958) for various Celebes languages are all different from the enigmatic Buruese 'donit'/'gonit'. Adriani's dictionary of Bare'e (a language centred on the Poso district) gives the same words as Mohr, variants of the stem word 'rari', also 'boibi' for the young.

Certainly the babirusa attracted widespread attention among both Indonesians and Europeans. Even if, with Mohr (1958: 67-68), we reject the notion that it was known to the Romans in the 1st century A.D., its first European description, by Piso in 1658 (Mohr, 1958: 52) is still remarkably early. It was kept and even bred by petty rulers in Celebes as a potential diplomatic gift (Dammerman, 1929: 154).

It is even plausible that it was incorporated into Balinese art. The 'Raksasa' — a demon, half-human, half-animal — is represented with a curly tusk emerging from either cheek (pl. 4 fig. a, b), a notion which seems rather difficult to account for unless the artists had a tradition of an animal which does actually have this disposition (Anthony Forge, pers. comm.). Bali was included in the Bugis (S. Celebes) trade network in the 18th (?) century (Tobing, 1977: 44) and there was a Buginese colony there in 1817 (Boon, 1977: 25); one of the tangible results of such trade will have been the introduction of Bali cattle into South Celebes, where they remain to this day the only domestic breed.

CONCLUSIONS

The original distribution of the babirusa is difficult to reconstruct, but it seems likely that it was originally confined to Celebes (including the Togean Is.). It is less ecologically resilient than the anoa, for example, and has vanished from the extensively cultivated southern peninsula of Celebes; on the other hand, its range has evidently been extended by human agency to Buru; its apparent absence from Peleng suggests that it may be intrusive also in the Sula group. As a skull from central Celebes approaches the Buru and Sula subspecies, the origin of the latter may perhaps be sought here. Further specimens are needed to solve this problem, but as the babirusa is a rare animal, they should not be obtained not by traditional "collecting" but by purchasing, or soliciting as gifts, trophy skulls kept in local villages, which is how the Moa skull was obtained.

Whether the hypothesis of its introduction into Buru and Sula is valid or not, the babirusa has quite evidently long been regarded as an extraordinary beast, adopted into Balinese art as the acme of animality, and made known in Europe at an unexpectedly early date.

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REFERENCES

BEAUFORT, F. DE, 1964. Catalogue des types d'ongulés du Muséum national d'Histoire naturelle, Paris et recherches sur ces types. — Bull. Mus. natn. Hist. nat., (2) 35: 551-579.

BOON, J. A., 1977. The anthropological romance of Bali, 1597-1972. Cambridge University Press.

DAMMERMAN, K. W., 1929. Fauna Buruana. Mammalia. — Treubia, 7: 149-163.

DAVIS, D. D., 1940. Notes on the anatomy of the Babirussa. — Field Mus. Nat. Hist. Chicago, (Zool. Ser.) 22: 363-411.

DENINGER, K., 1909. Über Babirusa. — Ber. Naturf. Ges. Freiburg, 17: 179-200.

GLOVER, I., 1970. Excavations in Timor. Ph. D. Thesis, Australian National University.

GUILLEMARD, F. H., 1886. The cruise of the Marchesa. Vol. 2. John Murray, London.

HOOIJER, D. A., 1948. Pleistocene vertebrates from Celebes. III. Anoa depressicornis (Smith) subsp., and Babyrousa babyrussa beruensis nov. subsp. — Proc. Kon. Ned. Akad. Wetensch. Amsterdam, 51: 3-11.

——, 1950. Man and other mammals from Toalian sites in south-eastern Celebes. — Verh. Kon. Ned. Akad. Wetensch. Amsterdam, (Afd. Natuurk., Tweede Sectie) 46 (2): 7-158.

LAURIE, E. M. O. & J. E. HILL, 1954. List of land mammals of New Guinea, Celebes and adjacent islands 1758-1952. Trustees of the British Museum, London.

LESSON, R.-P., 1827. Manuel de mammalogie, ou histoire naturelle des mammifères. Roret, Librairie, Paris.

MOHR, E., 1958. Zur Kenntnis des Hirschebers, Babirussa babyrussa Linné 1758. — Zool. Garten, (NF) 25: 50-69.

MULVANEY, D. J. & R. P. SOEJONO, 1970. Archeology in Sulawesi, Indonesia. — Antiquity, 45: 26-33.

SABAN, R., 1968. Musculature de la tête. In: P.-P. GRASSÉ, ed. Traité de zoologie. Tome 16 (2): 229-471.

SODY, H. J. V., 1949. Notes on some Primates, Carnivora and the Babirusa from the Indo-Malayan and Indo-Australian regions. — Treubia, 20: 121-190.

STRESEMANN, E., 1925. Begegnungen mit dem Hirscheber (Babirussa babyrussa) auf Buru. — Pallasia, 3: 49-56.

THENIUS, E., 1970. Zur Evolution und Verbreitungsgeschichte der Suidae (Artiodactyla, Mammalia). — Z. Säugetierk., 35: 321-342.

THOMAS, O., 1920. Some notes on Babirussa. — Ann. Mag. Nat. Hist., 9 (5): 185-188.

TOBING, P. O. L., 1977. Hukum pelayaran dan perdagangan Amanna Gappa. Ujung Pandan.

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THE KARYOTYPE OF BABYROUSA BABYRUSSA (SUIDÆ, MAMMALIA)

by

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(Received for publication on 25th November 1980)

INTRODUCTION

The family Suidæ includes five living genera : *Babyrousa*, *Sus*, *Phacochoerus*, *Potamochoerus* and *Hylochoerus*. All these genera except for *Sus* comprise only one living species.

Chromosome studies have been performed on the domestic pig and the wild boar (both *Sus scrofa*), the wart hog *Phacochoerus æthiopicus*, the African bush pig *Potamochoerus porcus*, and the giant forest hog *Hylochoerus meinertzhageni*, revealing diploid chromosome numbers of 38, 36-37-38, 34, 34 and 32, respectively. G-banding patterns in the domestic pig have been described by Berger (1972), Hageltorn and Gustavsson (1973), Hansen (1977), Hansen and Melander (1974), Miyake and Ishikawa (1978), Pace *et al.* (1975) and Watt (1977), Q-banding patterns by Gustavsson *et al.* (1972) and Hansen (1972 and 1977). G-banding patterns in the wild boar and the wart hog have been studied by Bosma (1976) and Tikhonov and Troshina (1975), and by Bosma (1978), respectively. These authors demonstrated that the differences in karyotype between the domestic pig, the wild boar and the wart hog, as well as the variation in chromosome number in the wild boar, are due to Robertsonian type rearrangements.

In this paper we present the karyotype, including G- and Q-banding patterns, of *Babyrousa babyrussa*. The babirusa is a pig with a weight as much as 90 kg, relatively long legs and a rough skin that usually hangs in loose folds and is almost devoid of hair. Prominent in the male are the large upper canines, which do not grow from the side of the jaw, but instead are directed upward, and curve

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backward and downward, often touching the forehead (Fig. 1). The species is indigenous to parts of Indonesia : North Celebes, the Togian Islands, the Sula Islands, and the island of Buru (Fig. 2).

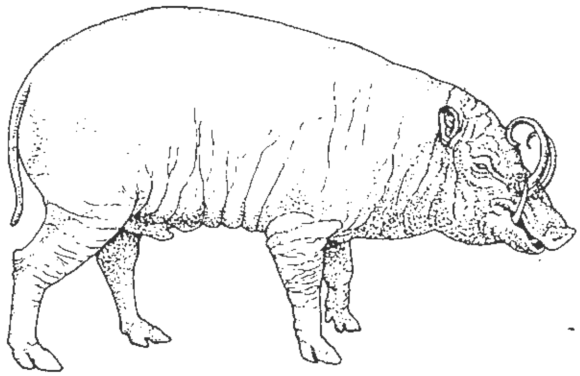

Fig. 1 – Male babirusa.

MATERIALS AND METHODS

We examined metaphase chromosomes from a male and a female babirusa, kept in Antwerp Zoo (Belgium).

The chromosome preparations were made from lymphocytes cultured by placing 1 ml of whole blood in a medium composed of 5 ml TC-Medium 199, 0.5 ml TC-Fetal Calf Serum, TC-Penicillin-Streptomycin (all Difco) and 0.3 ml of phytohemagglutinin (PHA). The PHA had been prepared according to the method described by Van Hemel (1971). The blood was incubated for 3 days at 37° C. Colchicine (Sandoz) (final concentration 0.5 μg/ml medium) was added 3 hours before harvesting. The preparative procedure included treatment of the cell suspensions with 0.075 *M* potassium chloride for 5 minutes at 37° C, fixation in a mixture of acetic acid and methanol (1 : 3, v/v), and air-drying. Conventional staining was carried out with aceto-orcein.

G-bands were produced according to the method of Hageltorn and Gustavsson (1973), which is a modification of that introduced by Seabright (1971). The method requires preparations to be incubated in a trypsin solution and stained with a buffered Giemsa solution.

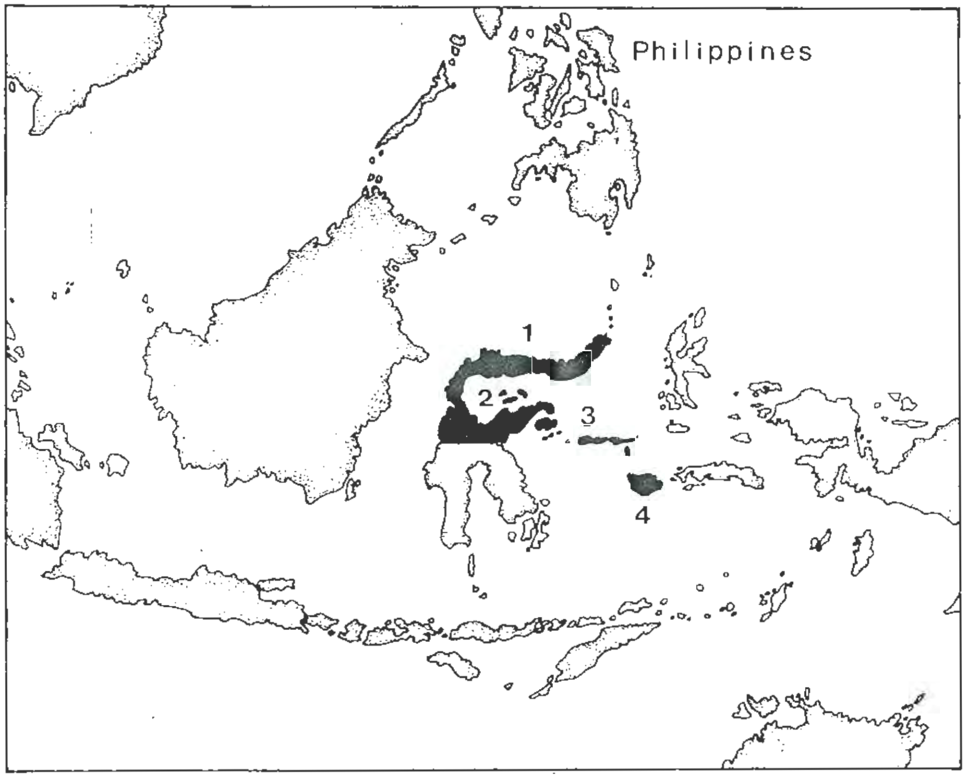

Fig. 2 – Sketch-map showing the geographical distribution of the babirusa (1 – Celebes, 2 – Togian Islands, 3 – Sula Islands, 4 – Buru).

To obtain Q-bands, preparations were stained for 20 minutes with an aqeous solution of quinacrine mustard (Sigma) (0.5 mg/ml distilled water), rinsed briefly in running tap water, and rinsed and mounted in McIlvaine's buffer at pH 5.5 (method personally communicated by Schnedl). Only the female specimen was examined with this technique.

The chromosomes were arranged and numbered according to the position of the centromere, and in order of decreasing length. The chromosomes of the domestic pig were numbered following the Reading Conference recommendations (Ford *et al.*, 1980), those of the wild boar and the wart hog following Bosma (1976 and 1978). The nomenclature used to describe the chromosome morphology in relation to the centromeric position is also that recommended at the Reading Conference (Ford *et al.*, 1980).

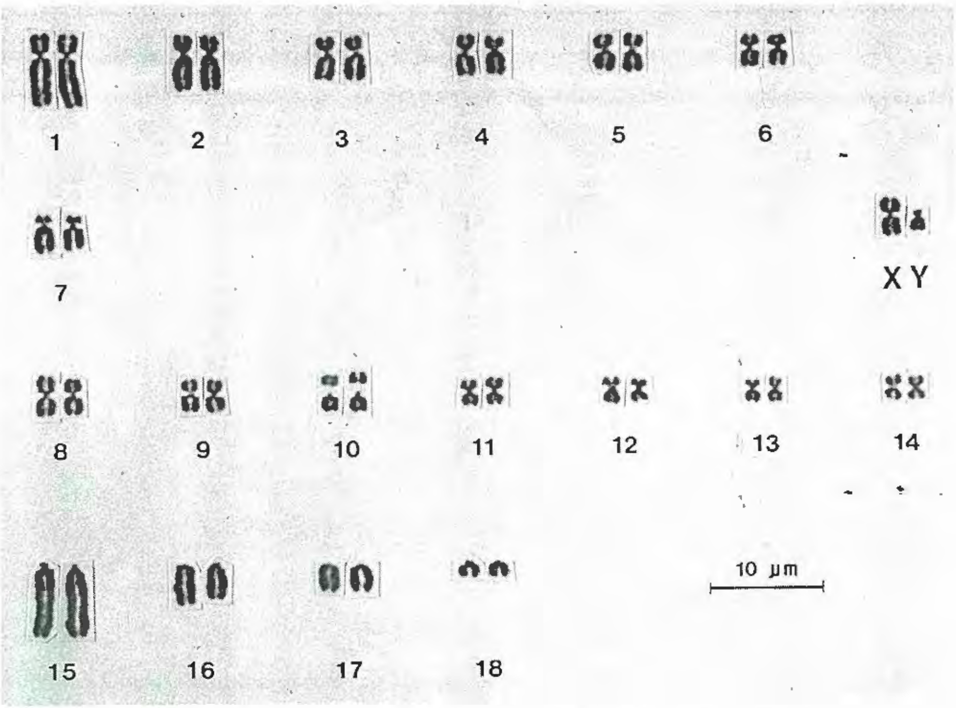

Fig. 3 – Karyogram showing orcein-stained chromosomes of a male babirusa.

RESULTS

The two investigated specimens of babirusa have a diploid chromosome number of 38. Karyograms of orcein-stained, G-banded and Q-banded chromosomes are presented in Figures 3-5.

Figure 3 shows that the autosomes include six pairs of submetacentrics (Nos. 1-6), one pair of subtelocentrics (No. 7), seven pairs of metacentrics (Nos. 8-14), and four pairs of telocentrics (Nos. 15-18). The X and Y chromosomes are metacentric and subtelocentric, respectively. Chromosomes No. 10 have a distinct secondary constriction.

DISCUSSION AND CONCLUSION

Comparison of the G- and Q-banding patterns in the babirusa with those in the domestic pig reveals that eleven pairs of autosomes, and the X chromosomes look almost identical. In addition, there is a close similarity in the distribution of these bands between : the long arm of babirusa chromosome 1 and chromosome 13 of the domestic pig, the short arm of babirusa chromosome 1 and chromosome 16 of the domestic pig, the long arm of babirusa chromosome 2 and chromosome 15 of the domestic pig, and the short arm of babirusa chromosome 2 and chromosome 17 of the domestic pig. Apparently, these chromosomes have been involved in Robertsonian translocations.

A complete list of corresponding chromosomes and parts of chromosomes of the babirusa, the domestic pig, the wild boar and the wart hog is given in Table I. In this table the wild boar occurs twice, due to the differences in karyotype between the European and Asian populations of this species (Tikhonov and Troshina, 1975; Bosma, 1976).

Table I shows that five pairs of babirusa autosomes (Nos. 6, 12, 14, 15 and 17) have no direct equivalents in domestic or wild *Sus scrofa*, or in *Phacochoerus*

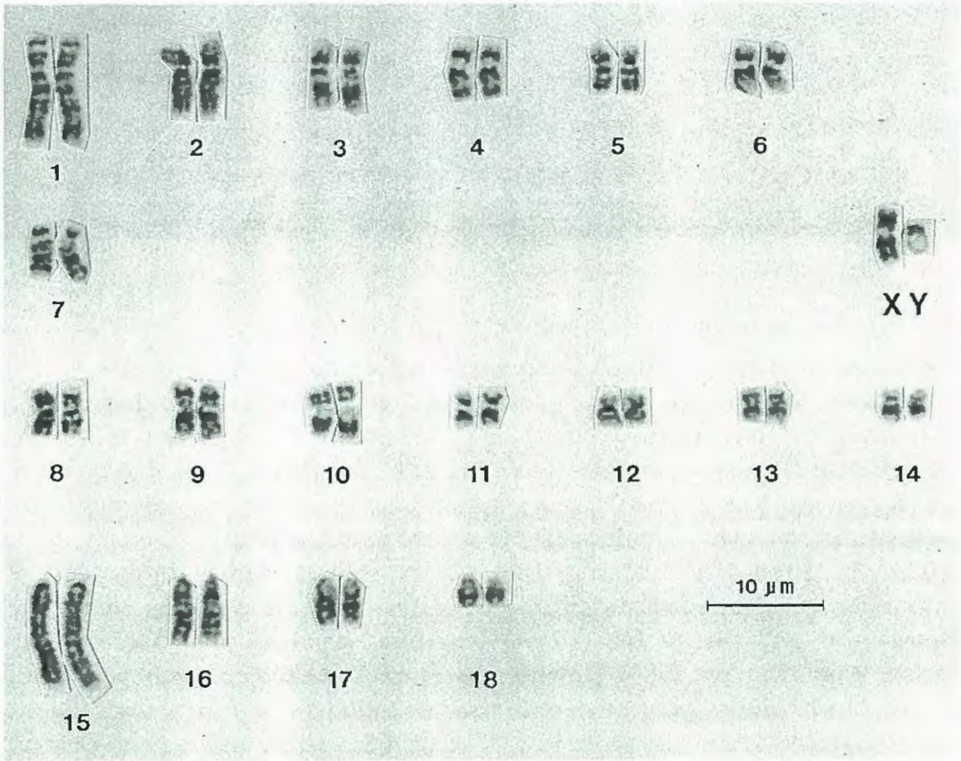

Fig. 4 – Karyogram showing G-banded chromosomes of a male babirusa.

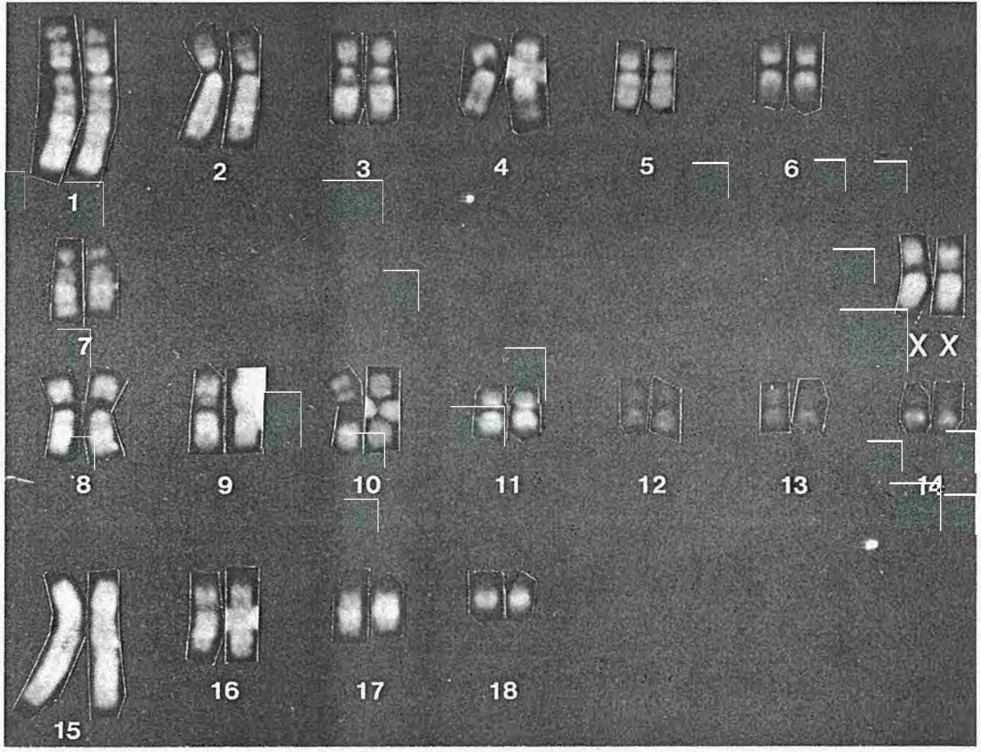

Fig. 5 – Karyogram showing Q-banded chromosomes of a female babirusa.

æthiopicus. G-banded chromosomes belonging to these autosomal pairs, and taken from six different cells (A-F) are presented separately in Figure 6.

Chromosome 15 of the babirusa has two prominent dark bands, separated by a distinct light band, at approximately one third from its distal end. A similar arrangement of bands is found in the centre of the long arms of chromosome 1 of the domestic pig and the wild boar, and chromosome 2 of the wart hog. This suggests that these chromosomes may be related to one another.

The Y chromosome of the babirusa is subtelocentric, unlike the Y chromosomes of the domestic pig, the wild boar and the wart hog, which are metacentric, and that of the African bush pig, which is submetacentric (cf. Melander and Hansen, 1980). However, using the G-banding procedure, the long and short arms of the babirusa Y chromosome stain pale and dark, respectively, which is a pattern seen also in domestic and wild *Sus scrofa* and in *Phacochoerus æthiopicus.*

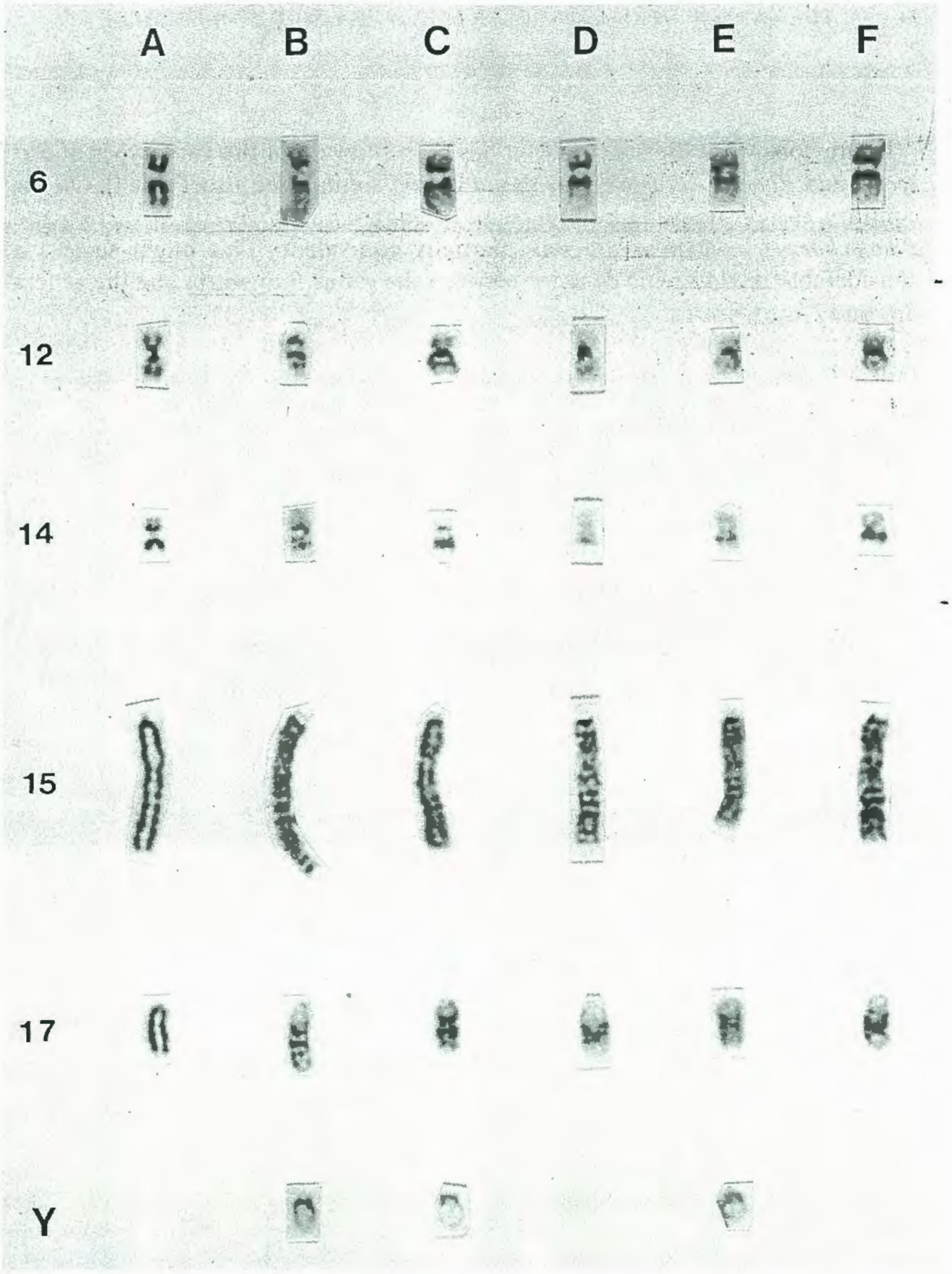

Fig. 6 – G-banded chromosomes of pairs Nos. 6, 12, 14, 15 and 17, and G-banded Y chromosomes from different cells (A-F). Cells B, C and E are from a male, cells A, D and F from a female babirusa.

In previous work (Bosma, 1978) it has been shown that the karyotypes of *Sus scrofa* and *Phacochoerus æthiopicus* are largely similar (see also Table I). On the contrary, the chromosome complements of *Babyrousa babyrussa*, *Sus scrofa* and *Phacochoerus æthiopicus* are only partially equivalent. This might suggest a considerable phylogenetic distance between the genus *Babyrousa* and the genera *Sus* and *Phacochoerus*.

Table I Corresponding chromosomes and parts of chromosomes of the babirusa *(Babyrousa babyrussa)*, the domestic pig *(Sus scrofa)*, the wild boar *(Sus scrofa)* and the wart hog *(Phacochoerus æthiopicus)*.
Data on the wild boar are confined to specimens with 36 chromosomes. Type I applies to animals from the Netherlands (Bosma, 1976) and Lithuania (Tikhonov and Troshina, 1975). Type II applies to animals from certain parts of Asia (Tikhonov and Troshina, 1975). The «extra» submetacentric chromosome found in type II of wild *Sus scrofa* is given the number 1b.

TABLE I

Babyrousa babyrussa	domestic *Sus scrofa*	wild *Sus scrofa* *(Type I)*	wild *Sus scrofa* *(Type II)*	*Phacochoerus æthiopicus*
–	1	1	1	2
3	2	2	2	4
–	3	3	3	5
4	4	4	4	6
5	5	5	5	7
–	6	6	6	8
7	7	7	7	9
8	8	8	8	10
9	9	9	9	11
10	10	10	10	12
11	11	11	11	13
13	12	12	12	14
1 (long arm)	13	13	13	1 (long arm)
16	14	14	14	15
2 (long arm)	15	1a (long arm)	15	3 (long arm)
1 (short arm)	16	16	1b (long arm)	1 (short arm)
2 (short arm)	17	1a (short arm)	1b (short arm)	3 (short arm)
18	18	18	18	16
6	–	–	–	–
12	–	–	–	–
14	–	–	–	–
15	–	–	–	–
17	–	–	–	–
X	X	X	X	X
–	Y	Y	Y	Y
Y	–	–	–	–

Babyrousa babyrussa is generally considered to be in an isolated position with regard to the other living suids, because it has a number of specialized morphological and anatomical characters, and has a very limited geographical distribution. Although the fossil record is limited to Pleistocene material from Celebes and Buru, the hypothesis has been put forward that Babyrousa has developed since Oligocene times along a separate evolutionary line (Stehlin, 1899 and 1900; Thenius, 1970). This concept is fully supported by our data.

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SUMMARY

The karyotype of the babirusa *Babyrousa babyrussa*, including G- and Q-banding patterns, is presented, and compared with those of the domestic pig, the wild boar (both *Sus scrofa*) and the wart hog *Phacochoerus æthiopicus*. It is shown that these karyotypes are only partially equivalent. This might suggest a considerable phylogenetic distance between the genus *Babyrousa* and the genera *Sus* and *Phacochoerus*.

