Berrendo Peninsular:

Evaluación de la Viabilidad de la Población y del Hábitat

La Paz, Baja California Sur, México, [illegible]

SEDESOL

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

Editado por
Edited by

Jorge Cancino, Philip Miller, Jose Bernal Stoopen, and Jim Lewis

Recopilado por los Participantes del Taller
Compiled by the Workshop Participants

Un Taller en Colaboración:
A Collaborative Workshop of:

Centro de Investigación Biológicas del Noroeste, S.C. (CIB)
Secretaría de Desarrollo Social (SEDESOL)
IUCN/SSC Conservation Breeding Specialist Group

SPECIES SURVIVAL COMMISSION

SEDESOL

A contribution of the IUCN/SSC Conservation Breeding Specialist Group.

Cover Photo: El Berrendo Peninsular (*Antilocapra americana peninsularis*)
Desierto de Vizcaíno, Baja California Sur, México
Photo by Patricio Robles Gil, Agrupación Sierra Madre, México.

Cancino, J., P. Miller, J. Bernal Stoopen, and J. Lewis (eds.). 1995. *Population and Habitat Viability Assessment for the Peninsular Pronghorn (*Antilocapra americana peninsularis*).* IUCN/SSC Conservation Breeding Specialist Group: Apple Valley, MN. 113pp.

The work of the Conservation Breeding Specialist Group is made possible by generous contributions from the following members of the CBSG Institutional Conservation Council

Conservators ($10,000 and above)

Australasian Species Management Prog.
Chicago Zoological Society
Columbus Zoological Gardens
Denver Zoological Gardens
Fossil Rim Wildlife Center
Friends of Zoo Atlanta
Greater Los Angeles Zoo Association
International Union of Directors of Zoological Gardens
Metropolitan Toronto Zoo
Minnesota Zoological Garden
Omaha's Henry Doorly Zoo
Saint Louis Zoo
Sea World, Inc.
White Oak Conservation Center
Wildlife Conservation Society - NY
Zoological Society of Cincinnati
Zoological Society of San Diego

Guardians ($5,000-$9,999)

Cleveland Zoological Society
John G. Shedd Aquarium
Loro Parque
Lubee Foundation
North Carolina Zoological Park
Toledo Zoological Society
Wild Animal Habitat
Zoological Parks Board of New South Wales

Protectors ($1,000-$4,999)

Africam Safari
Audubon Institute
Bristol Zoo
Burgers' Zoo
Caldwell Zoo
Calgary Zoo
Cologne Zoo
Copenhagen Zoo
Detroit Zoological Park
El Paso Zoo
Federation of Zoological Gardens of Great Britain and Ireland
Fort Wayne Zoological Society
Fort Worth Zoo
Gladys Porter Zoo
Houston Zoological Garden
Indianapolis Zoological Society
International Aviculturists Society
Japanese Association of Zoological Parks & Aquariums
Jersey Wildlife Preservation Trust
Living Desert
Marwell Zoological Park
Milwaukee County Zoo
NOAHS Center
North of England Zoological Society, Chester Zoo
Oklahoma City Zoo
Paignton Zoological & Botanical Gardens
Parco Natura Viva Garda Zoological Park
Penscynor Wildlife Park
Philadelphia Zoological Garden
Phoenix Zoo
Pittsburgh Zoo
Riverbanks Zoological Park
Royal Zoological Society of Antwerp
Royal Zoological Society of Scotland
San Francisco Zoo
Schoenbrunner Tiergarten
Sedgwick County Zoo
Sunset Zoo (10 year commitment)
Taipei Zoo
The WILDS
The Zoo, Gulf Breeze, FL
Urban Council of Hong Kong
Washington Park Zoo
Wassenaar Wildlife Breeding Centre
Wilhelma Zoological Garden
Woodland Park Zoo
Yong-In Farmland
Zoological Parks Board of Victoria
Zoological Park Organization
Zoological Society of London
Zurich Zoological Garden

Stewards ($500-$999)

Aalborg Zoo
Arizona-Sonora Desert Museum
Banham Zoo
Cotswold Wildlife Park
Dutch Federation of Zoological Gardens
Erie Zoological Park
Fota Wildlife Park
Givskud Zoo
Granby Zoological Society
International Zoo Veterinary Group
Knoxville Zoo
Lincoln Park Zoo
National Geographic Magazine
National Zoological Gardens of South Africa
Odense Zoo
Orana Park Wildlife Trust
Paradise Park
Perth Zoological Gardens
Porter Charitable Trust
Rolling Hills Ranch (5 year commitment)
Rostock Zoo
Royal Zoological Society of Southern Australia
Rotterdam Zoo
Tierpark Rheine
Twycross Zoo
Union of German Zoo Directors
Wellington Zoo
World Parrot Trust
Zoo de la Casa de Campo-Madrid
Welsh Mt. Zoo/Zool. Society of Wales
Zoologischer Garten Frankfurt

Curators ($250-$499)

Camperdown Wildlife Center
Emporia Zoo
Edward D. Plotka
Racine Zoological Society
Roger Williams Zoo
Thrigby Hall Wildlife Gardens
Topeka Zoological Park
Tropical Bird Garden

Sponsors ($50-$249)

African Safari
Apenheul Zoo
Belize Zoo
Claws 'n Paws
Darmstadt Zoo
Dreher Park Zoo
Fota Wildlife Park
Great Plains Zoo
Hancock House Publisher
Kew Royal Botanic Gardens
Lisbon Zoo
Miller Park Zoo
Nagoya Aquarium
National Audubon Society-Research Ranch Sanctuary
National Aviary in Pittsburgh
Ocean World Taipei Incorporation
PAAZAB
Parco Faunistico "La Torbiera"
Potter Park Zoo
Tenerife Zoo
Tokyo Zoological Park
Touro Parc-France

Supporters ($25-$49)

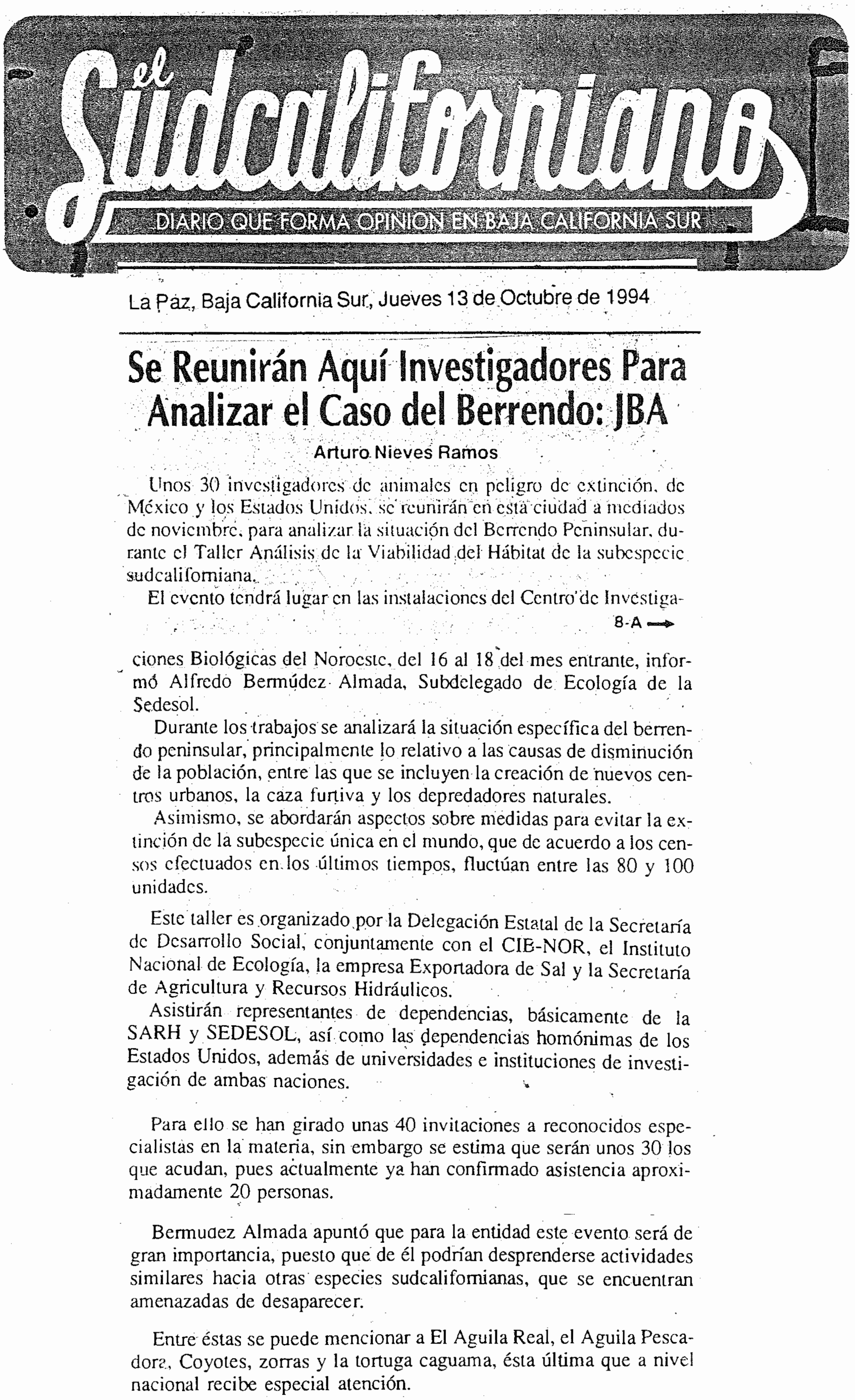
Alameda Park Zoo
American Loriinae Conservancy
Bighorn Institute
Brandywine Zoo
DGHT Arbeitsgruppe Anuren
Folsom Children's Zoo & Botanical Garden
International Crane Foundation
Jardin aux Oiseaux
Lee Richardson Zoo
Natal Parks Board
Oglebay's Good Children's Zoo
Speedwell Bird Sanctuary

1 August 1995

CONTENIDO
CONTENTS

CONTENIDO (Continuación)
CONTENTS (Continued)

CONTENIDO (Continuación)
CONTENTS (Continued)



el Sudcaliforniano
DIARIO QUE FORMA OPINION EN BAJA CALIFORNIA SUR

La Paz, Baja California Sur, Jueves 13 de Octubre de 1994

Se Reunirán Aquí Investigadores Para Analizar el Caso del Berrendo: JBA

Arturo Nieves Ramos

Unos 30 investigadores de animales en peligro de extinción, de México y los Estados Unidos, se reunirán en esta ciudad a mediados de noviembre, para analizar la situación del Berrendo Peninsular, durante el Taller Análisis de la Viabilidad del Hábitat de la subespecie sudcaliforniana.

El evento tendrá lugar en las instalaciones del Centro de Investigaciones Biológicas del Noroeste, del 16 al 18 del mes entrante, informó Alfredo Bermúdez Almada, Subdelegado de Ecología de la Sedesol.

8-A →

Durante los trabajos se analizará la situación específica del berrendo peninsular, principalmente lo relativo a las causas de disminución de la población, entre las que se incluyen la creación de nuevos centros urbanos, la caza furtiva y los depredadores naturales.

Asimismo, se abordarán aspectos sobre medidas para evitar la extinción de la subespecie única en el mundo, que de acuerdo a los censos efectuados en los últimos tiempos, fluctúan entre las 80 y 100 unidades.

Este taller es organizado por la Delegación Estatal de la Secretaría de Desarrollo Social, conjuntamente con el CIB-NOR, el Instituto Nacional de Ecología, la empresa Exportadora de Sal y la Secretaría de Agricultura y Recursos Hidráulicos.

Asistirán representantes de dependencias, básicamente de la SARH y SEDESOL, así como las dependencias homónimas de los Estados Unidos, además de universidades e instituciones de investigación de ambas naciones.

Para ello se han girado unas 40 invitaciones a reconocidos especialistas en la materia, sin embargo se estima que serán unos 30 los que acudan, pues actualmente ya han confirmado asistencia aproximadamente 20 personas.

Bermudez Almada apuntó que para la entidad este evento será de gran importancia, puesto que de él podrían desprenderse actividades similares hacia otras especies sudcalifornianas, que se encuentran amenazadas de desaparecer.

Entre éstas se puede mencionar a El Aguila Real, el Aguila Pescadora, Coyotes, zorras y la tortuga caguama, ésta última que a nivel nacional recibe especial atención.

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 1

RESUMEN EJECUTIVO
EXECUTIVE SUMMARY

RESUMEN EJECUTIVO

Históricamente la población del berrendo peninsular (*Antilocapra americana peninsularis*) ocupaba aproximadamente 40,000 km^2 desde San Felipe y San Quintín en el norte hasta Bahía Magdalena en el sur. En 1925 se estimó que el tamaño de la población era de 500 individuos. Entre 1950 y 1980 debido principalmente al impacto de actividades humanas esta distribución y abundancia rápidamente declinó hasta niveles muy críticos: en la actualidad solamente de 100-200 individuos se distribuyen en 3600 km^2 aproximadamente. Este población se localiza unicamente en el Desierto de Vizcaino.

Este Taller de Análisis de la Viabilidad de la Población y del Habitat del berrendo peninsular se propuso para analizar la situación con un grupo de especialistas representantes de diversas instituciones mexicanas y norteamericanas, tanto gubernamentales como no gubernamentales, siendo este Taller el primer evento de esta naturaleza que se realiza en México con la participación del CBSG/IUCN.

Participaron un total de 30 personas de 17 instituciones. El evento se realizó del 16 al 18 de noviembre de 1994 en el Centro de Investigaciones Biológicas del Noroeste, S. C. situado en La Paz, Baja California Sur, México.

Se proporcionó una extensa explicación sobre el programa VORTEX y sus potencialidades.

Las metas que se marcaron para ser cubiertas por este taller fueron:

1. Elaboración de un programa de manejo para la recuperación del berrendo peninsular.

2. Identificación de las instituciones (presentes y potenciales) con interés y compromiso en el programa de manejo para la recuperación.

3. Definición de las necesidades y prioridades para la recuperación de esta subespecie.

4. Reunir y compilar la información básica y fundamentos teóricos, de los factores biológicos, no biológicos y sociales que influyen sobre la población del berrendo peninsular.

Se formaron siete subgrupos de trabajo que abordaron los siguientes temas: biología básica y modelaje; distribución y estado; factores de riesgo; calidad del habitat y tendencias; y estrategias de conservación (educación ambiental, investigación, y manejo). Se generaron los siete reportes respectivos, que ilustran:

a. El modelaje con VORTEX de la población del berrendo peninsular indicó que la población es muy sensible al incremento de la mortalidad de crías, y que la mortalidad de adultos también es un factor importante.

b. La distribución de la subespecie se redujo históricamente en más de un 90%. El berrendo peninsular está considerado, nacional e internacionalmente, en peligro de extinción.

c. Las amenazas identificadas incluyen el furtivismo, la transformación y reducción del habitat y la alta mortalidad de crías y juveniles.

d. La calidad del habitat se considera de una baja capacidad de carga que se refleja en una baja densidad.

En cuanto a las estrategias de conservación se propuso:

e.1. Realizar una campaña de educación ambiental a niveles local, estatal, nacional e internacional, que involucra a organizaciones gubernamentales y no gubernamentales. Algunas de las acciones que se señalaron ya están iniciadas.

e.2. Se señalaron las prioridades de investigación en lo que se refiere a la población destacando: biología básica, monitoreo y uso del habitat.

e.3. De manera similar al punto anterior se priorizaron las medidas a tomar, de las cuales las principales son: presencia en el área, gestión interinstitucional, análisis y reglamentación del uso del suelo, monitoreo de la población y crianza en semicautiverio.

Se definieron temporalidades para el inicio y/o continuación de los diferentes rubros mencionados, asi como también se definieron las prioridades, responsabilidades e instituciones participantes y de apoyo.

EXECUTIVE SUMMARY

Historically, the peninsular pronghorn (*Antilocapra americana peninsularis*) population occupied approximately 40,000 km^2 from San Felipe and San Quintin in the north to Magdalena Bay in the south. In 1925 the population contained an estimated 500 individuals. Between 1950 and 1980, due principally to the impact of human activities, population distribution and abundance rapidly declined to very critical levels: presently, about 100-200 individuals are distributed within approximately 3,600 km^2. This population is localized primarily within a portion of the Vizcaino Desert.

A Population Habitat and Viability Assessment (PHVA) Workshop was conducted for the peninsular pronghorn to analyze the current situation. A group of specialists representing various governmental and nongovernment institutions from Mexico and the United States participated in the Workshop. This was the first such workshop developed in Mexico with the participation of IUCN/CBSG.

Thirty persons from 17 institutions participated in the workshop held November 16 to 18, 1994, at the Center for Biological Research (N.W.), S.C. in La Paz, Baja California Sur, Mexico. Participants were given an extensive explanation of the VORTEX population simulation software package and its uses.

Goals identified by Workshop participants were:

1. To develop a management plan for recovery of the peninsular pronghorn.
2. To identify the institutions (present and potential), their interests and commitment to the recovery program.
3. To define the need and priorities for recovery of the subspecies.
4. To collect and record basic and fundamental information on social, biological, and nonbiological factors.

Working groups were organized on the following topics: life history/modelling; distribution and status; threats; habitat quality and trends; conservation education; research; and general management. The following were among the key points discussed in these groups:

a. VORTEX modelling of the pronghorn population indicated that the population was very sensitive to increases in fawn mortality, with adult mortality also an important factor.

b. Distribution of the subspecies has been reduced by more that 90%. The peninsular pronghorn has been declared an endangered species nationally and internationally.

c. Threats to the population include poaching, habitat loss, habitat quality reduction, and high mortality of both fawns and yearlings.

d. The habitat quality is believed to be reduced in carrying capacity and it is reflected in the low pronghorn density.

Regarding conservation strategies, the participants:

e1. Proposed to develop an environmental education campaign at local, state, national, and international levels with the participation of government and nongovernmental organizations. Some of the actions that were identified are currently being developed.

e2. Identified research priorities for the population considering mainly basic biology and monitoring of the subspecies and land use.

e3. Prioritized recovery measures, the most important being: law enforcement in the area, interinstitutional analysis and regulation of the use of the land, monitoring of the population, and rearing in semicaptivity.

A schedule was identified to initiate and continue recovery activities. Work priorities and responsibilities were defined and the role of participating institutions identified (e.g., funding or legal support).

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 2

BIOLÓGIA DE LA POBLACIÓN Y MODELOS
POPULATION BIOLOGY AND MODELLING

BIOLÓGIA DE LA POBLACIÓN Y MODELAJE

Introducción

La necesidad de las estrategias intensivas del manejo y los efectos de estas pueden ser modeladas para suguerir que prácticas pueden ser las mas efectívas para conservar esta población. VORTEX, un programa de simulación de modelaje escrito por Robert Lacy y Kim Hughes, fue utilizado como una herramienta para estudiar la interacción de varias variables estocásticas.

El programa VORTEX es una simulación Monte Carlo sobre los efectos tanto de las fuerzas determinísticas, como de los eventos demográficos, ambientales y genéticos estocásticos en las poblaciones silvestres. VORTEX modela las dinámicas de las poblaciones como eventos discretos y secuenciales (por ejemplo, nacimientos, muertes, relación de sexos, catástrofes etc.) que ocurren de acuerdo a probabilidades definidas de distribucion. Las probabilidades de eventos son modeladas como variables constantes o al azar que siguen distribuciones específicas. El paquete simula una población considerando una serie de eventos que describen el ciclo de vida tipico de organismos diploídes con reproducción sexual.

VORTEX no pretende dar respuestas absolutas. debido a que proyecta estocásticamente las interacciones de los varios parametros que entran en el modelo y debido también a los procesos aleatorios que ocurren en la naturaleza. La interpretación de los resultados depende de nuestro conocimiento de la biología del berrendo, de las condiciones que afectan a la población y, de los posibles cambios que pueden ocurrir en el futúro. Mas especificamente, debido a que la cantidad de información sobre la historia de vida específica para el berrendo peninsular es limitada, utilizamos información de la población silvestre del berrendo de Sonora (*Antilocapra americana sonorensis*) cuando fue apropiado. Estas dos subespecies son ecologicamente similares, hecho que permite utilizar información de esta poblacion mayormente estudiada.

Parámetros de Entrada para la Simulación

Sistema de Apareamiento : Polígamos.

Edad Promedio a Primera Reproducción: VORTEX define a la reproducción como la edad en que las crías nacen, no la edad de madurez sexual. La edad en que las hembras entran en madurez sexual es de alrededor de 16 meses, mientras que los machos alcanzan la madurez sexual antes de cumplir un año de vida. Sin embargo, debido a que el periódo de gestación para esta subespecie es de aproximadamente 8 meses, determinamos la edad de primera reproducción para las hembras a los dos años y para los machos al primer año de vida.

Edad de Senectud: VORTEX asume que los animales pueden reproducirse (en una tasa normal) a lo largo de su vida adulta. Información del berrendo de Sonora indica que tanto los machos como las hembras cuentan con capacidad reproductiva hasta los 10 anos.

Producción de Crías: Con base a observaciones de campo para el berrendo de Sonora, estimamos que aproximadamente el 25% de las hembras con capacidad reproductiva no producen crías cada ano. Asi mismo, debido a que las hembras tipicamente tienen una sola cría durante su primera gestación, subdividimos el tamaño de la camada de tal forma que el 7.5% de la población de hembras tuviera una cría y el 67.5% tuviera dos crías. La variación en la reproducción se modela en VORTEX introduciendo una desviación standard (DS) para la proporción de hembras adultas que no producen crías. Debido a la falta de datos empíricos con respecto a esta variable, asumimos que esta variación (resultante de las fluctuaciones en la abundancia de alimentos y en la variación en las que las hembras alcanzan la madurez sexual) fue de 25% del valor de la media. VORTEX entonces determina el porcentaje de hembras que se reproducen cada año de la simulación, a partir de un distribución binomial con la media especificada (25%) y la DS (6.25%). Las proporciones relativas de las camadas de 1 y 2 crías se mantienen constantes.

Machos en el Pool Reproductivo: La proporción de machos con capacidad reproductiva anual inicialmente fue establecida en un 50%. Debido a que existe una jerarquía para los machos reproductivos, creemos que los machos más maduros conforman el pool reproductivo. Debido a que las densidades de las poblaciones en los desiertos son bajas, utilizamos porcentajes mayores de machos reproductivos que los que han sido reportados en la literatura debido al intervalo de tiempo que requiren los machos para encontrar hembras. Nosotros establecimos un porcentaje mayor correspondiente al 75%.

Relación de Sexos al Nacimiento: Debido a que no existe información para el berrendo peninsular que indique una relación de sexos en el nacimiento diferente a 50:50 utilizamos una relación igual para todas las simulaciones.

Mortalidad: La sobrevivencia de las crías entre las poblaciones de berrendos de Norteamérica pueden ser influenciada altamente por depredación, principalmente por depredadores tales como los coyotes y gato montes. Por ejemplo, la mortalidad en crías debido a la depredación por coyote en Alberta, Canada fue de cerca del 50% (Barrett, 1984). Este nivel de mortalidad ocurrió en una área con relativamente baja densidad de coyotes, estimada conservativamente en un ejemplar por cada 13 km^2. Las investigaciones desarrolladas en el Desierto del Vizcaíno, sugieren que las densidades de coyotes pueden ser mucho mayores. En forma consecuente, inicialmente fijamos una tasa de mortalidad en juveniles correspondientes al 60%. Esta decisión estuvo también basada en los resultados de las relaciones de sexo y edad reportados en los mas recientes rastreos del berrendo peninsular. Así mismo, los datos de las poblaciones de berrendos Americanos en los zoológicos indican que la mortalidad en juveniles es de cerca del 50%, por lo que la estimación de un 60% de mortalidad en vida silvestre parece muy razonable. Por supuesto, esta discusión no implica que toda la mortalidad en el berrendo se debe a depredación. Muchos otros factores juegan un papel en la mortalidad natural. Nosotros investigamos un aumento adicional en la densidad de depredadores incrementando la mortalidad juvenil a un 70% y hasta a un 80%.

No existen datos específicos de mortalidad en adultos para el berrendo Peninsular, pero datos provenientes de las poblaciones del berrendo Sonorense indican que esta es aproximadamente del 10% para ambos sexos. Para investigar los efectos del aumento en la depredación y en la cacería ilegal en el componente adulto de la población, establecimos valores de mortalidad adulta en un 15% y 20% en una submuestra de la simulaciones.

Depresión por Consanguinidad: No existe información específica de la prevalencia y de los efectos de la consangunidad en las poblaciones de berrendos peninsulares. De acuerdo a datos de censos recientes, puede ser razonable el inferir que el reducido tamano de las poblaciones observadas recientemente pueda ser resultado de un grado medible de consanguinidad. Por lo tanto, hemos incluído a la depresión por consanguinidad en una submuestra de los escenarios de modelaje.

Utilizamos el modelo de heterósis de depresión por consanguinidad. En este modelo los individuos que son heterozigótos para un locus genético particular tienen un vigor superior que aquellos que son homocigótos para este locus. Debido a que los alelos detrimentales particulares no son removidos en el curso del tiempo por la selección natural en este modelo, puede ser que los efectos deletéreos de la consanguinidad en las poblaciones de berrendos anteriormente modeladas esten sobreetimados.

La severidad de depresión por consanguinidad en las poblaciones de mamíferos puede ser medida como el número de "equivalentes letales" contenidos en el genoma de la población de interés. Información de algunas especies de cérvidos en cautiverio, sugiere que estas especies albergan alrededor de 3 equivalentes letales, un valor muy cercano al de la mediana obtenido en una muestra mayor que incluye a 40 especies de mamíferos analizada por Ralls et al. (1988). En forma consecuente, modelamos la depresión por consanguinidad utilizando el valor de la mediana de equivalentes letales.

Tamaño de la Población Inicial: El tamaño de la población fue inicialmente establecido en 100 animales. Este valor fue primordialmente seleccionado con base al juicio profesional, debido a la considerable variación de los censos obtenidos en los años recientes. Es importante el senalar que los últimos dos censos indicaron una cuenta mínima de entre 51 y 175 animales, correspondiendo el valor menor al censo mas reciente (Abril, 1994). El valor de 100 no es una media para estos dos censos. El promedio de los dos últimos censos es mayor pero los grupos alcanzaron un concenso de que la población real estaba constituída por alrededor de 100 individuos.

Sin embargo, es posible que las técnicas de muestreo utilizadas en el censo, revelaron unicamente una proporción de la poblacion real. Por lo tanto, empezamos un número de simulaciones considerando 200 animales. Iniciamos todos los escenarios con una distribución estable de edades, que distribuye a la población inicial entre cada una de las clases por edad y sexo, de acuerdo con la mortalidad existente y la calendarización reproductiva.

Capacidad de Carga: La capacidad de carga (K) define un límite superior para el tamaño de la población, arriba del cual se impone una mortalidad equitativa a través de las clases de edad y sexo, regresando la población a este valor o límite.

Nelson (1925) indicó que el tamaño total de la población del berrendo peninsular a lo largo de la península, con base en métodos de censo disponible entonces, era de 500 individuos. La distribución actual del berrendo, dentro de la Reserva del Desierto del Vizacaíno, incluye unicamente una parte de la distribución histórica. Debido a que los números reportados por Nelson probablemente subestimaron del tamaño real de la población y, debido a la superficie del hábitat de la Reserva de la Biosfera, nosotros estimamos una capacidad de carga de 500 individuos para la distribución actual. Debido a que casí no existe información sobre la capacidad de carga en la región para el berrendo, esta estimación está basada principalmnte en la intuición disponible. Debido a que la distribución actual del berrendo se encuentra dentro de la Reserva de la Biosfera, no modelamos una reducción determinística en la disponibilidad del hábitat ni tampoco la capacidad de carga del berrendo resultante de la degradación del habitat por motivos humanos.

Catástrofes: Las catástrofes son eventos singulares que ocurren fuera de los límites de la variación ambiental normal que afecta la reproducción y sobrevivencia. Estos eventos pueden ser huracanes, inundaciones, sequías, incendios, enfermedades y otras circunstancas similares. Los catástrofes son modeladas asignando una probabilidad anual de ocurrencia y un factor de severidad con un rango de 0.0 (efecto máximo o absoluto) a 1.0 (sin efecto).

Nosotros incluimos un 100 - año de sequía en un conjunto de escenarios. Este evento por lo tanto tiene una probabilidad de ocurrencia anual del 1.0% y reduce la probabilidad de sobrevivencia de todos los individuos en un 50% en comparación con aquellos años en los que no se registra ninguna sequía.

Repeticiones y Años de Proyección: Los escenarios que no incluyen depresión por consanguinidad fueron simulados 500 veces y aquellos que incorporaron depresión por consanguinidad fueron simulados 100 veces, debido a limitantes de computación. Las proyecciones de las poblaciones fueron extendidas a 100 años. Los resultados fueron resumidos en periódos o intervalos de 10 años para su utilización en figuras y tablas que mostramos a continuación. Todas las simulaciones fueron desarrolladas utilizando el paquete software VORTEX 6.3.

Resultados del Modelaje de Simulación

Resultados Determinísticos

Tasa de crecimiento (r_d) Las tasas de crecimiento determinísticas calculadas utilizando los métodos de la matriz Leslie (Ricklefs 1979) se muestran para cada escenario en la columna 6 de las Tablas 1 - 8. Los valores positívos indican crecimiento de poblaciones, mientras que los valores negativos indican una disminución de la poblacion. Un valor deterministico r<0 corresponde a una disminución determinística (por ejemplo, las muertes sobrepasan los nacimientos) y la población se extinguirá aun en ausencia de cualquier fluctuación estocástica. La diferencia entre la tasa del crecimiento determinístico de la población y la tasa de crecimiento que resulta de simulaciones (r_s, referirse abajo) puede mostrar una indicación del impacto de los factores estocásticos en la persistencia de las poblaciones.

Estas tasas determinísticas de crecimiento se calculan a partir de la mortalidad y de la calendarización reproductiva para cada escenario de modelaje. Como resultado, parámetros tales como la proporción de machos adultos disponibles para reproducción, el tamaño inicial de la población, y la inclusión de depresión por consanguinidad no alteran las tasas de crecimiento para una mortalidad particular. Este hecho es evidente en estas tablas. Sin embargo, observese que la inclusión de una catástrofe - en este caso, una sequía de 100 años, si reduce la tasa determinística de crecimiento, aunque solo ligeramente (Tablas 5 - 8).

Independientemente de la severidad de la mortalidad adulta, las poblaciones siempre se encuentran en crecimiento determinístico cuando la mortalidad de las crías es del 60%. Sin embargo, la tasa de crecimiento se reduce casi al 75% cuando la mortalidad de los adultos es mayor, en comparación con una reducida mortalidad adulta. Cuando la mortalidad de las crías es del 67.5%, las poblaciones se encuentran en una declinación determinística unicamente en aquellas condiciones en las que la mortalidad adulta es elevada. Tal y como se espera, las poblaciones se encuentran en declinación determinística cuando la mortalidad de las crías es alta (75%). En forma cualitativa, estas observaciones son similares cuando se adiciona una sequia al modelo.

Baja Mortalidad en Crías (60%)

Resultados del escenario de modelaje base - baja mortalidad de crías, tamaño inicial de la población de 100 animales, sin catástrofes y sin depresión por consanguinidad- se muestran en la Tabla 1 y en la Figura 1. Bajo condiciones de baja mortalidad adulta, el riesgo de extinción durante el periódo de tiempo de 100 años es de virtualmente 0 (Fig. 1a), conforme la población se incrementa rapidamente hacia la capacidad de carga bajo un crecimiento del 5 - 9 % (Fig. 1b). Cuando la mortalidad adulta es alta, el riesgo de extinción de la población es de unicamente 3% y la población se incrementa en una tasa anual de entre 1.5% a casi el 50% de la capacidad de carga asumida (Fig. 1b). En este y en todos los escenarios subsecuentes, el incrementar la porporcion de machos adultos disponibles para reproducción del valor base de 50 al 75% produce valores casi idénticos. Esto es de esperarse, debido al sistema polígamo de esta subespecie. Por lo tanto, podemos concluir que la persistencia de la población del berrendo es de cierta forma insensible a este parámetro; consecuentemente, consideraremos unicamente aquellos escenarios utilizando el valor base de 50% en todas las discusiones que siguen.

Si asumimos un tamaño inicial de la población de 200 individuos y una baja mortalidad de crías, el riesgo de extinción es de virtualmente cero bajo todos los escenarios de mortalidad (Tabla 3, Fig. 2a). Es más, las poblaciones se incrementan de una forma muy similar a aquellas de los escenarios base. Si se incorpora la depresión por consanguinidad al modelo, el riesgo de extinción se incrementa considerablemente, a más del 40%, si el tamaño inicial de la poblacion es reducido y la mortalidad adulta es alta (Tabla 2, Fig. 1a). Aún cuando el tamano inicial de la población es de 200, el riesgo de extinción se incrementa a 13% si la población esta sufriendo de depresión por consanguinidad (Tabla 4, Fig. 2a). Sin embargo, bajo condiciones de alta mortalidad adulta, independientemente del tamaño inicial de la población, las poblaciones muestran un incremento inicial seguido por un decremento en su tamano original debido a la alta la mortalidad que ocurre por consanguinidad (Figs. 1b, 2b). Es claro que, bajo estas condiciones, la depresión por consanguinidad tiene un efecto pronunciado en las dinámicas de esta población. Sin embargo, es importante recordar, que el modelo de heterósis de depresión por consanguinidad utilizado en estas simulaciones puede sobreestimar los efectos deletéreos de la consanguinidad (referirse a **Parámetros de Entrada para la Simulación**).

La adición de sequías a los modelos incrementá el riesgo de extinción y disminuye ligeramente los tamaños finales de la población, particularmente bajo condiciones de una alta mortalidad de adultos y de depresión por consanguinidad (Tablas 5 y 6, Figs. 7 y 8). Aún cuando estos eventos tienen una baja probabilidad de ocurrencia anual, sus efectos pueden ser muy severos y pueden conducir a la inestabilidad en las poblaciones.

Mortalidad Intermedia de Crías (67.5%)

En todos los casos una alta mortalidad de crías conduce a una mayor inestabilidad de la población. Cuando la mortalidad adulta es baja, el riesgo de extinción de la población disminuye para ambos tamaños iniciales de la población, aun en la presencia de depresión por consanguinidad (Tablas 1-4, Figs. 3a y 4a). El riesgo se incrementa considerablemente conforme la mortalidad adulta se incrementa. El riesgo se incrementa a casí 1.0 bajo condiciones de una alta mortalidad de adultos y de depresión por cosanguinidad, con una media en el tiempo de extinción de aproximadamente 50 a 60 años. Los efectos de la depresión por consanguinidad son particulamente pronunciados cuando el tamaño inicial de la población es bajo y la mortalidad de adultos es intermedia: el riesgo de extinción se incrementa de 9% a 63%, en escenarios excentos de sequías, y de entre 18% al 69% en aquellos escenarios que incorporan sequías. Cuando las poblaciones iniciales son grandes, los efectos de la consanguinidad en el riesgo de extinción no son tan pronunciados, aunque deben ser considerados.

Si la depresión por consanguinidad y la sequía estan ausentes, las poblaciones continuán incrementándose en un 0.2 - 4.1% por año para los niveles bajos e intermedios de mortalidad adulta. Sin embargo, una alta mortalidad adulta conduce a una declinación consistente de la población cercana al cero (Tablas 1 y 3, Figs. 3 y 4). El adicionar depresión por consanguinidad reduce la tasa de crecimiento estocástica para todos los niveles de mortalidad adulta; de hecho, bajo un nível intermedio de mortalidad adulta, el crecimiento estocástico cambia de positívo a negativo (Figs. 3b y 4b). El incluir el componente de sequías en el modelo tiende a aumentar estos efectos.

Mortalidad Alta de Crías (75%)

Cuando se incrementa la mortalidad de crías al 75%, ocurre una rapida destabilización de la población. Aún bajo condiciones relativamente óptimas, como por ejemplo, de un tamaño inicial de la población de 200 individuos, sin depresión por consanguinidad y sin sequía, el riesgo de extinción es del 24% con una media en el tiempo de extinción de 72 años (Tabla 3, Fig. 6a). El riesgo se incrementa rapidamente a 100% al adicionarse sequías, depresión por consanguinidad y una mayor mortalidad de adultos (por ejemplo Fig. 12a). Bajo estas condiciones mayormente severas, la extinción ocurre en un periódo de 30-40 años. Los efectos de depresión por consanguinidad se pronuncian mayormente cuando la mortalidad en adultos es baja; estos efectos son más pronunciados bajo condiciones de mayor mortalidad de adutos (Figs. 5a, 6a, 11a y 12a).