SAMENVATTING

In dit artikel worden de resultaten van cytogenetisch onderzoek aan het hertezwijn *Babyrousa babyrussa* beschreven. Gebruik is gemaakt van een conventionele kleuringstechniek, en van een G- en een Q-banderingsmethode. Het diploïde chromosoomaantal blijkt 38 te bedragen. Zes paar autosomen zijn submetacentrisch, één paar subtelocentrisch, zeven paar metacentrisch, en vier paar telocentrisch. Het X chromosoom is metacentrisch en het Y chromosoom subtelocentrisch.

De G- en Q-bandpatronen van het hertezwijn worden vergeleken met die van het gedomesticeerde varken, het wilde zwijn (beide *Sus scrofa*) en het

wrattenzwijn *Phacochoerus æthiopicus.* Het blijkt dat het karyotype van het hertezwijn meer verschilt van dat van de overige genoemde varkensachtigen, dan de karyotypes van het gedomesticeerde varken, het wilde zwijn en het wrattenzwijn onderling van elkaar verschillen. Hieruit zou geconcludeerd kunnen worden dat de fylogenetische verwantschap tussen het geslacht *Babyrousa* enerzijds, en de geslachten *Sus* en *Phacochoerus* anderzijds, geringer is dan de fylogenetische verwantschap tussen *Sus* en *Phacochoerus* onderling.

REFERENCES

BERGER, R. (1972): Etude du caryotype du porc avec une nouvelle technique, Expl. Cell Res. 75, 298-300.

BOSMA, A.A. (1976): Chromosomal polymorphism and G-banding patterns in the wild boar (Sus scrofa L.) from the Netherlands, Genetica 46, 391-399.

BOSMA, A.A. (1978): The chromosomal G-banding pattern in the wart hog, Phacochoerus æthiopicus (Suidæ, Mammalia) and its implications for the systematic position of the species, Genetica 49, 15-19.

FORD, C.E., POLLOCK, D.L. and GUSTAVSSON, I. (1980): Proceedings of the first international conference for the standardisation of banded karyotypes of domestic animals, University of Reading, Reading, England, 2nd-6th August 1976. Hereditas 92, 145-162.

GUSTAVSSON, I., HAGELTORN, M., JOHANSSON, C. and ZECH, L. (1972): Identification of the pig chromosomes by the quinacrine mustard fluorescence technique, Expl. Cell Res. 70, 471-474.

HAGELTORN, M. and GUSTAVSSON, I. (1973): Giemsa staining patterns for identification of the pig mitotic chromosomes, Hereditas 75, 144-146.

HANSEN, K.M. (1972): The karyotype of the pig (Sus scrofa domestica), identified by quinacrine mustard staining and fluorescence microscopy, Cytogenetics 11, 286-294.

HANSEN, K.M. (1977): Identification of the chromosomes of the domestic pig (Sus scrofa domestica). An identification key and a landmark system, Ann. Génét. Sél. Anim. 9, 517-526.

HANSEN-MELANDER, E. and MELANDER, Y. (1974): The karyotype of the pig, Hereditas 77, 149-158.

HEMEL, J.O. van (1971): Studies on human chromosome satellite association. Thesis, University Utrecht.

MELANDER, Y. and HANSEN-MELANDER, E. (1980): Chromosome studies in African wild pigs (Suidæ, Mammalia), Hereditas 92, 283-289.

MIYAKE, Y.I. and ISHIKAWA, T. (1978): The possibility of chromosome classification as identified by trypsin-Giemsa banding patterns, Zuchthyg. (Berl.) 13, 33-37.

PACE, J.W., SRIVASTAVA, P.K. and LASLEY, J.F. (1975): G-band patterns of swine chromosomes, J. Hered. 66, 344-348.

SEABRIGHT, M. (1971): A rapid banding technique for human chromosomes. Lancet, 1971, 971-972.

STEHLIN, H.G. (1899) : Ueber die Geschichte des Suiden-Gebisses. I. Teil, Abh. Schweiz. paläont. Ges. 26, 1-336.

STEHLIN, H.G. (1900) : Ueber die Geschichte des Suiden-Gebisses. II. Teil, Abh. Schweiz. paläont. Ges. 27, 337-527.

THENIUS, E. (1970): Zur Evolution und Verbreitungsgeschichte der Suidæ (Artiodactyla, Mammalia), Z.f. Säugetierkunde 35, 321-342.

TIKHONOV, V.N. and TROSHINA, A.I. (1975) : Chromosome translocations in the karyotypes of wild boars Sus scrofa L. of the European and the Asian areas of USSR, Theor. Appl. Genetics 45, 304-308.

WATT, J.L. (1977) : G-and C-banded karyotypes obtained after mitotic stimulation of bone marrow cells of the domestic pig (Sus scrofa), Genetica 47, 149-153.

NOTE:

In the interest of brevity, the following paper by K. Leus does not include the lengthy Appendix entitled "Annotated list of trees and palms of Sulawesi forest with special reference to the fruiting trees". For a complete copy of this paper including the Appendix, please contact Dr. Leus at her current address noted at the bottom of page 121.

The habitat and diet of the Sulawesi babirusa (*Babyrousa babyrussa celebensis*)

by

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1. Introduction

Information on the diet of babirusa in the wild is scarce and anecdotal in nature. Valentijn wrote in 1726:

> "De spijs van dit dier is niet dezelve, als die van de andere Bosch verkens, die canari (een soort van Indiaanse amandelen) eeten; maar alleen, of gras, of wel bladeren van de waringin en andere wilde bomen. Men heeft van't zelve ook niet te vrezen, dat het, gelijk andere verkens, de thuinen verwoesten, de heiningen doorwroeten, en't gezaaide, of geplantende verderven zal, alzoo't zich meest met boombladeren behelpt, en geen quaad ter wereld doet."
> (The food of these animals is not the same as that of the other forest pigs, which eat canari, a sort of Indian almond; but they only eat grass or leaves of the waringi and other wild trees. One should also not fear that they, like other pigs, will ravage gardens, uproot fences and destroy that which is planted, whilst they only feed themselves with tree leaves and don't do any harm at all.)

He also added that animals kept in captivity in local gardens were generally fed on rice, batata (= sweet potato), leaves, canari, padi and fish, including the intestines. It later appeared that Valentijn's descriptions were not based on his personal

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observations but were a summary of an unpublished and now missing manuscript by Rumphius (1628-1702) entitled "Amboinsch Dierboek" (Polman, 1983).

During the following centuries, basically the same information, with a few additions here and there, has been repeated over and over again in encyclopaedic works by Halle (1757), Batsch (1788), Desmarest (1820), Goldsmith (1822), Schreber and Wagner (1835), Tjeenk Willink (1905), Haltenorth (1963), Morris (1965) and others. Some of these additions, such as the inclusion of water plants, fruit and invertebrates in the diet, appear to be extrapolated from first hand reports by Lesson and Garnot (1825), Wallace (1870), Sarasin and Sarasin (1905) and Deninger (1910). Other additions, however, appear to be based on reports of food items fed to babirusa in captivity such as fish (Valentijn, 1726) and roots (Geoffroy Saint-Hillaire and Cuvier, 1842).

More recently, new information was obtained by Selmier (1978, 1983) who visited Sulawesi and the Togian islands in search of babirusa. Residents of Lore Kalamanta (Sulawesi) reported to her that babirusa and *Sus celebensis* ate the same greens and acorns, but that they had different preferences. Both in Lore Kalamanta and on the Togian islands *Elatostema* (Urti.*) was reported as a favourite babirusa food. The babirusa on Pangempan, one of the Togian islands, were observed to eat fruits (e.g. mango and coconuts) and various fungi. They would also visit the small village gardens in search of maize, millet, sweet potatoes, sugar cane and small herb-trees among others.

Since Selmier (1983), the only first hand information to be published on the diet of babirusa in the wild was a note by Whitten et al. (1987a) stating that the major fruit eaten by the babirusa in the west of the Dumoga-Bone National Park was said to be the pangi fruit *Pangium edule* Reinw. (Flac.).

The above information represents all that is available on the composition of the diet of babirusa in the wild. However, from the results of the work by Leus (1994), Conklin et al. (1994) and Leus and Morgan (1996) the following assumption can be made: Babirusa are likely to be non-ruminant foregut fermenters specialised in the fermentation of the more easily digestible cell wall fractions and cell solubles. These substances are most abundant in fruits and dicotyledonous plant parts rather than some monocotyledonous plants such as grasses. We can therefore assume that fruit

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* All genus and species names of the plants of Sulawesi mentioned in this paper will be followed by a 4-letter abbreviation of the family they belong to. More information about these plants can be found in Appendix 1 which is organised in alphabetical order according to the plant families.

and leaves will form important ingredients in the babirusa diet, supplemented with smaller quantities of herbs, grass, roots and animal matter.

This paper will investigate some of the trees and plants available to the babirusa of Sulawesi (*B. b. celebensis*) with special reference being paid to the fruiting trees and the type of fruits they produce. The nature of the plants available to the babirusa will of course depend on the habitats and forest types frequented by them. For this reason, a short description of the forest types of Sulawesi will be presented first together with notes on the likelihood of babirusa being found in these forests.

2. The forest types of Sulawesi

2.1. Lowland evergreen rain forest:

Lowland evergreen rain forest occurs in ever-wet, well drained inland locations up to about 1200m altitude. It is characterised by a very dense, lofty green vegetation with very high trees (up to 45m) (van Steenis, 1950). The Sulawesi lowland rain forest is markedly different from that of Borneo and other islands on the Sunda Shelf. Lowland rain forests on the Sunda Shelf are often dominated by trees of the Dipterocarpaceae family (Lack and Kevan, 1984; Whitmore, 1984a; Whitmore and Sidiyasa, 1986). East of the Wallace Line this family is not so common, and there is a much more diverse floral composition (Whitten et al., 1987a). More information with respect to the plants of lowland evergreen rain forest in Sulawesi may be found in the papers by Hickson (1889), Steup (1931, 1932, 1933, 1935, 1939a, b), Verhoef (1938), Bloembergen (1940), Meijer (1974), Lack and Kevan (1984, 1987), Soewanda et al. (1984), Whitmore (1984b), Whitmore and Sidiyasa (1986), Whitten et al. (1987a) and Whitmore et al. (1989). There have been several reports of the presence of babirusa in the lowland evergreen rainforest (Macdonald, pers. comm.; Selmier, 1978, 1983; Patry and Capiod, 1989; Patry, 1990; Patry et al., 1995) although recent reports suggest that the babirusa may have now largely moved from the lower lying coastal areas to the more inland, higher and less accessible regions (Macdonald, 1993).

2.2. Fresh water swamp forest:

Fresh water swamp forest occurs on land subjected to occasional flooding with mineral rich fresh water (≥ pH6) (Whitmore, 1984a). The floral composition of fresh water swamps can vary with the local soil and drainage conditions but travelling from the edge of the open water to the drier areas one typically finds grassy vegetation followed by palms and pandans followed by a forest very much like dryland lowland forest with shrubs and trees (Whitmore, 1984a; Whitten et al., 1987a). Further information about fresh water swamp forest plants in Sulawesi may be found in the papers by Bloembergen (1940), Whitten et al. (1987a) and Whitmore et al. (1989). In

1825 inhabitants of Buru reported to Lesson and Garnot that the babirusa in the interior of the island "se plait au milieu des joncs et des plantes aquatiques" (amuse themselves in the middle of rushes (or rattans) and water plants). Since then there have been several reports, mostly in encyclopaedic works, stating that babirusa tend to live in swampy and marshy areas and along rivers (Lesson and Garnot, 1826; Jennison, 1927; Temminck, 1835; Boitard, 1851; Haltenorth, 1963).

2.3. Peat swamp forest:

The only major peat swamp in Sulawesi is the Rawa Aopa swamp, 100km west of Kendari (Whitten et al., 1987a; Zwahlen, 1992). The vegetation in the swamp itself includes water plants in various forms and shapes. Swamp forest can be found towards the edges of the swamp where, although the soil is still flooded for a large part of the year, the water is less deep (Zwahlen, 1992). Information additional to that found in the papers by Whitten et al. (1987a) and Zwahlen (1992) may be obtained in Whitmore et al. (1989). The presence of the babirusa in the Rawa Aopa peat swamp forest has recently been verified (Zwahlen, 1992).

2.4. Mangrove forest:

The typical tropical coastline mangrove forests have become rare in Sulawesi. Mangrove trees are tolerant of saline conditions but can also grow in fresh water and can therefore sometimes be found more inland along rivers. A typical mangrove forest contains practically no understorey vegetation and contains trees provided with specially developed root systems to cope with the regular flooding of saline sea water (Whitten et al., 1987a). Babirusa have been reported to swim and dive in the sea (Valentijn, 1726; Selmier, 1983) but it is more likely that they, like rats, macaques, other pigs and lizards, visit the edges of the mangrove forest to forage for fruits and various animal products (Whitten et al., 1987a). Further information about the mangrove forests of Sulawesi may be found in the paper by Whitmore et al. (1989)

2.5. Riverine forest:

The riverine forest is usually not very distinct from the surrounding lowland forest and not many of the trees recorded in riverine forest are restricted to it (Whitten et al., 1987a). Additional information on riverine forest plants in Sulawesi may be found in the papers by Steup (1933) and Whitmore and Sadiayasa (1986). Video recordings have been made of babirusa visiting salt licks alongside a river in the north of Sulawesi (Patry and Capiod, 1989; Patry, 1990; Patry et al., 1995)

2.6. Forest on ultrabasic soils:

When considering the exceptional soil conditions formed over ultrabasic rocks (low silica and a high iron and magnesium content), it can be expected that most of the plants found in these areas are more or less restricted to them (Whitmore, 1984a; Whitten et al., 1987a). It is generally agreed that low densities of vertebrate animals are found living in regions with ultrabasic soils in Sulawesi. Whether this is related to low productivity, high levels of defence compounds in the leaves, or imbalanced nutrient and mineral concentrations in the plant parts is not yet known (Whitten et al., 1987a). There is no information on the presence of babirusa in the forests on ultrabasic soils of Sulawesi.

2.7. Forest on limestone:

A limestone landscape is very rugged with steep slopes, vertical walls, crevices, overhanging precipices and only very few gentle sloping surfaces (Whitmore, 1984a; Whitten et al., 1987a). Soils on limestone are particularly rich in calcium and magnesium (Whitten et al., 1987a). The plant species found in limestone areas must be tolerant of high levels of calcium and have been selected by their ability to cope with both this and the physical nature of the landscape. The result is a very specific community of trees which are found mainly in the gentler sloping areas. The steep cliffs and rock faces are colonised with a distinctive, more herbaceous flora (Whitmore, 1984a; Whitten et al., 1987a). More information for Sulawesi may be found in Bloembergen (1940). The babirusa are hunted by the people of Toradja land, a limestone rich area in Central Sulawesi (Bloembergen, 1940). Babirusa are therefore certainly present in this area but their presence on particular sites is likely to be related to the accessibility of the terrain (steepness of slopes etc.).

2.8. Monsoon forest:

Tropical rain forests are replaced by monsoon or seasonal forests in those regions where water is periodically seriously limiting to the vegetation (Whitmore, 1984b). Most monsoon forests are largely deciduous. Little monsoon forest remains in Sulawesi because of its susceptibility to fire. Repeated burning of a monsoon forest eventually turns the vegetation into grassland (Whitten et al., 1987a). Additional information on the monsoon forest plants of Sulawesi may be found in the papers by Sarasin and Sarasin (1905), Steup (1929, 1939a, b), Bloembergen (1940) and Whitten et al. (1987a). It is conceivable that the babirusa will venture into the monsoon forests, if only during the wetter months. Since recent investigations have indicated that babirusa tend to disappear from a region as soon as the forest disappears (Whitten et al, 1987), it is unlikely that they will frequent the dry grassy savannahs.

2.9. Montane forest:

Above the lowland forest the lower montane forest is found with shorter, less massive trees, epiphytes and orchids. At higher altitudes the trees become even shorter with small, relatively thick leaves. This is called the upper montane forest.

At even higher altitude, the trees are shorter still, with smaller leaves, epiphytic lichens but practically no orchids. This is the subalpine forest. In valleys and waterlogged places in this zone there are virtually no trees but a covering of shrubs, herbs and tough grasses (Robbins and Wyatt-Smith, 1964; Whitmore, 1984a; Whitten et al., 1987a). The altitudes at which the different montane forest types occur are mainly governed by temperature and cloud level. A useful altitude scheme suggested by Whitten et al. (1987a) for Sulawesi is:

lowland and hill forest	0 - 1500m
lower montane forest	1500 - 2400m
upper montane forest	2400 - 3000m
subalpine forest	>3000m

Additional information on montane forest composition on Sulawesi is contained within the papers by Steup (1931, 1939a, b), Bloembergen (1940), Wemmer and Watling (1986) and Whitten et al. (1987a). According to Deninger (1910) the babirusa on Buru were mainly confined to the mountainous regions and are present at altitudes of at least 1000m. On Sulawesi, Bloembergen (1940) visited the forests in the region of the Lindu-lake at 1000m altitude and reported that the local people hunt wild pigs, babirusa, deer and anoa in this region. Babirusa are definitely present in the Central Sulawesi Lore Lindu reserve and the latter now even has a picture of the babirusa as its logo. More recent studies indicated that only 10% of the land in the reserve lies below 1000m whereas about 70% lies between 1000-1500m (Wemmer and Watling, 1986). The babirusa are therefore likely to be present at these heights. No further information on the altitudinal zonation of the babirusa is available in the literature. It can be expected that they will frequent the lower montane forest if only because of the important food source represented by the fruits of the Fagaceae trees which often dominate this forest type (Wemmer and Watling, 1986; Whitten et al., 1987a). From the lower montane forest upwards, their occurrence remains an open question.

For more detailed information on the nature and composition of the vegetation in these regions the reader is referred to the references linked with each forest type and to Appendix 1. The latter gives a detailed annotated list of most of the tree species reported from the Sulawesi forests, together with information on the appearance, habitat, fruits and local use of some of the trees. A lot of the more recently gathered information on the composition of the Sulawesi forests is to be found in unpublished reports, mostly to Institutions of the Indonesian Government, and are not readily accessible. Nevertheless, some of the information from these reports has been assembled and discussed by Whitmore (1984b), Whitten et al. (1987a), Whitmore et al.

(1989) and Zwahlen (1992) and it is these references that have been consulted for the purposes of this paper.

3. The diet of wild babirusa

The diet of babirusa in the wild can be summarised as consisting of herbs, leaves, roots, fruits, cultivated plants from gardens and animal material(Valentijn, 1726; Lesson and Garnot, 1825; Wallace, 1870; Sarasin and Sarasin, 1905; Deninger, 1910; Selmier, 1978, 1983).

3.1. Herbs:

In the herbal category, grass, water plants and *Elatostema* (Urti.) were mentioned. Relatively few herbs tend to be found on the floor of mature rain forests. However, herbs do appear in forest gaps during the younger phases of forest development (Whitmore, 1984a; Whitten et al., 1987a). Grasses are especially dominant in those regions which are frequently subjected to fires (Whitten et al., 1987a). The grassy patches in the enclosures of captive babirusa tend not to show signs of extensive grazing, but animals have been observed eating from the grass in their enclosure and will eat fresh grass that is offered to them (Leus, 1994; Leus and Morgan, 1996; Leus and Vercammen, 1996). When given the opportunity, captive babirusa include grass and herbs in their diet, but not to such an extent that they can be described as grazers. Babirusa also appear less able to digest cellulose and lignin of grass origin than the domestic pigs (Leus, 1994). Grass is therefore unlikely to be one of the main constituents of the babirusa diet.

The herb *Elatostema* is a non-stinging member of the nettle family (Urticaceae) and generally grows on rocks, in streams or under shrubs (Ridley, 1924). It is said to be one of the favourite foods of the babirusa in Lore Kalamanta (Sulawesi) as well as on the Togian islands (Selmier, 1978). In most of the European zoos that were visited for this study, the common nettle *Urtica dioica* L. (Urti.) was found to grow untouched inside the enclosures of the animals. Only once was a young female in Antwerp Zoo observed to eat some leaves of this plant. Since the common nettle has the stinging hairs typical of the nettle family, this character may be an important deterrent against the selection of this plant as a source of food in Europe.

A well known water plant which is consumed as a vegetable by man *Ipomoea aquatica* Forsk. (Conv.), is better known in Indonesia as "kangkung" (Ooststroom, 1948; Hanerwald, 1991). There are four reasons why kangkung is likely to be consumed by the wild babirusa:

1) it can form very dense masses in marshy areas such as at the delta of the Djenemaedja river, south of Palopo in Sulawesi (Ooststroom, 1948)
2) babirusa are known to frequent swampy habitats
3) it is a regular food of wild pigs in Malaya (Ooststroom, 1948) and
4) it forms an important part of the diet of the babirusa in Jakarta and Surabaya Zoo, Indonesia, where is readily eaten by those animals.

Considering the affinity of babirusa for mud and water, as well as their ability to swim (Valentijn, 1726; Selmier, 1983; Melish, 1994), it seems likely that they will frequent marshes and swamps of various types and will consume water plants growing in these areas.

3.2. Leaves:

According to Valentijn (1726) and Desmarest (1820) wild babirusa eat leaves of trees such as those of the "waringi" and banana trees (*Musa*). The consumption of a variety of tree leaves by the wild babirusa would not be surprising considering the enthusiasm with which babirusa in captivity eat the leaves, buds and twigs of trees and branches (Leus 1994; Leus and Vercammen 1996). Female babirusa in Surabaya Zoo would go to great lengths to reach the leaves of the few trees in their enclosure. They would raise themselves off the ground and balance on their hind legs without support while stretching out to reach the leaves with their mouths (Macdonald et al., 1993). Valentijn (1726) reported that wild babirusa would stand on their hind legs with their front legs leaning against a tree, even though the function given to this behaviour by him was "the sampling of smells of approaching enemies". Captive babirusa have often been observed standing on their hind legs while leaning against uprights of their enclosures in order to reach the leaves of suspended branches, or food items offered over the fence by the public. This seems a more likely explanation for the behaviour of the animals in the wild than that mentioned by Valentijn (1726).

3.3. Roots:

The babirusa's inability to root in compact ground has been confirmed several times in recent years: both in captivity and in the wild babirusa were only seen to turn over soil in areas where it comprised loose sand or wet mud (Selmier, 1978; Leus et al., 1992; Patry et al., 1995; Leus et al., 1996; Leus and Vercammen, 1996). These observations make subterranean plant parts less likely food items for the wild babirusa, perhaps with the exception of roots from plants growing in loose, muddy or sandy soils. Hunters and guides of Lore Kalamanta even claim to be able to distinguish between furrows made by *Sus celebensis* and those produced by babirusa. Babirusa are said to make shallow, straight-lined furrows whereas *Sus celebensis* dig deeper and thrust their snouts in lines that radiate from one spot (Selmier, 1978).

3.4. Fruits:

Wild babirusa are said to eat fruit, but the only fruits specified were "canari, a sort of Indian almond" (Valentijn, 1726), acorns (Selmier, 1978), "pangi" (*Pangium edule* Reinw. (Flac.)) (Whitten et al., 1987a), mangos (Selmier, 1983) and coconuts (Sarasin and Sarasin, 1905; Selmier, 1978, 1983).

3.4.1. Canari

The name "canari" most likely refers to the seeds of the fruits produced by trees of the genus *Canarium* (Burs.); possibly *Canarium vulgare* Leenh. (Burs.) or *Canarium indicum* L. (Burs.), the almond-like seeds of which are edible to man. There are approximately 11 species of *Canarium* (Burs.) on Sulawesi (see Appendix 1). The plum-shaped fruits are reasonably large (often about 3 by 2 cm) and usually have a fleshy pericarp which encloses a hard woody shell in which the seed is found (Leenhouts, 1956). Dried canari fruits offered to babirusa in Jakarta zoo could only be cracked open by the adult-sized animals. The younger animals would rush towards the adults as soon as they noticed a nut had been cracked and would try to obtain some of the pieces. Although the almond like seed was eaten first, the hard shell was also easily crushed and eaten (Leus and Macdonald, unpubl. obs.). *Canarium* (Burs.) trees can become locally abundant (Leenhouts, 1956) and are therefore a potentially important food source for the babirusa, especially since the seeds are very oily (Leenhouts, 1956) and therefore energy rich.

3.4.2. Acorns and chestnuts

Oaks (*Lithocarpus* (Faga.)) and chestnuts (*Castanopsis* (Faga.)) are important components of especially the lower montane forest of Sulawesi, where they can come to dominate the forest (Steup, 1931; Bloembergen, 1940; Wemmer and Watling, 1986; Whitten et al., 1987a). For example, the dominant forest type in the Lore Lindu reserve is the lower montane forest (between 1000 and 2650m) with especially *Castanopsis* (Faga.) and *Lithocarpus* (Faga.) as the dominant tree species (Wemmer and Watling, 1986). Because of the high nutritional contents of the starch and/or oil-rich fruits and because of their long or frequent fruiting seasons, the Fagaceae often represent an important part of the diet of many vertebrates living in Fagaceae containing forests around the world. For example, they are thought to be of great importance to the Sundaic bearded pigs (*Sus barbatus barbatus* and *Sus barbatus oi*) (Caldecott, 1991a, b). Acorns are also one of the favourite food items of the European wild boar (*Sus scrofa*) (Briedermann, 1990). During good fruiting years, between the months of October and February, acorns and beechnuts can come to represent around 80% of the food components in the diet of this species. Considering the dominance of Fagaceae trees in the Lore Lindu reserve, it is very likely that oaks and chestnuts will also be part of the staple diet of the babirusa in the reserve. Babirusa in captivity are often offered small quantities of acorns (*Quercus* (Faga.)) and chestnuts (sweet chestnut *Castanea sativa* Miller (Faga.)) which are readily eaten (Leus, 1994).

3.4.3. Pangi

The major fruit eaten by babirusa in the west of the Dumoga-Bone National Park is said to be the large pangi fruit, *Pangium edule* Reinw. (Flac.) (Whitten et al., 1987a). It grows in a wide variety of habitats mainly below 300m but sometimes reaching up to 1000m (Sleumer, 1954; Appendix 1). It is not known whether the babirusa eat just the soft and mushy pericarp, or the entire fruit including the seeds with their arils. The seeds contain high concentrations of the potentially toxic substance gynocardin, a cyanogenic glucoside. Many fruits employ chemical defence compounds in order to avoid predation of seeds (Whitten et al., 1987a). Some animals demonstrate an ability to avoid toxic foods behaviourally. Also, whether or not a potentially toxic compound will have an adverse effect on a certain animal depends on a wide range of factors. These include: the amount of the toxin ingested; whether or not there was previous experience with the toxin; the energy content of the food item; the nature and amount of the other nutritional components of the food item and the abilities and efficiency of the animal's detoxification system (Freeland and Janzen, 1974; Klaassen et al., 1986). It is therefore not possible to reject a certain fruit as a potential food item for the babirusa based solely on the presence of a potentially hazardous substance. For example, the babirusa in Antwerp Zoo eat the horse-chestnuts (*Aesculus hippocastanum* L. Hippocastanaceae) that fall into their enclosure from the tree alongside the fence. The horse-chestnut contains a saponin glucoside called aesculin. Ingestion of large amounts of the fruits has been known to cause illness in cattle, horses, pigs and man (Cooper and Johnson, 1984). So far, no negative effects following ingestion of the horse-chestnuts were observed in the Antwerp babirusa.

3.4.4. Mango

The mango tree (*Mangifera indica* L. (Anac.) was native to South Asia but is now extensively cultivated in the tropical regions of Asia, Africa and America (Hill, 1952). Although it is mostly found in cultivation or as a village tree, it can become naturalised in lowland forests (Ding Hou, 1978). Young mangos are astringent, acidic and rich in vitamin C. As the fruit grows, starch is accumulated in both peel and pulp. During the ripening process, this starch is converted into sucrose so that ripe mangos taste sweet (Nagy and Shaw, 1980). Mangos, together with fruits produced by trees of the same genus, or indeed the same family (Anacardiaceae), are well known to provide a source of food for many animals such as birds, squirrels, monkeys, pigs and elephants (Ding Hou, 1954; Appendix 1). It is highly likely that babirusa will eat the fruits produced by the wild Anacardiaceae trees. They may also visit village borders and plantations to feed on the fruits of the cultivated trees.

3.4.5. Coconut

The babirusa are not able to break open intact coconuts and will only feed on coconut pieces or germinating nuts. They are therefore not regarded as pests, and their presence in the plantations is reported to be tolerated by the (Muslim) coconut farmers (Selmier, 1978, 1983). Because of the continuous flowering and fruiting of the cocos palm (Hill, 1952) and the high oil content (and therefore energy value) of the nut endosperm, the coconut is a potentially important item in the diet of the wild babirusa. It may also form an important "backup food" during times when wild forest fruits and greens are scarce. Inhabitants of the Togian islands believe that babirusa prefer to eat wild forest foods and will only come to the coconut groves when the wild food is in limited supply (Selmier, 1978).