Todos los escenarios muestran decrementos rápidos y consistentes en el tamaño de las población, con tasas de crecimiento estocásticas que presentan un rango del -2% al -13%. Al igual que con las mediciones del riesgo de extinción, la depresión por consanguinidad muestra los mayores efectos cuando la mortalidad adulta es reducida.

Conclusiones

Los resultados del modelaje discutidos aquí representan una gran variedad de situaciones. El escenario mas optimístico, con una mortalidad adulta y de crías reducida, sin sequías o depresión por consanguinidad y con un tamaño inicial de la población largo, presenta una tasa anual de crecimiento de casí el 9% sin riesgo de extinción en los proximos 100 años (Tabla 1, Fig. 1). En el otro extremo, el escenario mas pesimista produce una población que se extinguirá dentro de 70 años, con una tasa anual de crecimiento de -13%. Es probable que actualmente la población se encuentre intermedia entre estos dos extremos, con un riesgo considerable de extinción de entre los próximos 100 años.

Los modelos indican que tanto la mortalidad de crías como la adulta parecen ser los factores primarios que influencian la variabilidad del berrendo peninsular en el Desierto de Vizacaíno. De hecho, los resultados sugieren que la población es igualmente sensible a incrementos en la mortalidad de crías como de adultos. Sin embargo, los esfuerzos del modelaje muestran claramente que una reducida mortalidad en crías, aun con una alta mortalidad de adultos, puede conducir a un crecimiento o estabilidad poblacional, mientras que una mortalidad alta en crías siempre resulta en una declinación de la poblacion y en la inestabilidad de la misma (refererise a Tabla 1). Estos datos sugieren que las acciones de manejo deben de dirigirse especificamente hacia la reducción en la mortalidad del berrendo, posiblemente haciéndo una enfasís en las crías. Parece ser que esto puede lograrse traves del control de depredadores y de la criánza bajo condiciones de semicautiverio. Para determinar el curso de acción mas apropiado, deben de realizarse análisis de costo-beneficio muy detallados.

Aún mas, la consecuencias deletéreas de la consanguinidad pueden ser considerables, particularmente cuando las poblaciones de los berrendos son pequeñas (por ejemplo de 100) y estos efectos deben de ser reconocidos y apreciados por aquellos responsables del manejo de la subespecie. Esfuerzos directos deben de desarrollarse para establecer y mantener una población mayor en vida silvestre en orden de reducir el impacto de la depresión por consanguinidad.

POPULATION BIOLOGY AND MODELLING

Introduction

The need for and effects of intensive management strategies can be modelled to suggest which practices may be the most effective in conserving this population. VORTEX, a simulation modelling package written by Robert Lacy and Kim Hughes, was used as a tool to study the interaction of multiple stochastic variables.

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, catastrophes, etc.) that occur according to defined probability distributions. The probabilities of events are modelled 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 cycle 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 enter 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 pronghorn, the conditions affecting the population, and possible changes in the future. More specifically, since the amount of life history data specific to the peninsular pronghorn is limited, we utilized data from wild population of Sonoran pronghorn (*Antilocapra americana sonoriensis*) when appropriate. These two subspecies are similar ecologically, allowing for the use of data from this well-studied population.

Input Parameters for Simulations

Mating System: Polygynous

Average Age of First Reproduction: VORTEX defines breeding as the time when young are born, not the age of sexual maturity. Age of sexual maturity for females is about 16 months, while males reach sexual maturity before one year of age. However, because the gestation period for this subspecies is approximately 8 months, we have set the age of first reproduction for females at two years and for males at one year.

Age of Senescence: VORTEX assumes that animals can breed (at the normal rate) throughout their adult life. Data from Sonoran pronghorn indicate that both males and females are reproductively capable until 10 years of age.

Fawn Production: Based on field observations for Sonoran pronghorn we estimated that approximately 25% of reproductively capable females did not have fawns each year. Further, because does typically have single fawns during their first pregnancy we subdivided litter size so that 7.5% of the female population had one offspring and 67.5 % had twin fawns.

Variation in reproduction is modelled in VORTEX by entering a standard deviation (SD) for the proportion of adult females producing no offspring. Because empirical data for this variable were lacking, we assumed that such variation (due to fluctuations in food abundance and variability in the age at which females reach sexual maturity) was 25% of the mean value. VORTEX then determines the percent of females breeding each year of the simulation by sampling from a binomial distribution with the specified mean (25%) and SD (6.25%). The relative proportions of litters of 1 and 2 offspring are held constant.

Male Breeding Pool: The proportion of adult males breeding each year was initially set at 50%. Because pronghorn have a social heirarchy for breeding males, we felt that only more mature bucks made up the breeding pool. Because densities in desert populations are low, we also used higher percentages of males actually breeding than reported in the literature due to the time interval required for bucks to find does. We set this higher figure at 75%.

Sex Ratio at Birth: As no data exist indicating other than a 50:50 sex ratio at birth for peninsular pronghorns, we used an equal sex ratio for all simulations.

Mortality: Fawn survival among pronghorn populations in North America can be heavily influenced by predation, primarily by such predators as coyotes and bobcats. For example, fawn mortality due to coyote predation in Alberta, Canada was nearly 50% (Barrett, 1984). This level of mortality was in an area of relatively low coyote density, estimated conservatively at one per 13 km^2. Research in the Vizcaino Desert suggests that coyote densities may be much higher. Consequently, we set an initial mortality rate for juveniles at 60%. This choice was also based on sex and age ratios from the most recent surveys of peninsular pronghorn. In addition, data from American pronghorn populations in zoos indicate juvenile mortalities approaching 50%, making 60% juvenile mortality in wild populations very reasonable. Of course, this discussion does not imply that all mortality in pronghorn is due to predation. Many other factors play a role in natural mortality. We modelled a further increase in predator density by increasing juvenile mortality to 70% and even 80%.

No specific data are available for adult mortality of peninsular pronghorn, but data from Sonoran pronghorn populations indicate that adult mortality is about 10% for both sexes. To investigate the effects of increased predation and poaching on the adult component of the population, we set adult mortality at 15% and 20% in a subset of simulations.

Inbreeding Depression: Specific data do not exist on the prevalence and effects of inbreeding in peninsular pronghorn populations. Given recent census data, it may be reasonable to infer that the small population sizes observed in the recent past may have resulted in some measurable degree of inbreeding. Therefore, we have included inbreeding depression in a subset of modelling scenarios.

We employed the heterosis model of inbreeding depression, in which individuals that are heterozygous at a given genetic locus have superior fitness to those that are homozygous at that locus. Because particular detrimental alleles are not removed by natural selection from the population over time in this model, the heterosis model may provide an overestimate of the deleterious effects of inbreeding in the pronghorn populations modelled below.

The severity of inbreeding depression in mammal populations can be measured as the number of "lethal equivalents" contained in the genome of the population of interest. Data for some captive cervid species suggests that these species harbor about 3 lethal equivalents, a value very close to the median value obtained in the larger dataset of 40 mammalian species analyzed by Ralls et al. (1988). Consequently, we modelled inbreeding depression using this median lethal equivalent value.

Initial Population Size: The initial population size was first set at 100 animals. This value was selected based primarily on professional judgement due to considerable variation in census results in recent years. It is important to note that the last two censuses indicated between 51 and 175 animals minimum count with the lower value being the most recent (April 1994). The value of 100 is not a mean for these two surveys. The average of the last two censuses is higher but the groups reached a concensus that the true population was closer to 100.

It is possible, however, that the survey techniques used in the censuses revealed only a proportion of the true population. We therefore began a number of simulations with 200 animals. We initialized all scenarios with a stable age distribution that distributes the starting population among each age-sex class in accordance with the existing mortality and reproductive schedules.

Carrying Capacity: The carrying capacity (K) defines an upper limit for the population size, above which additional mortality is imposed equally across age and sex classes in order to return the population to this value.

Nelson (1925) stated that the total population size for peninsular pronghorn across the peninsula, based on census methods available at that time, was 500 individuals. The current distribution of the pronghorn, within the Vizcaino Desert Biosphere Reserve, encompasses only a part of the historical distribution. Since Nelson's number probably underestimated the true population size, and given the current size of Biosphere Reserve habitat, we estimated a carrying capacity of 500 individuals for the current distribution. As there are virtually no data that provide substantial insight into the pronghorn carrying capacity of the region, this estimate is based primarily on available intuition.

Because the current distribution of pronghorn is within the Biosphere Reserve, we did not model a deterministic reduction in habitat availability and, by extension, pronghorn carrying capacity due to human-mediated habitat degradation.

Catastrophes: Catastrophes are singular events outside the bounds of normal environmental variation affecting reproduction and survival. These events can be tornadoes, floods, droughts, fire, disease, or other similar circumstances. Catastrophes are modelled by assigning an annual probability of occurrence and a severity factor ranging from 0.0 (maximum or absolute effect) to 1.0 (no effect).

We included a 100-year drought in a set of scenarios. This event therefore has an annual probability of occurrence of 1.0% and reduces the probability of survival for all individuals by 50% compared to non-drought years.

Iterations and Years of Projection: Those scenarios not including inbreeding depression were simulated 500 times, while scenarios incorporating inbreeding depression were simulated 100 times because of computational limitations. Population projections extended for 100 years. Output results were summarized at 10-year intervals for use in the Figures and Tables that follow. All simulations were conducted using the VORTEX 6.3 software package.

Results from Simulation Modelling

Deterministic Results

Growth rate (r_d) The deterministic growth rates calculated using Leslie matrix methods (Ricklefs 1979) are shown for each scenario in column 6 of Tables 1-8. Positive values indicate population growth, while negative values indicate population decline. A deterministic $r < 0$ is in deterministic decline (i.e., deaths outpace births), and will go extinct even in the absence of any stochastic fluctuations. The difference between the deterministic population growth rate and the growth rate resulting from the simulation (r_s, see below) can give an indication of the impact of stochastic factors on population persistence.

These deterministic growth rates are calculated from the mortality and fecundity schedules for each modelling scenario. As a result, parameters such as the proportion of adult males available for breeding, the initial population size, and the inclusion of inbreeding depression do not alter the growth rates for a particular mortality schedule. This is evident in the Tables. Note, however, that the inclusion of a catastrophe—in this case, a 100-year drought—does reduce the deterministic growth rate, although only slightly (Tables 5-8).

Regardless of the severity of adult mortality, the populations are always in deterministic growth when fawn mortality is 60%. However, the growth rate is reduced by nearly 75% when adult mortality is highest, compared to conditions of low adult mortality. When fawn mortaltiy is 67.5%, populations are in deterministic decline only under conditions of high adult mortality. As may be expected, the populations are in deterministic decline when fawn mortality is high (75%). These observations are qualitatively the same when drought is added to the models.

Stochastic Simulation Results

Low Fawn Mortality (60%)

Results from the base modelling scenario—low fawn mortality, initial population size of 100 animals, with no catastrophes and no inbreeding depression—are shown in Table 1 and Figure 1. Under conditions of low adult mortality, risk of extinction over the 100-year time span is virtually zero (Fig. 1a), as the population rapidly increases to carrying capacity under 5-9% annual growth (Fig. 1b). When adult mortality is high, the risk of population extinction is only 3% and the population increases at an annual rate of about 1.5% to nearly 50% of the assumed carrying capacity (Fig. 1b). In these and all subsequent scenarios, increasing the proportion of adult males available for breeding from the base value of 50% to 75% yields nearly identical results. This is to be expected, given the polygynous breeding system in this subspecies. We can therefore conclude that the persistence of the pronghorn population is quite insensitive to this parameter; consequently, we will consider only those scenarios using the base 50% value in all discussions to follow.

If we assume an initial population size of 200 individuals and low fawn mortality, the extinction risk is virtually zero under all adult mortality scenarios (Table 3, Fig. 2a). Furthermore, the populations increase in a manner very similar to those in the base scenarios. If inbreeding depression is incorporated into the model, extinction risk is increased considerably, to over 40%, if the initial population size is low and adult mortality is high (Table 2, Fig. 1a). Even if the initial population size is 200, the risk of extinction increases to 13% if the population is suffering from inbreeding depression (Table 4, Fig. 2a). However, under conditions of high adult mortality, regardless of initial size, the populations show an initial increase followed by a decrease to their original size as increased mortality occurs through inbreeding (Figs. 1b, 2b). It is clear that, under these conditions, inbreeding depression does have a pronounced effect on the dynamics of this population. It is important to remember, however, that the heterosis model of inbreeding depression used in these simulations may provide an overestimate of the deleterious effects of inbreeding (see **Input Parameters for Simulations** above).

The addition of drought to the models increases the extinction risk and slightly decreases the final population sizes, particularly under conditions of high adult mortality and inbreeding depression (Tables 5 and 6, Figs. 7 and 8). Even though these events have a low annual probability of occurrence, their effects can be quite severe and can lead to population instability.

Intermediate Fawn Mortality (67.5%)

Overall, higher fawn mortality leads to greater population instability. When adult mortality is low, the risk of population extinction is negligible for both initial population sizes, even in the presence of inbreeding depression (Tables 1-4, Figs. 3a and 4a). This risk is greatly increased, however, as adult mortality is increased. This risk increases to nearly 1.0 under conditions of high adult mortality and inbreeding depression, with a mean time to extinction of approximately 50-60 years. The effects of inbreeding depression are particularly pronounced when the initial population size is low and adult mortality is intermediate: the risk of extinction increases from 9% to 63% in non-drought scenarios, and from 18% to 69% in scenarios incorporating drought. When initial populations are larger in size, the effects of inbreeding on extinction risk are not as pronounced, but are nevertheless considerable.

If inbreeding depression and drought are absent, populations continue to increase at 0.2-4.1% per year for low and intermediate levels of adult mortality. However, high adult mortality leads to consistent population decline to near zero (Tables 1 and 3, Figs. 3 and 4). Adding inbreeding depression further reduces the stochastic growth rate for all levels of adult mortality; in fact, under intermediate adult mortality, stochastic growth changes from positive to negative (Figs. 3b and 4b). Including drought into the models tends to magnify these effects.

High Fawn Mortality (75%)

When fawn mortality is further increased to 75%, rapid population destabilization occurs. Even under relatively optimal conditions, i.e., initial population size of 200 individuals, no inbreeding depression, and no drought, the risk of extinction is 24% with a mean time to extinction of 72 years (Table 3, Fig. 6a). This risk increases rapidly to 100% as drought, inbreeding depression, and higher adult mortality are factored into the models (i.e., Fig. 12a). Under these more severe conditions, extinction occurs in 30-40 years. The effects of inbreeding depression are most pronounced when adult mortality is low; these effects are swamped out under conditions of higher adult mortality (Figs. 5a, 6a, 11a, and 12a).

All scenarios show consistent, and in many cases rapid, decline in population size, with stochastic growth rates ranging from -2% to -13%. As with measures of extinction risk, inbreeding depression shows the greatest effect when adult mortality is low.

Conclusions

The modelling results discussed here represent a great variety of outcomes. The most optimistic scenario, with low adult and fawn mortality, no drought or inbreeding depression, and large initial population size, has an annual growth rate of nearly 9% with no risk of extinction in 100 years (Table 1, Fig. 1). At the other extreme, the most pessimistic scenario yields a population that is certain to be extinct within 70 years, with an annual growth rate of -13%. It is likely that the population currently is intermediate between these two extremes, with a considerable risk of extinction within the next 100 years.

The models indicate that both fawn and adult mortality appear to be the primary factors influencing the viability of the pronghorn population in the Vizcaino Desert. In fact, the results suggest that the population is roughly equally sensitive to increases in both fawn and adult mortality. Nevertheless, the modelling efforts clearly show that reduced fawn mortality, even with high adult mortality, can lead to population growth or stability, while higher fawn mortality always results in population decline and instability (Table 1). Together, these data suggest that management actions should be directed specifically toward reducing pronghorn mortality, perhaps with an emphasis on fawns. It appears that this can be accomplished through predator control and/or semi-captive rearing. Detailed cost-benefit analyses must be undertaken to determine the most appropriate course of action.

Furthermore, the deleterious consequences of inbreeding can be considerable, particularly when pronghorn populations are quite small (i.e., <100), and these effects must be recognized and appreciated by those responsible for subspecies management. Direct efforts should be made to establish and maintain larger wild population sizes in order to reduce the impact of inbreeding depression.

Sample VORTEX Input File

```
PRONG320.OUT     ***Output Filename***
Y      ***Graphing Files?***
N      ***Each Iteration?***
100     ***Simulations***
100      ***Years***
10      ***Reporting Interval***
1      ***Populations***
Y      ***Inbreeding Depression?***
H      ***Model of Inbreeding Depression***
3.140000      ***Number of Lethal Equivalents?***
Y      ***EV correlation?***
1      ***Types Of Catastrophes***
P      ***Monogamous, Polygynous, or Hermaphroditic***
2      ***Female Breeding Age***
1      ***Male Breeding Age***
10      ***Maximum Age***
0.500000     ***Sex Ratio***
2      ***Maximum Litter Size***
N      ***Density Dependent Breeding?***
25.000000     ***Population 1: Percent Litter Size 0***
7.500000     ***Population 1: Percent Litter Size 1***
67.500000     ***Population 1: Percent Litter Size 2***
2.500000     ***EV--Reproduction***
60.000000     ***Female Mortality At Age 0***
14.770979     ***EV--FemaleMortality***
10.000000     ***Female Mortality At Age 1***
2.500000     ***EV--FemaleMortality***
20.000000     ***Adult Female Mortality***
5.000000     ***EV--AdultFemaleMortality***
60.000000     ***Male Mortality At Age 0***
14.770979     ***EV--MaleMortality***
25.000000     ***Adult Male Mortality***
6.250000     ***EV--AdultMaleMortality***
1.000000     ***Probability Of Catastrophe 1***
1.000000     ***Severity--Reproduction***
0.500000     ***Severity--Survival***
N       ***All Males Breeders?***
Y       ***Answer--A--Known?***
75.000000     ***Percent Males In Breeding Pool***
Y      ***Start At Stable Age Distribution?***
100     ***Initial Population Size***
500     ***K***
0.000000     ***EV--K***
N      ***Trend In K?***
N      ***Harvest?***
N      ***Supplement?***
Y      ***AnotherSimulation?***
```

Table 1. Peninsular pronghorn population analysis: initial population size = 100, no catastrophes, no inbreeding depression.

	Mortality (%)									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
201	60	10	15	50	.090	.088 (.114)	0.0	488 (26)	0.940	—
210				75	.090	.086 (.114)	0.0	489 (23)	0.943	—
202		15	20	50	.057	.052 (.129)	0.0	464 (50)	0.924	—
211				75	.057	.052 (.129)	0.0	459 (54)	0.927	—
203		20	25	50	.023	.016 (.151)	0.028	321 (148)	0.840	—
212				75	.023	.015 (.152)	0.026	309 (148)	0.843	—
204	67.5	10	15	50	.047	.041 (.133)	0.0	438 (84)	0.919	—
213				75	.047	.042 (.134)	0.0	438 (84)	0.926	—
205		15	20	50	.013	.002 (.164)	0.090	205 (162)	0.770	—
214				75	.013	.004 (.160)	0.074	214 (154)	0.809	—
206		20	25	50	-.022	-.043 (.217)	0.704	42 (52)	0.559	60
215				75	-.022	-.040 (.215)	0.662	41 (50)	0.573	62
207	75	10	15	50	-.003	-.023 (.194)	0.424	101 (118)	0.682	65
216				75	-.003	-.021 (.191)	0.394	101 (119)	0.700	62
208		15	20	50	-.039	-.066 (.234)	0.900	20 (19)	0.509	52
217				75	-.039	-.064 (.233)	0.900	28 (57)	0.529	52
209		20	25	50	-.076	-.110 (.266)	1.0	—	—	36
218				75	-.076	-.110 (.267)	0.998	2 (—)	0.375	36

% Males refers to the proportion of males available for breeding; r_d is the deterministic growth rate calculated from the life table; r_s (SD) is the stochastic growth (standard deviation) calculated from the simulations; P(E) is the probability of population extinction after 100 years; N_{100} (SD) is the mean final population size (standard deviation) of those simulated populations surviving to 100 years; H_{100} is the mean population heterozygosity after 100 years; and T(E) is the mean time to population extinction for those scenarios in which at least 20% of the populations went extinct.

Table 2. Peninsular pronghorn population analysis: initial population size = 100, no catastrophes, heterosis model of inbreeding depression (3.14 lethal equivalents). Table heading definitions are as in Table 1.

	Mortality									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
273	60	10	15	50	.090	.073 (.111)	0.0	481 (31)	0.940	—
282				75	.090	.074 (.111)	0.0	483 (28)	0.944	—
274		15	20	50	.057	.037 (.128)	0.01	419 (108)	0.916	—
283				75	.057	.040 (.126)	0.0	428 (77)	0.923	—
275		20	25	50	.023	-.018 (.167)	0.41	145 (140)	0.815	74
284				75	.023	-.023 (.175)	0.49	151 (148)	0.826	72
276	67.5	10	15	50	.047	.028 (.131)	0.02	377 (131)	0.921	—
285				75	.047	.027 (.132)	0.02	373 (139)	0.909	—
277		15	20	50	.013	-.035 (.185)	0.63	93 (126)	0.771	70
286				75	.013	-.030 (.173)	0.54	69 (97)	0.784	67
278		20	25	50	-.022	-.075 (.226)	0.98	25 (27)	0.755	52
287				75	-.022	-.073 (.220)	0.98	7 (4)	0.676	52
279	75	10	15	50	-.003	-.046 (.197)	0.80	94 (106)	0.735	68
288				75	-.003	-.051 (.200)	0.79	39 (53)	0.776	63
280		15	20	50	-.039	-.088 (.230)	1.0	—	—	44
289				75	-.039	-.088 (.230)	1.0	—	—	44
281		20	25	50	-.076	-.123 (.258)	1.0	—	—	32
290				75	-.076	-.131 (.266)	1.0	—	—	30

Table 3. Peninsular pronghorn population analysis: initial population size = 200, no catastrophes, no inbreeding depression. Table heading definitions are as in Table 1.

	Mortality									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
219	60	10	15	50	.090	.086 (.113)	0.0	489 (23)	0.950	—
228				75	.090	.087 (.113)	0.0	490 (22)	0.954	—
220		15	20	50	.057	.052 (.128)	0.0	460 (54)	0.943	—
229				75	.057	.052 (.127)	0.0	462 (52)	0.945	—
221		20	25	50	.023	.016 (.145)	0.01	348 (130)	0.906	—
230				75	.023	.016 (.146)	0.004	340 (137)	0.905	—
222	67.5	10	15	50	.047	.040 (.132)	0.0	441 (79)	0.942	—
231				75	.047	.040 (.133)	0.0	438 (76)	0.945	—
223		15	20	50	.013	.005 (.153)	0.028	253 (146)	0.867	—
232				75	.013	.005 (.154)	0.032	268 (155)	0.875	—
224		20	25	50	-.022	-.040 (.204)	0.554	54 (68)	0.611	68
233				75	-.022	-.041 (.206)	0.570	59 (81)	0.670	69
225	75	10	15	50	-.003	-.020 (.183)	0.238	108 (123)	0.752	72
234				75	-.003	-.020 (.181)	0.260	120 (125)	0.775	71
226		15	20	50	-.039	-.065 (.224)	0.858	39 (60)	0.579	60
235				75	-.039	-.065 (.224)	0.856	30 (45)	0.583	61
227		20	25	50	-.076	-.107 (.258)	0.994	11 (4)	0.272	43
236				75	-.076	-.108 (.258)	0.990	13 (9)	0.266	42

Table 4. Peninsular pronghorn population analysis: initial population size = 200, no catastrophes, heterosis model of inbreeding depression (3.14 lethal equivalents). Table heading definitions are as in Table 1.

	Mortality									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
291	60	10	15	50	.090	.079 (.111)	0.0	489 (24)	0.951	—
300				75	.090	.078 (.113)	0.0	483 (27)	0.953	—
292		15	20	50	.057	.043 (.125)	0.0	437 (80)	0.944	—
301				75	.057	.043 (.125)	0.0	451 (81)	0.942	—
293		20	25	50	.023	-.004 (.154)	0.13	201 (145)	0.863	—
302				75	.023	-.004 (.150)	0.11	206 (147)	0.878	—
294	67.5	10	15	50	.047	.029 (.132)	0.01	382 (114)	0.936	—
303				75	.047	.033 (.130)	0.0	396 (102)	0.945	—
295		15	20	50	.013	-.018 (.163)	0.28	154 (139)	0.852	81
304				75	.013	-.018 (.162)	0.27	133 (131)	0.856	74
296		20	25	50	-.022	-.068 (.207)	0.95	26 (27)	0.777	62
305				75	-.022	-.067 (.211)	0.94	44 (61)	0.781	64
297	75	10	15	50	-.003	-.039 (.185)	0.56	75 (104)	0.758	70
306				75	-.003	-.042 (.186)	0.58	65 (104)	0.777	68
298		15	20	50	-.039	-.079 (.223)	0.96	27 (40)	0.665	57
307				75	-.039	-.086 (.225)	0.98	7 (0)	0.714	53
299		20	25	50	-.076	-.121 (.253)	1.0	—	—	38
308				75	-.076	-.118 (.248)	1.0	—	—	40

Table 5. Peninsular pronghorn population analysis: initial population size = 100, catastrophe (100-year drought), no inbreeding depression. Table heading definitions are as in Table 1.

	Mortality									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
237	60	10	15	50	.085	.079 (.134)	0.0	477 (50)	0.937	—
246				75	.085	.080 (.133)	0.0	475 (56)	0.939	—
238		15	20	50	.052	.046 (.146)	0.002	440 (89)	0.913	—
247				75	.052	.046 (.148)	0.002	437 (91)	0.916	—
239		20	25	50	.018	.006 (.173)	0.106	255 (164)	0.798	—
248				75	.018	.007 (.174)	0.078	254 (155)	0.798	—
240	67.5	10	15	50	.042	.034 (.151)	0.008	391 (120)	0.902	—
249				75	.042	.032 (.153)	0.014	395 (121)	0.904	—
241		15	20	50	.008	-.005 (.183)	0.178	171 (147)	0.760	—
250				75	.008	-.006 (.182)	0.182	166 (149)	0.762	—
242		20	25	50	-.027	-.054 (.236)	0.842	33 (35)	0.498	58
251				75	-.027	-.052 (.233)	0.808	39 (40)	0.557	56
243	75	10	15	50	-.008	-.030 (.207)	0.518	74 (94)	0.668	65
252				75	-.008	-.029 (.210)	0.498	69 (87)	0.665	62
244		15	20	50	-.044	-.072 (.248)	0.946	23 (28)	0.400	50
253				75	-.044	-.076 (.251)	0.950	19 (18)	0.488	48
245		20	25	50	-.081	-.123 (.280)	1.0	—	—	32
254				75	-.081	-.120 (.281)	0.998	9 (—)	0.346	33

Table 6. Peninsular pronghorn population analysis: initial population size = 100, catastrophe (100-year drought), heterosis model of inbreeding depression (3.14 lethal equivalents). Table heading definitions are as in Table 1.

	Mortality									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
309	60	10	15	50	.085	.066 (.132)	0.0	446 (89)	0.934	—
318				75	.085	.068 (.132)	0.0	469 (64)	0.938	—
310		15	20	50	.052	.022 (.148)	0.06	348 (142)	0.897	—
319				75	.052	.025 (.148)	0.05	357 (140)	0.908	—
311		20	25	50	.018	-.034 (.196)	0.62	90 (94)	0.809	67
320				75	.018	-.031 (.192)	0.56	99 (134)	0.783	67
312	67.5	10	15	50	.042	.014 (.154)	0.07	293 (165)	0.877	—
321				75	.042	.016 (.157)	0.08	301 (166)	0.878	—
313		15	20	50	.008	-.041 (.199)	0.69	57 (92)	0.732	65
322				75	.008	-.037 (.196)	0.71	89 (90)	0.785	71
314		20	25	50	-.027	-.085 (.241)	1.0	—	—	46
323				75	-.027	-.084 (.243)	0.99	3 (—)	0.0	47
315	75	10	15	50	-.008	-.051 (.208)	0.83	43 (64)	0.726	62
324				75	-.008	-.056 (.210)	0.86	36 (42)	0.716	61
316		15	20	50	-.044	-.099 (.249)	1.0	—	—	40
325				75	-.044	-.099 (.244)	1.0	—	—	40
317		20	25	50	-.081	-.133 (.274)	1.0	—	—	30
326				75	-.081	-.142 (.278)	1.0	—	—	28

Table 7. Peninsular pronghorn population analysis: initial population size = 200, catastrophe (100-year drought), no inbreeding depression. Table heading definitions are as in Table 1.

	Mortality									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
255	60	10	15	50	.085	.079 (.133)	0.0	478 (50)	0.949	—
264				75	.085	.079 (.134)	0.0	473 (55)	0.951	—
256		15	20	50	.052	.046 (.144)	0.0	445 (78)	0.937	—
265				75	.052	.044 (.146)	0.0	438 (94)	0.937	—
257		20	25	50	.018	.011 (.162)	0.022	300 (145)	0.881	—
266				75	.018	.008 (.166)	0.030	284 (151)	0.869	—
258	67.5	10	15	50	.042	.034 (.152)	0.002	393 (117)	0.932	—
267				75	.042	.035 (.150)	0.0	415 (104)	0.939	—
259		15	20	50	.008	-.004 (.174)	0.092	196 (156)	0.831	—
268				75	.008	-.005 (.176)	0.106	202 (157)	0.828	—
260		20	25	50	-.027	-.048 (.218)	0.692	45 (54)	0.616	66
269				75	-.027	-.049 (.221)	0.682	37 (43)	0.633	66
261	75	10	15	50	-.008	-.028 (.200)	0.358	86 (112)	0.721	70
270				75	-.008	-.030 (.203)	0.402	85 (107)	0.730	69
262		15	20	50	-.044	-.069 (.239)	0.890	34 (34)	0.639	58
271				75	-.044	-.070 (.238)	0.898	25 (40)	0.521	58
263		20	25	50	-.081	-.114 (.268)	0.996	14 (3)	0.546	40
272				75	-.081	-.111 (.269)	0.996	5 (1)	0.0	42

Table 8. Peninsular pronghorn population analysis: initial population size = 200, catastrophe (100-year drought), heterosis model of inbreeding depression (3.14 lethal equivalents). Table heading definitions are as in Table 1.

	Mortality									
		Adult								
File #	Fawn	♀	♂	% Males	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
327	60	10	15	50	.085	.071 (.132)	0.0	472 (57)	0.949	—
336				75	.085	.069 (.133)	0.0	460 (71)	0.949	—
328		15	20	50	.052	.031 (.147)	0.02	395 (127)	0.928	—
337				75	.052	.033 (.143)	0.0	402 (127)	0.929	—
329		20	25	50	.018	-.020 (.179)	0.32	137 (134)	0.844	78
338				75	.018	-.013 (.172)	0.20	154 (133)	0.860	79
330	67.5	10	15	50	.042	.024 (.148)	0.0	355 (142)	0.931	—
339				75	.042	.024 (.149)	0.01	349 (144)	0.930	—
331		15	20	50	.008	-.032 (.190)	0.49	109 (108)	0.831	73
340				75	.008	-.025 (.186)	0.41	150 (156)	.843	77
332		20	25	50	-.027	-.080 (.227)	0.99	12 (—)	0.722	58
341				75	-.027	-.077 (.231)	0.96	12 (5)	0.514	59
333	75	10	15	50	-.008	-.055 (.212)	0.77	53 (62)	0.725	67
342				75	-.008	-.048 (.205)	0.72	78 (107)	0.821	68
334		15	20	50	-.044	-.099 (.240)	1.0	—	—	47
343				75	-.044	-.092 (.235)	0.99	22 (—)	0.871	49
335		20	25	50	-.081	-.137 (.259)	1.0	—	—	34
344				75	-.081	-.133 (.268)	1.0	—	—	36

Figure Legends

Figure 1. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 60% and an initial population size of 100 under different adult mortality scenarios:

A: 10% female, 15% male
B: 15% female, 20% male
C: 20% female, 25 % male
(A-C)/F: Scenarios incorporating inbreeding depression.

In these and all subsequent figures, only scenarios incorporating 50% of adult males into the breeding pool are shown.

Figure 2. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 60% and an initial population size of 200 under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 3. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 67.5% and an initial population size of 100 under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 4. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 67.5% and an initial population size of 200 under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 5. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 75% and an initial population size of 100 under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 6. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 75% and an initial population size of 200 under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 7. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 60%, an initial population size of 100, and exposure to drought under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 8. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 60%, an initial population size of 200, and exposure to drought under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 9. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 67.5%, an initial population size of 100, and exposure to drought under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 10. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 67.5%, an initial population size of 200, and exposure to drought under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 11. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 75%, an initial population size of 100, and exposure to drought under different adult mortality scenarios. Curves defined as in Figure 1.

Figure 12. Probability of population extinction (a) and final population size (b) for pronghorn populations with juvenile mortality = 75%, an initial population size of 200, and exposure to drought under different adult mortality scenarios. Curves defined as in Figure 1.