3.4.6. Other fruits

The literature does not provide any further information on specific fruits eaten by the babirusa. From Appendix 1 it becomes clear that there is still an enormous array of other fruits being produced in the Sulawesi forest, all of which could potentially be consumed by the babirusa. However, each fruit is not eaten by the same range of animals. Whether or not a certain fruit is consumed by a certain animal will depend on its nutritional composition, accessibility and morphological characteristics among other factors. The three specified factors will be discussed briefly below.

3.4.6.1. Nutritional composition

Fruits tend to be divisible into two groups, "cheap" fruits and "expensive" fruits, according to the seed dispersal strategy used by the plant (Howe and Smallwood, 1982). Most plants employ the first strategy which is to produce large numbers of "cheap" fruits which will attract a wide variety of animals many of which are seed predators. These "cheap" fruits generally contain a lot of carbohydrates (typically sugar) but often contain less than 0.5% protein in their wet weight (Thomas, 1984). Figs (*Ficus* (Mora.)) are often considered as examples of cheap fruits (Whitten et al., 1987a). They are said to be abundant, rich in sugar, containing no secondary compounds in their fruits and they are fed upon by practically every fruit-consuming vertebrate in the tropical forest (Janzen, 1979). Recent studies have however indicated that the nutritional composition of figs is not as uniform as was once thought. For example, figs are not necessarily sugary, a number of them having quite a low sugar and metabolisable energy content and a relatively high fibre content (Conklin and Wrangham, 1994). Only a limited number of plants employ the second seed dispersal strategy which is to produce a limited number of "expensive" fruits which are searched for by obligate frugivore seed dispersers. These expensive fruits generally have a high lipid content and offer up to 6%-7% protein in their wet weight (Thomas, 1984). Examples of expensive fruits include nutmegs (Myristiceae) and laurels

(Lauraceae) (Whitten et al., 1987a). One Sulawesi tree which produces particularly protein rich fruits is the introduced pioneer tree *Piper aduncum* L. (Pipe.) which produces fruit with up to 10% protein (Whitten et al., 1987a).

Obligate frugivores need to find fruits that will provide them with an adequate diet balanced in protein, lipids and carbohydrates and they therefore need to specialise in selecting the so-called expensive fruits (Thomas, 1984; Whitten et al., 1987a). As was discussed above, babirusa are known to ingest plant material other than fruits. They also include invertebrates in their diet (Deninger, 1910; Selmier, 1983) and captive babirusa have proved to be efficient hunters of small mammals and birds (Leus et al., 1992). Because of this ability to supplement their diet with other plant material as well as animal products, it is likely that babirusa will exploit both "cheap" and "expensive" fruits and will not to be limited to the latter.

3.4.6.2. Accessibility

An animal can only feed on a particular fruit if the latter is accessible to it both in time and space. For example, one of the most important food items for the Sundaic bearded pigs (*Sus barbatus barbatus* of Borneo and *Sus barbatus oi* of Malaya and Sumatra) are the oil rich seeds of the Dipterocarpaceae (Caldecott, 1991a, b). The dipterocarps strongly influence food availability because they dominate the lowland rain forest of islands on the Sunda shelf and they all tend to fruit together at long but irregular intervals of five to seven years (Whitten et al., 1987a; Caldecott, 1991b). The Sundaic bearded pigs have adapted to this scarce and unpredictable food supply in a number of ways among which the ability to travel (large body, long legs, swimming ability), flexible foraging behaviour (variable group size and the use of predictable food sources through migrations) and a vigorous response to food supply opportunities (potentially high growth rates, early maturation, relatively large litter size and short gestation length) (Caldecott, 1991a). None of the dipterocarp trees contributing to the diet of the bearded pigs (Caldecott, 1991b) are present on Sulawesi. In their stead are seven species all of which produce rather small, long winged nuts adapted for wind dispersal (Appendix 1) (Symington, 1943-1974; Ashton, 1984; Whitmore and Sidiyasa, 1986; Whitmore et al., 1989). The seeds of these Dipterocarp species are therefore unlikely to be a staple food for the babirusa.

The place of the dipterocarps in Sulawesi is taken by trees that do not appear to fruit gregariously (Whitten et al., 1987a). We can therefore expect fruit supply to be less scarce and more continuous. The smaller litter size and longer gestation length of the babirusa seem to fit within this schema. It is not clear when and how often babirusa in the wild tend to give birth and it is therefore not known whether this is related to food supply. Recent studies suggest that babirusa live in groups of up to eight individuals, usually composed of a few adult females with their offspring, while the large adult males appear to be more solitary (Patry et al., 1995). However, there is no information on the stability and movements of these groups and the relation of these factors to food supply. There are no reports of babirusa mass migrations such as those known for the bearded pigs. Should fruit shortages occur, then migration is not the only possible solution to this problem. Another strategy which is typical for animals with a fixed home range, comprises a change in diet composition whereby fruits are replaced by other food items such as animal matter (Whitten et al., 1987a). The omnivorous nature of the babirusa suggests the latter strategy as the more likely solution to a limited fruit supply. Other "backup foods" for the babirusa could include cultivated fruit and vegetables collected from local village gardens and plantations.

3.4.6.3. Morphological characteristics

Although some fruits, such as the rather fleshy fruits of the Moraceae (figs) and Rubiaceae, are consumed by most fruit eating vertebrates (Janzen, 1979; Gautier-Hion et al., 1985), studies investigating the dispersal of seeds by tropical forest animals have indicated that certain categories of frugivores tend to select fruits with specific morphological characteristics (Ridley, 1930; van der Pijl, 1957, 1969; Gautier-Hion et al., 1985; Dubost, 1984). None of these studies, however, included pigs and a syndrome of "pig-fruits" is as yet undescribed. "Bird and Monkey fruits" (=brightly coloured, often sweet tasting fruits with succulent flesh containing arillate seeds e.g. Apocynaceae, Anacardiaceae, Lauraceae, Lecythidaceae, Meliaceae, Myristicaceae and Sapotaceae (Appendix 1)) are known to be eaten by ground dwelling animals such as pigs after they have been partially eaten and discarded by the birds and monkeys (Ridley, 1930; Ng, 1972; Whitmore, 1973; Gautier-Hion et al., 1985; Corner, 1988; Kochummen, 1989; Durrell, 1993; Appendix 1). Those parts of the fruits available to the terrestrial animals are usually the skins and seeds with some remaining pieces of flesh (Ng, 1972; Whitmore, 1973; Corner, 1988; Kochummen, 1989). Recent video recordings of babirusa in Northern Sulawesi showed babirusa and Sulawesi macaques in close proximity to one another (Patry and Capiod, 1989; Patry, 1990; Florence 1995; Patry, pers. comm.). Since fruits are an important component in the diet of the Sulawesi macaques, the possibility exists that the babirusa will feed on fruit remains discarded by these foraging primates. Fruit species eaten by the macaques include figs (*Ficus* (Mora.)), *Dracontomelum* (Anac.), *Syzygium* (Myrt.), *Spondias pinnata* (L. f.) Kurz (Anac.) and *Pangium edule* (Flac.) (Whitten et al., 1987a; Watanabe & Brotoisworo, 1982). Other arboreal fruit eaters making fruits and seeds available to terrestrial mammals are squirrels (Sciuridae), fruit bats (Pteropodidae) and civets (Viverridae). For example, bearded pigs in Sarawak, Borneo, have been observed feeding on the remains of *Dracontomelum* (Anac.) fruits that were dropped by squirrels after they had eaten part of the pulp (Ding Hou, 1978).

Fruits falling off the trees without the interference of arboreal animals tend to be either young, unripe aborted fruits or very ripe fruits. Many of the ripe fruits that fall to the ground have already lost, or will quickly loose, their bright colours, turn brown and start to rot (Gautier-Hion et al., 1985). Fallen fruits nevertheless form an important part of the diet of many terrestrial animals.

4. Concluding summary

A study of the available literature suggested that babirusa may be present in most of the forest types of Sulawesi. Based on the results of previous studies it was hypothesised that the main items in the diet of wild babirusa are likely to be fruits and leaves supplemented with smaller amounts of herbs, grass, roots and animal matter. A large number of specific trees and plants available to the babirusa of Sulawesi were investigated. Special reference was paid to the fruiting trees, the type of fruits they produce, and the suitability of these fruits as food for the babirusa. The hypotheses formulated in this paper now need to be tested in the field. A detailed study of the diet of the babirusa in the wild is urgently required, not in the least in order to improve the diet fed to the captive babirusa which form part of the conservation breeding program. The babirusa in northern Sulawesi could be observed fairly easily as they came to drink at a salt lick, but they were never observed to eat in that area (Patry and Capiod, 1989; Patry, 1990; Patry, pers. comm.; Florence, 1995). Both the vigilant nature of the babirusa (they will run into cover at the least sound (Patry, pers. comm.)) and the dense vegetation in the jungle will make it extremely difficult to follow the animals closely enough to allow detailed observations of what exactly they are eating. Analyses of faecal material could be complicated by the fact that the habitat of the babirusa is shared with that of the other wild pig species on Sulawesi, *Sus celebensis*. Nevertheless, faeces of even relatively closely related species can often be distinguished by smell, differences in diets, the presence of protozoa, differences in body size of the producer etc. The detailed list (Appendix 1) of the species of trees of Sulawesi, the habitat in which they occur and the type of fruit they produce will form an important basis for this type of study.

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References

Airy Shaw, HK. 1948. Thymelaeaceae-Gonystyloideae. Flora Malesiana I **4**, 349-365.

Airy Shaw, H.K. 1982. The Euphorbiaceae of Central Malesia (Celebes, Moluccas, Lesser Sunda Islands). Kew Bulletin **37**, 1-40.

Ashton, P.S. 1978. Flora Malesiana Precursores: Dipterocarpaceae. The garden's Bulletin, Singapore, **31**, 5-48.

Ashton, P. 1984. Dipterocarpaceae. Flora Malesiana **I 9**, 237-552.

Backer, C.A. 1948a. Amaranthaceae. Flora Malesiana I **4**, 69-98.

Backer, C.A. 1948b. Crassulaceae. Flora Malesiana I **4**, 197-202.

Backer, C.A. and Bakhuizen van den Brink, R.C. 1965. Flora of Java. Vol. II. NV. P. Noordhoff: Groningen, The Netherlands. 641 pp.

Balgooy, M.M.J. van and Tantra, I.G.N. 1986. The vegetation in two areas in Sulawesi. Bull. Balai Pen. Hutan. 1-61.

Batsch, A.J. 1788. Versuch einer Anleitung zur kenntnis und Geschichte der Thiere und Mineralien. I. Algemeine Geschichte der Natur, besondre der Säugethiere, Vogel, Amphibien und Fische. Der Akademischen Buchhandlung: Jena.

Bloembergen, S. 1940. Verslag van een exploratie-tocht naar Midden-Celebes (Lindoe-meer en Goenoeng Ngilalaki ten zuiden van Paloe in Juli 1939). Tectona **33**, 377-418.

Bloembergen, S. 1948. Aceraceae. Flora Malesiana I **4**, 3-4.

Boitard, P. 1851. Le Jardin des Plantes - description et moeurs des mammifères de la menagerie et du museum d'histoire naturelle. G. Barba: Paris. 308 pp.

Briedermann, L. 1990. Schwarzwild. VEB Deutscher Landwirtschaftsverlag, Berlin. 540 pp.

Burkill, I.H. 1966. Dictionary of the economic products of the Malay Peninsula. Department of Agriculture: Kuala Lumpur.

Buwalda, P. 1948. Umbelliferae. Flora Malesiana I **4**, 113-140.

Caldecott, J. 1991a. Monographie des Bartschweines (*Sus barbatus*). Bongo **18**, 54-68.

Caldecott, J. 1991b. Eruptions and migrations of bearded pig populations. Bongo **18**, 233-243.

Conklin, N.L. and Wrangham, R.W. 1994. The value of figs to a hind-gut fermenting frugivore: a nutritional analysis. Biochemical Systematics and Ecology **22**, 137-151.

Conklin, N.L., Dierenfeld, E.S. and MacLaughlin, K. 1994. Digestibility and passage of a zoo diet fed to babirusa (*Babyrousa babyrussa*). D. Zool. Garten N.F. **64**, 357-365.

Cooper, M.R. and Johnson, A.W. 1984. Poisonous plants in Britain and their effects on animals and man. Ministry of Agriculture, Fisheries and Food: London. 305 pp.

Corner, E.J.H. 1988. Wayside Trees of Malaya (3rd ed.) Vols. **1** & **2**. Malayan Nature Society: Kuala Lumpur.

Cossalter 1980. Location and ecological data of some provenances of *Eucalyptus deglupta* Blume in the Celebes and Ceram Islands. Characteristics of the natural stands. For. Gen. Res. Info. **6**, 16-23.

Deninger, K. 1910. Uber Babyrusa. Berichte der Naturforschenden Gesellschaft zu Freiburg i. Br. **18**, 1-22.

Desmarest, A.G. 1820. Mammalogie. Veuve Agasse: Paris, 391-392.

Ding Hou. 1954. Rhizophoraceae. Flora Malesiana I **5**, 429-493.

Ding Hou. 1978. Anacardiaceae. Flora Malesiana I **8**, 395-548.

Dransfield, J. 1976. A note on the habitat of Pigafetta filaris in North Celebes. Principes **20**, 48.

Dransfield, J. 1979. A manual of the rattans of the Malay Peninsula. Forest Department, Ministry of Primary Industries, Malaysia. 270 pp.

Dransfield, J. 1981. Palms and Wallace's Line. In: Wallace's Line and Plate Tectonics (ed. T.C. Whitmore), Clarendon: Oxford, 43-56.

Dubost, G. 1984. Comparison of the diets of frugivorous forest ruminants of Gabon. J. Mamm. **65**, 298-316.

Durrell, G. 1993. Preface. In: Oliver, W.L.R. (ed.) IUCN Status Survey and Conservation Action Plan for Pigs, Peccaries and Hippos. IUCN: Gland, Switzerland.

Everett, B. and Whitmore, T.C. 1973. Lythraceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 2. Forest department, Ministry of Agriculture and Lands, Malaysia, 276-280.

Exell, A.W. 1948. Combretaceae. Flora Malesiana I **4**, 533-589.

Florence, A. 1995. Sulawesi: an island bewitched. BBC 'Natural World' film. BBC: Bristol.

Freeland, W.J. and Janzen, D.H. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Am. Nat. **108**, 269-289.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L. Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. and

Thiollay, J.-M. 1985. Fruit characteristics as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia **65**, 324-337.

Geoffroy-St-Hillaire, T.E. and Cuvier, F. 1842. Histoire naturelle des mammifères. Blaise, Paris. **7**, 1-4.

Goldsmith, O. 1822. A history of the earth and animated nature. William Baynes-Son: London, **2**, 162-181.

Halle, J.S. 1757. Die Naturgeschichte der Thiere in sistematischer Ordnung. Deel 1. Christian Friedrich Voss: Berlin.

Haltenorth, T. 1963. Klassifikation der Säugetiere: Artiodactyla. Handbuch der Zoologie. W. de Gruyter: Berlin. **8.1**, (18) 4-27.

Hartley, T.G. 1974. A revision of the genus *Acronychia* (Rutaceae). J. Arnold Arboretum **55**, 469-567.

Hickson, S.J. 1889. A naturlist in North Celebes, a narrative of travels in Minahassa, the Sangir and Talaut stands with notices of the fauna, flora and ethnology of the districts visited. London, 392 pp.

Hill, A.F. 1952. Economic botany. McGraw-Hill: New York, Toronto, London. 560 pp.

Howe, H.F. and Smallwood, J. 1982. Ecology of seed dispersal. Ann. Rev. Ecol. Syst. **13**, 201-228.

Janzen, D.H. 1979. How to be a fig. Annu. Rev. Ecol. Syst. **10**, 13-51.

Jennison, G. 1927. Natural history, animals. A&C Black: London, 313-314.

Kalkman, C. 1993. Rosaceae. Flora Malesiana I **11**, 227-351.

Keng, H. 1974. Labiateae. Flora Malesiana I 8, 301-394.

Kevan, P.G. 1985. Pollination in a cryptically diocious plant Decaspermum parviflorum (Lam.) A.J. Scott (Myrtaceae) by pollen-collecting bees in Sulawesi, Indonesia. Biol. J. Linnean Society **25**, 319-330.

Klaassen, C.D., Andrew, H.O. and Doull, J. (eds.) 1986. Casarett and Doull's Toxicology: the basic science of poisons. Collier Macmillan: London. 974 pp.

Kochummen, K.M. 1972a. Annonaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **1**. Forest department, Ministry of Agriculture and Lands, Malaysia, 61-99.

Kochummen, K.M. 1972b. Bombacaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **1**. Forest department, Ministry of Agriculture and Lands, Malaysia, 100-120.

Kochummen, K.M. 1973a. Loganiaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **2**. Forest department, Ministry of Agriculture and Lands, Malaysia, 267-275.

Kochummen, K.M. 1973b. Simaroubaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **2**. Forest department, Ministry of Agriculture and Lands, Malaysia, 345-352.

Kochummen, K.M. 1973c. Sterculiaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **2**. Forest department, Ministry of Agriculture and Lands, Malaysia, 353-382.

Kochummen, K.M. 1973d. Tiliaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **2**. Forest department, Ministry of Agriculture and Lands, Malaysia, 392-412.

Kochummen, K.M. 1978a. Moraceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **3**. Forest department, Ministry of Agriculture and Lands, Malaysia, 119-168.

Kochummen, K.M. 1978b. Myrtaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **3**. Forest department, Ministry of Agriculture and Lands, Malaysia, 169-254.

Kochummen, K.M. 1978c. Verbenaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **3**. Forest department, Ministry of Agriculture and Lands, Malaysia, 297-313.

Kochummen, K.M. 1989. Lauraceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **4**. Forest department, Ministry of Agriculture and Lands, Malaysia, 98-178.

Koster, J. Th. 1935. The Compositae of the Malay archipelago. Blumea **1**, 351-536.

Lack, A.J. and Kevan, P.G. 1984. On the reproductive biology of a canopy tree, *Syzygium syzygioides* (Myrtaceae), in a rain forest in Sulawesi, Indonesia. Biotropica **16**, 31-36. + erratum in Biotropica 1985. **17**, 14.

Lack, A.J. and Kevan, P.G. 1987. The reproductive biology of a distylous tree, *Sarcotheca celebica* (Oxalidaceae) in Sulawesi, Indonesia. Bot. J. Linn. Soc. **95**, 1-8.

Latiff, A. 1989. Rhamnaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **4**. Forest department, Ministry of Agriculture and Lands, Malaysia, 297-301.

Laubenfels, D.J. de 1969. A revision of the Malesian and Pacific rainforest conifers. I. Podocarpaceae, in part. J. Arn. Arb. **50**, 274-369.

Laubenfels, D.J. de 1986a. Araucariaceae. Flora Malesiana I **10**, 419-442.

Laubenfels, D.J. de 1986b. Podocarpaceae. Flora Malesiana I **10**, 351-419.

Laubenfels, D.J. de 1986c. Taxaceae. Flora Malesiana I **10**, 347-351.

Leenhouts, P.W. 1954. Connaraceae. Flora Malesiana I **5**, 495-541.

Leenhouts, P.W. 1956. Burseraceae. Flora Malesiana I **5**, 209-296.

Leenhouts, P.W. 1957. Goodeniaceae. Flora Malesiana I **5**, 335-344.

Lesson, R.P. and Garnot, P. [and Guerin-Meneville, F-E.] 1826. Voyage autour de monde. Zoologie. Bertrand: Paris. **1**, 21 and 124-127.

Leus, K. 1994. Foraging behaviour, food selection and diet digestion of *Babyrousa babyrussa* (Suidae, Mammalia). PhD thesis. The University of Edinburgh: Edinburgh. 302pp.

Leus, K. and Morgan, C.A. 1996. Analyses of diets fed to babirusa (*Babyrousa babyrussa*) in captivity with respect to their nutritional requirements. IBEX J.M.E. **3**, 41-44.

Leus, K.Y.G. and Vercammen, P. 1996. Behaviour of a male and female babirusa (*Babyrousa babyrussa*, Suidae, Mammalia) during the first five days after their move to a semi-natural enclosure. D. Zool. Garten N.F. **66**, 133-155.

Leus, K., Bowles, D., Bell, J. and Macdonald, A.A. 1992. Behaviour of the babirusa (*Babyrousa babyrussa*) with suggestions for husbandry. Acta Zool. Pathol. Antverpiensia **82**, 9-27.

Leus, K., Bland, K.P., Dhondt, A.A. and Macdonald, A.A. 1996. Ploughing behaviour of *Babyrousa babyrussa* (Suidae, Mammalia) suggests a scent marking function. J. Zool. **238**, 209-219.

Macdonald, A.A. 1993. The Babirusa *(Babyrousa babyrussa)*. In: Oliver, W.L.R. (ed.) Status Survey and Conservation Action Plan for Pigs, Peccaries and Hippos. IUCN: Gland, Switzerland, 161-170.

Meijer, W. 1974. Field Guide to the trees of West Malesia. University of Kentucky, Kentucky.

Melish, R. 1994. Observation of swimming Babirusa *Babyrousa babyrussa* in Lake Poso, Central Sulawesi, Indonesia. Malayan Nature Journal **47**, 431-432.

Morris, D. 1965. The mammals, a guide to the living species. Hodder and Stoughton/ Zoological Society of London/ Granada T.V. Network: London, p 372.

Nagy, S. and Shaw, P.E. 1980. Tropical and subtropical fruits, composition, properties and uses. Avi Publishing Inc: Westport, Connecticut.

Ng, F.S.P. 1972. Sapotaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **1**. Forest department, Ministry of Agriculture and Lands, Malaysia, 388-389.

Ng, F.S.P. 1978a. Casuarinaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **3**. Forest department, Ministry of Agriculture and Lands, Malaysia, 45-46.

Ng, F.S.P. 1978b. Ebenaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **3**. Forest department, Ministry of Agriculture and Lands, Malaysia, 56-94.

Ng, F.S.P. 1978c. Ericaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **3**. Forest department, Ministry of Agriculture and Lands, Malaysia, 95-107.

Ng, F.S.P. 1989. Elaeocarpaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **4**. Forest department, Ministry of Agriculture and Lands, Malaysia, 82-97.

Nooteboom, H.P. 1986. Magnoliaceae. Flora Malesiana I **10**, 561-605.

Ooststroom, S.J. 1948. Convolvulaceae. Flora Malesiana I **4**, 388-512.

Patry, M. 1990. Babirussa: une Vie Jusqu'au Bout du Rêve. Fixot: Paris, 221 pp.

Patry, M. and Capiod, J. 1989. Pour la première fois le Babiroussa à l'état naturel. Connaissance de la Chasse **156**, 45-46.

Patry, M., Leus, K. and Macdonald, A.A. 1995. Group structure and behaviour of babirusa (*Babyrousa babyrussa*) in Northern Sulawesi. Austr. J. Zool. **43**, 643-655.

Payens, J.P.D.W. 1954. Erythroxylaceae. Flora Malesiana I **5**, 543-552.

Philipson, W.R. 1986. Monimiaceae. Flora Malesiana I **10**, 255-326.

Pijl, L. van der 1957. The dispersal of plants by bats (chiropterochory). Acta Bot. Neerl. **6**, 291-315.

Polman, K. 1983. The Central Moluccas, an annotated bibliography. Foris Publications Holland, Dordrecht. 324 pp.

Prance, G.T. and Whitmore, T.C. 1973. Rosaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **2**. Forest department, Ministry of Agriculture and Lands, Malaysia, 321-343.

Raven, P.H. 1974. Onagraceae. Flora Malesiana I **8**, 98-113.

Ridley, H.N. 1924. The flora of the Malay Peninsula. L. Reeve & co.: London.

Ridley, H.N. 1930. Dispersal of plants throughout the world. L. Reeve & co.: Ashford.

Ridsdale, C.E. 1978. A revision of the tribe Naucleeae s.s. (Rubiaceae). Blumea **27**, 307-366.

Robbins, R.G. and Wyatt-Smith, J. 1964. Dry land forest Formations and forest types in the Malay Peninsula. Malay. For. **27**, 188-217.

Robson, N.K.B. 1974. Hypericaceae. Flora Malesiana I **8**, 1-29.

Sarasin, P. and Sarasin, F. 1905. Reisen in Celebes ausgefuehrt in den Jahren 1893-1896 und 1902-1903. Kriedel: Wiesbaden.

Saw, L.G. 1989. Urticaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **4**. Forest department, Ministry of Agriculture and Lands, Malaysia, 472-478.

Schreber, J.C.D. and Wagner, J.A. 1835. Die Säugethiere in abbildungen nach der Natur. L.D. Weigel: Leipzig. **6**, 462-468.

Selmier, V.J. 1978. Only in Indonesia - the babirusa. (Unpubl.) report to LIPI and PPA, Indonesia: 40 pp.

Selmier, V.J. 1983. Bestandsgroße und Verhalten des Hirschebers (*Babyrousa babyrussa*) auf den Togian-Inseln. Bongo **7**, 51-64.

Sleumer, H. 1954. Flacourtiaceae. Flora Malesiana I **5**, 1-106.

Sleumer, H. 1956. Proteaceae. Flora Malesiana I **5**, 147-206.

Soepadmo, E. 1972. Fagaceae. Flora Malesiana I **7**, 265-403.

Soepadmo, E. 1973. Ulmaceae. Flora Malesiana I **8**, 31-76.

Soewanda, A., Prawira, Tantra, I.G.M. and Whitmore, T.C. 1984. Pocket checklist of Indonesian timber trees. Fl. Males. Bull. **37**, 47-48.

Steenis, C.G.G.J. van 1948a. Datiscaceae. Flora Malesiana I **4**, 382-387.

Steenis, C.G.G.J. van 1948b. Droseraceae. Flora Malesiana I **4**, 377-381.

Steenis, C.G.G.J. van 1948c. Sonneratiaceae. Flora Malesiana I **4**, 280-289 & 513-515.

Steenis, C.G.G.J. van 1950. The delimination of Malaysia and its main plant geographical divisions. Flora Malesiana I, **1**, lxx-lxxv.

Steenis, C.G.G.J. van 1974. Bignoniaceae. Flora Malesiana I **8**, 114-186.

Steup, F.K.M. 1929. Plantengeografische schets van het Paloedal. Tectona **22**, 576-596.

Steup, F.K.M. 1931. Bijdragen tot de kennis der bosschen van Noord- en Midden Celebes II. Een verkenningstocht door Midden-Celebes. Tectona **24**, 1121-1135.

Steup, F.K.M. 1932. Bijdragen tot de kennis der bosschen van Noord- en Midden Celebes III. Het zoogenaamde tjempaka-hoetan complex in de Minahasa. Tectona **25**, 119-147.

Steup, F.K.M. 1933. Bijdragen tot de kennis der bosschen van Noord- en Midden Celebes IV. Over de boschgesteldheid in de onderafdeeling Bolaang Mongondow. Tectona **26**, 26-49.

Steup, F.K.M. 1935. De lasi-bosschen van de onderafdeeling Boalemo. Tectona **28**, 95-107.

Steup, F.K.M. 1939a. Vegetatieschetsen van Zuid Celebes. Trop. Natuur **27**, 140-146.

Steup, F.K.M. 1939b. Over vegetatietypen op Celebes. Natuurk. Tijds. Ned.-Indie **98**, 283-293.

Stone, B.C. 1972. Rutaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 1. Forest department, Ministry of Agriculture and Lands, Malaysia, 367-387.

Stone, B.C. 1983. Studies in Malesian Pandanaceae 19. New species of Freycinetia and Pandanus from Malesia, Southeast Asia. J. Arn. Arb. **64**, 309-324.

Stover, R.H. and Simmonds, N.W. 1987. Bananas. 3rd edition. Longman Scientific and Technical, Essex, 468 pp.

Sugden, A. 1992. Longman Botany Handbook. Longman - York Press, Essex, 192 pp.

Symington, C.F. 1943-1974. Foresters' Manual of Dipterocarps. Malayan For. Rec. **16**, 244 pp.

Temmink, C.J. 1835. Coup d'oeil sur la faune des iles de la sonde et de l'empire du Japon. In P.F.B. von Siebold - Fauna Japonica. J.G. Lalau: Lugduni Batavorum. pp xv-xvi.

Thomas, D.W. 1984. Fruit intake and energy budgets of frugivorous bats. Physiol. Zool. **57**, 457-467.

Tjeenk Willink, H.D. 1905. Mammalia voorkomende in Nederlandsch-Indie. Natuurk. Tijdschr. Ned-Ind. **65**, 153-345.

Tootill, E. (ed.) 1984. The penguin dictionary of botany. Penguin Books, London, 390 pp.

Uhl, N.W. and Dransfield, J. 1987. Genera Palmarum, A classification of palms based on the work of Harald E. Moore, Jr. Allen Press, Lawrence, Kansas. 610pp.

Valentijn, F. 1726. Oud en nieuw Oost-Indie. J. van Braam: Dordrecht/ Amsterdam. **5**, 268-269.

Veldkamp, J.F. 1972. Oxalidaceae. Flora Malesiana I 7, 151-178.

Verhoef, L. 1938. Bijdragen tot de kennis der bosschen van Noord- en Midden-Celebes. V. Het boschgebied Ongkak Doemoga (Bolaang Mongondow). Tectona **31**, 7-29.

Wallace, A.R. 1870. Insulinde, het land van den Orang-oetan en den Paradijsvogel. Eerste deel. P.N. van Kampen, Amsterdam. xxiv+528 pp.

Watanabe, K. and Brotoisworo, E. 1982. Field observations on Sulawesi macaques. In: Kyoto University Overseas Research Report on Studies on Non-human Primates. **2**, 3-9 Kyoto University, Kyoto.

Wemmer, C. and Watling, D. 1986. Ecology and status of the Sulawesi palm civet *Macrogalidia musschenbroekii* Schlegel. Biol. Cons. **35**, 1-17.

Whitmore, T.C. (ed.) 1972a. Tree flora of Malaya Vol **1**. Forest Department, Ministry of Agricuture and lands, Malaysia.

Whitmore, T.C. 1972b. Leguminosae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **1**. Forest department, Ministry of Agriculture and Lands, Malaysia, 237-304.

Whitmore, T.C. 1972c. Myristicaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **1**. Forest department, Ministry of Agriculture and Lands, Malaysia, 315-345.

Whitmore, T.C. 1973a. Apocynaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 2. Forest department, Ministry of Agriculture and Lands, Malaysia, 3-24.

Whitmore, T.C. 1973b. Capparidaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 2. Forest department, Ministry of Agriculture and Lands, Malaysia, 25-26.

Whitmore, T.C. 1973c. Euphorbiaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 2. Forest department, Ministry of Agriculture and Lands, Malaysia, 34-136.

Whitmore, T.C. 1973d. Guttiferae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 2. Forest department, Ministry of Agriculture and Lands, Malaysia, 162-236.

Whitmore, T.C. 1973e. Lecythidaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 2. Forest department, Ministry of Agriculture and Lands, Malaysia, 257-266.

Whitmore, T.C. 1973f. Santalaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. 2. Forest department, Ministry of Agriculture and Lands, Malaysia, 341-344.

Whitmore, T.C. (ed.) 1984a. Tropical rain forests of the Far East, 2nd ed. O.U.P.: Oxford.

Whitmore, T.C. 1984b. A vegetation map of Malesia at scale 1:5 million. J. Biogeog. **11**, 461-471.

Whitmore, T.C. and Sidiyasa, K. 1986. Report on the forests at Toraut, Dumoga-Bone proposed National Park. Kew Bull. **41**, 747-756.

Whitmore, T.C.; Tantra, I.G.M. and Sutisma, U. (eds.) 1989. Tree flòra of Indonesia, checklist for Sulawesi. Agency for Forestry Reseach and Development, Forest Research and Development Centre, Bogor, Indonesia.

Whitten, A.J. 1980. Arenga as a fruit for gibbons. Principes **26**, 143-146.

Whitten, A.J., Mustafa, M. and Henderson, G.S. 1987a. The Ecology of Sulawesi. Gadja Mada University Press: Yogyakarta (Indonesia), 414pp.

Whitten, A.J., Damanik, S.J., Anwar, J. and Hisyam, N. 1987b. The ecology of Sumatra. Gadja Mada University Press: Yogyakarta (Indonesia), 583 pp.

Wilde, W.J.J.O. de 1972. Passifloraceae. Flora Malesiana I 7, 405-434.

Wilde, W.J.J.O. de 1981. Supplementary data on Malesian Knema (Myristicaceae) including three new taxa. Blumea **27**, 223-234.

Wong, K.M. 1989. Rubiaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **4**. Forest department, Ministry of Agriculture and Lands, Malaysia, 324-425.

Yap, S.K. 1989. Sapindaceae. In: Whitmore, T.C. (ed.) Tree Flora of Malaya. Vol. **4**. Forest department, Ministry of Agriculture and Lands, Malaysia, 434-461.
Whitmore, T.C. (ed.) 1984a. Tropical rain forests of the Far East, 2nd ed. O.U.P.: Oxford.

Zwahlen, R. 1992. The ecology of Rawa Aopa, a Peat-swamp in Sulawesi, Indonesia. Envir. Cons. **19**, 226-234.

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Group Structure and Behaviour of Babirusa (*Babyrousa babyrussa*) in Northern Sulawesi

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Abstract

Studies were carried out at two 'salt-licks' in lowland tropical forest on North Sulawesi, Indonesia. During 60 days of observation 586 sightings of babirusa were made, comprising 161 adult males, 155 adult females, 11 adults of unknown sex, 78 subadult males, 53 subadult females and 34 subadults of indeterminate sex; juveniles were observed 94 times, 19 males, 12 females and 63 of unknown sex. We saw 226 groups ranging in size from one to eight animals (median = 2). Almost half the sightings were of solitary animals, usually adult males. Bachelor groups of four or more babirusa were never seen. Adult females were rarely seen without company, often both juveniles and subadults being sighted together with them. There were never more than three adult females in a group. There were about twice as many family groups without adult males as there were with males. Agonistic behaviour between males was confined to 'threat at a distance', 'nose in the air', 'head under jaw submission' and 'front half supported' behaviours. Incidents of female–female agonistic behaviour were fewer, but in two, the dominant female chased her inferior off the 'salt-lick'.

Introduction

The babirusa (*Babyrousa babyrussa*) is a wild pig endemic to the Indonesian island of Sulawesi, some of the Togian and Sula islands, and the island of Buru (Fig. 1). The available geological and fragmentary paleontological evidence indicates an early evolutionary separation from the other Suidae (Römer 1966; Audley-Charles 1981) and analysis of its karyotype concurs with this view (Bosma *et al.* 1991). Recent studies in the field have shown the species to be directly vulnerable to hunting, and indirectly to logging and mining pressures, which are threatening its position in the wild (Smiet 1982; Blouch 1989; Oliver 1993). One consequence is that there is now an international captive breeding programme (Plasa 1994) based in zoological gardens in Asia, Europe and North America.

The earliest fragments of information about the behaviour of the babirusa in the wild were collected from the island of Buru by Rumphius and subsequently published by Valentijn (1726). Other comments may be found in the 'hunting' reports of Guillemard (1886) and Stresemann (1925). More recently, some behavioural studies were conducted on the Togian Islands by Selmier (1978, 1983). Despite the sum of these efforts, no information on the group structure of the babirusa in the wild exists. Studies of babirusa in zoological collections suggest that the animals may be gregarious (Macdonald *et al.* 1989). There is also some evidence of close bonding between the adult female and her young which may extend beyond the first year of life. Other studies of the babirusa in captivity have indicated the nature of activity patterns during

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the day, agonistic and marking behaviour, courtship and reproduction (Bowles 1986; Leus *et al.* 1992, 1995; Leus 1993, 1994; Macdonald *et al.* 1993). The results reported in the present paper comprise the most extensive documentation of a population of babirusa in the wild, and the first description of group sizes, group structure, agonistic and reproductive behaviour. The taxonomic nomenclature used throughout the paper is that presented in Oliver (1993).

Study Area

The study area was situated south of the Paleleh mountain range in the northern watershed draining into the Paguyaman river on the Minahasa peninsula of North Sulawesi (Sulawesi Utara) (Fig. 1). The altitude is approximately 100 m, and the average annual rainfall is approximately 2000 mm and is slightly seasonal, the months between August and October tending to be somewhat dryer (Whitten *et al.* 1987). The observations were carried out at two 'salt-lick' sites about 15 km apart, named 'Marisa' and 'Lantolo'. The 'Marisa' site had a surface area of about 4800 m^2 and was approximately rectangular in shape (Fig. 2). The 'Lantolo' site was smaller, with a surface area of about 900 m^2 (Fig. 2). Both sites were located in dense lowland tropical forest.

Materials and Methods

The detailed background to the videotaped observations reported in this paper have been published elsewhere (Patry 1990; Poulard and Patry 1990; Collet 1995). Observations were made from about 0700 or 0800 hours in the morning until 1700 or 1800 hours in the late afternoon between 18 and 19 March 1988, 2 and 5 October 1988, 4 and 13 May 1989, 18 and 30 July 1990, and 10 August and 9 November 1990. This represented a total of 60 days and approximately 600 h of observation. The periphery of the study sites was checked each morning for traces of animals that may have visited in the hours of darkness. Additional observations were carried out within the forest on three groups of babirusa. Videotape recordings commenced when one or more babirusa was seen to enter the study site and continued for the duration of the time that it/they were in view. A total of 8 h, 37 min of tape containing images of babirusa was obtained in this manner.

The age of each animal was classified according to the following scheme, which was based upon personal observations and the accumulated knowledge of staff responsible for babirusa care in zoological

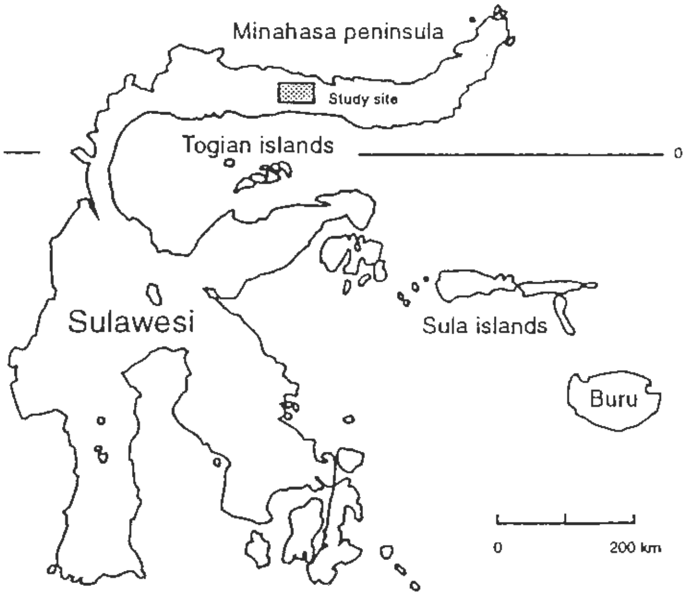

Fig. 1. The group of Indonesian islands upon which babirusa are found. The region of the study sites is indicated by the shaded area on the Minahasa peninsula of Sulawesi.

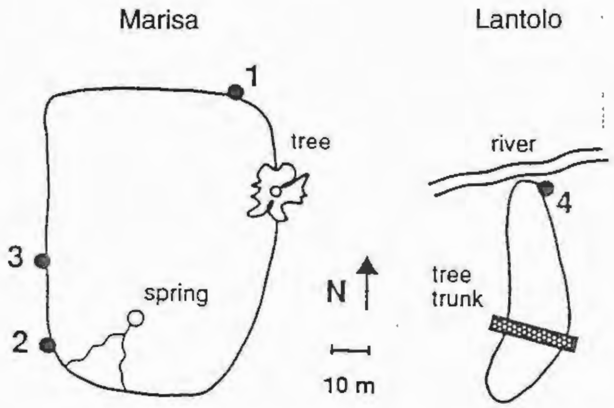

Fig. 2. Schematic diagrams to illustrate the layout of the 'Marisa' and 'Lantolo' study sites with the positions of the observation hides (1, 2, 3, 4) and the prominent 'tree', 'spring' and fallen 'tree trunk' landmarks indicated. The sites were situated approximately 15 km apart.

Fig. 3. A solitary adult male babirusa beside the tree at the 'Marisa' study site. A water source existed between the tree's roots where many babirusa came to drink.

collections. Adult males were designated as animals with maxillary canines that had pierced the skin and had formed a semicircular curve of tooth through which daylight could be clearly seen (Fig. 3). Subadult males were animals that showed short maxillary canine teeth that either formed a very tight semicircular curve through which very little or no daylight could be seen, or had just protruded through the skin, or showed no teeth through the skin but the developed bony alveolus under the skin of the nose. Juvenile males were smaller animals without sign of growth of the maxillary canines or their alveoli. Adult females were identified from subadult females by means of their size.

The animals were identified according to sex, age class, group size, and, where possible, individuals were identified. This was relatively easy to undertake in the case of males because of the shape of their canines. Some individual males were seen to visit the 'salt-licks' more than once. However, babirusa teeth are susceptible to breakage and over the time span of the study the same male may have had a changed appearance. It was impossible to identify females one from another. Additionally, in a number of instances the animals were recorded on tape for a very short time, and their sex or identity may not have been clear if the angle of view was inappropriate. For these reasons the results were not adjusted for recurring visits.

The behaviour expressed by the babirusa was classified into agonistic, 'ploughing', reproductive and mother–infant behaviours. The agonistic behaviours were further categorised with reference to the classifications 'threat at a distance', 'nose in the air', 'head under jaw submission' and 'front half supported' used to describe the agonistic behaviour of babirusa in zoos (Macdonald *et al.* 1993). The 'ploughing' behaviour has likewise been described in detail from zoo-based studies by Leus *et al.* (1995).

Results

Group Structure

The total number of babirusa sightings recorded on videotape was 586, comprising 161 adult males, 155 adult females and 11 adults of unknown sex; 78 subadult males, 53 subadult females and a further 34 cases where it was not possible to determine the sex of the subadult animal; and 94 juveniles of which 19 could be identified as males and 12 as females, the sex of the other 63 remaining unclear. The babirusa were present in groups that ranged in size from one to eight animals, with 160 groups observed at the 'Marisa' site and 66 groups at the 'Lantolo' site (Table 1). The median group size (including solitary animals) was two babirusa for both 'Marisa' and 'Lantolo'. There was no difference between the two sites in the frequency with which each group size was seen ($\chi^2 = 2{\cdot}964$, d.f. = 7, $P > 0{\cdot}9$), and also no significant difference in the proportions of male, female, subadult or juvenile animals observed at the two sites. The observations made at each site have therefore been combined and the percentage of times that each group size was seen calculated (Table 1). Almost half the sightings were of single animals, whereas groups of five or more animals represented less than 20% of the groups recorded. No groups larger than eight animals were observed; when two groups were present at the 'salt-lick' at any one time they moved about the open area as separate entities. The animals filmed in the forest were excluded from the analyses because the group size and composition could not be determined with certainty.

Most sightings of solitary animals were of adult males (Fig. 3) (84% of all solitary animals), with pairs or trios of males rarely seen (Table 2). Single adult males were seen with single adult females, but never with two or more females unless young animals were present. Bachelor groups of four or more adult babirusa were never seen. Very few adult males (6) were seen together with young animals without adult females also being in the group (28). Adult females were rarely seen without company, sometimes together with other adult animals, but most often with young babirusa (Figs 4 and 5, Table 2). Groups containing adult females and young numbered 84, of which two-thirds (56) had no adult males present (Table 2).

Table 1. The numbers of groups of babirusa of different size recorded at the 'Marisa' and 'Lantolo' study sites and the percentage of the total represented by each group size

Group size	'Marisa'	'Lantolo'	Total	Total (%)
1	74	30	104	46·0
2	21	6	27	11·9
3	26	9	35	15·5
4	14	6	20	8·9
5	10	5	15	6·6
6	8	4	12	5·3
7	4	3	7	3·1
8	3	3	6	2·7
Totals	160	66	226	100

Single adult females with young and no adult male (38 sightings) comprised the second most frequently observed grouping of babirusa; the group size ranged from two to six animals (Tables 2 and 3). The largest number of 'female' groups (17) contained one adult female and two young (Table 3). There were never more than three adult females in a group and no group had more than five young. On 12 occasions adult female(s) were seen with only juveniles. On 20 occassions adult female(s) were seen with only subadult animals. On another 24 occasions both juveniles and subadults were sighted together with the adult female(s).

No group of adult females and young were seen with more than two adult males present (Tables 2 and 4). There were about twice as many family groups without adult males (56) as there were with males (28). Of those, 21 were with one adult male and only 7 were with two adult males (Tables 2 and 3). In 18 of 28 cases where one or two adult males were present in the family group, juvenile animals were also present (Table 4).

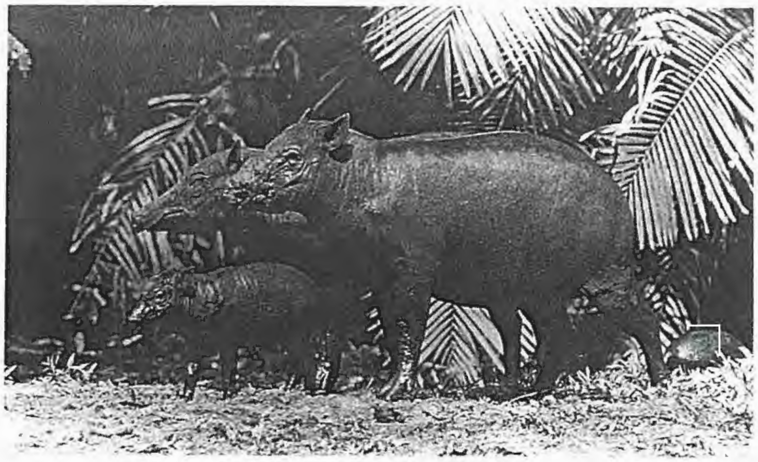

Fig. 4. A group of four babirusa, comprising two adult females and two juveniles, by the edge of the forest near the spring at the 'Marisa' study site.

Fig. 5. A group of eight babirusa, comprising adult, subadult and juvenile animales, sampling the 'salt-lick' just in front of the shadow cast by the large fallen tree trunk at the 'Lantolo' study site.

Table 2. Numbers of groups of babirusa arranged according to the number of adult males and females present and according to the presence or absence of youngsters

Groups containing adults of unknown sex are not included

	Adult males			
	0	1	2	3
Adult females				
0 female only	–	87	5	2
0 female + young	–	6	0	0
Total	–	93	5	2
1 female only	6	7	2	1
1 female + young	38	11	2	0
Total	44	18	4	1
2 females only	3	0	0	0
2 females + young	13	7	4	0
Total	16	7	4	0
3 females only	1	0	0	
3 females + young	5	2	1	
Total	6	2	1	
4 females only	0	0		
4 females + young	0	1		
Total	0	1		

Table 3. The number of groups with young of both sexes seen together with adult female, but not adult male, babirusa

The young animals are subdivided into Subadult and Juvenile classes

		Adult females	
Young animals	1	2	3
1 Subadult	5	0	0
1 Juvenile	4	1	0
2 Subadults	5	2	0
1 Subadult + 1 Juvenile	10	0	0
2 Juveniles	2	4	1
3 Subadults	3	3	1
1 Subadult + 2 Juveniles	1	0	0
2 Subadults +1 Juvenile	3	0	0
4 Subadults	0	0	1
3 Subadults + 1 Juvenile	3	0	0
2 Subadults + 2 Juveniles	1	3	0
3 Subadults + 2 Juveniles	1	0	0
2 Subadults + 3 Juveniles	0	0	1
1 Subadult + 4 Juveniles	0	0	1

Table 4. The number of groups with young of both sexes seen together with adult female and male babirusa

The young animals are subdivided into Subadult and Juvenile classes

	Adult females			
	1	2	3	4
One adult male +				
1 subadult	1	0	0	0
1 juvenile	3	0	0	0
2 subadults	2	0	0	0
1 subadult + 1 juvenile	0	2	0	0
2 juveniles	1	0	0	0
3 subadults	0	1	0	0
2 subadults + 1 juvenile	2	0	0	0
1 subadult + 2 juveniles	1	0	1	0
3 juveniles	0	1	0	1
4 subadults	0	1	0	–
1 subadult + 3 juveniles	1	0	1	–
3 subadults + 1 juvenile	0	1	0	–
4 subadults + 1 juvenile	0	1	–	–
Two adult males +				
1 subadult	1	0	0	0
2 subadults	1	1	1	0
1 subadult + 1 juvenile	0	1	0	0
3 juveniles	0	1	0	0
3 subadults + 1 juvenile	0	1	–	–

Agonistic Behaviour

Twelve groups of animals demonstrated some form of identifiable agonistic behaviour on video. Usually these interactions were between male animals in which one male glanced over at another ('threat at a distance') and the other lowered his head, or animals when approaching one another would lift their heads and put their noses in the air ('nose in the air'), or one male would place his ears tight back against his head which he then lowered below the mandible of the other, often older adult male whose head was held higher and whose ears were are held upright ('head under jaw submission'). The lower, submissive male would sometimes utter a long rattling screech; no sound was recorded from the dominant male.

On four occasions the behaviour known as 'front half supported' was observed. In one of these, because of partial forest obstruction, it was not clear whether it was like the second occasion, which was partly play behaviour between younger animals. Of the other two incidents the following is illustrative of the behaviour. An old male babirusa (Male A) walked in the direction of two other males on the 'salt-lick', but was temporarily diverted from them by the presence of a female. She placed her snout under his mandible. He continued walking in the direction of the other males. Male B, with his head held high and his ears pointed forward walked towards Male A. Old Male A lowered his head in response. Male B then diverted his attention to the other older Male C which did not have his head lower. Male B climbed with his fore limbs onto the head and shoulder of Male C who screamed throughout this procedure. The scream went down in pitch and intensity during the confrontation. Male B ended the confrontation by dismounting. He then walked in the direction of Male A with his ears held forward. Meanwhile, Male C kept his head down and moved the rear of his body round so that his lowered head always pointed towards Male B. The latter approached Male A which by now had also raised his head. The approach of Male B was made side-ways on with the left shoulder leading, head and ears raised. Male A had lowered his head; meanwhile, Male B put his weight onto his back legs and climbed onto the head and shoulders of Male A. Male A lifted one fore leg off the ground but never got both fore limbs into the air. Male A screamed as Male B dismounted with his head raised. Male A again faced his attacker with a lowered head and started to retreat. As he was retreating, Male C was approaching him with its ears forward. Male A spun around to face the new potential danger. He then lowered his head to Male C and the two did not fight. Male B walked off the site.

Two female–female interactions were observed. In one, Female A closest to the camera lowered her head and the other female (Female B) reached high. Female A lunged forward with her head down. Both females then attempted to go onto their hind legs with heads raised. Female A was pushed over by Female B. Female A then immediately lunged back for the feet of Female B on two occasions, one quickly followed by the other. The animals ended up side by side, with their heads pointing in opposite directions. The head of Female A was thumped into the thorax and abdomen of Female B, and Female B was thrown a short distance. Female A immediately thumped her again on the same part of the body, this time with even more force, and Female B was thrown at least 2 m away. Female B then rapidly ran towards the forest, pursued for a distance of 5–6 m by Female A. Two juvenile babirusa that were present during the fight showed no signs of anxiety, and only moved out of the way if there was a suggestion that the fight was coming towards them. After Female B had left the scene, one of the juveniles came to nose the snout of Female A, and then ran off after Female B. A deep-throated growling was recorded during the fight and a short 'woh' sound was heard at the end. It was not clear which animals were vocalising. In an encounter between two other female babirusa, the departing female uttered a long scream as she was chased.

'Ploughing' Behaviour

This behaviour was observed at the 'salt-lick' on six occasions, three times by adult males, once by a subadult male and twice by juvenile animals. In the clearest example, an adult male stood in the mud which he lifted with his nose for a few seconds. He then pushed the mud forward with his nose, knelt down and, using his hind limbs for propulsion, slid forward onto his chest with his nose in the mud for a couple of seconds. He then rolled to the right and to the left on his belly with his feet under him. After rolling to the left once more he lay straight for a short time before getting to his feet.

Reproductive Behaviour

Three short periods of reproductive behaviour were observed. In each an adult male was seen following an adult female and appeared to be sniffing and mouthing her perineal region. In one this behaviour was interrupted by the arrival of a juvenile animal.

Mother–Piglet Behaviour

Three sequences of video film were shot of singleton infants suckling, and one sequence of twins suckling. In the former the young piglets appeared to be obtaining milk for a long period of time despite their mothers moving about the 'salt-lick'. Despite this movement repeatedly breaking the physical contact between sow and piglets, the youngsters also sometimes managed to retain the teat in their mouths and continued suckling as the sow moved. This maintenance of contact was most often seen when piglets suckled from behind the mother, alternating between the two hind teats. One piglet seemed to obtain milk from both fore and hind teats by moving in front of or behind the hind limb of its mother. However, in this very small sample, the hind teats appeared to be suckled most often. The piglet occasionally nudged its nose lightly into the udder (a gentle fluent movement rather than a banging movement), used tongue movements with the teat, and occasionally pulled on the teat.

It is interesting to note a single sequence where two similarly sized piglets approached the udder of a sow at the same time, and the animal that had been suckling chased the other piglet away. In the sequence where twin piglets were suckling, one approached the udder from the rear of the standing sow, and the other from her left side. The piglet from the rear suckled the right hind teat and the one from the left suckled both of the fore teats.

Discussion

This study represents the first description of group structure in a large population of babirusa in the wild. The largest proportion of sightings of babirusa was of a solitary animal, a finding that is comparable to observations made on other species of pig (Table 5). Groups of 2–5 animals were also relatively frequently observed in other pig species; approximately the same range of group sizes seems to apply to the pigmy hog (*Sus salvanius*) and the Javan warty pig (*Sus verrucosus*) although no detailed studies have yet been carried out on these threatened pig species (Oliver 1980; Oliver and Deb Roy 1993; Blouch 1988, 1993). The main difference the babirusa shows with respect to the other pig species is in the maximum group size observed (Table 5). Groups of the Eurasian wild pig (*Sus scrofa*) in the Camargue, France, occasionally reached sizes of 23 animals (Dardaillon 1988), and about 9% of all observations made during a study in Germany were represented by groups of more than 20 individuals (Briedermann 1990). Common warthog (*Phacochoerus africanus*) groups can occasionally contain up to 16 individuals (Cumming 1975). Two other pig species appear to travel in much bigger groups. The only detailed field study carried out on the Red River hog (*Potamochoerus porcus*) reported an average group size of 10·56 animals (Oduro 1989, reported by Vercammen *et al.* 1993). The sundaic bearded pig (*Sus barbatus barbatus*) of Borneo is well known to aggregate in groups of hundreds of individuals that migrate together (Caldecott 1991*a*, 1991*b*). No published records of such large gatherings of babirusa exist, the largest group size recorded during the present study being of eight individuals.

Pig group size can be influenced by climatic conditions, food availability, hunting and deforestation pressure, the timing of the reproductive cycle, the numbers of young born, predation and so on (Cumming 1975; d'Huart 1978; Dardaillon 1988; Briedermann 1990; Caldecott 1991*a*, 1991*b*). It is important to bear in mind, therefore, that most of the recordings of babirusa were made during August–November, towards the end of the 'dry' season. The abundance of larger groups of common warthog is said to increase during the rainy season (Cumming 1975). We do not have comparable year-round information on babirusa group size from north Sulawesi to be able to carry out this type of analysis.

The information available on the digestion of food by the babirusa suggests that fruits may be an important component of the diet (Leus 1994). Unfortunately, no information is available on the fruiting pattern of the trees in the forests of the Minahasa peninsula, nor on the precise nature of the diet in the wild. The bearded pig demonstrates the most dramatic relationship between large increases in group size and the increases in the availability of fruit within the forests of Borneo (Caldecott 1991*a*, 1991*b*). Other studies of the diet in the wild and the fruiting patterns of the forest are also required to help explain how diet availability may influence group size, structure and home range.

Recent reports presented not only evidence of deforestation, but also of hunting and mining pressure in the broad valley where the video filming of babirusa took place (Florence 1995; Collet 1995). Studies of the Eurasian wild pig in Europe have indicated that larger associations of animals will split up into smaller groups as hunting pressure increases (Briedermann 1990). Whether group fragmentation of the babirusa has taken place in a similar way is unclear. Our

Table 5. Relative abundance (%) of different group sizes in four species of wild pig

Species	Relative abundance (%) *Babyrousa babyrussa*	 *Potamochoerus larvatus*^{A}	 *Sus scrofa*^{B}	 *Phacochoerus africanus*^{C}
Sample size	(n = 226)	(n = 153)	(n = 872)	(n = 1332)
Group size				
1	46·0	33·3	34·3	20·0
2	11·9	28·9	11·7	19·0
3	15·5	16·3	10·6	15·3
4	8·9	13·1	8·7	11·7
5	6·6	3·9	8·7	12·7
6	5·3	2·0	5·5	9·0
7	3·1	1·3	4·6	7·0
8	2·7	0	3·6	2·3
9	0	0·7	3·3	2·3
10	0	0·7	2·2	0·7
11–15	0	0	4·9	1·4
16–20	0	0	1·4	0·2
>20	0	0	0·1	0

^{A} Seydack (1990). ^{B} Dardaillon (1988). ^{C} Cumming (1975).

results suggest that further studies of babirusa in less disturbed areas of Sulawesi may be necessary in order to reveal whether their group size is larger as the amount of disturbance is reduced.