Fig. 1. Juvenile Mortality = 60%
$N_0 = 100$

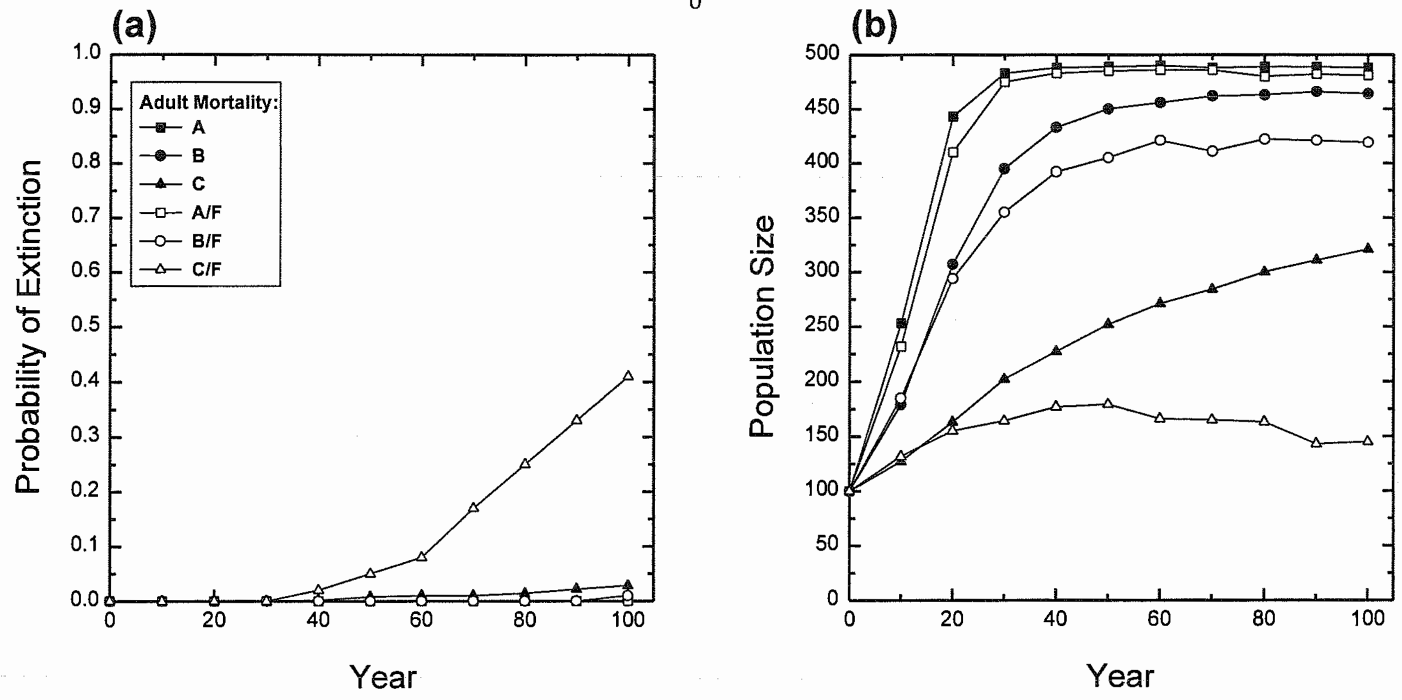


Fig. 2. Juvenile Mortality = 60%
$N_0 = 200$

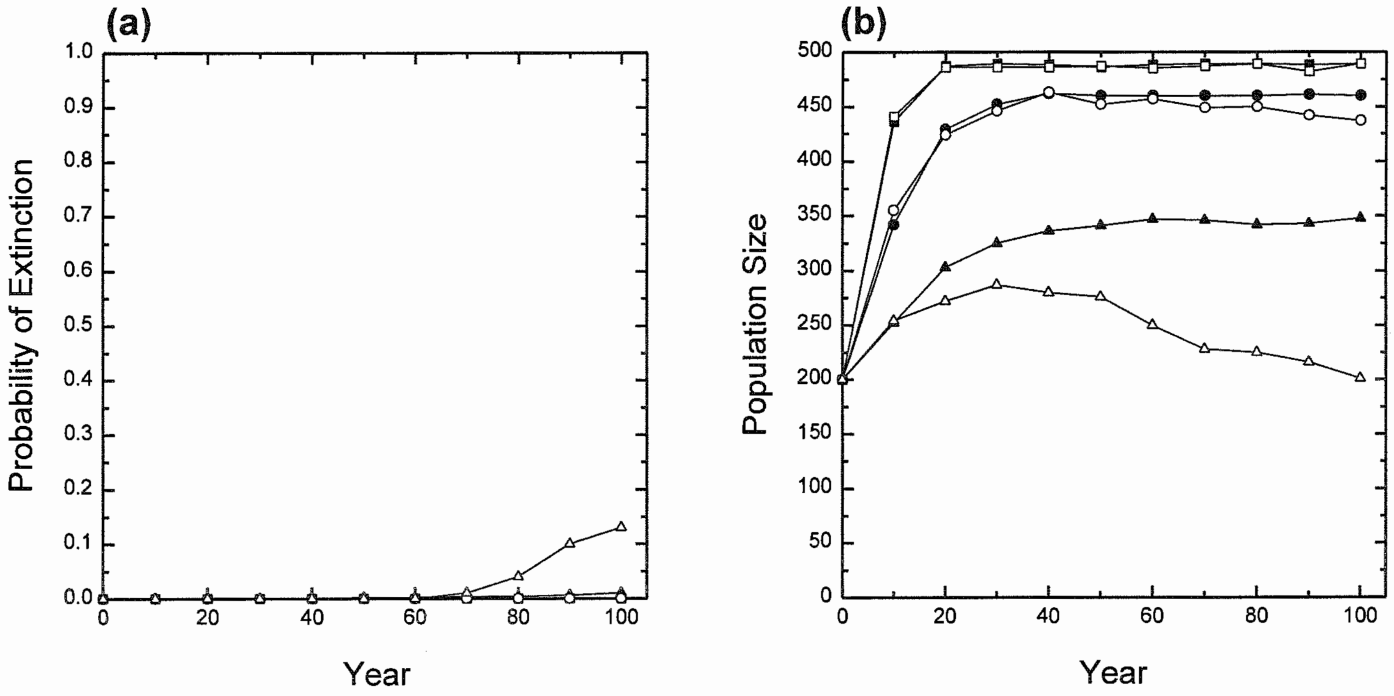


Fig. 3. Juvenile Mortality = 67.5%
$N_0 = 100$

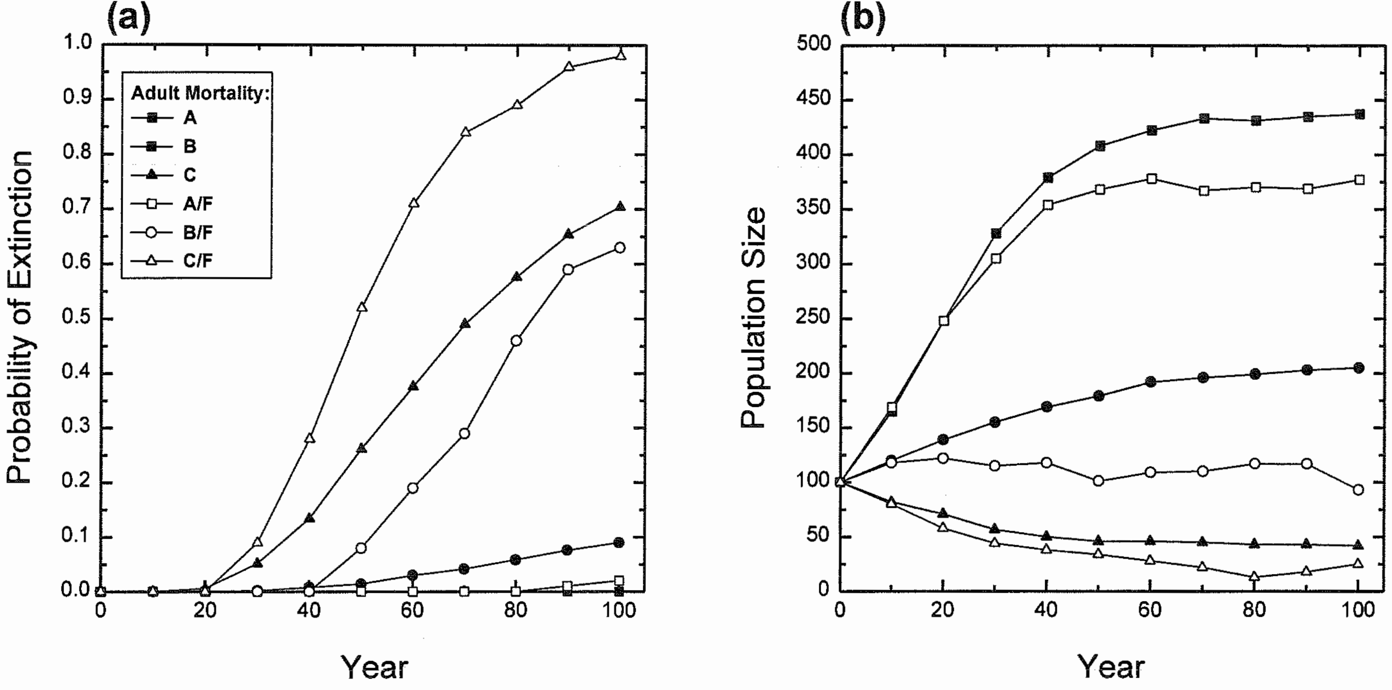


Fig. 4. Juvenile Mortality = 67.5%
$N_0 = 200$

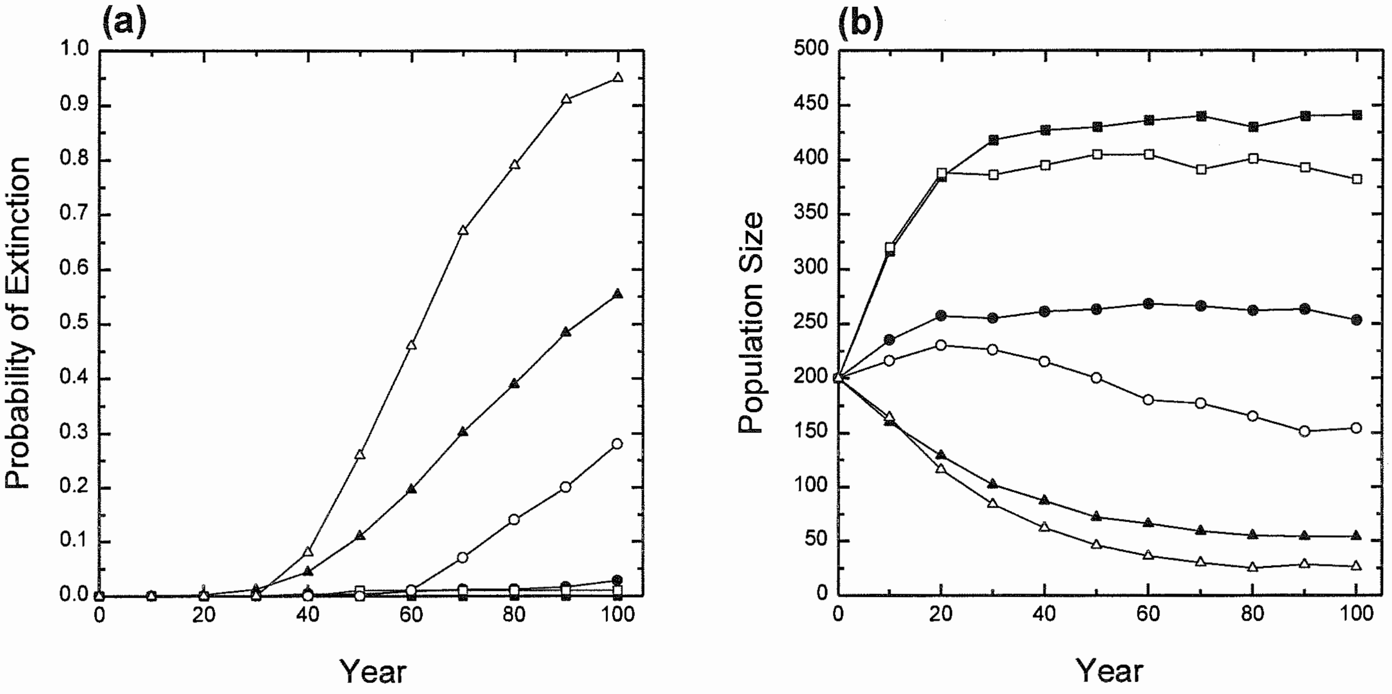


Fig. 5. Juvenile Mortality = 75%
$N_0 = 100$

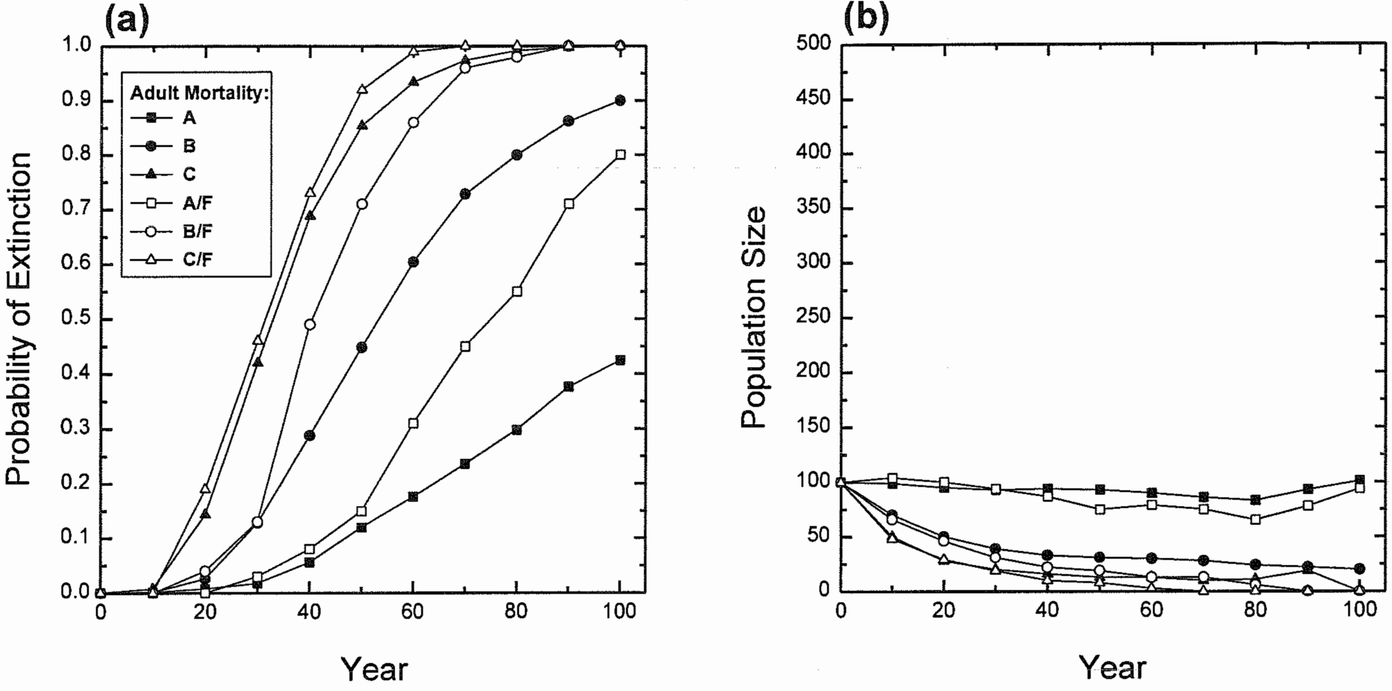


Fig. 6. Juvenile Mortality = 75%
$N_0 = 200$

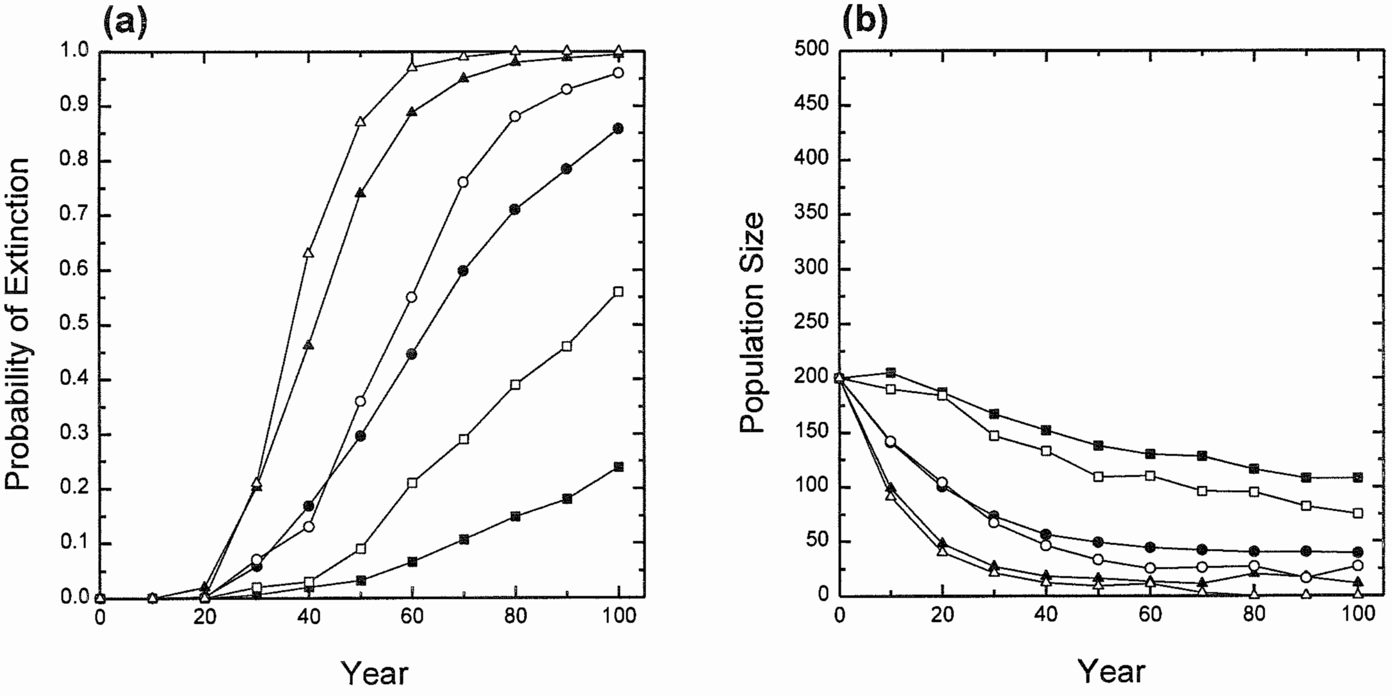


Fig. 7. Juvenile Mortality = 60%
N_0 = 100; Drought

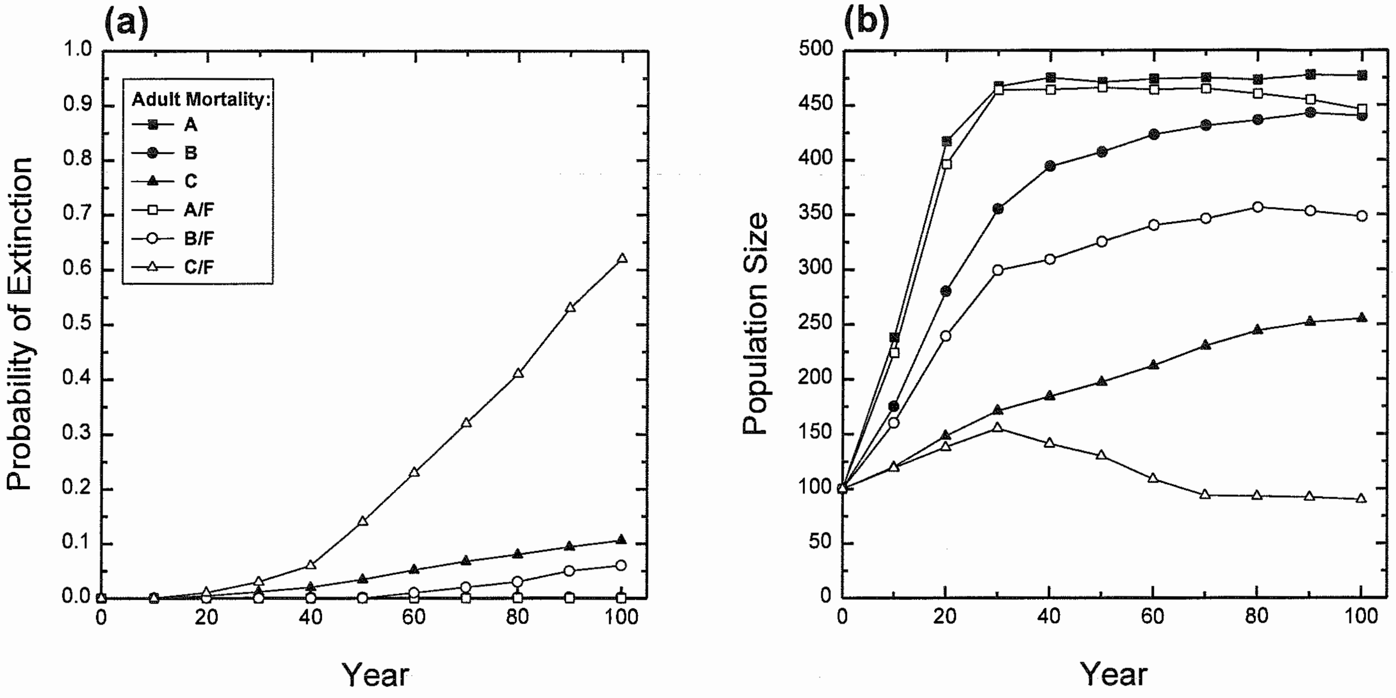


Fig. 8. Juvenile Mortality = 60%
N_0 = 200; Drought

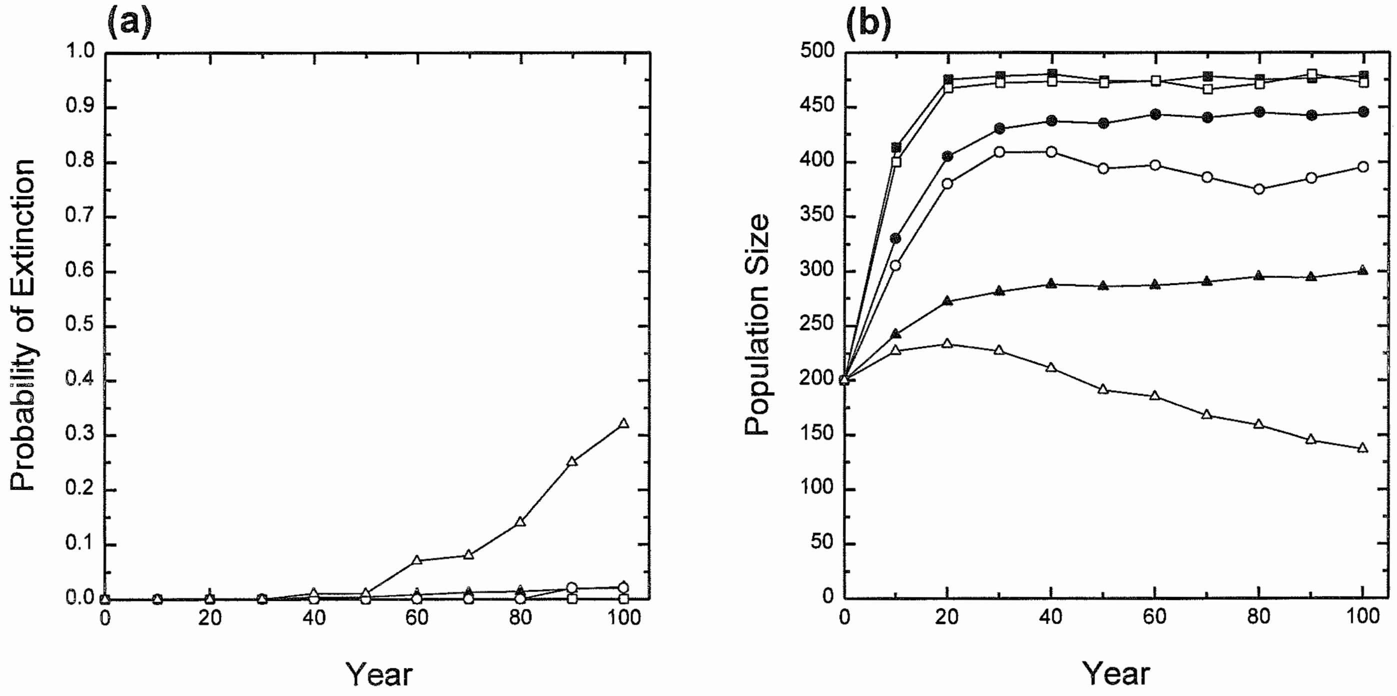


Fig. 9. Juvenile Mortality = 67.5%
N_0 = 100; Drought

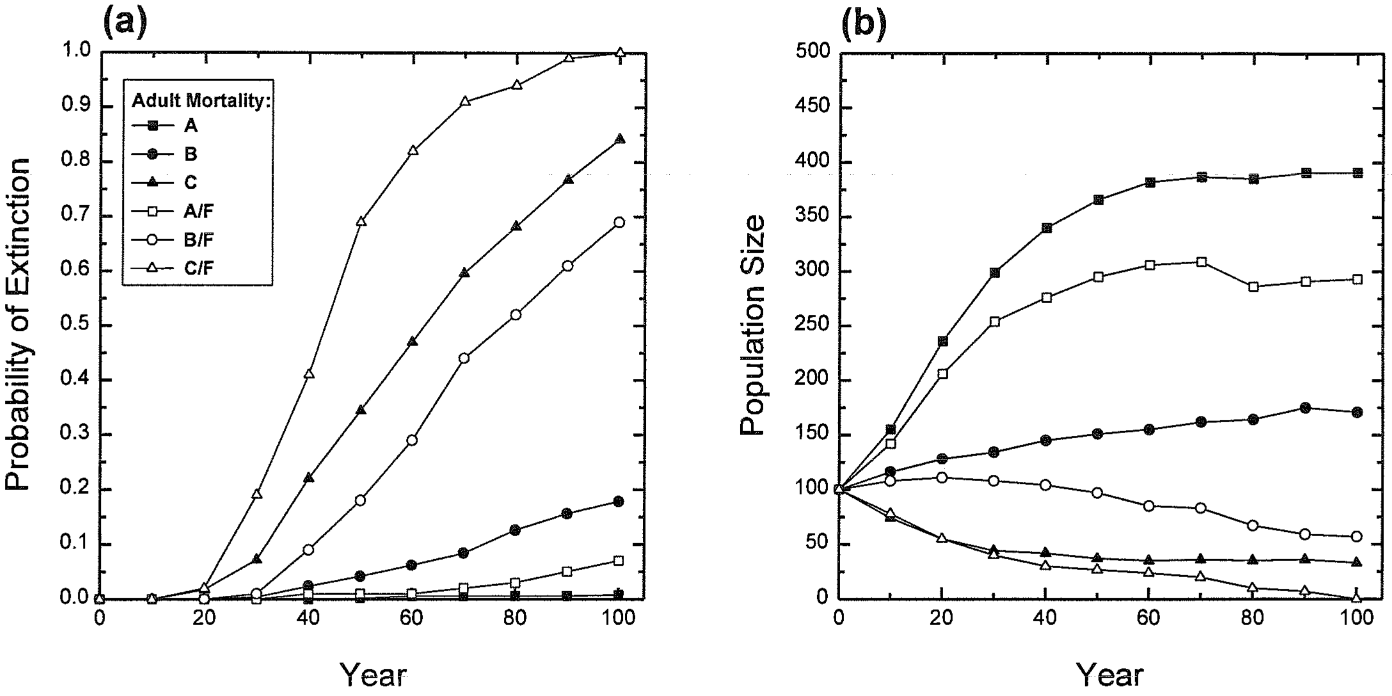


Fig. 10. Juvenile Mortality = 67.5%
N_0 = 200; Drought

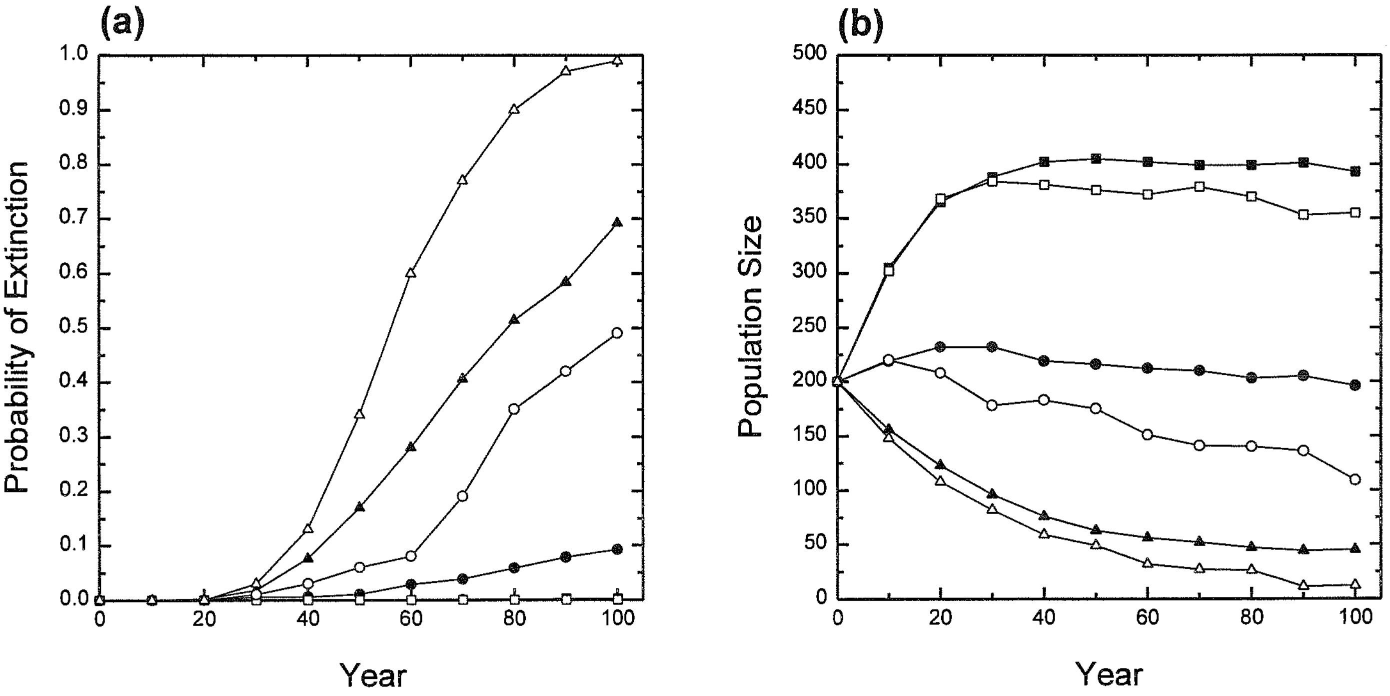


Fig. 11. Juvenile Mortality = 75%
N_0 = 100; Drought

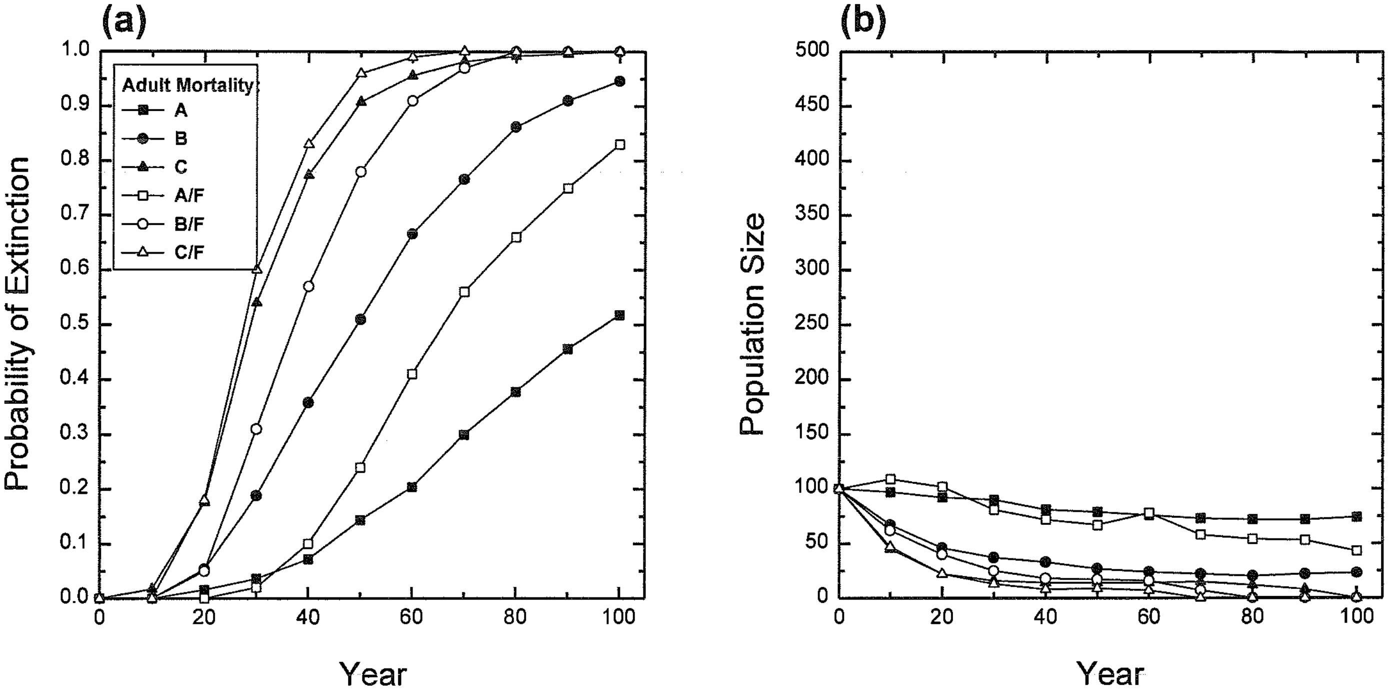
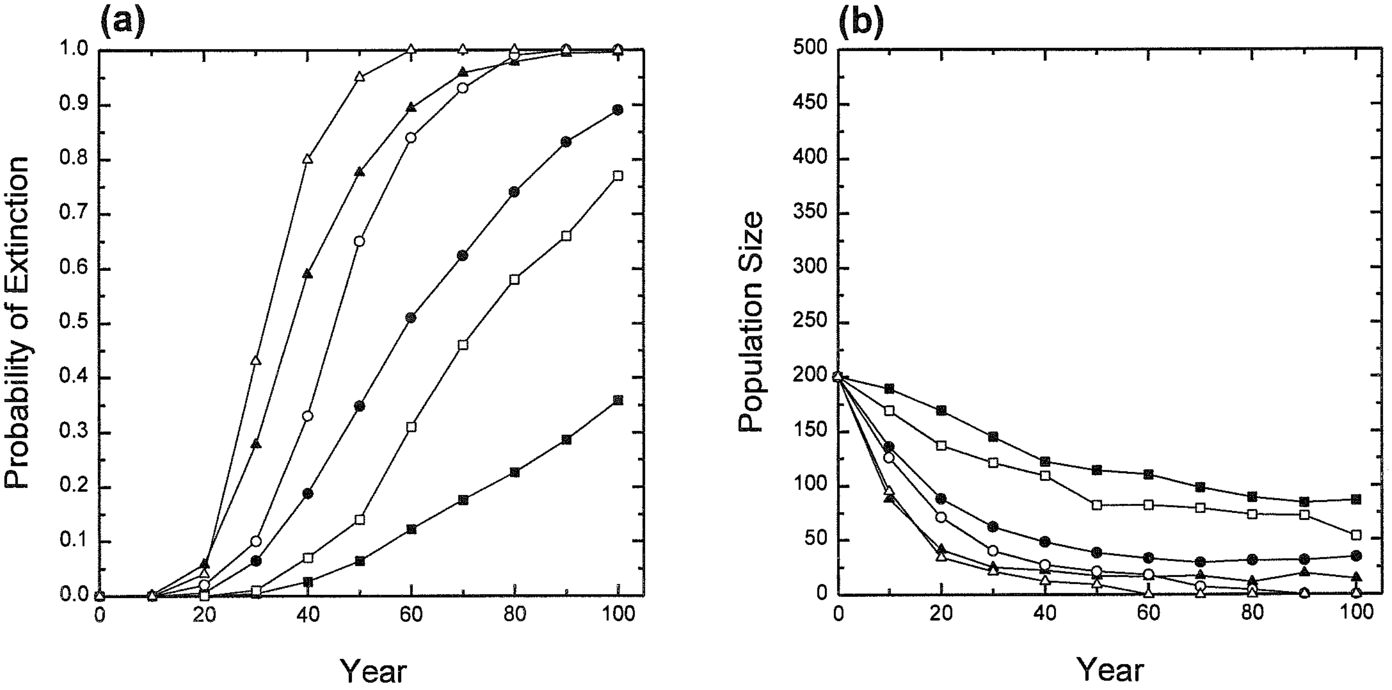


Fig. 12. Juvenile Mortality = 75%
N_0 = 200; Drought



EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 3

DISTRIBUCIÓN Y ESTADO DE CONSERVACIÓN
DISTRIBUTION AND CONSERVATION STATUS

DISTRIBUCIÓN Y ESTADO DE CONSERVACIÓN

Distribución Histórica

La subespecie endémica de la península (Hall y Kelson 1959) se distribuía históricamente en gran parte de ella, siendo los registros marginales los siguientes: Cañón de la Esperanza (Elliot 1903); Bahía de San Felipe (Elliot 1903); Tierra adentro de la Bahía de Santa Rosalía (Townsend 1912); al sur, mas allá de la Bahía de Magdalena (Nelson 1925), 73 km al sur de Calmallí; Bahía de Vizcaíno (Nelson 1925), Desierto de Vizcaíno (Orihuela 1977); San Quintín (Elliot 1903). Se estima que históricamente se distribuyó en aproximadamente 40,000 km^2.