There is no information from the wild relating the time of birth of babirusa to climatic change. Studies in zoological collections demonstrate that babirusa have oestrus cycle lengths of 28–42 days and are able to breed all the year (Macdonald 1993; Plasa 1994). Gestation length is usually 155–158 days, although up to 171 days has been reported (Reinhard and Frädrich 1983; Macdonald 1993). The normal litter size is one or two, although a low incidence of triplet births has been recorded both in captivity and in the wild, and four fetuses have been reported in utero in a wild female (Patry 1990). The present study indicated the presence of singletons and twins, but there was no clear evidence of triplets (Table 3). The small size of the litter, therefore, contributes directly to the small size of the groups of babirusa when compared with groups of *Sus* species. The close bonding between female babirusa and her young, seen in zoological collections, seemed to be reflected in the sow plus two litter structure of a number of the family groups reported in the present study (Table 3 and Fig. 5). The precise role played by young from the previous litter is not clear.

Although the open nature of the study sites and the fact that the proceedings were videotaped permitted detailed analyses of the composition of the groups, care must be exercised in the interpretation of observations made on animals in the open at a 'salt-lick' during daytime. Likewise, care must be taken in the extrapolation of behaviour so observed to the type of behaviour that the same animals may express within the forest and at night. The few glimpses of male babirusa in the forest lent support to the notion that they are mainly solitary. Our only observations of night-time behaviour of animals in the wild was that babirusa did not come to the 'salt-lick' after dark. Studies in zoos suggest that in the late afternoon and at night-fall they may sleep together in groups (Macdonald *et al.* 1989; Leus *et al.* 1992; Macdonald 1993). The gathering of groups of Red River hog to sleep together has been observed in West Africa (Ben Voysey, personal communication). Babirusa nests on the Togian Islands, however, have been described as single-animal-sized structures (Selmier 1978, 1983). Further studies in the forest are required to resolve these apparent contradictions.

During the present study solitary adult males (Fig. 3) were observed most frequently (38·5%). The only times that adult male Eurasian wild pig associate with matriarchal groups were when the females were in oestrus; at other times they were solitary (Dardaillon 1988; Briedermann 1990). Adult male common warthog either live alone or in bachelor groups and are found with females almost exclusively during the mating season (Cumming 1975; Mason 1982; Vercammen and Mason 1993). Adult male bushpigs (*Potamochoerus larvatus*) associate with the female and her offspring for a much longer time, the association often continuing even after the young are weaned (Seydack 1991). This type of relationship seems to be taken a step further by adult male forest hogs (*Hylochoerus meinertzhageni*) which live with the family group at all times, and usually become solitary only after they have been expelled from the group by another male (d'Huart 1978, 1991). In case of the babirusa, matriarchal groups seemed to occur more frequently, and family groups (groups including one or more adult males) less frequently than was the case for the bushpig and the forest hog (d'Huart 1978, 1991; Seydack 1990, 1991). The babirusa exhibited almost no reproductive behaviour on the 'salt-lick' throughout the period of the present study. Seasonal differences in the degree of association between adult male and female babirusa remain to be studied.

Observation of the babirusa in zoological collections has revealed a series of behaviours that male animals appear to use in order to establish rank with respect to other males (Macdonald *et al.* 1993). The increasing levels of threat behaviour, 'threat at a distance', 'nose in the air' and 'front half supported' that were described from the agonistic behaviour of groups of captive male babirusa, were all observed at the 'salt-lick' in the course of the present study. Subadult and smaller males appeared to defer to larger adult males. However, as in the zoos, where the animals were more evenly matched for size, the dominant animal seemed to possess other characteristics (willingness to promote the threat, perhaps) from which he derived that status. The details of each behaviour were indistinguishable from those observed under captive conditions. Only about 5% of the interactions between zoo males resulted in the next level of threat, 'boxing' behaviour. This behaviour is often a progression from 'front half supported' in which both animals raise their front legs off the ground, and while standing on their hind legs facing one another, paddle for some minutes against the chest and shoulders of their opponent. The reason we did not observe this behaviour may be due to differences in the relative benefits individuals derived from sampling the 'salt-lick', as opposed to exerting dominance. Not infrequently the sounds of strenuous agonistic behaviour were heard near the 'salt-lick' but out of sight in the forest, but it was never clear which species of pig, *Babyrousa babyrussa*, or the more common Sulawesi warty pig (*Sus celebensis*), was responsible for this. The relative infrequency with which males demonstrated 'ploughing' behaviour on the 'salt-lick' may similarly be related to some, currently unclear, lack of need to mark this piece of land. 'Ploughing' behaviour in zoological collections has been associated with the deposition of pheromones on the soil by mature males when introduced to a fresh enclosure, or to one previously occupied by another adult male (Leus *et al.* 1995). Other unpublished studies suggest that this marking behaviour may take place elsewhere in the forest.

The majority of groups with females tended to have a single adult female with young, although more than one female babirusa with young may be found together (Fig. 4). This relative preponderance of single females with young may be an adaptation to safeguard against opportunistic cannibalism by adult babirusa of the newborn young of other babirusa, which has been observed in zoological gardens (Bowles 1986; Macdonald *et al.* 1989; Leus *et al.* 1992). These observations on group structure may be related to the attacks we observed being made by one female on another. It was not clear whether either of the combatants was pregnant. Immediately prior to parturition the babirusa sow tends to be much more aggressive (Leus *et al.* 1992).

In conclusion, babirusa in North Sulawesi were diurnal in their use of the 'salt-licks'. They travelled in small groups, the adult males tending to be solitary whereas the adult females tended to be accompanied by young animals of one or two generations. Large bachelor groups were not seen. Groups rarely contained three or more adult females. The range of agonistic and ploughing behaviours observed were indistinguishable from those exhibited by babirusa in zoological collections.

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References

Audley-Charles, M. G. (1981). Geological history of the region of Wallace's Line. In 'Wallace's Line and Plate Tectonics'. (Ed. T. C. Whitmore.) pp. 24–35. (Clarendon Press: Oxford).

Blouch, R. A. (1988). Ecology and conservation of the Javan warty pig *Sus verrucosus* Müller, 1840. *Biological Conservation* **43**, 295–307.

Blouch, R. A. (1989). Report from the field: Indonesia. Smithsonian Institute Conservation and Research Center Newsletter, National Zoo, Washington DC, No. 1, pp. 6–8.

Blouch, R. A. (1993). The Javan warty pig (*Sus verrucosus*). In 'Status Survey and Conservation Action Plan: Pigs, Peccaries and Hippos'. pp. 129–36. (IUCN: Gland, Switzerland.)

Bosma, A. A., de Haan, N. A., and Macdonald, A. A. (1991). The current status of cytogenetics of the Suidae: a review. *Bongo, Berlin* **18**, 260–72.

Bowles, D. (1986). Social behaviour and breeding of babirusa *Babyrousa babyrussa* at the Jersey Wildlife Preservation Trust. *Dodo* **23**, 86–94.

Briedermann, L. (1990). 'Schwarzwild.' (VEB Deutscher Landwirtschaftsverlag: Berlin.)

Caldecott, J. (1991*a*). Monographie des Bartschweines (*Sus barbatus*). *Bongo, Berlin* **18**, 54–68.

Caldecott, J. (1991*b*). Eruptions and migrations of bearded pig populations. *Bongo, Berlin* **18**, 233–43.

Collet, J.-Y. (1995). Foux d'animaux: les aventures de Papiroussa. Léo productions (film): Boulogne, France.

Cumming, D. H. M. (1975). A field study of the ecology and behaviour of warthog. Museum Memoir 7, Salisbury, Rhodesia.

Dardaillon, M. (1988). Wild boar social groupings and their seasonal changes in the Camargue, southern France. *Zeitschrift für Säugetierkunde* **53**, 22–30.

d'Huart, J. P. (1978). Écologie de l'Hylochère (*Hylochoerus meinertzhageni* Thomas) au Parc National des Virunga. *Fondations pour favoriser les recherches scientifiques en Afrique, 2e Série, fascilule* **25**, 156 pp.

d'Huart, J. P. (1991). Monographie des Riesenwaldschweines (*Hylochoerus meinertzhageni*). *Bongo, Berlin* **18**, 103–18.

Florence, A. (1995). Sulawesi: an island bewitched. BBC 'Natural World' film: BBC, Bristol.

Guillemard, F. H. H. (1886). 'The Cruise of the Marchesa to Kamschatka and New Guinea.' Chapter 2, pp. 190–1, 200–5. (J. Murray: London.)

Leus, K. (1993). La grande expedition des babiroussas dans la 'presque-jungle' de St-Martin. *Magazine Trimestriel, Espace Zoologique, St Martin la Plaine* **30**, 4.

Leus, K. (1994). Foraging behaviour, food selection and diet digestion of *Babyrousa babyrussa* (Suidae, Mammalia). Ph. D. Thesis, University of Edinburgh, Scotland.

Leus, K., Bowles, D., Bell, J., and Macdonald, A. A. (1992). Behaviour of the babirusa (*Babyrousa babyrussa*) with suggestions for husbandry. *Acta Zoologica et Pathologica Antverpiensia* **82**, 1–19.

Leus, K., Bland, K. P., Dhondt, A. A., and Macdonald, A. A. (1995). Ploughing behaviour of the babirusa (*Babyrousa babyrussa*) suggests a scent marking function. *Journal of Zoology (London)* **237** (in press).

Macdonald, A. A. (1993). The babirusa (*Babyrousa babyrussa*). In 'Status Survey and Conservation Action Plan: Pigs, Peccaries and Hippos'. pp. 161–71. (IUCN: Gland, Switzerland.)

Macdonald, A. A., Bell, J., Munro, S. A., Kaspe, L., Harwono Gepak, V., Sasmita, R., and Bowles, D. (1989). Observations on the behaviour and health of captive babirusa. In 'Prociding Simposium Nasional Penyakit Satwa Liar'. pp. 244–53. (Universitas Airlangga dan Kebun Binatang: Surabaya, Indonesia.)

Macdonald, A. A., Bowles, D., Bell, J., and Leus, K. (1993). Agonistic behaviour in captive babirusa (*Babyrousa babyrussa*). *Zeitschrift für Säugetierkunde* **58**, 18–30.

Mason, D. R. (1982). Studies on the biology and ecology of the warthog *Phacochoerus aethiopicus sundevalli* Lönnberg, 1908 in Zululand. D. Sc. (Wildlife Mangement), University of Pretoria, South Africa.

Oduro, W. (1989). Ecology of the Red River hog in Southern Nigeria. Ph. D. Thesis, University of Ibadan, Nigeria.

Oliver, W. L. R. (1980). The pigmy hog. The Jersey Wildlife Preservation Trust Special Scientific Report No. 1, Trinity, Jersey.

Oliver, W. L. R. (Ed.) (1993). 'Status Survey and Conservation Action Plan: Pigs, Peccaries and Hippos.' (IUCN: Gland, Switzerlaud.)

Oliver, W. L. R., and Deb Roy, S. (1993). The pygmy hog (*Sus salvanius*). In 'Status Survey and Conservation Action Plan: Pigs, Peccaries and Hippos'. pp. 121–9. (IUCN: Gland, Switzerland.)

Plasa, L. (1994). 'Internationales Zuchtbuch für den Hirscheber (International studbook for the babirusa) *Babyrousa babyrussa* 1993.' (Wilhelma Zoologisch-botanischer Garten: Stuttgart.)

Patry, M. (1990). 'Babiroussa, une vie jusqu'au bout du rêve.' (Paris: Fixot.)

Poulard, J., and Patry, M. (1990). Geheimnisvolle Hirsch-Eber. *Das Tier* Januari 1990, 70–5.

Reinhard, R., and Frädrich, H. (1983). Bemerkung zur Zucht Hirschebern (*Babyrousa babyrussa* L.) im Zoo Berlin. *Bongo, Berlin* 7, 65–70.

Römer, A. S. (1966). 'Vertebrate Paleontology.' 3rd Edn. (Chicago University Press: Chicago.)

Selmier, V. J. (1978). Only in Indonesia: the babirusa. Unpublished report to Lembaga Ilmu Pengetahuan Indonesia and Direktorat Perlindungan Dan Pengawetan Alam: Jakarta.

Selmier, V. J. (1983). Bestandsgröße und Verhalten des Hirschebers *Babyrousa babyrussa* auf den Togian-Inseln. *Bongo, Berlin* 7, 51–64.

Seydack, A. H. W. (1990). Ecology of the bushpig *Potamochoerus porcus* Linn. 1758 in the Cape Province, South Africa. Ph. D. Thesis, Univeristy of Stellenbosch, South Africa.

Seydack, A. (1991). Monographie des Buschschweines (*Potamochoerus porcus*). *Bongo, Berlin* 18, 85–102.

Smiet, F. (1982). Threats to the spice islands. *Oryx* 14, 323–8.

Stresemann, E. (1925). Begegnungen mit dem Hirscheber (*Babirussa babyrussa*) auf Buru. *Pallasia* 3, 49–56.

Valentijn, F. (1726). 'Oud en Nieuw Oost-Indien.' Chapter 5, pp. 268–9. (J. van Braam: Dordrecht, Amsterdam.)

Vercammen, P., and Mason, D. R. (1993). The warthogs (*Phacochoerus africanus* and *P. aethiopicus*). In 'Status Survey and Conservation Action Plan: Pigs, Peccaries and Hippos'. (Ed. W. L. R. Oliver.) pp. 75–84. (IUCN: Gland, Switzerland.)

Vercammen, P., Seydack, A. H. W., and Oliver, W. L. R. (1993). The bush pigs (*Potamochoerus larvatus* and *P. porcus*). In 'Status Survey and Conservation Action Plan: Pigs, Peccaries and Hippos'. (Ed. W. L. R. Oliver.) pp. 93–101. (IUCN: Gland, Switzerland.)

Whitten, A. J., Mustafa, M., and Henderson, G. S. (1987). 'The Ecology of Sulawesi.' (Gadjah Mada University Press: Yogyakarta, Indonesia.)

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Notes on the distribution and status of Babirusa *babyrousa babyrussa* in Buru, Maluku Province, Indonesia.

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The status and distribution of Babirusa *Babyrousa babyrussa* on Buru island is little known. Teams from PHPA/Bird Life International has conducted field surveys in Buru for a total of 80 days in the period October 1995 to June 1996. The purpose of the surveys was to collect data on vertebrate fauna and vegetation in order to establish the biodiversity value of different habitats and to evaluate the boundaries for the proposed protected Gunung Kepalat Made area. Although the teams spent more than 50 days in the forest, all information on babirusa was obtained by interviewing local residents.

Babirusa were reported to be rather common in forested hills and mountains in western Buru, present in forested hills and mountains in south-eastern Buru, but absent from the Wai Apu folld plain and monsoon forest of central and north-eastern Buru. It was reported to be uncommon close to the coast and said not to enter cultivated areas. These reports are supported by good descriptions.

Skulls or lower jaws of babirusa have been shown to the team (and photographed) in three places. A hunter had kept remains of pigs, including a lower jaw of babirusa, in his hut inland from Fogi (S 03°12'24", E126°04'37"). This hut was at 700m altitude within selectively-logged forest. Judging from these remains, *Sus* sp. (presumably *S. scrofa*) is the most numerous pig in this area. Skulls of babirusa (adult males) was shown to the teams in the villages of Selwadu (S 03°05'28", E126°07'28") and Waihotong (S 03°05'52", E126°07'28").

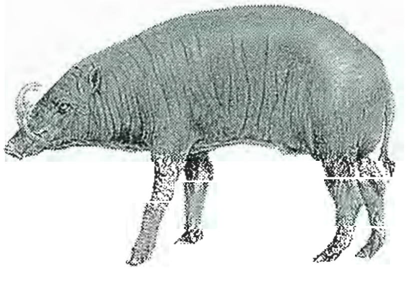
Residents of 10 villages visited in the western part of Buru all reported that babirusa could be found inland from their villages. None of the informants suspected that the population had been declining. However, babirusa's preference for remote areas was believed to be a result of hunting pressure. Babirusa is hunted for meat for personal consumption. A man from Leksula reported that babirusa are known from forests in south-east Buru and that he had seen a dead male on the beach near Lena in 1994. Local hunters from the village Metar in central Buru reported that wild pigs were common within the monsoon forest above the village, but that they never had found babirusa there. They also told that they never had heard about from the Kayu Putih Melaleuca leucadendron dominated monsoon forest which covers most of central and north-west Buru. Babirusa were not known to residents of the Wai Apu flood plain.

Anecdotal information on ecology and behavior of babirusa was collected from local people in villages in the Bara Bay area (Desa Bara, Desa Wairuba, Desa Waihotong, Desa Waikase and Desa Selwadu). Informants reported that babirusa prefer rocky areas, steep slopes, ridges and other areas where they are difficult to reach. They usually occur as solitary individuals or in small family groups. The number of piglets was said to be one or two. They do not bathe in mud but prefer clean rivers. Babirusa were said to feed on fruits or leaves fallen from Meranti *Shorea* spp., "Kayu Kuning" and "Gondal".

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 8
Appendix III:
IUCN Policy Guidelines



THE IUCN POLICY STATEMENT ON CAPTIVE BREEDING

Prepared by the
SSC Captive Breeding Specialist Group

As approved by the 22nd Meeting of the IUCN Council Gland, Switzerland

4 September 1987

SUMMARY: Habitat protection alone is not sufficient if the expressed goal of the World Conservation Strategy the maintenance of biotic diversity, is to be achieved. Establishment of self-sustaining captive populations and other supportive intervention will be needed to avoid the loss of many species, especially those at high risk in greatly reduced, highly fragmented, and disturbed habitats captive breeding programmes need to be established before specks are reduced to critically low numbers, and thereafter need to be coordinated Internationally according to sound biological principles, with a view to the maintaining or re establishment of viable populations in the wild.

PROBLEM STATEMENT

IUCN data indicate that about 3 per cent of terrestrial earth is gazetted for protection. Some of this and much of the other 97 per cent is becoming untenable for many species, and remaining populations are being greatly reduced and fragmented. From modern population biology one can predict that many species will be lost under these conditions. On average more than one mammal, bird, or reptile species has been bst in each year this century. Since extinctions of most taxa outside these groups are not recorded, the loss rate for all species is much higher.

Certain groups of species are at particularly high risk, especially forms with restricted distribution, those of large body size, those of high economic value, those at the top of food chains, and those which occur only in climax habitats. Species in these categories are likely to be bst first, but a wide range of other 10rms are also at risk. Conservation over the bng term will require management to reduce risk, including *ex situ* populations which could support and interact demographically and genetically with wild populations.

FEASIBILITY

Over 3,000 vertebrate species are being bred in zoos and other captive animal facilities. When a serious attempt is made, most species breed in captivity, and viable populations can be maintained over the long term. A wealth of experience is available in these institutions, including husbandry, veterinary medicine, reproductive biology, behaviour, and genetics. They offer space for supporting populations of many threatened taxa, using resources not competitive with those for *in situ* conservation. Such captive stocks have in the past provided critical support for some wild populations (e.g. American bison, *Bison bison*), and have been the sole escape from extinction for others which have since been re-introduced to the wild (e.g. Arabian oryx, *Otyx leucoryx*).

RECOMMENDATION

IUCN urges that those national and international organizations and those individual institutions concerned with maintaining wild animals in captivity commit themselves to a general policy of developing demographically self-sustaining captive populations of endangered species wherever necessary.

SUGGESTED PROTOCOL

WHAT: The specific problems of the species concerned need to be considered, and appropriate aims for a captive breeding programme made explicit.

WHEN: The vulnerability of small populations has been consistently under estimated. This has erroneously shifted the timing of establishment of captive populations to the last moment, when the crisis is enormous and when extinction is probable. Therefore, timely recognition of such situations is critical, and is dependent on information on wild population status, particularly that provided by the IUCN Conservation Monitoring Centre. Management to best reduce the risk of extinction requires the establishment of supporting captive populations much earlier, preferably when the wild population is still in the thousands. Vertebrate taxa with a current census below one thousand individuals in the wild require close and swift cooperation between field conservationists and captive breeding specialists, to make their effort complementary and minimize the likelihood of the extinction of these taxa.

HOW: Captive populations need to be founded and managed according to sound scientific principles for the primary purpose of securing the survival of species through stable, self-sustaining captive populations. Stable captive populations preserve the options of reintroduction and/or supplementation of wild populations.

A framework of international cooperation and coordination between captive ~ breeding institutions holding species at risk must be based upon agreement to cooperatively manage such species for demographic security and genetic diversity. The IUCN/SSC Captive Breeding Specialist Group is an appropriate advisory body concerning captive breeding science and resources.

Captive programmes involving species at risk should be conducted primarily for the benefit of the species and without commercial transactions. Acquisition of animals for such programmes should not encourage commercial ventures or trade. Whenever possible, captive programmes should be carried out in parallel with field studies and conservation efforts aimed at the species in its natural environment.

IUCN GUIDELINES FOR THE PLACEMENT OF CONFISCATED LIVE ANIMALS[1]

Statement of Principle:

When live animals are confiscated by government authorities, these authorities have a responsibility to dispose of them appropriately. Within the confines of national and international law, the ultimate on disposition of confiscated animals must achieve three goals: 1) to maximise conservation value of the specimens without in any way endangering the health, behavioral repertoire, genetic characteristics, or conservation status of wild or captive populations of the species[1]; 2) to discourage further illegal or irregular[2] trade in the species; and 3) to provide a humane solution, whether this involves maintaining the animals in captivity, returning them to the wild, or employing euthanasia to destroy them.

Statement of Need:

Increased regulation of trade in wild plants and animals and enforcement of these regulations has resulted in an increase in the number of wildlife shipments intercepted by government authorities as a result of non-compliance with these regulations. In some instances, the interception is a result of patently illegal trade; in others, it is in response to other irregularities. While in some cases the number of animals in a confiscated shipment is small, in many others the number is in the hundreds. Although in many countries confiscated animals have usually been donated to zoos and aquaria, this option is proving less viable with large numbers of animals and, increasingly, for common species. The international zoo community has recognized that placing animals of low conservation priority in limited cage space may benefit those individuals but may also detract from conservation efforts as a whole. They are, therefore, setting conservation priorities for cage space (IUDZG/CBSG 1993).

With improved interdiction of the illegal trade in animals there is an increasing demand for information to guide confiscating agencies in the disposal of specimens. This need has been reflected in the formulation of specific guidelines for several groups of organisms such as parrots (Birdlife International in prep) and primates (Harcourt in litt.). However, no general guidelines exists.

In light of these trends, there is an increasing demand - and urgent need - for information and advice to guide confiscating authorities in the disposition of live animals. Although specific guidelines have been formulated for certain groups of organisms, such as parrots (Birdlife International in prep.) and primates (Harcourt 1987), no general guidelines exist.

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[1] Although this document refers to species, in the case of species with well-defined subspecies and races, the issues addressed will apply to lower taxonomic units.

When disposing of confiscated animals, authorities must adhere to both national and international law. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) requires that confiscated individuals of species listed on the treaty's Appendices be returned to the "state of export . . . or to a rescue centre or such other place as the Management Authority deems appropriate and consistent with the purpose of the Convention." (Article VIII). However the treaty does not elaborate on this requirement, and CITES Management Authorities must act according to their own interpretation, not only with respect to repatriation but also as regards what constitutes disposition that is "appropriate and consistent" with the treaty. Although the present guidelines are intended to assist CITES Management Authorities in making this assessment, they are designed to be of general applicability to all confiscated live animals.

The lack of specific guidelines has resulted in confiscated animals being disposed of in a variety of ways. In some cases, release of confiscated animals into existing wild populations has been made after careful evaluation and with due regard for existing guidelines (IUCN 1987, IUCN 1995). In other cases, such releases have not been well planned and have been inconsistent with general conservation objectives and humane considerations, such as releasing animals in inappropriate habitat, dooming these individuals to starvation or certain death from other causes against which the animals are not equipped or adapted. Such releases may also have strong negative conservation value by threatening existing wild populations as a result of: 1) diseases and parasites acquired by the released animals while in captivity spreading into existing wild populations; 2) individuals released into existing populations, ro in areas near to existing populations, not being of the same race or sub-species as those in the wild population, resulting in mixing of distinct genetic lineages; 3) animals held in captivity, particularly juveniles and immatures, acquiring an inappropriate behavioral repertoire from individuals of other species, and/or either losing certain behaviors, or not developing the full behavioral repertoire, necessary for survival in the wild. Also, it is possible that release of these animals could result in inter-specific hybridisation.

Disposition of confiscated animals is not a simple process. Only on rare occasions will the optimum course to take be clear-cut or result in an action of conservation value. Options for the disposition of confiscated animals have thus far been influenced by the public's perception that returning animals to the wild is the optimal solution in terms of both animals welfare and conservation. A growing body of scientific study of re-introduction of captive animals suggests that such actions may be among the least appropriate options for many reasons. This recognition requires that the options available to confiscating authorities for disposition be carefully reviewed.

Management Options:

In deciding on the disposition of confiscated animals, priority must be given to the well-being and conservation of existing wild populations of the species involved, with all efforts made to ensure the humane treatment of the confiscated individuals. Options for disposition fall into three

principal categories: 1) maintenance of the individual(s) in captivity; 2) returning the individual(s) in question to the wild; and 3) euthanasia.
Within a conservation perspective, by far the most important consideration in reviewing the options for disposition is the conservation status of the species concerned. Where the confiscated animals represent an endangered or threatened species, particular effort should be directed towards evaluating whether and how these animals might contribute to a conservation programme for the species. The decision as to which option to employ in the disposition of confiscated animals will depend on various legal, social, economic and biological factors. The "Decision Tree"[1] provided in the present guidelines is intended to facilitate consideration of these options. The tree has been written so that it may be used for both threatened and common species. However, it recognizes that the conservation status of the species will be the primary consideration affecting the options available for placement, particularly as the expense and difficulty of returning animals to the wild (see below) will often only be justified for threatened species. International networks of experts, such as the IUCN-Species Survival Commission Specialist Groups, should be able to assist confiscating authorities, and CITES Scientific and Management Authorities, in their deliberations as to the appropriate disposition of confiscated specimens.

Sending animals back automatically to the country from which they were shipped, the country in which they originated (if different), or another country m which the species exists, does not solve any problems. Repatriation to avoid addressing the question of disposition of confiscated animals is irresponsible as the authorities in these countries will face the same issues concerning placement as the authorities in the original confiscating country.

OPTION 1-- **CAPTIVITY**

Confiscated animals are already in captivity; there are numerous options for maintaining them in captivity. Depending on the circumstances, animals can be donated, loaned, or sold. Placement may be in zoos or other facilities, or with private individuals. Finally, placement may be either in the country of origin, the country of export (if different), the country of confiscation. or in a country with adequate and/or specialised facilities for the species in question. If animals are maintained in captivity, in preference to either being returned to the wild or euthanized, they must be afforded humane conditions and ensured proper care for their natural lives.

Zoos and aquaria are the captive facilities most commonly considered for disposition of animals, but a variety of captive situations exist where the primary aim of the institution or individuals involved is not the propagation and resale of wildlife. These include:

> **Rescue centres**, established specifically to treat injured or confiscated animals, are sponsored by a number of humane organisations in many countries.
>
> **Life-time care facilities** devoted to the care of confiscated animals have been built in a few countries.

Specialist societies or clubs devoted to the study and care of single taxa or species(e.g., reptiles, amphibians, birds) have, in some instances, provided an avenue for the disposition of confiscated animals without involving sale through intermediaries. Placement may be made directly to these organisations or to individuals who are members.

Humane Societies may be willing to ensure placement of confiscated specimens with private individuals who can provide humane life-time care.

Research laboratories (either commercial or non-commercial, e.g. universities) maintain collections of exotic animals for many kinds of research (e.g. behavioural, ecological, physiological, psychological, medical). Attitudes towards vivisection, or even towards the non-invasive use of animals in research laboratories as captive study populations, vary widely from country to country. Whether transfer of confiscated animals to research institutions is appropriate will therefore engender some debate. However, it should be noted that transfer to facilities involved in research conducted under humane conditions may offer an alternative -- and one which may eventually contribute information relevant to the species' conservation. In many cases, the lack of known provenance and the risk that the animal in question has been exposed to unknown pathogens will make transfer to a research institution an option that will be rarely exercised or desired.

CAPTIVITY - Sale, Loan or Donation

Animals can be placed with an institution or individual in a number of ways. It is critical, however. that two issues be separated: the ownership of the animals and/or their progeny, and the payment of a fee by the institution/individual receiving the animals. Paying the confiscating authority, or the country of origin, does not necessarily give the person or institution making the payment any rights (these may rest with the confiscating authority). Similarly, ownership of an animal can be transferred without payment. Confiscating authorities and individuals or organizations participating in the placement of confiscated specimens must clarify ownership. both of the specimens being transferred and their progeny. Laws dictating right of ownership of wildlife differ between nations, in some countries ownership remains with the government, in others the owner of the land inhabited by the wildlife has automatic rights over the animals.