El impacto de las actividades humanas como son la construcción de la carretera transpeninsular, exploraciones de Pemex en Vizcaíno, construcción del acueducto Vizcaíno-Bahía Tortugas y de caminos vecinales en la región, entre 1950 y 1980, fueron factores que determinaron la rápida declinación de las poblaciones del berrendo.

Aunque la distribución del berrendo peninsular presentada por Hall (1981) no incluye el sur de California, existe la posibilidad de que esta subespecie en realidad ocupara también esta región.

Distribución Actual

La distribución actual de acuerdo a los registros realizados entre 1977 y 1994, es de 362,385 ha aproximadamente (SEDESOL, 1993, mas obs pers. B. Sanabria). Dicha área cubre una superficie plana, topográficamente simple, incluída entre el paralelo 28 en el norte, 113 grados y 18 minutos en el este, 26 grados 47 minutos en el sur, y el meridiano 114 grados 30 minutos en el oeste (Figura 3-1, página 45).

Líneas de Investigación

- Es necesario desarrollar estudios de investigación que establezcan la identidad taxonómica en las poblaciones distribuidas en la frontera entre Baja California Norte y California, E. U. Entre las herramientas a usar puede estar la nueva técnica para extraer DNA de cavidad pulpar de dientes de ejemplares de museo.

- Es necesario identificar las áreas geográficas de criánza y distribución estacional, a través de observaciones directas y de técnicas de radiotelemetría.

- Dada la variación en el esfuerzo de muestreo en los censos en el pasado, es necesario estandarizar los métodos y períodos en que se realizan los censos y hacer un análisis más profundo de los datos ya existentes. En los censos se podrían utilizar métodos como los instrumentados en el caso de Sonora, que incluyen dobles conteos, transectos lineales, radiotelemetría, corrección para visibilidad (visibility bias).

Estado de Conservación del Berrendo

El berrendo peninsular históricamente fue protegido legalmente por primera vez en 1922, año en el cual el Presidente Obregón decretó su veda permanente. Posteriormente, en 1951, se decretó la Ley Federal de Caza, la cual le dió continuidad a aquella disposición. Después, a nivel internacional esta subespecie fue incluída en el Red Data Book de la IUCN en 1988. En el "Federal Register" el USFWS incluyó igualmente al berrendo peninsular bajo estado de "amenazado". Así mismo, en el Diario Oficial de 1991 se reiteró la protección legal de esta subespecie. El más reciente decreto oficial en nuestro país en el cual se le otorga protección es el del 21 de mayo de 1994. El impacto de estas disposiciones legales ha permitido al menos la sobrevivencia de una pequeña población estimada en aproximadamente 200 ejemplares hasta la fecha.

Se han recopilado datos en 23 censos en el área de distribución actual en un período que va desde 1977 a 1986 (Figura 3-2, página 46). A partir de esta fecha hubo un período de cuatro años en los que se carece de datos, siendo hasta el año de 1990 en el que nuevamente se continuaron a partir del mes de noviembre, realizándose seis censos más. De éstos, el más notable fue el de noviembre de 1993. En este censo se observaron 175 animales: 48 machos, 56 hembras y 71 no identificados. En el gráfica anterior, mostramos el censo estandorizado para una observación anual. Aunque la tendencia parece indicar un comportamiento constante de la poblacion con algunos momentos de gran abundancia como 1985, 1986, y 1993. Esto puede ser resultado de esfuerzos de muestreo desiguales, distintas áreas y extensiones muestreadas, y diferentes capacidades de detección por los observadores, o bien representar realmente el comportamiento de la población durante ese lapso.

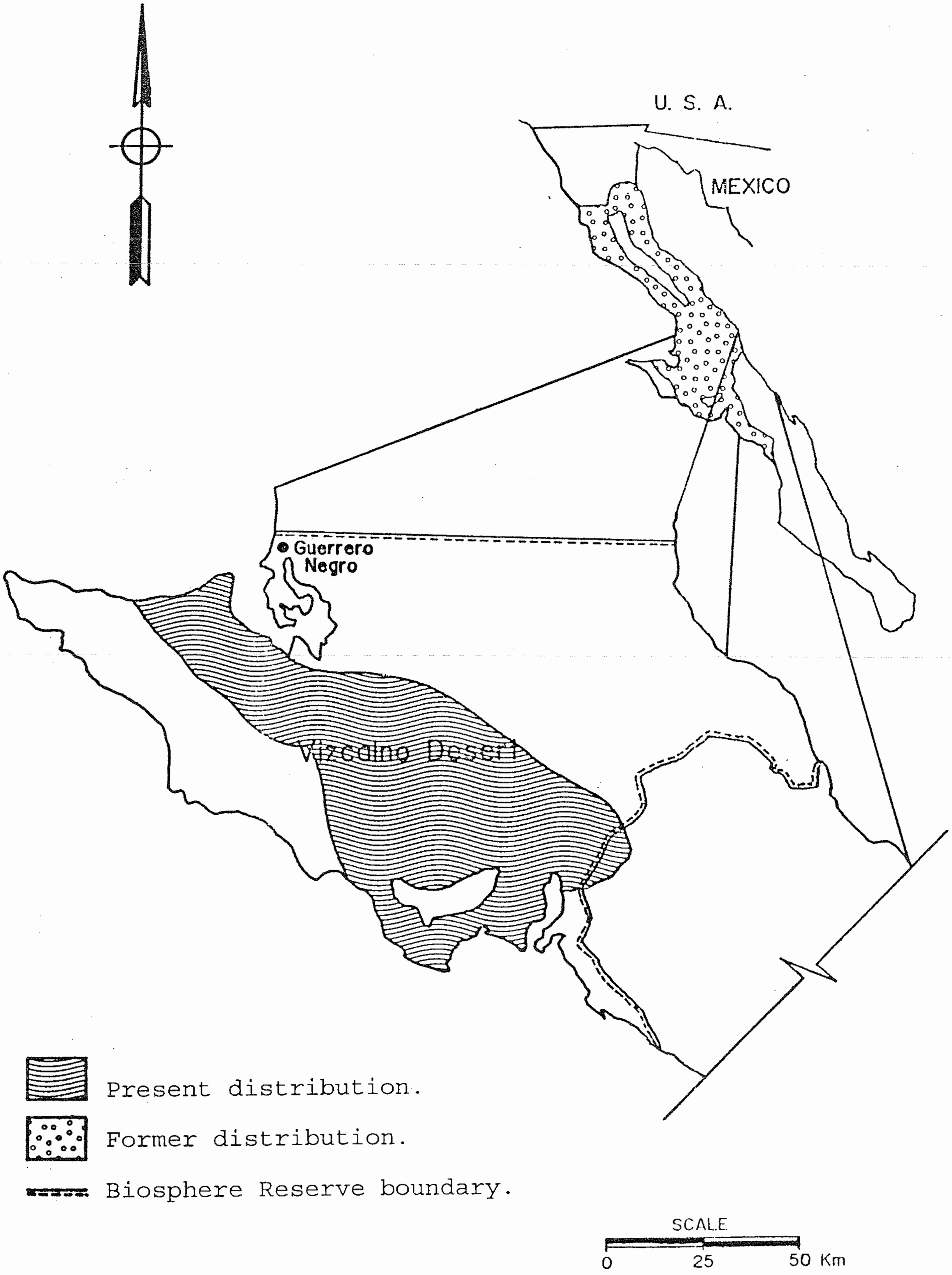


Figure 3-1. Historic and present distribution of the peninsular pronghorn in the Lower California peninsula, Mexico.

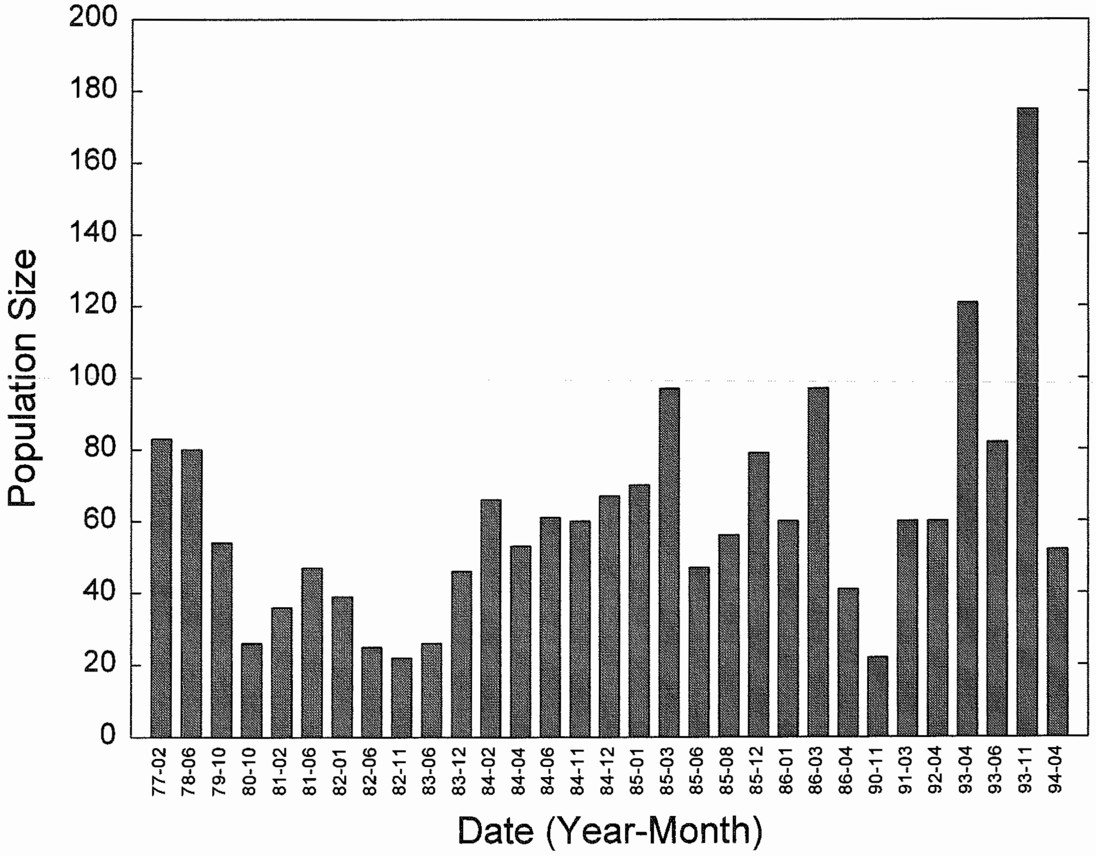


Figure 3-2. Population census of the peninsular pronghorn in the Vizcaino Desert from 1977 to 1994.

DISTRIBUTION AND CONSERVATION STATUS

Historical Distribution

The peninsular pronghorn (Hall and Kelson 1959) was historically distributed over a large part of the peninsula, based on the following records: Canon de la Esperanza (Elliott 1903); Bahia de San Felipe (ibid.); Litoral de la Bahia de Santa Rosalia (Townsend, 1912); to the south beyond Bahia de Magdelena (Nelson, 1925), 73 km to the south of Calmalli; Bahia de Vizcaino (Nelson, 1925); Desierto de Vizcaino; San Quentin (Elliot, 1903). It has been estimated that the subspecies was distributed over approximately 40,000 km2.

The impact of human activities, such as construction of the transpeninsular highway, explorations by PEMEX in the Vizcaino area, and construction of the aqueduct Vizcaíno-Bahia Tortugas and small roads in the region, were factors contributing to the rapid decline of pronghorn populations during 1950-1970.

Although the distribution of the peninsular pronghorn presented by Hall (1981) does not include southern California, there is a possibility that this subspecies was also distributed in this area.

Current Distribution

The present occupied range is approximately 362,385 ha (SEDESOL 1993; B. Sanabria pers. obs.). This area covers a topographically flat expanse, including the 28th parallel to the north, 113 degrees, 18 minutes East, 26 degrees, 47 minutes to the south. Towards the west it is bounded by the meridian at 114 degrees, 30 minutes (Figure 3-1, page 45).

Research Needs

- Develop research studies which establish the taxonomic identity of those populations distributed in the border between Baja California Norte and California, USA. Among the techniques that can be used for this study, a new method involves extraction of DNA from tooth pulp of museum specimens.

- Identify the geographical areas of rearing and the seasonal distribution, through the direct observations of females isolated from the group and through radiotelemetry.

- Due to the variation in the survey efforts in the past, it is necessary to standardize the methods and seasons in which the censuses are done and to conduct more thorough analysis of the data which already exist. In the censuses, it may be possible to use methods similar to those implemented in the case of the Sonoran pronghorn, which include double counts, lineal transects, rediotelemetry, and visibility bias.

Conservation Status of the Pronghorn

Historically, the peninsular pronghorn was protected by law for the first time in 1922 when President Obregon decreed that hunting was prohibited. In 1951, Ley Federal de Caza, or the Federal Hunting Law, continued this level of protection. At the international level, the subspecies was listed in the Convention on International Trade in Endangered Species (CITES) of wild flora and fauna in 1975 as an Appendix I species and included in the IUCN Red Data Book in 1988. Appendix I species are those threatened with extinction. Similarly, in the Diario Oficial of 1991, its level of protection was decreed and the last official decree for protection of the pronghorn was 21 May, 1994. These legal actions have permitted the survival of a small population, estimated at 100-200 animals.

Data from 23 censuses (1977 to 1986) in the occupied range have been compiled (Figure 3-2, page 46). There was a period 1986-1990 in which there was no census. Censuses were resumed in November 1990 and six censuses have been conducted since then. Among these six censuses, the most important was the one done in November 1993. In this census, 175 animals were observed: 48 males, 56 females, and 71 unidentified. In the preceding graph, we show the census standardized for one annual observation. The population appears stable, with some increases in 1985, 1986, and 1993. This can be the result of different survey efforts, different areas and extents of coverage, and different capacities of detection for the observers, as well as real population trends during this period.

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 4

CALIDAD DE HABITAT Y TENDENCIAS
HABITAT QUALITY AND TRENDS

CALIDAD DE HABITAT Y TENDENCIAS

Antecedentes

Desde la década de los 60's el área de distribución del berrendo peninsular ha tenido variaciones, en un principio se estimó que ocupada 8000 km^2. En la actualidad se estima que entre el área ocupada y la que potencialmente pueden usar los berrendos, se alcanza una extensión de 5000 km^2, ya que en su mayor parte conserva las condiciones de vegetación, topografía, y accesibilidad para esta subespecie.

Existen estudios que presentan información sobre la dieta del berrendo. El primero (Cancino 1988) ofrece un listado de especies vegetales consumidas. El segundo (Cancino in press) describe los habitos alimentarios basados en analisis de excretas.

Referencia general sobre las causas por las que se modificó la estructura y extensión del hábitat en Vizcaíno (Jaramillo 1989).

Otra publicación (Cancino 1988) que cuantifica de los cambios en la extensión del hábitat histórico y causas asociadas al hombre.

Necesidades de Investigación

1) Se necesita información sobre los cambios en el uso del suelo y desarrollos urbanos para finalmente relacionarlo con la distribución histórica y actual. Se require de un estudio cuantitativo de la transformación y/o reducción del hábitat debido a los siguientes factores.

   -Agricultura
   -Nuevos centros de población
   -Inundación de salitrales (industriales)
   -Construcción de acueductos y diques
   -Construcción de caminos y brechas
   -Desarrollos turísticos
   -Uso de recursos que afectan la calidad del hábitat: leña y posterías; mineria y extractivas; uso de agua, y sobrexplotación de acuíferos.

   Herramientas: Mapas INEGI, DETENAL, SARH, COTECOCA, Reforma Agraria (tenencia de la tierra), usos del suelo y planes de desarrollo urbano (gobierno del estado), Pemex.

2) Información sobre datos climáticos lo más antiguos posibles.

3) Determinar características estructurales de la vegetación actuales para conocer los requerimientos del habitat cuantitativamente (número de estratos, especies dominantes, y fenología)

4) Determinar las características topográficas y de altitud donde ha sido registrado el berrendo.

5) Determinar la selección de sitios de pernoctación y reproducción.

6) Capacidad de carga.

7) Impacto de la fauna asociada: posibles depradadores (coyote, aguila, zorra) y competidores (liebres y ganado)

Esta información podrá ampliar el conocimiento de la disponibilidad del hábitat adecuado actual y del histórico, y las causas posibles del decremento de la población, y ayudará a determinar las posibilidades de reintroducción en estas áreas.

HABITAT QUALITY AND TRENDS

Background

Since the 1960's the distribution area of the peninsular pronghorn has been variable, but was generally considered to be about 8000 km^2. At present it is estimated that about 5000 km^2 of pronghorn habitat exists, based on vegetation conditions, topography, and accessibility for this subspecies. Only a portion of this available habitat is currently used by pronghorn.

Two studies present information about the diet of pronghorn. The first is a listing of plant species consumed (Cancino 1988). The second describes food habits based on fecal analysis (Cancino in press). Jaramillo (1989) discusses the reasons why the size and shape of habitat in the Vizcaino Desert was modified. Furthermore, Cancino (1988) quantifies changes in size and extent of the historical habitat and human related factors causing the changes.

Research Needs

1. We need information about changes in land use and urban development to relate them to the historical distribution of the pronghorn. We require quantitative study of the transformation and/or reduction of the habitat due to the following:

   - Agriculture
   - New human population centers
   - Mining of salt
   - Construction of aqueducts and canals
   - Construction of paved and unpaved roads
   - Development of tourism
   - Use of resources which affect habitat quality: firewood, power lines; mining; extractive industries; use of water; overexploitation of aquifers.

   Tools: Maps of National Institute of Geography, DETENAL, SARH, COTECOCA, Agrarian Reform (land tenancy), land use, and urban development plan (state government), Petroleos Mexicanos (PEMEX)

2. Historical information about climatological data.

3. To determine the structural characteristics of the vegetation to understand the quantitative habitat requirements of the pronghorn (habitat strata, dominant species, and phenology)

4. To determine topographic and elevation characteristics where the pronghorn has been recorded.

5. To determine the habitat characteristics of selected sites.

6. Carrying capacity.

7. Impact of associated wildlife like potential predators (coyote, eagle, and fox) and competitors (hares and cattle).

This information should increase our knowledge of the distribution and characteristics of the present and historical habitat, identify possible causes of the population decline, and help determine the potential for reintroduction into unoccupied habitat.

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 5

AMENAZAS
THREATS

AMENAZAS

Entre las amenazas a la sobrevivencia del berrendo en el Desierto del Vizcaíno que se han observado en las últimas decádas y en la actualidad, estan las siguientes:

A. Transformación y reducción de hábitat
B. Cacería ilegal
C. Ganadería extensiva
D. Factores naturales

Transformación y Reducción de Habitat

Dentro de las actividades humanas que han contribuído a la transformación y reducción del hábitat del berrendo, se encuentran las siguientes:

Zonas inundadas	33,000 ha
Ganadería extensiva	500,000 ha
Agricultura	6,847 ha
Brechas y caminos	2,200 ha
Asentamientos humanos	1,583 ha
Aislamiento de la Mesa de la Choya	25,550 ha

Desde la década de los 60's el área de distribución del berrendo peninsular ha tenido variaciones, en un principio se estimó que ocupada 8000 km^2. En la actualidad se estima que entre el área ocupada y la que potencialmente pueden usar los berrendos, se alcanza una extensión de 5000 km^2, ya que en su mayor parte conserva las condiciones de vegetación, topografía, y accesibilidad para esta subespecie.

Cacería Ilegal

La causa más evidente para la disminución del berrendo en el Desierto del Vizcaíno es la intensa y contínua cacería ilegal a la que ha estado sometido, la anterior se infiere por las siguientes razones: relatos y denuncias de los habitantes del área sobre; incursiones de cazadores ilegales, infracciones por violación a la legislación vigente en materia de cacería, decomiso de armas a cazadores furtívos y restos de berrendos con evidencia de caza ilegal y múltiples rastros (rodadas y casquillos do alto poder) en las zonas que actualmente habita el berrendo.

Ganadería Extensiva

Existen aproximadamente 5400 cabezas de ganado vacuno en la porción oriental del Desierto del Vizcaíno, dentro del área de distribución del berrendo de las cuales más del 60% del ganado se localiza en la principal zona de concentración del berrendo. También hay varias manadas de burros y caballos. El ganado doméstico puede representar una fuerte competencia para el berrendo sobre todo en la época de secas en que ambos se concentran en los cauces de los arroyos y es probable que el ganado constituya además una fuente de transmisión de emfermedades para el berrendo a las que éste no sea resistente.