When drawing up the terms of transfer many items must be considered, including:

-- ownership of both the animals involved and their offspring (dictated by national law) must be specified as one of the terms and conditions of the transfer (it may be necessary to insist there is no breeding for particular species, e.g. primates). Either the country of origin or the country of confiscation may wish to retain ownership of the animals and/or their progeny. Unless specific legal provisions apply, it is impossible to assure the welfare of the animals following a sale which includes a transfer of ownership.

-- sale or payment of a fee to obtain certain rights (e.g. ownership of offspring) can provide a means of placement that helps offset the costs of confiscation.

--sale and transfer of ownership should only be considered in certain circumstances, such as where the animals in question are not threatened and not subject to a legal proscription on trade (e.g., CITES Appendix I) and there is no risk of stimulating further illegal or irregular trade.

--sale to commercial captive breeders may contribute to reducing the demand for wild-caught individuals.

--sale may risk creating a public perception of the confiscating State perpetuating or benefitting from illegal or irregular trade.

--if ownership is transferred to an organization to achieve a welfare or conservation goal, the confiscating authority should stipulate what will happen to the specimens should the organization wish to sell/transfer the specimens to another organization or individual.

--confiscating authorities should be prepared to make public the conditions under which confiscated animals have been transferred and, where applicable, the basis for any payments involved.

CAPTIVITY-- **Benefits**

The benefits of placing confiscated animals in a facility that will provide life-time care under humane conditions include;

a) educational value;
b) potential for captive breeding for eventual re-introduction;
c) possibility for the confiscating authority to recoup from sale costs of confiscation;
d) potential for captive bred individuals to replace wild-caught animals as a source for trade.

CAPTIVITY- **Concerns**

The concerns raised by placing animals in captivity include:

A) **Disease.** Confiscated animals may serve as vectors for disease. The potential consequences of the introduction of alien disease to a captive facility are more serious than those of introducing disease to wild populations (see discussion page 9); captive conditions might encourage disease spread to not only conspecifics. As many diseases can not be screened for, even the strictest quarantine and most extensive screening for disease can not ensure that an animal is disease free. Where quarantine cannot adequately ensure that an individual is disease free, isolation for an indefinite period, or euthanasia, must be carried out.

B) **Escape**. Captive animals maintained outside their range can escape from captivity and become pests. Accidental introduction of exotic species can cause tremendous damage and in certain cases, such as the escape of mink from fur farms in the United

Kingdom, the introduction of exotics can result from importation of animals for captive rearing.

C) **Cost of Placement**. While any payment will place a value on an animal, there is little evidence that trade would be encouraged if the institution receiving a donation of confiscated animals were to reimburse the confiscating authority for costs of care and transportation. However, payments should be explicitly for reimbursement of costs of confiscation and care, and, where possible, the facility receiving the animals should bear all such costs directly.

D) **Potential to Encourage Undesired Trade**. Some (e.g., Harcourt 1987) have maintained that any transfer - whether commercial or non-commercial - of confiscated animals risks promoting a market for these species and creating a perception of the confiscating state being involved in illegal or irregular trade.

Birdlife International (in prep.) suggests that in certain circumstances sale of confiscated animals does not necessarily promote undesired trade. They offer the following requirements that must be met for permissible sale by the confiscating authority: I) the species to be sold is already available for sale legally in the confiscating country in commercial quantities; and 2) wildlife traders under indictment for; or convicted of, crimes related to import of wildlife are prevented from purchasing the animals in question. However, experience in selling confiscated animals in the USA suggests that it is virtually impossible to ensure that commercial dealers suspected or implicated in illegal or irregular trade are excluded, directly or indirectly, in purchasing confiscated animals.

In certain circumstances sale or loan to commercial captive breeders may have a clearer potential for the conservation of the species, or welfare of the individuals, than non-commercial disposition or euthanasia. However, such breeding programmes must be carefully assessed as it may be difficult to determine the effects of these programmes on wild populations.

OPTION 2-- RETURN **TO THE WILD**

These guidelines suggest that return to the wild would be a desirable option in only a very small number of instances and under very specific circumstances. The rationale behind many of the decision options iii this section are discussed in greater detail in the IUCN Re-introduction Guidelines (IUCN/SSC RSG 1995) which, it is important to note, make a clear distinction between the different options for returning animals to the wild. These are elaborated below.

I) **Re-introduction**: an attempt to establish a population in an area that was once part of the range of the species but from which it has become extirpated.
Some of the best known re-introductions have been of species that had become extinct in the wild. Examples include: Pere David's deer (*Elaphurus davidanus*) and the Arabian

oryx (*Oryx leucoryx.*). Other re-introduction programmes have involved species that exist in some parts of their historical range but have been eliminated from other areas; the aim of these programmes is to re-establish a population in all area, or region, from which the species has disappeared. An example of this type of r~introduction is the recent re-introduction of the swift fox (*Vulpes velox*) in Canada.

2) **Reinforcement of an Existing Population**: the addition of individuals to all existing population of the same taxon.

Reinforcement can be a powerful conservation tool when natural populations are diminished by a process which, at least in theory, can be reversed. An example of a successful reinforcement project is the golden lion tamarin *(Leontopithecus rosalia)* project in Brazil. Habitat loss, coupled with capture of live animals for pets, resulted in a rapid decline of the golden lion tamarin. when reserves were expanded, and capture for the pet trade curbed, captive-bred golden lion tamarins were then used to supplement depleted wild populations.

Reinforcement has been most commonly pursued when individual animals injured by human activity have been provided with veterinary care and released. Such activities are common in many western countries, and specific programmes exist for species as diverse as hedgehogs and birds of prey. However common an activity, reinforcement carries with it the very grave risk that individuals held in captivity, even temporarily, are potential vectors for the introduction of disease into wild populations.

Because of inherent disease risks and potential behavioural abnormalities, reinforcement should only be employed in instances where there is a direct and measurable conservation benefit (demographically and/or genetically, and/or to enhance conservation in the public's eye), for example when reinforcement will significantly add to the viability of the wild population into which an individual is being placed.

3) **Conservation Introductions:** (also referred to as Beneficial or Benign Introductions - IUCN 1995): an attempt to establish a species, for the purpose of conservation, outside its recorded distribution but within a suitable habitat in which a population can be established without predicted detriment to native species.

Extensive use of conservation introductions has been made in New Zealand, where endangered birds have been transferred to off-shore islands that were adjacent to, but not part of the animals' original range. Conservation introductions can also be a component of a larger programme of re-introduction, an example being the breeding of red wolves on islands outside their natural range and subsequent transfer to mainland range areas (Smith 1990).

RETURN To THE WILD - CONCERNS

Before return to the wild of confiscated animals is considered, several issues of concern must be considered in general terms; welfare, conservation value, cost, and disease.

a) **Welfare**. While some consider return to the wild to be humane, ill-conceived projects may return animals to the wild which then die from starvation or suffer an inability to adapt to an unfamiliar or inappropriate environment. This is not humane. Humane considerations require that each effort to return confiscated animals to the wild be thoroughly researched and carefully planned. Such returns also require long-term commitment in terms of monitoring the fate of released individuals. Some (e.g., International Academy of Animal Welfare Sciences 1992) have advocated that the survival prospects for released animals must at least approximate those of wild animals of the same sex and age class in order for return to the wild to be seriously considered. While such demographic data on wild populations are, unfortunately, rarely available, the spirit of this suggestion should be respected -- there must be humane treatment of confiscated animals when attempting to return them to the wild.

b) **Conservation Value And Cost**. In cases where returning confiscated animals to the wild appears to be the most humane option, such action can only be undertaken if it does not threaten existing populations of conspecifics or populations of other interacting species, or the ecological integrity of the area in which they live. The conservation of the species as a whole, and of other animals already living free, must take precedent over the welfare of individual animals that are already in captivity.

Before animals are used in programmes in which existing populations are reinforced, or new populations are established, it must be determined that returning these individuals to the wild will make a significant contribution to the conservation of the species, or populations of other interacting species. Based solely on demographic considerations, large populations are less likely to go extinct, and therefore reinforcing existing very small wild populations may reduce the probability of extinction. In very small populations a lack of males or females may result in reduced population growth or population decline and, therefore, reinforcing a very small population lacking animals of a particular sex may also improve prospects for survival of that population. However, genetic and behavioural considerations, as well as the possibility of disease introduction, also play a fundamental role in determining the long term survival of a population.

The cost of returning animals to the wild in an appropriate manner can be prohibitive for all but the most endangered species (Stanley Price 1989; Seal et al. 1989). The species for which the conservation benefits clearly outweigh these costs represent a tiny proportion of the species which might, potentially, be confiscated In the majority of cases, the costs of appropriate, responsible (re)introduction will preclude return to the wild. Poorly planned or executed (re)introduction programmes are no better than dumping animals in the wild and should be vigorously opposed on both conservation and humane grounds.

c) **Founders And Numbers Required**. Most re-introductions require large numbers of founders, usually released in smaller groups over a period of time. Hence, small groups of confiscated animals may be inappropriate for re-introduction programmes, and even larger groups will require careful management if they are to have any conservation value for re-introduction programmes. In reality, confiscated specimens will most often only be of potential value for reinforcing an existing population, despite the many potential problems this will entail.

c) **Source of Individuals**. If the precise provenance of the animals is not known (they may be from several different provenances), or if there is any question of the source of animals, supplementation may lead to inadvertent pollution of distinct genetic races or sub~species. If particular local races or sub-species show specific adaptation to their local environments mixing in individuals from other races or sub-species may be damaging to the local population. Introducing an individual or individuals into the wrong habitat type may also doom that individual to death.

a) **Disease**. Animals held in captivity and/or transported, even for a very short time, may be exposed to a variety of pathogens. Release of these animals to the wild may result in introduction of disease to con-specifics or unrelated species with potentially catastrophic effects. Even if there is a very small risk that confiscated animals have been infected by exotic pathogens, the potential effects of introduced diseases on wild populations are so great that this will often prevent returning confiscated animals to the wild (Woodford and Rossiter 1993, papers in *J Zoo and Wildlife Medicine* 24(3), 1993).

Release of any animal into the wild which has been held in captivity is risky. Animals held in captivity are more likely to acquire diseases and parasites. While some of these diseases can be tested for, tests do not exist for many animal diseases. Furthermore, animals held in captivity are frequently exposed to diseases not usually encountered in their natural habitat. Veterinarians and quarantine officers, taking that the species in question is only susceptible to certain diseases, may not test for the diseases picked up in captivity. It should be assumed that all diseases are potentially contagious.

Given that any release incurs some risk, the following "precautionary principle" must be adopted: *if there is no conservation value in releasing confiscated specimens, the possibility of accidentally introducing a disease, or behavioural and genetic aberrations into the environment which are not already present, however unlikely, may rule out returning confiscated specimens to the wild as a placement option.*

RETURN TO THE WILD: BENEFITS

There are several benefits of returning animals to the wild, either through re-introduction for the establishment of a new population or reinforcement of an existing population.

a) **Threatened Populations**: In situations where the existing population is severely threatened, such an action might improve the long-term conservation potential of the species as a whole, or of a local population of the species (e.g., golden lion tamarins).

b) **Public Statement**: Returning animals to the wild makes a strong political/educational statement concerning the fate of animals (e.g., orangutans (*Pongo pygmaeus*) and chimpanzees (*Pan troglodytes*) - Aveling & Mitchell 1982, but see Rijksen & Rijksen-Graatsma 1979) and may serve to promote local conservation values. However, as part of any education or public awareness programmes, the costs and difficulties associated with the return to the wild must be emphasized.

OPTION 3- EUTHANASIA

Euthanasia: the killing of animals carried out according to humane guidelines -- is unlikely to be a popular option amongst confiscating authorities for disposition of confiscated animals. However, it cannot be over-stressed that euthanasia may frequently be the most feasible option available for economic, conservation and humane reasons. In many cases, authorities confiscating live animals will encounter the following situations:

a) Return to the wild in some manner is either unnecessary (e.g., in the case of a very common species), impossible, or prohibitively expensive as a result of the need to conform to biological (IUCN/SSC RSG ~995) and animal welfare guidelines (International Academy of Welfare Sciences 1992).

b) Placement in a captive facility is impossible, or there are serious concerns that sale will be problematic or controversial.

c) During transport, or while held in captivity, the animals have contracted a chronic disease that is incurable and, therefore, are a risk to any captive or wild population. In such situations, there may be no practical alternative to euthanasia.

EUTHANASIA -ADVANTAGES:

a) From the point of view of conservation of the species involved, and of protection of existing captive and wild populations of animals, euthanasia carries far fewer risks (e.g. loss of any unique behavioural/genetic/ecological variations within an individual representing variation within the species) when compared to returning animals to the wild.

b) Euthanasia will also act to discourage the activities that gave rise to confiscation, be it smuggling or other patently illegal trade, incomplete or irregular paperwork, poor packing, or other problems, as the animals in question are removed entirely from trade.

c) Euthanasia may be in the best interest of the welfare of the confiscated animals. Release to the wild will carry enormous risks for existing wild populations and may pose severe challenges to the survival prospects of the individual animals, who may, as a result, die of starvation, disease or predation.

d) Cost: euthanasia is cheap compared to other options. There is potential for diverting resources which might have been used for re-introduction or lifetime care to conservation of the species in the wild.

When animals are euthanized, or when they die a natural death while in captivity, the dead specimen should be placed in the collection of a natural history museum, or another reference collection in a university or research institute. Such reference collections are of great importance to studies of biodiversity. if such placement is impossible, carcasses should be incinerated to avoid illegal trade in animal parts or derivatives.

EUTHANASIA- RISKS

a) There is a risk of losing unique behavioural, genetic and ecological material within an individual or group of individuals that represents variation within a species.

DECISION TREE ANALYSIS

For decision trees dealing with "Return to the Wild" and "Captive Options" the confiscating party must first ask the question:

Question 1: Will "Return to the Wild" make a significant contribution to the conservation of the species?

The most important consideration in deciding on placement of confiscated specimens is the conservation of the species in question. Conservation interests are best served by ensuring the survival of as many individuals as possible. The release of confiscated animals therefore must improve the prospects for survival of the existing wild population. Returning an individual to the wild that has benn held in captivity will always involve some level of risk to existing populations of the same or other species in the ecosystem to which the animal is returned because there can never be absolute certainty that a confiscated animal is disease- and parasite-free. In most instances, the benefits of return to the wild will be outweighed by the costs and risks of such an action. If returning animals to the wild is not of conservation value, captive options pose fewer risks and may offer more humane alternatives.

Q1 Answer: No: Investigate "Captive Options"
Yes: Investigate "Return to the Wild Options"

DECISION TREE ANALYSIS: CAPTIVITY

The decision to maintain confiscated animals in captivity involves a simpler set of considerations than that involving attempts to return confiscated animals to the wild.

Question 2: Have animals been subjected to a comprehensive veterinary screening and quarantine?

Animals that may be transferred to captive facilities must have a clean bill of health because of the risk of introducing disease to captive populations.

Theses animals must be placed in quarantine to determine if they are disease-free before being transferred to a captive-breeding facility.

Q2 Answer: Yes: Proceed to Question 3.
No: Quarantine and screen and move to Question 3.

Question 3: Have animals been found to be disease-free by comprehensive veterinary screening and quarantine or can they be treated for any infection discovered?

If; during quarantine animals are found to harbour diseases that cannot reasonably be cured, they must be euthanized to prevent infection of other animals. If the animals are suspected to have come into contact with diseases for which screening is impossible, extended quarantine, donation to a research facility, or euthanasia must be considered.

Q3 Answer: Yes: Proceed to Question 4
No: If chronic and incurable infection, first offer animals to research institutions. impossible to place in such institutions, euthanize.

Question 4: Are there grounds for concern that sale will stimulate further illegal or irregular trade?

Commercial sale of Appendix I species is not permitted under the Convention as it is undesirable to stimulate trade in these species. Species not listed in any CITES appendix, but which are nonetheless seriously threatened with extinction, should be afforded the same caution.

Sale of confiscated animals, where legally permitted, is a difficult option to consider. while the benefits of sale -- income and quick disposition -- are clear, there are many problems that may arise as a result of further commercial transactions of the specimens involved. Equally, it should be noted that there may be circumstances where such problems arise as a result of a non-commercial transaction or that, conversely, sale to commercial captive breeders may contribute to production of young offsetting the capture from the wild.

More often than not, sale of threatened species should not take place. Such sales or trade in threatened species may be legally proscribed in some countries, or by CITES. There may be rare cases where a commercial captive breeding operation may purchase or receive individuals for breeding, which may reduce pressure on wild populations subject to trade. In all circumstances, the confiscating authority should be satisfied that:

1) those involved in the illegal or irregular transaction that gave rise to confiscation cannot obtain the animals;
2) the sale does not compromise the objective of confiscation; and, finally,
3) the sale will not increase illegal, irregular or otherwise undesired trade in the species.

Previous experience with sale in some countries (e.g., the USA) has indicated that selling confiscated animals is beset by both logistic and political problems and that, in addition to being controversial, it may also be counter-productive to conservation objectives.

Q4 Answer: Yes: Proceed to Question 5a.
No: Proceed to Question 5b.

Question 5a: Is space available in a non-commercial captive facility (e.g., life-time care facility, zoo, rescue centre, specialist society, their members or private individuals)?

Question 5b: Is space available in a non-commercial captive facility (e.g., life-time care facility, zoo, rescue centre, specialist society, their members or private individuals) or is there a commercial facility breeding this species, and is the facility interested in the animals?

Transfer of animals to non-commercial captive-breeding facilities, if sale may stimulate further illegal or irregular trade, or commercial captive breeding facilities, an option only if sale will not stimulate further illegal or irregular trade, should generally provide a safe and acceptable means of disposition of confiscated animals. when a choice must be made between several such institutions, the paramount consideration should be which facility can:

1) offer the opportunity for the animals to participate in a captive breeding programme;
2) provide the most consistent care; and
3) ensure the welfare of the animals.

The terms and conditions of the transfer should be agreed between the confiscating authority and the recipient institution. Terms and conditions for such agreements should include:

I) a clear commitment to ensure life-time care or, in the event that this becomes impossible, transfer to another facility that can ensure life-time care, or euthanasia;
2) clear specification of ownership of the specimens concerned (as determined by national law) and, where breeding may occur, the offspring. Depending on the circumstances, ownership may be vested with the confiscating authority, the country of origin or export, or with the recipient facility.
3) clear specification of conditions under which the animal(s) or their progeny may be sold.

In the majority of instances, there will be no facilities or zoo or aquarium space available in the country in which animals are confiscated. Where this is the case other captive options should be investigated. This could include transfer to a captive facility outside the country of confiscation particularly in the country of origin, or, if transfer will not stimulate further illegal trade, placement in a commercial captive breeding facility. However, these breeding programmes must be carefully assessed and approached with caution. It may be difficult to monitor these programmes and such programmes may unintentionally, or intentionally, stimulate trade in wild animals. The conservation potential of this transfer, or breeding loan, must be carefully weighed against even the smallest risk of stimulating trade which would further endanger the wild population of the species.

In many countries, there are active specialist societies or clubs of individuals with considerable expertise in the husbandry and breeding of individual Species or groups of Species. Such societies can assist in finding homes for confiscated animals without involving sale through intermediaries. In this case, individuals receiving confiscated animals must have demonstrated expertise in the husbandry of the species concerned and must be provided with adequate information and advice by the club or society concerned. Transfer to specialist societies or individual members must be made according to terms and conditions agreed with the confiscating authority. Such agreements may be the same or similar to those executed with Lifetime Care facilities or zoos. Placement with these societies or members is an option if sale of the confiscated animals may or may not stimulate trade.

Q5 Answer: Yes: Execute agreement and Sell
No: Proceed to Question 6.

Question 6: Are institutions interested in animals for research under humane conditions?

Many research laboratories maintain collections of exotic animals for research conducted under humane conditions. If these animals are kept in conditions that ensure their welfare, transfer to such institutions may provide an acceptable alterative to other options, such as sale or euthanasia. As in the preceding instances, such transfer should be subject to terms and conditions agreed with the confiscating authority; in addition to those already suggested, it may be advisable to include terms that stipulate the types of research the confiscating authority considers permissible. If no placement is possible, the animals should be euthanized.

Q6 Answer: Yes: Execute Agreement and Transfer.
No: Euthanize.

DECISION TREE ANALYSIS -- RETURN TO THE WILD

Question 2: Have animals been subjected to a comprehensive veterinary screening and quarantine?

Because of the risk of introducing disease to wild populations, animals that may be released must have a clean bill of health. These animals must be placed in quarantine to determine if they are disease free before being considered for released.

Q2 Answer: Yes: Proceed to Question 3.
No: Quarantine and screen and move to Question 3

Question 3: Have animals been found to be disease free by comprehensive veterinary screening and quarantine or can they be treated for any infection discovered?

1. If during quarantine, the animals are found to harbour diseases that cannot reasonably be cured, unless any institutions are interested in the animals for research under humane conditions, they must be euthanized to prevent infection of other animals. If the animals are suspected to have come into contact with diseases for which screening is impossible, extended quarantine, donation to a research facility, or euthanasia must be considered.

Q3 Answer: Yes: Proceed to Question 4
No: if chronic and incurable infection, first offer animals to research institutions. if impossible to place in such institutions, euthanize.

Question 4: Can country of origin and site of capture be confirmed?

The geographical location from which confiscated individuals have been removed from the wild must be determined if these individuals are to be re-introduced or used to supplement existing populations. In most cases, animals should only be returned to the population from which they were taken, or from populations which are known to have natural exchange of individuals with this population.

If provenance of the animals is not known, release for reinforcement may lead to inadvertent hybridisation of distinct genetic races or sub-species. Related species of animals that may live in sympatry in the wild and never hybridise have been known to hybridise when held in captivity or shipped in multi-Species groups. This type of generalisation of species recognition under abnormal conditions can result in behavioural problems compromising the success of any future release and can also pose a threat to wild populations by artificially destroying reproductive isolation that is behaviourally mediated.

Q4 Answer: Yes: Proceed to Question 5.
No: Pursue 'Captive Options'.

Question 5: Do the animals exhibit behavioural abnormalities which might make them unsuitable for return to the wild?

Behavioural abnormalities as a result of captivity can result in animals which are not suitable for release into the wild. A wide variety of behavioural traits and specific behavioural skills are necessary for survival, in the short-term for the individual, and in the long-term for the population. Skills for hunting, avoiding predators, food selectivity etc. are necessary to ensure survival.

Q5 Answer: Yes: Pursue 'Captive Options'.
No; Proceed to Question 6.

Question 6:Can individuals be returned expeditiously to origin (specific location), and will benefits to conservation of the species outweigh any risks of such action?

Repatriation of the individual and reinforcement of the population will only be options under certain conditions and following the IUCN/RSG 1995 guidelines:

1) Appropriate habitat for such an operation still exists in the specific location that the individual was removed from; and
2) sufficient funds are available, or can be made available.

Q6 Answer: Yes: Repatriate and reinforce at origin (specific location) following IUCN guidelines.
No: Proceed to Question 7.

Question 7: For the species in question, does a generally recognized programme exist whose aim is conservation of the species and eventual return to the wild of confiscated individuals and or their progeny? Contact IUCN/SSC, IUDZG, Studbook Keeper, or Breeding Programme Coordinator.

In the case of Species for which active captive breeding and or re-introduction programmes exist, and for which further breeding stock/founders are required, confiscated animals should be transferred to such programmes after consultation with the appropriate scientific authorities. If the Species in question is part of a captive breeding programme, but the taxon (sub-species or race) is not part of this programme (e.g. Maguire & Lacy 1990), other methods of disposition must be considered. Particular attention should be paid to genetic screening to avoid jeopardizing captive breeding programmes through inadvertent hybridisation.

Q7 Answer: Yes: Executer agreement and transfer to existing programme.
No: Proceed to Question 8.

Question 8: Is there a need and is it feasible to establish a new r~introduction programme following IUCN Guidelines?

In cases where individuals cannot be transferred to existing r~introduction programmes, return to the wild, following appropriate guidelines, will only be possible under the following circumstances: 1) appropriate habitat exists for such an operation; 2) sufficient funds are available, or can be made available, to support a programme over the many years that (re)introduction will require; and 3) either sufficient numbers of animals are available so that re-introduction efforts are potentially viable, or only reinforcement of existing populations is considered. In the majority of cases, at least one, if not all, of these requirements will fail to be met. In this instance, either conservation introductions outside the historical range of the Species or other options for disposition of the animals must be considered.

It should be emphasized that if a particular species or taxon is confiscated with some frequency, consideration should be made as to whether to establish a re-introduction, reinforcement, or introduction programme. Animals should not be held by the confiscating authority indefinitely while such programmes are planned, but should be transferred to a holding facility after consultation with the organization which is establishing the new programme.

Q8 Answer: Yes: Execute agreement and transfer to holding facility or new programme.
No: Pursue 'Captive Options'.

References

Aveling, R. & Mitchell A.H. (1982). Is rehabilitating orang utans worthwhile? Oryx 16: 263-271.

BirdLife International (in prep). Parrots: An Action Plan for their Conservation. (BirdLife International, Cambridge: England).

Harcourt, A. H. (1987). *Options for unwanted or confiscated primates.* Primate Conservation 8:111-113.

International Academy of Animal Welfare Sciences (1992). *Welfare guidelines for the re-introduction of captive-bred mammals to the wild.* (Universities Federation for Animal Welfare, Potters Bar: United Kingdom).

IUCN (1987). *The IUCN position statement on translocation of living organisms: introductions, re-introductions and restocking.* (IUCN, Gland: Switzerland).

IUCN/SSC RSG (1995). *Draft guidelines for re-introductions.* Species Survival Commission Re-introduction Specialist Group, IUCN - The World Conservation Union.

IUDZG/CBSG (IUCN/SSC) 1993. *The World Zoo Conservation Strategy. The Role of Zoos and Aquaria of the World in Global Conservation.* IUDZG - the World Zoo Organization.

Maguire, L.A. and Lacy, W. C. (1990). Allocating scarce resources for conservation of endangered sub-Species: partitioning zoo space for tigers. Conservation Biology 4, 156-157.

Rijksen, H. D. & Rijksen-Graatsma, A. (1979). Rehabilitation, a new approach is needed. Tigerpaper 6:16-18.

Seal, U.S. & Foose, T. (1992). Captive Animal Management Program (CAMP) Summary Report. (IUCN-CBSG, Apple Valley, Minnesota: USA).

Smith, R. (1990). Island Update. Red Wolf Newsletter 2(1): 2-3.

Stanley Price, M. W. (1989) *Animal re-introduction: the Arabian oryx in Oman.* Cambridge studies in applied ecology and resource management. (Cambridge University Press, Cambridge).

DRAFT GUIDELINES FOR RE-INTRODUCTIONS

Introduction

These policy guidelines have been drafted by the Re-introduction Specialist Group of the IUCN's Species Survival Commission (Guidelines for determining procedures for disposal of species confiscated in trade are being developed separately by IUCN for CITES.) in response to the increasing occurrence of reintroduction projects world-wide, and consequently, to the growing need for specific policy guidelines to help ensure that the re-introductions achieve their intended conservation benefit, and do not cause adverse side-effects of greater impact. Although the IUCN developed a Position Statement on the Translocation of Living Organisms in 1987, more detailed guidelines were felt to be essential in providing more comprehensive coverage of the various factors involved in re-introduction exercises.

These guidelines are intended to act as a guide for procedures useful to re-introduction programmes and do not represent an inflexible code of conduct. Many of the points are more relevant to re-introductions using captive-bred individuals than to translocation of wild species. Others are especially relevant to globally endangered species with limited numbers of founders. Each re-introduction proposal should be rigorously reviewed on its individual merits. On the whole, it should be noted that re-introduction is a very lengthy and complex process.

This document is very general, and worded so that it covers the full range of plant and animal taxa. It will be regularly revised. Handbooks for re-introducing individual groups of animals and plants will be developed in future.

1. Definition of Terms

a. "Re-introduction":

An attempt to establish a species (The taxonomic unit referred to throughout the document is species: it may be a lower taxonomic unit [e.g. sub-species or race] as long as it can be unambiguously defined.) in an area which was once part of its historical range, but from which it has become extinct (CITES criterion of "extinct": species not definitely located in the wild during the past 50 years of conspecifics.). ("Re-establishment" is a synonym, but implies that the re-introduction has been successful) .

b. Translocation":

Deliberate and mediated movement of wild individuals or populations from one part of their range to another.

c. "Reinforcement/Supplementation:

Addition of individuals to an existing population.

d. Conservation/Benign Introductions:

An attempt to establish a species, for the purpose of conservation, outside its recorded distribution but within an appropriate habitat and eco-geographical area.

2. Aims and Objectives of the Re-Introduction

a. Aims:

A re-introduction should aim to establish a viable, free-ranging population in the wild, of a species or subspecies which was formerly globally or locally extinct (extirpated). In some circumstances, a re-introduction may have to be made into an area which is fenced or otherwise delimited, but it should be within the species' former natural habitat and range, and require minimal long-term management.

b. Objectives:

The objectives of a re-introduction will include: to enhance the long-term survival of a species; to re-establish a keystone species (in the ecological or cultural sense) in an ecosystem; to maintain natural biodiversity; to provide long-term economic benefits to the local and/or national economy; to promote conservation awareness; or a combination of these.

Re-introductions or translocation of species for short-term, sporting or commercial purposes - where there is no intention to establish a viable population - are a different issue, beyond the scope of these guidelines. These include fishing an(I hunting activities.

3. Multi disciplinary Approach

A re-introduction requires a Multi disciplinary approach involving a team of persons drawn from a variety of backgrounds. They may include persons from: governmental natural resource management agencies; non-governmental organizations; funding bodies; universities; veterinary institutions; zoos (and private animal breeders) and/or botanic gardens, with a full range of suitable expertise. Team leaders should be responsible for coordination between the various bodies and provision should be made for publicity and public education about the project.

4. Pre-Project Activities

a. Biological:

(I) Feasibility study and background research

- An assessment should be made of the taxonomic status of individuals to be re-introduced. They must be of the same subspecies as those which were extirpated, unless adequate numbers are not available. An investigation of historical information about the loss and fate of individuals from the re-introduction area, as well as molecular genetic studies, should be undertaken in case of doubt. A study of genetic variation within and between populations of this and related taxa can also be helpful. Special care is needed when the population has long been extinct.

- Detailed studies should be made of the status and biology of wild populations (if they exist) to determine the species' critical needs; for animals, this would include descriptions of habitat preferences, intra specific variation and adaptations to local ecological conditions, social behavior, group composition, home range size, shelter and food requirements, foraging and feeding behavior, predators and diseases. For plants it would include biotic and abiotic habitat requirements, dispersal mechanisms, reproductive biology, symbiotic relationships (e.g. with mycorrhizae, pollinators), insect pests and diseases. Overall, a firm knowledge of the natural history of the species in question is crucial to the entire re-introduction scheme.

- The build-up of the released population should be modeled under various sets of conditions, in order to specify the optimal number and composition of individuals to be released per year and the numbers of years necessary to promote establishment of a viable population.

- A Population and Habitat Viability Analysis will aid in identifying significant environmental and population variables and assessing their potential interactions, which would guide long-term population management.

(ii) Previous Re-introductions

- Thorough research into previous re-introductions of the same or similar species and wide-ranging contacts with persons having relevant expertise should be conducted prior to and while developing re-introduction protocol.

(iii) Choice of release site

- Site should be within the historic range of species and for an initial reinforcement or re-introduction have very few, or no, remnant wild individuals (to prevent disease spread, social disruption and introduction of alien genes). A conservation/ benign introduction should be undertaken only as a last resort when no opportunities for re-introduction into the original site or range exist.

- The re-introduction area should have assured, long-term protection (whether formal or otherwise).

(iv) Evaluation of re-introduction site

- Availability of suitable habitat: re-introductions should only take place where the habitat and landscape requirements of the species are satisfied, and likely to be sustained for the for-seeable future. The possibility of natural habitat change since extirpation must be considered. The area should have sufficient carrying capacity to sustain growth of the re-introduced population and support a viable (self-sustaining) population in the long run.

- Identification and elimination of previous causes of decline: could include disease; over-hunting; over-collection; pollution; poisoning; competition with or predation by introduced species; habitat loss; adverse effects of earlier research or management programmes; competition with domestic livestock, which may be seasonal.

- Where the release site has undergone substantial degradation caused by human activity, a habitat restoration programme should be initiated before the reintroduction is carried out.

(v) Availability of suitable release stock

- Release stock should be ideally closely-related genetically to the original native stock.

- If captive or artificially propagated stock is to be used, it must be from a population which has been soundly managed both demographically and genetically, according to the principles of contemporary conservation biology.

- Re-introductions should not be carried out merely because captive stocks exist, nor should they be a means of disposing of surplus stock.

- Removal of individuals for re-introduction must not endanger the captive stock population or the wild source population. Stock must be guaranteed available on a regular and predictable basis, meeting specifications of the project protocol.

- Prospective release stock must be subjected to a thorough veterinary screening process before shipment from original source. Any animals found to be infected or which test positive for selected pathogens must be removed from the consignment, and the uninfected, negative remainder must be placed in strict quarantine for a suitable period before retest. If clear after retesting, the animals may be placed for shipment.

- Since infection with serious disease can be acquired during shipment, especially if this is intercontinental, great care must be taken to minimize this risk.

- Stock must meet all health regulations prescribed by the veterinary authorities of the recipient country and adequate provisions must be made for quarantine if necessary.

- Individuals should only be removed from a wild population after the effects of translocation on the donor population have been assessed, and after it is guaranteed that these effects will not be negative.

b. Socio-Economic and Legal Activities

- Re-introductions are generally long-term projects that require the commitment of long-term financial and political support.

- Socio-economic studies should be made to assess costs and benefits of the e-introduction programme to local human populations.

- A thorough assessment of attitudes of local people to the proposed project is necessary to ensure long term protection of the re-introduced population, especially if the cause of species' decline was due to human factors (e.g. over-hunting, over-collection, loss of habitat). The programme should be fully understood, accepted and supported by local communities.

- Where the security of the re-introduced population is at risk from human activities, measures should be taken to minimize these in the re-introduction area. If these measures are inadequate, the re-introduction should be abandoned or alternative release areas sought.

- The policy of the country to re-introductions and to the species concerned should be assessed. This might include checking existing national and international legislation and regulations, and provision of new measures as necessary. Re-introduction must take place with the full permission and involvement of all relevant government agencies of the recipient or host country. This is particularly important in re-introductions in border areas, or involving more than one state.

- If the species poses potential risk to life or property, these risks should be minimized and adequate provision made for compensation where necessary; where all other solutions fail, removal or destruction of the released individual should be considered.

In the case of migratory/mobile species, provisions should be made for crossing of international/state boundaries.

5. Planning. Preparation and Release Stages

- Construction of a Multi disciplinary team with access to expert technical advice for all phases of the programme.

- Approval of all relevant government agencies and land owners, and coordination with national and international conservation organizations.

- Development of transport plans for delivery of stock to the country and site of re-introduction, with special emphasis on ways to minimize stress on the individuals during transport.

- Identification of short-and long-term success indicators and prediction of programme duration, in context of agreed aims and objectives.

- Securing adequate funding for all programme phases.

- Design of pre- and post- release monitoring programme so that each re-introduction is a carefully designed experiment, with the capability to test methodology with scientifically collected data.

- Appropriate health and genetic screening of release stock. Health screening of closely related species in re-introduction area.

- If release stock is wild-caught, care must be taken to ensure that: a) the stock is free from infectious or contagious pathogens and parasites before shipment and b) the stock will not be exposed to vectors of disease agents which may be present at the release site (and absent at the source site) and to which it may have no acquired immunity.

- If vaccination prior to release, against local endemic or epidemic diseases of wild stock or domestic livestock at the release site, is deemed appropriate, this must be carried out during the "Preparation Stage" so as to allow sufficient time for the development of the required immunity.

- Appropriate veterinary or horticultural measures to ensure health of released stock throughout programme. This is to include adequate quarantine arrangements, especially where founder stock travels far or crosses international boundaries to release site.

- Determination of release strategy (acclimatization of release stock to release area; behavioral training - including hunting and feeding; group composition, number, release patterns and techniques; timing).

- Establishment of policies on interventions (see below).

- Development of conservation education for long-term support; professional training of individuals involved in long-term programme; public relations through the mass media and in local community; involvement where possible of local people in the programme.

- The welfare of animals for release is of paramount concern through all these stages.

6. Post-Release Activities

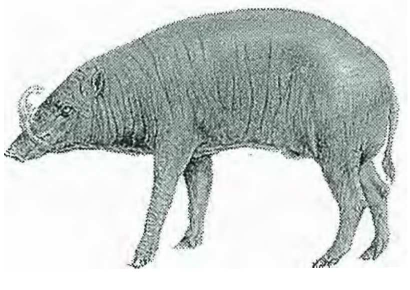
- Post release monitoring of all (or sample of) individuals. This most vital aspect may be by direct (e.g. tagging, telemetry) or indirect (e.g. spoor, informants) methods as suitable.

- Demographic, ecological and behavioral studies of released stock.
- Study of processes of long-term adaptation by individuals and the population.
- Collection and investigation of mortalities.
- Interventions (e.g. supplemental feeding; veterinary aid; horticultural aid) when necessary.
- Decisions for revision rescheduling, or discontinuation of programme where necessary.
- Habitat protection or restoration to continue where necessary.
- Continuing public relations activities, including education and mass media coverage.
- Evaluation of cost-effectiveness and success of re- introduction techniques.
- Regular publications in scientific and popular literature.

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE BABIRUSA (*Babyrousa babyrussa*)

Taman Safari Indonesia
22 - 26 July 1996

Section 9
Appendix IV:
VORTEX Technical Reference



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VORTEX: A Computer Simulation Model for Population Viability Analysis

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Abstract

Population Viability Analysis (PVA) is the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process. Extrinsic forces, such as habitat loss, over-harvesting, and competition or predation by introduced species, often lead to population decline. Although the traditional methods of wildlife ecology can reveal such deterministic trends, random fluctuations that increase as populations become smaller can lead to extinction even of populations that have, on average, positive population growth when below carrying capacity. Computer simulation modelling provides a tool for exploring the viability of populations subjected to many complex, interacting deterministic and random processes. One such simulation model, VORTEX, has been used extensively by the Captive Breeding Specialist Group (Species Survival Commission, IUCN), by wildlife agencies, and by university classes. The algorithms, structure, assumptions and applications of VORTEX are described in this paper.

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, to determine the number of progeny produced by each female each year, and to determine which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Fecundity is assumed to be independent of age after an animal reaches reproductive age. Mortality rates are specified for each pre-reproductive age–sex class and for reproductive-age animals. Inbreeding depression is modelled as a decrease in viability in inbred animals.

The user has the option of modelling density dependence in reproductive rates. As a simple model of density dependence in survival, a carrying capacity is imposed by a probabilistic truncation of each age class if the population size exceeds the specified carrying capacity. VORTEX can model linear trends in the carrying capacity. VORTEX models environmental variation by sampling birth rates, death rates, and the carrying capacity from binomial or normal distributions. Catastrophes are modelled as sporadic random events that reduce survival and reproduction for one year. VORTEX also allows the user to supplement or harvest the population, and multiple subpopulations can be tracked, with user-specified migration among the units.

VORTEX outputs summary statistics on population growth rates, the probability of population extinction, the time to extinction, and the mean size and genetic variation in extant populations.

VORTEX necessarily makes many assumptions. The model it incorporates is most applicable to species with low fecundity and long lifespans, such as mammals, birds and reptiles. It integrates the interacting effects of many of the deterministic and stochastic processes that have an impact on the viability of small populations, providing opportunity for more complete analysis than is possible by other techniques. PVA by simulation modelling is an important tool for identifying populations at risk of extinction, determining the urgency of action, and evaluating options for management.

Introduction

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat, have been reduced to one or more small, isolated populations. The causes of the original decline are often obvious, deterministic forces, such as over-harvesting,

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habitat destruction, and competition or predation from invasive introduced species. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990). Of particular impact on small populations are stochastic processes. With the exception of aging, virtually all events in the life of an organism are stochastic. Mating, reproduction, gene transmission between generations, migration, disease and predation can be described by probability distributions, with individual occurrences being sampled from these distributions. Small samples display high variance around the mean, so the fates of small wildlife populations are often determined more by random chance than by the mean birth and death rates that reflect adaptations to their environment.

Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The use of simulation modelling, often in conjunction with other techniques, to explore the dynamics of small populations has been termed Population Viability Analysis (PVA). PVA has been increasingly used to help guide management of threatened species. The Resource Assessment Commission of Australia (1991) recently recommended that 'estimates of the size of viable populations and the risks of extinction under multiple-use forestry practices be an essential part of conservation planning'. Lindenmayer *et al.* (1993) describe the use of computer modelling for PVA, and discuss the strengths and weaknesses of the approach as a tool for wildlife management.

In this paper, I present the PVA program VORTEX and describe its structure, assumptions and capabilities. VORTEX is perhaps the most widely used PVA simulation program, and there are numerous examples of its application in Australia, the United States of America and elsewhere.

The Dynamics of Small Populations

The stochastic processes that have an impact on populations have been usefully categorised into demographic stochasticity, environmental variation, catastrophic events and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate and sex ratio of a population even if the probabilities of birth and death remain constant. On the assumption that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be important to population viability only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means. The distribution of annual adult survival rates observed in the remnant population of whooping cranes (*Grus americana*) (Mirande *et al.* 1993) is shown in Fig. 1. The innermost curve approximates the binomial distribution that describes the demographic stochasticity expected when the probability of survival is 92·7% (mean of 45 non-outlier years).

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The second narrowest curve on Fig. 1 shows a normal distribution that statistically fits the observed frequency histogram of crane survival in non-outlier years. The difference between this curve and the narrower distribution describing demographic variation must be accounted for by environmental variation in the probability of adult survival.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analysed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease,

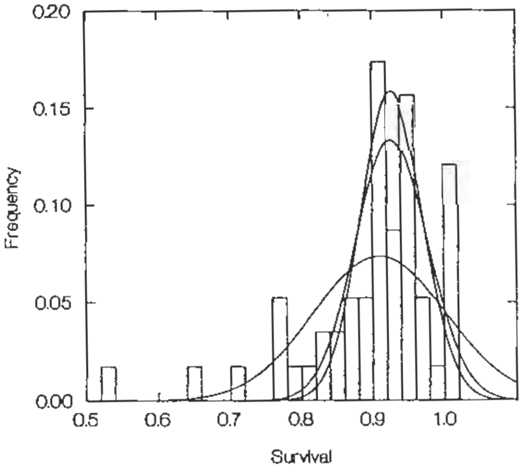

Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938–90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution that most closely fits the histogram, excluding the five leftmost bars (7 outlier 'catastrophe' years). The narrowest and tallest curve is the normal approximation to the binomial distribution expected from demographic stochasticity. The difference between the tallest and second tallest curves is the variation in annual survival due to environmental variation.

hurricanes, large-scale fires, and floods are outliers in the distribution of environmental variation (e.g. five leftmost bars on Fig. 1). As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls *et al.* 1988; Lacy *et al.* 1993). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations have a negative impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerate genetic drift (Crow and Kimura 1970). These synergistic destabilising effects of stochastic process on small populations of wildlife have been described as an 'extinction vortex' (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered a 'minimum viable population' (MVP) (Seal and Lacy 1989), although Shaffer (1981) first defined a MVP more stringently as a population that has a 99% probability of persistence for 1000 years. The estimation of MVPs or, more generally, the investigation of the probability of extinction constitutes PVA (Gilpin and Soulé 1986; Gilpin 1989; Shaffer 1990).

Methods for Analysing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction–recolonisation dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991). Because demographic and genetic processes in small populations are inherently unpredictable, the expected fates of wildlife populations can be described in terms of probability distributions of population size, time to extinction, and genetic variation. These distributions can be obtained in any of three ways: from analytical models, from empirical observation of the fates of populations of varying size, or from simulation models.

As the processes determining the dynamics of populations are multiple and complex, there are few analytical formulae for describing the probability distributions (e.g. Goodman 1987; Lande 1988; Burgmann and Gerard 1990). These models have incorporated only few of the threatening processes. No analytical model exists, for example, to describe the combined effect of demographic stochasticity and loss of genetic variation on the probability of population persistence.

A few studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g. Belovsky 1987; Berger 1990; Thomas 1990), but presently only order-of-magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). Threatened species are, by their rarity, unavailable and inappropriate for the experimental manipulation of population sizes and long-term monitoring of undisturbed fates that would be necessary for precise empirical measurement of MVPs. Retrospective analyses will be possible in some cases, but the function relating extinction probability to population size will differ among species, localities and times (Lindenmayer *et al.* 1993).

Modelling the Dynamics of Small Populations

Because of the lack of adequate empirical data or theoretical and analytical models to allow prediction of the dynamics of populations of threatened species, various biologists have turned to Monte Carlo computer simulation techniques for PVA. By randomly sampling from defined probability distributions, computer programs can simulate the multiple, interacting events that occur during the lives of organisms and that cumulatively determine the fates of populations. The focus is on detailed and explicit modelling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations. Computer programs available to PVA include SPGPC (Grier 1980*a*, 1980*b*), GAPPS (Harris *et al.* 1986), RAMAS (Ferson and Akçakaya 1989; Akçakaya and Ferson 1990; Ferson 1990), FORPOP (Possingham *et al.* 1991), ALEX (Possingham *et al.* 1992), and SIMPOP (Lacy *et al.* 1989; Lacy and Clark 1990) and its descendant VORTEX.

SIMPOP was developed in 1989 by converting the algorithms of the program SPGPC (written by James W. Grier of North Dakota State University) from BASIC to the C programming language. SIMPOP was used first in a PVA workshop organised by the Species Survival Commission's Captive Breeding Specialist Group (IUCN), the United States Fish and Wildlife Service, and the Puerto Rico Department of Natural Resources to assist in planning and assessing recovery efforts for the Puerto Rican crested toad (*Peltophryne lemur*). SIMPOP was subsequently used in PVA modelling of other species threatened with extinction, undergoing modification with each application to allow incorporation of additional threatening processes. The simulation program was renamed VORTEX (in reference to the extinction vortex) when the capability of modelling genetic processes was implemented in 1989. In 1990, a version allowing modelling of multiple populations was briefly named VORTICES. The only version still supported, with all capabilities of each previous version, is VORTEX Version 5.1.

VORTEX has been used in PVA to help guide conservation and management of many species, including the Puerto Rican parrot (*Amazona vittata*) (Lacy *et al.* 1989), the Javan rhinoceros (*Rhinoceros sondaicus*) (Seal and Foose 1989), the Florida panther (*Felis concolor coryi*) (Seal and Lacy 1989), the eastern barred bandicoot (*Perameles gunnii*) (Lacy and Clark 1990; Maguire *et al.* 1990), the lion tamarins (*Leontopithecus rosalia* ssp.) (Seal *et al.* 1990), the brush-tailed rock-wallaby (*Petrogale penicillata penicillata*) (Hill 1991), the mountain pygmy-possum (*Burramys parvus*), Leadbeater's possum (*Gymnobelideus leadbeateri*), the long-footed potoroo (*Potorous longipes*), the orange-bellied parrot (*Neophema chrysogaster*) and the helmeted honeyeater (*Lichenostomus melanops cassidix*) (Clark *et al.* 1991), the whooping crane (*Grus americana*) (Mirande *et al.* 1993), the Tana River crested mangabey (*Cercocebus galeritus galeritus*) and the Tana River red colobus (*Colobus badius rufomitratus*) (Seal *et al.* 1991), and the black rhinoceros (*Diceros bicornis*) (Foose *et al.* 1992). In some of these PVAs, modelling with VORTEX has made clear the insufficiency of past management plans to secure the future of the species, and alternative strategies were proposed, assessed and implemented. For example, the multiple threats to the Florida panther in its existing habitat were recognised as probably insurmountable, and a captive breeding effort has been initiated for the purpose of securing the gene pool and providing animals for release in areas of former habitat. PVA modelling with VORTEX has often identified a single threat to which a species is particularly vulnerable. The small but growing population of Puerto Rican parrots was assessed to be secure, except for the risk of population decimation by hurricane. Recommendations were made to make available secure shelter for captive parrots and to move some of the birds to a site distant from the wild flock, in order to minimise the damage that could occur in a catastrophic storm. These recommended actions were only partly implemented when, in late 1989, a hurricane killed many of the wild parrots. The remaining population of about 350 Tana River red colobus were determined by PVA to be so fragmented that demographic and genetic processes within the 10 subpopulations destabilised population dynamics. Creation of habitat corridors may be necessary to prevent extinction of the taxon. In some cases, PVA modelling has been reassuring to managers: analysis of black rhinos in Kenya indicated that many of the populations within sanctuaries were recovering steadily. Some could soon be used to provide animals for re-establishment or supplementation of populations previously eliminated by poaching. For some species, available data were insufficient to allow definitive PVA with VORTEX. In such cases, the attempt at PVA modelling has made apparent the need for more data on population trends and processes, thereby helping to justify and guide research efforts.

Description of VORTEX

Overview

The VORTEX computer simulation model is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events, on wildlife populations. VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables, following user-specified distributions. The input parameters used by VORTEX are summarised in the first part of the sample output given in the Appendix.

VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. The program was designed to model long-lived species with low fecundity, such as mammals, birds and reptiles. Although it could and has been used in modelling highly fecund vertebrates and invertebrates, it is awkward to use in such cases as it requires complete specification of the percentage of females producing each possible clutch size. Moreover, computer memory limitations often hamper such analyses. Although VORTEX iterates life events on an annual cycle, a user could model 'years' that are other than 12 months' duration. The simulation of the population is itself iterated to reveal the distribution of fates that the population might experience.

Demographic Stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination and death with a pseudo-random number generator. The probabilities of mortality and reproduction are sex-specific and pre-determined for each age class up to the age of breeding. It is assumed that reproduction and survival probabilities remain constant from the age of first breeding until a specified upper limit to age is reached. Sex ratio at birth is modelled with a user-specified constant probability of an offspring being male. For each life event, if the random value sampled from the uniform 0–1 distribution falls below the probability for that year, the event is deemed to have occurred, thereby simulating a binomial process.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), according to the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value, according to

$$N = p(1-p)/s^2 .$$

N binomial trials are then simulated by sampling from the uniform 0–1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

The 'carrying capacity', or the upper limit for population size within a habitat, must be specified by the user. VORTEX imposes the carrying capacity via a probabilistic truncation whenever the population exceeds the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation.

Environmental Variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions. Environmental variation in carrying capacity is modelled as a normal distribution. The variance across years in the frequencies of births and deaths resulting from the simulation model (and in real populations) will have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and additional fluctuations due to environmental variation and catastrophes (see Fig. 1 and section on The Dynamics of Small Populations, above).

Data on annual variations in birth and death rates are important in determining the probability of extinction, as they influence population stability (Goodman 1987). Unfortunately, such field information is rarely available (but see Fig. 1). Sensitivity testing, the examination of a range of values when the precise value of a parameter is unknown, can help to identify whether the unknown parameter is important in the dynamics of a population.

Catastrophes

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. Any number of types of catastrophes can be modelled. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors by 50% for the year. Such a catastrophe would be modelled as a random event with 0·02 probability of occurrence each year, and severity factors of 0·75 for survival and 0·50 for reproduction.

Genetic Processes

Genetic drift is modelled in VORTEX by simulation of the transmission of alleles at a hypothetical locus. At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring is randomly assigned one of the alleles from each parent. Inbreeding depression is modelled as a loss of viability during the first year of inbred animals. The impacts of inbreeding are determined by using one of two models available within VORTEX: a Recessive Lethals model or a Heterosis model.

In the Recessive Lethals model, each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive lethal allele in its genome. The fact that the simulation program assumes that all the lethal alleles are at the same locus has a very minor impact on the probability that an individual will die because of homozygosity for one of the lethal alleles. In the model, homozygosity for different lethal alleles are mutually exclusive events, whereas in a multilocus model an individnal could be homozygous for several lethal alleles simultaneously. By virtue of the death of individuals that are homozygous for lethal alleles, such alleles would be removed slowly by natural selection during the generations of a simulation. This reduces the genetic variation present in the population relative to the case with no inbreeding depression, but also diminishes the subsequent probability that inbred individuals will be homozygous for a lethal allele. This model gives an optimistic reflection of the impacts of inbreeding on many species, as the median number of lethal equivalents per diploid genome observed for mammalian populations is about three (Ralls *et al.* 1988).

The expression of fully recessive deleterious alleles in inbred organisms is not the only genetic mechanism that has been proposed as a cause of inbreeding depression. Some or most of the effects of inbreeding may be a consequence of superior fitness of heterozygotes (heterozygote advantage or 'heterosis'). In the Heterosis model, all homozygotes have reduced fitness compared with heterozygotes. Juvenile survival is modelled according to the logarithmic model developed by Morton *et al.* (1956):

$$\ln S = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is a measure of the rate at which survival decreases with inbreeding. B is termed the number of 'lethal equivalents' per haploid genome. The number of lethal equivalents per diploid genome, $2B$, estimates the number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual (as in the Recessive Lethals model, above), it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles that equate in effect with one lethal allele per individual. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at heterotic loci because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under the Heterosis model, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.

Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects varies considerably among species (Falconer 1981; Ralls *et al.* 1988; Lacy *et al.* 1993). Moreover, whether a Recessive Lethals model or a Heterosis model better describes the underlying mechanism of inbreeding depression and therefore the response to repeated generations of inbreeding is not well-known (Brewer *et al.* 1990), and could be determined empirically only from breeding studies that span many generations. Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterosis), applications of PVA must make assumptions about the effects of inbreeding on the population being studied. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in accord with the median (3·14 lethal equivalents per diploid) reported in the survey by Ralls *et al.* (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0·90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5·62 lethal equivalents).

Deterministic Processes

VORTEX can incorporate several deterministic processes. Reproduction can be specified to be density-dependent. The function relating the proportion of adult females breeding each year to the total population size is modelled as a fourth-order polynomial, which can provide a close fit to most plausible density-dependence curves. Thus, either positive population responses to low-density or negative responses (e.g. Allee effects), or more complex relationships, can be modelled.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodelled) population. The numbers of additions and removals are specified according to the age and sex of animals. Trends in the carrying capacity can also be modelled in VORTEX, specified as an annual percentage change. These changes are modelled as linear, rather than geometric, increases or decreases.

Migration among Populations

VORTEX can model up to 20 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. This probability is independent of the age and sex. Because of between-population migration and managed supplementation, populations can be recolonised. VORTEX tracks the dynamics of local extinctions and recolonisations through the simulation.

Output

VORTEX outputs (1) probability of extinction at specified intervals (e.g., every 10 years during a 100-year simulation), (2) median time to extinction if the population went extinct in at least 50% of the simulations, (3) mean time to extinction of those simulated populations that became extinct, and (4) mean size of, and genetic variation within, extant populations (see Appendix and Lindenmayer *et al.* 1993).

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction (SE) is reported by VORTEX as

$$SE(p) = \sqrt{[p \times (1-p)/n]} \, ,$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Availability of the VORTEX Simulation Program

VORTEX Version 5.1 is written in the C programming language and compiled with the Lattice 80286C Development System (Lattice Inc.) for use on microcomputers using the MS-DOS (Microsoft Corp.) operating system. Copies of the compiled program and a manual for its use are available for nominal distribution costs from the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124, U.S.A. The program has been tested by many workers, but cannot be guaranteed to be error-free. Each user retains responsibility for ensuring that the program does what is intended for each analysis.

Sequence of Program Flow

(1) The seed for the random number generator is initialised with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for input and output devices, population parameters, duration of simulation, and number of interations.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as

$$N_{max} = (K + 3s) \times (1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change linearly for a number of years in a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size. It is theoretically possible, but very unlikely, that a simulated population will exceed the calculated N_{max}. If this occurs then the program will give an error message and abort.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning it has been adjusted downward because of limiting memory often will not hamper the analyses. Except for limitations imposed by the size of the computer memory (VORTEX can use extended memory, if available), the only limit to the size of the analysis is that no more than 20 populations exchanging migrants can be simulated.

(5) The expected mean growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also estimated. Life-table estimations assume no limitation by carrying capacity, no limitation of mates, and no loss of fitness due to inbreeding depression, and the estimated intrinsic growth rate assumes that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life-table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7–26 below. For exploratory modelling, 100 iterations are usually sufficient to reveal gross trends among sets of simulations with different input parameters. For more precise examination of population behaviour under various scenarios, 1000 or more simulations should be used to minimise standard errors around mean results.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age–sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. VORTEX therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy–Weinberg equilibrium, is given by

$$H_e = 1 - \Sigma(p_i^2)\,,$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1·0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity by means of random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (assuming that the initial value was not zero) (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by VORTEX is the mean inbreeding coefficient of the population.

(9) The user specifies one of three options for modelling the effect of inbreeding: (a) no effect of inbreeding on fitness, that is, all alleles are selectively neutral, (b) each founder individual has one unique lethal and one unique non-lethal allele (Recessive Lethals option), or (c) first-year survival of each individual is exponentially related to its inbreeding coefficient (Heterosis option). The first case is clearly an optimistic one, as almost all diploid

populations studied intensively have shown deleterious effects of inbreeding on a variety of fitness components (Wright 1977; Falconer 1981). Each of the two models of inbreeding depression may also be optimistic, in that inbreeding is assumed to have an impact only on first-year survival. The Heterosis option allows, however, for the user to specify the severity of inbreeding depression on juvenile survival.

(10) Years are iterated via steps 11–25 below.

(11) The probabilities of females producing each possible litter size are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percentage of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates for their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) of the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for linear changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of breeding-age males specified to be breeding.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified sex ratio at birth. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) If the Heterosis option is chosen for modelling inbreeding depression, the genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between a new animal, A, and another existing animal, B is

$$f_{AB} = 0{\cdot}5 \times (f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_{AA} = 0{\cdot}5 \times (1 + F)$. [See Ballou (1983) for a detailed description of this method for calculating inbreeding coefficients.]

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If the Heterosis model of inbreeding depression is used and an individual is inbred, the survival probability is multiplied by e^{-bF} in which b is the number of lethal equivalents per haploid genome.

If the Recessive Lethals model is used, all offspring that are homozygous for a lethal allele are killed.

(18) The age of each animal is incremented by 1, and any animal exceeding the maximum age is killed.

(19) If more than one population is being modelled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age–sex class, VORTEX continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age class are created. Each immigrant is assigned two unique alleles, one of which will be a recessive lethal in the Recessive Lethals model of inbreeding depression. Each immigrant is assumed to be genetically unrelated to all other individuals in the population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N-K)/N$, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported. A simulated population is determined to be extinct if one of the sexes has no representatives.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate, are calculated across iterations and printed out.

Assumptions Underpinning VORTEX

It is impossible to simulate the complete range of complex processes that can have an impact on wild populations. As a result there are necessarily a range of mathematical and biological assumptions that underpin any PVA program. Some of the more important assumptions in VORTEX include the following.

(1) Survival probabilities are density independent when population size is less than carrying capacity. Additional mortality imposed when the population exceeds K affects all age and sex classes equally.

(2) The relationship between changes in population size and genetic variability are examined for only one locus. Thus, potentially complex interactions between genes located on the same chromosome (linkage disequilibrinm) are ignored. Such interactions are typically associated with genetic drift in very small populations, but it is unknown if, or how, they would affect population viability.

(3) All animals of reproductive age have an equal probability of breeding. This ignores the likelihood that some animals within a population may have a greater probability of breeding successfully, and breeding more often, than other individuals. If breeding is not at random among those in the breeding pool, then decay of genetic variation and inbreeding will occur more rapidly than in the model.

(4) The life-history attributes of a population (birth, death, migration, harvesting, supplementation) are modelled as a sequence of discrete and therefore seasonal events. However, such events are often continuous through time and the model ignores the possibility that they may be aseasonal or only partly seasonal.

(5) The genetic effects of inbreeding on a population are determined in VORTEX by using one of two possible models: the Recessive Lethals model and the Heterosis model. Both models have attributes likely to be typical of some populations, but these may vary within and between species (Brewer *et al.* 1990). Given this, it is probable that the impacts of inbreeding will fall between the effects of these two models. Inbreeding is assumed to depress only one component of fitness: first-year survival. Effects on reproduction could be incorporated into this component, but longer-term impacts such as increased disease susceptibility or decreased ability to adapt to environmental change are not modelled.

(6) The probabilities of reproduction and mortality are constant from the age of first breeding until an animal reaches the maximum longevity. This assumes that animals continue to breed until they die.

(7) A simulated catastrophe will have an effect on a population only in the year that the event occurs.

(8) Migration rates among populations are independent of age and sex.

(9) Complex, interspecies interactions are not modelled, except in that such community dynamics might contribute to random environmental variation in demographic parameters. For example, cyclical fluctuations caused by predator–prey interactions cannot be modelled by VORTEX.

Discussion

Uses and Abuses of Simulation Modelling for PVA

Computer simulation modelling is a tool that can allow crude estimation of the probability of population extinction, and the mean population size and amount of genetic diversity, from data on diverse interacting processes. These processes are too complex to be integrated intuitively and no analytic solutions presently, or are likely to soon, exist. PVA modelling focuses on the specifics of a population, considering the particular habitat, threats, trends, and time frame of interest, and can only be as good as the data and the assumptions input to the model (Lindenmayer *et al.* 1993). Some aspects of population dynamics are not modelled by VORTEX nor by any other program now available. In particular, models of single-species dynamics, such as VORTEX, are inappropriate for use on species whose fates are strongly determined by interactions with other species that are in turn undergoing complex (and perhaps synergistic) population dynamics. Moreover, VORTEX does not model many conceivable and perhaps important interactions among variables. For example, loss of habitat might cause secondary changes in reproduction, mortality, and migration rates, but ongoing trends in these parameters cannot be simulated with VORTEX. It is important to stress that PVA does not predict in general what will happen to a population; PVA forecasts the likely effects only of those factors incorporated into the model.

Yet, the use of even simplified computer models for PVA can provide more accurate predictions about population dynamics than the even more crude techniques available previously, such as calculation of expected population growth rates from life tables. For the purpose of estimating extinction probabilities, methods that assess only deterministic factors are almost certain to be inappropriate, because populations near extinction will commonly be so small that random processes dominate deterministic ones. The suggestion by Mace and Lande (1991) that population viability be assessed by the application of simple rules (e.g., a taxon be considered Endangered if the total effective population size is below 50 or the total census size below 250) should be followed only if knowledge is insufficient to allow more accurate quantitative analysis. Moreover, such preliminary judgments, while often important in stimulating appropriate corrective measures, should signal, not obviate, the need for more extensive investigation and analysis of population processes, trends and threats.

Several good population simulation models are available for PVA. They differ in capabilities, assumptions and ease of application. The ease of application is related to the number of simplifying assumptions and inversely related to the flexibility and power of the model. It is unlikely that a single or even a few simulation models will be appropriate for all PVAs. The VORTEX program has some capabilities not found in many other population simulation programs, but is not as flexible as are some others (e.g., GAPPS; Harris *et al.* 1986). VORTEX is user-friendly and can be used by those with relatively little understanding of population biology and extinction processes, which is both an advantage and a disadvantage.

Testing Simulation Models

Because many population processes are stochastic, a PVA can never specify what will happen to a population. Rather, PVA can provide estimates of probability distributions describing possible fates of a population. The fate of a given population may happen to fall at the extreme tail of such a distribution even if the processes and probabilities are assessed precisely. Therefore, it will often be impossible to test empirically the accuracy of PVA results by monitoring of one or a few threatened populations of interest. Presumably, if a population followed a course that was well outside of the range of possibilities predicted by a model, that model could be rejected as inadequate. Often, however, the range of plausible fates generated by PVA is quite broad.

Simulation programs can be checked for internal consistency. For example, in the absence of inbreeding depression and other confounding effects, does the simulation model predict an average long-term growth rate similar to that determined from a life-table calculation? Beyond this, some confidence in the accuracy of a simulation model can be obtained by comparing observed fluctuations in population numbers to those generated by the model, thereby comparing a data set consisting of tens to hundreds of data points to the results of the model. For example, from 1938 to 1991, the wild population of whooping cranes had grown at a mean exponential rate, r, of 0·040, with annual fluctuations in the growth rate, SD (r), of 0·141 (Mirande *et al.* 1993). Life-table analysis predicted an r of 0·052. Simulations using VORTEX predicted an r of 0·046 into the future, with a SD (r) of 0·081. The lower growth rate projected by the stochastic model reflects the effects of inbreeding and perhaps imbalanced sex ratios among breeders in the simulation, factors that are not considered in deterministic life-table calculations. Moreover, life-table analyses use mean birth and death rates to calculate a single estimate of the population growth rate. When birth and death rates are fluctuating, it is more appropriate to average the population growth rates calculated separately from birth and death rates for each year. This mean growth rate would be lower than the growth rate estimated from mean life-table values.

When the simulation model was started with the 18 cranes present in 1938, it projected a population size in 1991 ($N \pm \mathrm{SD} = 151 \pm 123$) almost exactly the same as that observed ($N = 146$). The large variation in population size across simulations, however, indicates that very different fates (including extinction) were almost equally likely. The model slightly underestimated the annual fluctuations in population growth [model SD (r)$=$0·112 *v.* actual SD (r)$=$0·141]. This may reflect a lack of full incorporation of all aspects of stochasticity into the model, or it may simply reflect the sampling error inherent in stochastic phenomena. Because the data input to the model necessarily derive from analysis of past trends, such retrospective analysis should be viewed as a check of consistency, not as proof that the model correctly describes current population dynamics. Providing another confirmation of consistency, both deterministic calculations and the simulation model project an over-wintering population of whooping cranes consisting of 12% juveniles (less than 1 year of age), while the observed frequency of juveniles at the wintering grounds in Texas has averaged 13%.

Convincing evidence of the accuracy, precision and usefulness of PVA simulation models would require comparison of model predictions to the distribution of fates of many replicate populations. Such a test probably cannot be conducted on any endangered species, but could and should be examined in experimental non-endangered populations. Once simulation models are determined to be sufficiently descriptive of population processes, they can guide management of threatened and endangered species (see above and Lindenmayer *et al.* 1993). The use of PVA modelling as a tool in an adaptive management framework (Clark *et al.* 1990) can lead to increasingly effective species recovery efforts as better data and better models allow more thorough analyses.

Directions for Future Development of PVA Models

The PVA simulation programs presently available model life histories as a series of discrete (seasonal) events, yet many species breed and die throughout much of the year. Continuons-time models would be more realistic and could be developed by simulating the time between life-history events as a random variable. Whether continuous-time models would significantly improve the precision of population viability estimates is unknown. Even more realistic models might treat some life-history events (e.g., gestation, lactation) as stages of specified duration, rather than as instantaneous events.

Most PVA simulation programs were designed to model long-lived, low fecundity (K-selected) species such as mammals, birds and reptiles. Relatively little work has been devoted to developing models for short-lived, high-fecundity (r-selected) species such as many amphibians and insects. Yet, the viability of populations of r-selected species may be highly affected by stochastic phenomena, and r-selected species may have much greater minimum viable populations than do most K-selected species. Assuring viability of K-selected species in a community may also afford adequate protection for r-selected species, however, because of the often greater habitat-area requirements of large vertebrates. Populations of r-selected species are probably less affected by intrinsic demographic stochasticity because large numbers of progeny will minimise random fluctuations, but they are more affected by environmental variations across space and time. PVA models designed for r-selected species would probably model fecundity as a continuous distribution, rather than as a completely specified discrete distribution of litter or clutch sizes; they might be based on life-history stages rather than time-increment ages; and they would require more detailed and accurate description of environmental fluctuations than might be required for modelling K-selected species.

The range of PVA computer simulation models becoming available is important because the different assumptions of the models provide capabilities for modelling diverse life histories. Because PVA models always simplify the life history of a species, and because the assumptions of no model are likely to match exactly our best understanding of the dynamics of a population of interest, it will often be valuable to conduct PVA modelling with several simulation programs and to compare the results. Moreover, no computer program can be guaranteed to be free of errors. There is a need for researchers to compare results from different PVA models when applied to the same analysis, to determine how the different assumptions affect conclusions and to cross-validate algorithms and computer code.

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References

Akçakaya, H. R., and Ferson, S. (1990). 'RAMAS/Space User Manual. Spatially Structured Population Models for Conservation Biology.' (Applied Biomathematics: Setauket, New York.)

Ballou, J. (1983). Calculating inbreeding coefficients from pedigrees. In 'Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations'. (Eds C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas.) pp. 509–20. (Benjamin/Cummings: Menlo Park, California.)

Belovsky, G. E. (1987). Extinction models and mammalian persistence. In 'Viable Populations for Conservation'. (Ed. M. E. Soulé.) pp. 35–57. (Cambridge University Press: Cambridge.)

Berger, J. (1990). Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4, 91–8.

Brewer, B. A., Lacy, R. C., Foster, M. L., and Alaks, G. (1990). Inbreeding depression in insular and central populations of *Peromyscus* mice. *Journal of Heredity* **81**, 257–66.

Burgmann, M. A., and Gerard, V. A. (1990). A stage-structured, stochastic model for giant kelp *Macrocystis pyrifera*. *Marine Biology* **105**, 15–23.

Clark, T. W. (1989). 'Conservation Biology of the Black-footed Ferret. Special Scientific Report.' (Wildlife Preservation Trust International: Philadelphia.)

Clark, T. W., and Seebeck, J. H. (Eds) (1990). 'Management and Conservation of Small Populations.' (Chicago Zoological Society: Brookfield, Illinois.)

Clark, T. W., Warneke, R. M., and George, G. G. (1990). Management and conservation of small populations. In 'Management and Conservation of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 1–18. (Chicago Zoological Society: Brookfield, Illinois.)

Clark, T. W., Backhouse, G. N., and Lacy, R. C. (1991). Report of a workshop on population viability assessment as a tool for threatened species management and conservation. *Australian Zoologist* 27, 28–35.

Crow, J. F., and Kimura, M. (1970). 'Introduction to Population Genetics Theory.' (Harper and Row: New York.)

Doughty, R. W. (1989). 'Return of the Whooping Crane.' (University of Texas Press: Austin.)

Falconer, D. S. (1981). 'Introduction to Quantitative Genetics.' 2nd Edn. (Longman: New York.)

Ferson, S. (1990). 'RAMAS/Stage. Generalized Stage-based Modeling for Population Dynamics.' (Applied Biomathematics: Setauket, New York.)

Ferson, S., and Akçakaya, H. R. (1989). 'RAMAS/Age User Manual. Modeling Fluctuations in Age-structured Populations.' (Applied Biomathematics: Setauket, New York.)

Fisher, R. A. (1958). 'The Genetical Theory of Natural Selection.' 2nd Edn. (Dover: New York.)

Foose, T. J., Lacy, R. C., Brett, R., and Seal, U. S. (1992). Kenya black rhinoceros population and habitat viability assessment. (Captive Breeding Specialist Group, SSC, IUCN: Apple Valley, Minnesota.)

Gilpin, M. E. (1987). Spatial structure and population vulnerability. In 'Viable Populations for Conservation'. (Ed. M. E. Soulé.) pp. 125–39. (Cambridge University Press: Cambridge.)

Gilpin, M. E. (1989). Population viability analysis. *Endangered Species Update* 6, 15–18.

Gilpin, M. E., and Soulé, M. E. (1986). Minimum viable populations: processes of species extinction. In 'Conservation Biology: the Science of Scarcity and Diversity'. (Ed. M. E. Soulé.) pp. 19–34. (Sinauer: Sunderland, Massachusetts.)

Goodman, D. (1987). The demography of chance extinction. In 'Viable Populations for Conservation'. (Ed. M. E. Soulé.) pp. 11–34. (Cambridge University Press: Cambridge.)

Grier, J. W. (1980*a*). A simulation model for small populations of animals. *Creative Computing* 6, 116–21.

Grier, J. W. (1980*b*). Modeling approaches for bald eagle population dynamics. *Wildlife Society Bulletin* **8**, 316–22.

Harris, R. B., Metzger, L. H., and Bevins, C. D. (1986). 'GAPPS. Version 3.0.' (Montana Cooperative Research Unit, University of Montana: Missoula.)

Hill, F. A. R. (1991). A research recovery plan for the brush-tailed rock wallaby *Petrogale pencillata* (Gray 1825). Report to Australian National Parks and Wildlife Service. (Department of Conservation and Environment: Melbourne.)

Kirkpatrick, S., and Stoll, E. (1981). A very fast shift-register sequence random number generator. *Journal of Computational Physics* **40**, 517.

Lacy, R. C. (1993). Impacts of inbreeding in natural and captive populations of vertebrates: implications for conservation. *Perspectives in Biology and Medicine*. (In press.)

Lacy, R. C., and Clark, T. W. (1990). Population viability assessment of eastern barred bandicoot. In 'The Management and Conservation of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 131–46. (Chicago Zoological Society: Brookfield, Illinois.)

Lacy, R. C., Flesness, N. R., and Seal, U. S. (1989). 'Puerto Rican Parrot Population Viability Analysis.' (Captive Breeding Specialist Group, SSC, IUCN: Apple Valley, Minnesota.)

Lacy, R. C., Petric, A. M., and Warneke, M. (1993). Inbreeding and outbreeding depression in captive populations of wild species. In 'The Natural History of Inbreeding and Outbreeding'. (Ed. N. W. Thornhill.) (University of Chicago Press: Chicago.) (In press.)

Lande, R. (1988). Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia* 75, 601–7.

Latour, A. (1986). Polar normal distribution. *Byte* August 1986, 131–2.

Lindenmayer, D. B., Clark, T. W., Lacy, R. C., and Thomas, V. C. (1993). Population viability analysis as a tool in wildlife management: a review with reference to Australia. *Environmental Management*. (In press.)

Mace, G. M., and Lande, R. (1991). Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5, 148–57.

Maguire, L. A., Lacy, R. C., Begg, R. J., and Clark, T. W. (1990). An analysis of alternative strategies for recovering the eastern barred bandicoot. In 'The Management and Conservation of Small Populations'. (Eds T. W. Clark and J. H. Seebeck.) pp. 147–64. (Chicago Zoological Society: Brookfield, Illinois.)

Maier, W. L. (1991). A fast pseudo random number generator. *Dr. Dobb's Journal* May 1991, 152–7.

Mirande, C., Lacy, R. C., and Seal, U. S. (1993). Whooping crane conservation viability assessment workshop. (Captive Breeding Specialist Group, SSC, IUCN: Apple Valley, Minnesota.)

Morton, N. E., Crow, J. F., and Muller, H. J. (1956). An estimate of the mutational damage in man from data on consanguineous marriages. *Proceedings of the National Academy of Sciences, U.S.A.* **42**, 855–63.

O'Brien, S. J., and Evermann, J. F. (1988). Interactive influence of infectious diseases and genetic diversity in natural populations. *Trends in Ecology and Evolution* 3, 254–9.

Possingham, H., Davies, I., and Noble, I. R. (1991). 'An Evaluation of Population Viability Analysis for Assessing the Risk of Extinction.' (Resource Assessment Commission: Canberra.)

Possingham, H. P., Davies, I., Noble, I. R., and Norton, T. W. (1992). A metapopulation simulation model for assessing the likelihood of plant and animal extinctions. *Mathematics and Computers in Simulation* **33**, 367–72.

Ralls, K., Ballou, J. D., and Templeton, A. R. (1988). Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* **2**, 185–93.

Resource Assessment Commission (1991). Forest and timber inquiry. Draft report. Vol. 2. July 1991. (Australian Government Publishing Service: Canberra.)

Ricklefs, R. E. (1979). 'Ecology.' 2nd Edn. (Chiron: New York.)

Robertson, A. (1960). A theory of limits in artificial selection. *Proceedings of the Royal Society of London* **153B**, 234–49.

Seal, U. S., and Foose, T. J. (1989). Javan rhinoceros population viability analysis and recommendations. (Captive Breeding Specialist Group, SSC, IUCN: Apple Valley, Minnesota.)

Seal, U. S., and Lacy, R. C. (1989). Florida panther population viability analysis. (Captive Breeding Specialist Group, SSC, IUCN: Apple Valley, Minnesota.)

Seal, U. S., Ballou, J. D., and Padua, C. V. (1990). *Leontopithecus* population viability analysis workshop report. (Captive Breeding Specialist Group, SSC, IUCN: Apple Valley, Minnesota.)

Seal, U. S., Lacy, R. C., Medley, K., Seal, R., and Foose, T. J. (1991). Tana River Primate Reserve Conservation Assessment Workshop. (Captive Breeding Specialist Group, SSC, IUCN: Apple Valley, Minnesota.)

Selander, R. K. (1983). Evolutionary consequences of inbreeding. In 'Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations'. (Eds C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde and W. L. Thomas.) pp. 201–15. (Benjamin/Cummings: Menlo Park, California.)

Shaffer, M. L. (1981). Minimum population sizes for species conservation. *BioScience* **31**, 131–4.

Shaffer, M. L. (1987). Minimum viable populations: coping with uncertainty. In 'Viable Populations for Conservation'. (Ed. M. E. Soulé.) pp. 69–86. (Cambridge University Press: Cambridge.)

Shaffer, M. L. (1990). Population viability analysis. *Conservation Biology* **4**, 39–40.

Simberloff, D. A. (1986). The proximate causes of extinction. In 'Patterns and Processes in the History of Life'. (Eds D. M. Raup and D. Jablonski.) pp. 259–76. (Springer-Verlag: Berlin.)

Simberloff, D. A. (1988). The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* **19**, 473–511.

Soulé, M. E. (Ed.) (1987). 'Viable Populations for Conservation.' (Cambridge University Press: Cambridge.)

Thomas, C. D. (1990). What do real population dynamics tell us about minimum population sizes? *Conservation Biology* **4**, 324–7.

Wright, S. (1977). 'Evolution and the Genetics of Populations. Vol. 3. Experimental Results and Evolutionary Deductions.' (University of Chicago Press: Chicago.)

Appendix. Sample Output from VORTEX

Explanatory comments are added in italics

```
VORTEX—simulation of genetic and demographic stochasticity
TEST
```

Simulation label and output file name

```
Fri Dec 20 09:21:18 1991
  2 population(s) simulated for 100 years, 100 runs
```

VORTEX first lists the input parameters used in the simulation:

```
  HETEROSIS model of inbreeding depression
    with 3·14 lethal equivalents per diploid genome

  Migration matrix:
          1       2
    1  0·9900  0·0100
    2  0·0100  0·9900
```

i.e. 1% probability of migration from Population 1 to 2, and from Population 2 to 1

```
  First age of reproduction for females: 2   for males: 2
  Age of senescence (death): 10
  Sex ratio at birth (proportion males): 0·5000

Population 1:
  Polygynous mating; 50·00 per cent of adult males in the breeding pool.
  Reproduction is assumed to be density independent.
    50·00 (EV=12·50 SD) per cent of adult females produce litters of size 0
    25·00 per cent of adult females produce litters of size 1
    25·00 per cent of adult females produce litters of size 2
```

EV is environmental variation

```
    50·00 (EV=20·41 SD) per cent mortality of females between ages 0 and 1
    10·00 (EV=3·00 SD) per cent mortality of females between ages 1 and 2
    10·00 (EV=3·00 SD) per cent annual mortality of adult females (2<=age<=10)
    50·00 (EV=20·41 SD) per cent mortality of males between ages 0 and 1
    10·00 (EV=3·00 SD) per cent mortality of males between ages 1 and 2
    10·00 (EV=3·00 SD) per cent annual mortality of adult males (2<=age<=10)
```

```
EVs have been adjusted to closest values possible for binomial distribution.
   EV in reproduction and mortality will be correlated.
   Frequency of type 1 catastrophes: 1·000 per cent
     with 0·500 multiplicative effect on reproduction
     and 0·750 multiplicative effect on survival
   Frequency of type 2 catastrophes: 1·000 per cent
     with 0·500 multiplicative effect on reproduction
     and 0·750 multiplicative effect on survival
   Initial size of Population 1: (set to reflect stable age distribution)
 Age  1    2    3    4    5    6    7    8    9    10     Total
      1    0    1    1    0    1    0    0    1    0        5  Males
      1    0    1    1    0    1    0    0    1    0        5  Females
    Carrying capacity=50 (EV=0·00 SD)
      with a 10·000 per cent decrease for 5 years.
   Animals harvested from population 1, year 1 to year 10 at 2 year intervals:
     1 females 1 years old
     1 female adults (2<=age<=10)
     1 males 1 years old
     1 male adults (2<=age<=10)
   Animals added to population 1, year 10 through year 50 at 4 year intervals:
     1 females 1 years old
     1 females 2 years old
     1 males 1 years old
     1 males 2 years old
```

Input values are summarised above, results follow.

VORTEX now reports life-table calculations of expected population growth rate.

```
Deterministic population growth rate (based on females, with assumptions of no limitation of mates
  and no inbreeding depression):
      r= -0·001      lambda=0·999      RO=0·997
   Generation time for:  females=5·28   males=5·28
```

Note that the deterministic life-table calculations project approximately zero population growth for this population.

```
Stable age distribution:   Age class   females   males
                              0         0·119     0·119
                              1         0·059     0·059
                              2         0·053     0·053
                              3         0·048     0·048
                              4         0·043     0·043
                              5         0·038     0·038
                              6         0·034     0·034
                              7         0·031     0·031
                              8         0·028     0·028
                              9         0·025     0·025
                             10         0·022     0·022
Ratio of adult (>=2) males to adult (>=2) females: 1·000
```

Population 2:

Input parameters for Population 2 were identical to those for Population 1.
Output would repeat this information from above.

Simulation results follow.

```
Population1
```

```
Year 10
    N[Extinct] =        0, P[E] = 0·000
    N[Surviving] =  100, P[S] = 1·000
    Population size =             4·36  (0·10 SE,  1·01 SD)
    Expected heterozygosity =  0·880 (0·001 SE, 0·012 SD)
    Observed heterozygosity =  1·000 (0·000 SE, 0·000 SD)
    Number of extant alleles = 8·57  (0·15 SE,  1·50 SD)
```

Population summaries given, as requested by user, at 10-year intervals.

```
Year 100
    N[Extinct] =     86, P[E] = 0·860
    N[Surviving] =  14, P[S] = 0·140
    Population size =             8·14  (1·27 SE,  4·74 SD)
    Expected heterozygosity =  0·577 (0·035 SE, 0·130 SD)
    Observed heterozygosity =  0·753 (0·071 SE, 0·266 SD)
    Number of extant alleles = 3·14  (0·35 SE,  1·29 SD)

In 100 simulations of 100 years of Population1:
  86 went extinct and 14 survived.
This gives a probability of extinction of 0·8600 (0·0347 SE),
  or a probability of success of           0·1400 (0·0347 SE).
99 simulations went extinct at least once.
Median time to first extinction was 5 years.
Of those going extinct,
  mean time to first extinction was 7·84 years (1·36 SE, 13·52 SD).
123 recolonisations occurred.
Mean time to recolonisation was 4·22 years (0·23 SE, 2·55 SD).
110 re-extinctions occurred.
Mean time to re-extinction was 54·05 years (2·81 SE, 29·52 SD).

Mean final population for successful cases was 8·14 (1·27 SE, 4·74 SD)
  Age 1     Adults     Total
  0·14       3·86       4·00   Males
  0·36       3·79       4·14   Females

During years of harvest and/or supplementation
  mean growth rate (r) was 0·0889 (0·0121 SE, 0·4352 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was  −0·0267 (0·0026 SE, 0·2130 SD)
```

Population growth in the simulation (r = −0·0267) was depressed relative to the projected growth rate calculated from the life table (r = −0·001) because of inbreeding depression and occasional lack of available mates.

```
Note:   497 of 1000 harvests of males and 530 of 1000 harvests of females could not be completed
        because of insufficient animals.

Final expected heterozygosity was     0·5768 (0·0349 SE, 0·1305 SD)
Final observed heterozygosity was     0·7529 (0·0712 SE, 0·2664 SD)
Final number of alleles was           3·14    (0·35 SE,    1·29 SD)

Population2
```

Similar results for Population 2, omitted from this Appendix, would follow.

```
  ********  Metapopulation Summary  ********
Year 10
    N[Extinct] =        0, P[E] = 0·000
    N[Surviving] =  100, P[S] = 1·000
    Population size =              8·65  (0·16 SE,  1·59 SD)
    Expected heterozygosity =   0·939 (0·000 SE, 0·004 SD)
    Observed heterozygosity =   1·000 (0·000 SE, 0·000 SD)
    Number of extant alleles = 16·92  (0·20 SE,  1·96 SD)
```

Metapopulation summaries are given at 10-year intervals.

```
Year 100
    N[Extinct] =     79,  P[E] = 0·790
    N[Surviving] =  21,  P[S] = 0·210
    Population size =             10·38  (1·37 SE,   6·28 SD)
    Expected heterozygosity =   0·600 (0·025 SE, 0·115 SD)
    Observed heterozygosity =   0·701  (0·050 SE, 0·229 SD)
    Number of extant alleles =  3·57   (0·30 SE,   1·36 SD)

In 100 simulations of 100 years of Metapopulation:
  79 went extinct and 21 survived.
This gives a probability of extinction of   0·7900 (0·0407 SE),
  or a probability of success of              0·2100 (0·0407 SE).
97 simulations went extinct at least once.
Median time to first extinction was 7 years.
Of those going extinct,
  mean time to first extinction was 11·40 years (2·05 SE, 20·23 SD).
91 recolonisations occurred.
Mean time to recolonisation was 3·75 years (0·15 SE, 1·45 SD).
73 re-extinctions occurred.
Mean time to re-extinction was 76·15 years (1·06 SE, 9·05 SD).

Mean final population for successful cases was 10·38 (1·37 SE, 6·28 SD)
  Age 1     Adults     Total
   0·48       4·71       5·19   Males
   0·48       4·71       5·19   Females

During years of harvest and/or supplementation
  mean growth rate (r) was 0·0545 (0·0128 SE, 0·4711 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was  −0·0314 (0·0021 SE, 0·1743 SD)

Final expected heterozygosity was   0·5997 (0·0251 SE, 0·1151 SD)
Final observed heterozygosity was   0·7009 (0·0499 SE, 0·2288 SD)
Final number of alleles was           3·57    (0·30 SE,    1·36 SD)
```

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