Factores Naturales

Los factores naturales también pueden estar influyendo en la reducción de la población relictual del berrendo, principalmente la escasa e irregular precipitación pluvial y los prolongados periodos de sequias, los que disminuyen la tasa de reproducción y viabilidad de crías, si a esto aunamos la gran abundancia de coyotes, los que pueden causar, como se ha demostrado para otras subespecies de berrendo, una gran depredación de crias recien nacidas, retardando de esta manera la recuperación del berrendo peninsular. Por otra parte lo reducido y aislado de la población e incluso de las manadas de berrendo pueden estar provocando la reproduccion entre parientes cercanos, con el consecuente incremento en la expresión de caracteres recesivos y por ende de malformaciones congénitas, lo cual puede ser una causa adicional de mortalidad.

Conclusiones

En base al conocimiento actual de la subespecie se considera que los principales amenazas a la sobrevivencia del berrendo en la actualidad se encuentran los siguientes:

1. Cacería
2. Modificación de habitat
3. Mortalidad de crías

Acciones

Entre las acciones más urgentes que deben de realizarse para la disminución o control de las amenazas del berrendo peninsular se recomienda las siguientes:

1. Campánas permanentes de vigilancia, divulgación y educación para prevenir y controlar la cacería furtiva e impactos ambientales negativos, asi como concientizar y lograr la participación activa de los habitantes locales en la recuperación de la subespecie.

2. Gestiones para la protección del habitat. Una medida decisiva es la operación de la Reserva de Biosfera el Vizcaino.

3. Llevar a cabo las gestiones para la coordinación intersectorial, así como para conseguir los fondos para la implementación del plan.

4. En cuanto a investigación se recomienda evaluar la competencia con el ganado domestico, la depredación y causas de mortalidad de crias.

5. Evaluación de la reducción del habitat en relación a la población del berrendo peninsular.

THREATS

Threats to survival of pronghorn observed in the last decade in the Vizcaino Desert are the following:

- A. Transformation and reduction of habitat
- B. Poaching
- C. Extensive livestock production
- D. Natural factors

Transformation and Reduction of Habitat

The following are human activities that have contributed to the transformation and reduction of pronghorn habitat:

Zones of inundation	33,000 ha
Livestock production	500,000 ha
Agriculture	6,847 ha
Paved and unpaved roads	2,200 ha
Human settlements	1,583 ha
Isolation of the Mesa de la Choya	25,550 ha

Since the 1960's the distribution area of the peninsular pronghorn has been variable, but was generally considered to be about 8000 km^2. At present it is estimated that about 5000 km^2 of pronghorn habitat exists, based on vegetation conditions, topography, and accessibility for this subspecies. Only a portion of this available habitat is currently used by pronghorn.

Poaching

The most apparent cause for the decline of the pronghorn in the Desert is intensive and continuous illegal hunting. We believe this to be true based on the following evidence: reports and official complaints by local inhabitants about the presence and actions of illegal hunters, violations of hunting legislation, confiscation of illegal firearms, and finding the remains of pronghorns killed by poachers and several trails (vehicle tracks and empty shotgun shells) in current pronghorn habitat.

Extensive Livestock Production

Approximately 5400 livestock occur in the Vizcaino Desert within the distribution area of the pronghorn. More than 60% of these livestock and many groups of burros and horses are located in the principal concentration zone of the pronghorn. The livestock are strong competitors for the food of pronghorn, especially in the dry season when both concentrate along the arroyos.

Livestock may also be a source of disease transmission to the pronghorn, disease to which they are not resistant.

Natural Factors

Natural factors, principally the low and irregular precipitation and prolonged dry periods, may also be reducing the remnant population of pronghorn by decreasing the reproductive rate and increasing mortality of the fawns. Another natural threat is the high population density of coyotes which may prey on recently born fawns, as has been demonstrated in studies of other pronghorn subspecies, thereby slowing or preventing population recovery of the peninsular pronghorn. The small and isolated populations of pronghorn may be resulting in inbreeding between closely related individuals, with consequent increase in recessive characters and congenital malformations, which may represent an additional cause of mortality.

Conclusions

Based on the current knowledge of the subspecies we consider that the following factors represent the main threats for the survival of the pronghorn:

1. Poaching
2. Habitat modification
3. Fawn mortality

Actions

Within the most urgent needs that have to be developed for the reduction or control of the peninsular pronghorn's threats, we recommend the following:

1. Permanent campaigns of patrolling, awareness and education to prevent and control the illegal hunting and the negative environmental impacts, and to increase consciousness and to make possible the active participation of the local inhabitants in recovery of the subspecies.

2. Actions to protect pronghorn habitat. One decisive action is operation of the Vizcaino Biosphere Reserve.

3. To coordinate actions between sectors, and to obtain funding to implement the plan.

4. In terms of research, it is recommended to evaluate the degree of competition with livestock, depredation and the main causes of fawn mortality.

5. Evaluation of reduction of habitat of the peninsular pronghorn population.

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 6

EDUCACIÓN AMBIENTAL
ENVIRONMENTAL EDUCATION

EDUCACIÓN AMBIENTAL

Campañas de Difusión

Hay que buscar un nombre para la campaña que la identifique, que llame la atención y que evoque a la subespecie, se propone: "Corre, berrendo, corre, la extinción es para siempre".

Toda esta implementación requerie de recursos financieros con instituciones interesadas:

- SEP (Secretaría de Educación Pública)
- ESSA (Compañia Exportadora de Sal, S.A.)
- Prestadores de servicios turisticos
- SEDESOL (Secretaría de Desarrollo Social)
- CIBNOR (Centro de Investigaciones Biológicas del Noroeste, S.C.)
- Grupos ecologicos
- SARH (Secretaría de Agricultura y Recursos Hidráulicos)
- Sierra Madre, S.C.
- Unidos para la Conservación, A.C.
- CBSG (Conservation Breeding Specialist Group)
- USFWS (United States Fish and Wildlife Service)
- NAPF (North American Pronghorn Foundation)
- PEMEX (Petroleos Mexicanos)
- CFE (Comisión Federal de Electricidad)
- WWF (World Wide Fund for Nature)
- Comité Conjunto México-Estados Unidos de América para la Conservación de la Vida Silvestre
- Conservación Internacional
- AGFD (Arizona Game and Fish Department)
- CFGD (California Fish and Game Department)
- Gobierno del estado de Baja California Sur
- CONACYT (Consejo nacional de Ciencia y Tecnología)
- The Nature Conservancy
- CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad)
- National Science Foundation
- National Wildlife Foundation
- Arizona Bighorn Sheep Society
- Wildlife Conservation Society
- Wildlife Management Institute
- National Geographic Society
- SIMAC (Sistema de Investigaciones del mar de Cortés)

Nivel Local, Regional, Nacional y Internacional

Local

Acciones en las poblaciones de la Reserva adyacentes a la distribución del berrendo (Gro. Negro, Vizcaíno, San Ignacio, Ejido, San José de Castro, etc.).

Regional

Principales centros poblacionales, cabeceras municipales y centros de interés turístico.

Acciones a Corto Plazo

- Poster: Puede ser patrocinado por un grupo internacional, Sierra Madre, ESSA, SEDESOL, CFE, y Pemex. La mitad se distribuye para difusión, y la otra mitad se vende para obtener fondos que puede servir para señalización.
- Señalizacion: En los principales caminos y berchas, de acuerdo al estudio de zonificación que se derive del estudio de inspección y vigilancia.
- Campaña en radio y periódico: Texto (ubicación de la subespecie, importancia de la subespecie, única y en peligro y que es un emblema).
- Capacitación: A maestros, grupo de la REBIVI y vigilantes.
- Audiovisual
- Documental
- Concursos (de dibujos y de otra indole)
- Tríptico (elaborado por turismo)
- Folleto didáctico para diferentes niveles, que incluya uno para obtener fondos.
- Publicación de artículos en revistas de difusion (Escala etc.).
- Libro sobre la Reserva de la Biosfera
- Spots
- Timbre

- Imagen en offset de 500 piezas que se venden a N$300.00.
- Recursos para señalización por patrocinadores.
- Materiales con slogan para obtener fondos: camisetas, gorras, calendario de la Reserva.

ENVIRONMENTAL EDUCATION

Advertising Campaign

A slogan that identifies and brings attention to the subspecies: "Run, berrendo, run, extinction is forever".

All of this implementation requires financial resources from all interested institutions:

- SEP (Secretary of Public Education)
- ESSA (Salt Mining and Export)
- Tourism Agencies
- SEDESOL (Secretary of Social Development)
- CIBNOR (Center for Biological Investigation of the Northeast)
- Ecological groups
- SARH (Secretary of Agriculture and Hydrology)
- Sierre Madre
- United for Conservation
- CBSG (Conservation Breeding Specialist Group)
- USFWS (U.S. Fish & Wildlife Service)
- NAPF (North American Pronghorn Foundation)
- PEMEX (Mexican Petroleum)
- CFE (Federal Electricity Commission)
- WWF (World Wide Fund for Nature)
- Joint Mexico-US Committee for Wildlife Conservation
- Conservation International
- AGFD (Arizona Game and Fish Department)
- CFGD (California Fish and Game Department)
- Government of the State of Baja California Sur
- CONACYT (National Council for Science and Technology)
- The Nature Conservancy
- CONABIO (National Commission for the Understanding and Use of Biodiversity)
- National Science Foundation
- National Wildlife Foundation
- Arizona Bighorn Sheep Society
- Wildlife Conservation Society
- Wildlife Management Institute
- National Geographic Society
- SIMAC (System for Research in the Sea of Cortes)

Local, Regional, National, and International Levels

Local

Actions in those towns adjacent to the Reserve that are close to the pronghorn distribution: Guerrero Negro, Vizcaino, San Ignacio, Ejido, San Jose de Castro, etc.

Regional

Main population centers, municipalities, and tourist centers of interest.

Short-term Actions

- Poster: It can be sponsored by an international group such as Sierre Madre, ESSA, SEDESOL, CFE, or PEMEX. Half of the posters can be distributed, and the other half sold to obtain funds that can help further education efforts.
- Sign production: On principal paved and unpaved roads, according to recent zoning studies which will result from studies on pronghorn distribution.
- Newspaper and Radio Campaign: Text (location of the subspecies, importance of the subspecies, unique, endangered, local symbol).
- Training: for scientists and managers of the Vizcaino Biosphere Reserve.
- Audio-visual
- Documentaries
- Contests: for drawings and other items
- Pamphlet: made by tourism agencies
- Educational brochures written on many levels, including one for obtaining funding.
- Publication of articles in non-scientific journals (Escala, etc.).
- Book about the Biosphere Reserve
- Short television and/or radio public service announcements
- Stamps

- 500 offset images of the berrendo, sold at N$300.00 each
- Resources for sign production by sponsors
- Materials with slogans to obtain funding: T-shirts, caps, and calendars of the Reserve.

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR

(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN

(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 7

INVESTIGACIÓN
RESEARCH

INVESTIGACIÓN
RESEARCH

En la siguiente tabla (pagina 74) se enlistan las áreas de estudio que es necesario abordar. Este listado no excluye ningún otro estudio (parcial o general) que no esté contenido en el mismo.

The following table (page 74) presents a list of studies needed. This list does not exclude any other study not explicitly considered.

A 1 = corto plazo/short-term
B 2 = mediano plazo/medium-term
C 3 = largo plazo/long-term
R = Nombres de los responsable/Names of those responsible:

JCH	Jorge Cancino Hernández
JDV	James DeVos Jr.
LC	Laura Colton
VSS	Victor Sánchez Sotomayor
LT	Laura Thompson-Olay
RRE	Ricardo Rodríguez-Estrella
RML	Rodrigo Medellin Legorreta
FRR	Felipe Ramírez Ruiz de Velasco

It is important to present detailed plans of every action that the group deems necessary.

Funding agencies: Ver lista en <u>Educación Ambiental</u>
See list in <u>Environmental Education</u>

	Prior.	Calen.	R
Monitoreo sistemático y censos *Systematic monitoring and surveying*	1	A:3	JCH/JDV
Biología (demografía, requerimeientos de agua, dieta, parásitos, enfermedades) *Life history (demography, water requirements, diet analysis, parasites, diseases)*	1-3	A:1-3	JCH/JDV
Taxonomía de la subespecie peninsular *Taxonomy of peninsular subspecies*	3	B:2	LC/VSS/LT/JCH
Uso estacional del habitat, preferencias de habitat, identificación de áreas críticas *Seasonal habitat use, habitat preferences, identifying critical areas (core areas)*	1	A:3	JCH/JDV
Evaluación del habitat (histórico y presente, fragmentación del habitat) *Assessment of the suitable habitat (historical and present, habitat fragmentation)*	1	A:3	RRE/JCH
Evaluación y monitoreo de la calidad del habitat *Evaluating and monitoring habitat quality*	1	A:2	RRE/JCH
Competencia, interacciones e impacto entre berrendo y ganado (hábitos de alimentación y disponibilidad de forreje, fenología vegetal) *Competition, interactions and impact between pronghorns and livestock (food habits and plant availability, plant phenology)*	2	B:2	RML/JCH
Depredación *Predation*	1	A:2	RML/JCH
Patrones climáticos *Climatic patterns*	2	A:1	RRE/LT
Evaluación de la cacería furtiva *Evaluation of poaching*	3	A:3	
Diversidad genética y consanguinidad *Genetic diversity and inbreeding*	1	A:1	LC/JCH
Crianza en semicautiverio y reintroducción *Fawn semi-captive rearing and reintroduction*	1	B:3	VSS/FRR

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 8

ESTRATEGIAS DE MANEJO
MANAGEMENT STRATEGIES

ESTRATEGIAS DE MANEJO

Manejo en Cautiverio y Semicautiverio

Tomando como base las experiencias del berrendo en cautiverio tanto en México como en E.U., las cuales no tuvieron éxito para alcanzar la sobrevivencia o adaptación de las crías en estado silvestre se recomienda que el manejo de la mayor parte de la población del berrendo peninsular en Vizcaíno sea en estado silvestre. En este sentido se recomienda seguir las siguientes estrategias de manejo.

Programa de Vigilancia

Se requiere un programa, sectorización del área y en el corto plazo hacer enfasis en las áreas de concentración del berrendo la base será de este programa el programa de vigilancia de la misma Reserva de la Biosfera "El Vizcaino".

Normatividad del Uso del Suelo del Área de Distribucion Actual del Berrendo

Tomando como base el ordenamiento de uso del suelo, se recomienda elaborar una normatividad específica para el uso del suelo en el área del berrendo.

Señalización

Se debe elaborar un programa de señalización específico para el berrendo en congruencia con el programa de manejo de La Reserva.

Tenencia de la Tierra y Uso del Suelo

Se deben elaborar convenios con los dueños de los predios para lograr la protección del berrendo, en compatibilidad con los programas de conservacion de la subespecie, haciendo especial enfasis en el desarrollo de la ganadería y agricultura. Gestionando con los diversos sectores que el desarrollo de obras de infraestructura se adecuén al ordenamiento de uso de suelo y vigilar su cumplimiento.

Programa de Control de Depredadores

Con base al resultados de las investigaciones en el área de podrán llevar en el mediano y largo plazo.

Manejo de Hábitat

Con base en los resultados de las investigaciones se podran llevar a cabo programas de restauración de habitat.

Estrategias de Manejo	Prior.	Calen.	Resp.
Inspección y vigilancia (presencia en el área)	1	A:3	S,P
Análisis y reglamentación en el uso del suelo	1	B:2	S,C
Gestión para coord. intersectoriales	1	A:3	C
Control de depredadores	2 *	B:1-3	S,C
Manejo de habitat	2 *	B:2-3	S,C
Control y seguimiento de población por telemetría	1 **	A:3	S,C,A
Manejo en semicautiverio	1 ***	B:3	B,C,E, S

* Este punto queda sujeta a los resultados de las investigaciones

** 10 ejemplares para capturar. De acuerdo con la experiencia de los participantes de Arizona y Sonora, se recomienda inicialmente empezar con el marcado de 10 animales.

*** La criánza en cautiverio entendida como la captura de crías y liberación de subadultos esta sujeta a la preparación de una propuesta que será evaluada por un grupo de expertos en criánza en cautiverio y berrendo. La realización de este programa es independiente del comportamiento de la población.

MANAGEMENT STRATEGIES

Captive and Semi-Captive Management

Captive-rearing experiences with the pronghorn in Mexico and the U.S. have not resulted in survival or adaptation of fawns in the wild. Therefore, we recommend that management of the pronghorn in the Vizcaino Desert should be accomplished in the wild.The management strategies listed below should be followed:

Vigilance Program

The occupied habitat should be categorized. For the short term, law-enforcement efforts should be emphasized in areas of pronghorn concentration. The basis for this program is the vigilance program for the Vizcaino Biosphere Reserve.

Land Use Regulations

Based upon land use ordinances, it is recommended that specific land use legislation be developed in the pronghorn range.

Radio Telemetry

It is necessary to develop a specific radio telemetry program for the pronghorn in accordance with the management program of the Reserve.

Land and Soil Use

Legal agreements should be developed with landowners to achieve the protect the pronghorn and its habitat. Such agreements should encourage land management actions beneficial to the pronghorn. The agreements are particularly needed with landowners involved with agriculture or livestock grazing.

Predator Control Program

Based on results of research conducted in the area, predator control should be developed in the near future and may be required for the long term.

Habitat Management

Habitat restoration programs may be developed based on the results of research.

Management Strategy	Prior.	Calen.	Resp.
Law Enforcement	1	A:3	S,P
Analysis and land-use regulations	1	B:2	S,C
Inter-institutional coordination	1	A:3	C
Predator control	2*	B:1-3	S,C
Habitat management	2*	B:2-3	S,C
Population monitoring using telemetry	1**	A:3	S,C,A
Semi-captive management	1***	B:3	B,C,E,S

* This strategy is dependent on results of research.

** 10 individuals to be captured. Based on experience from participants from Arizona and Sonora, it is recommended that the program be initiated with 10 animals.

*** Rearing in captivity, defined as the capture of wild fawns and subsequent release of subadults, is subjected to the development of a proposal that will be evaluated by a group of experts in captive rearing and in pronghorn biology. Development of this program is independent of the demographic characteristics of the population.

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 9

REFERENCIAS
REFERENCES

REFERENCIAS
REFERENCES

Barrett, M.W. 1984. Movements, habitat use, and predation on pronghorn fawns in Alberta. J. Wildl. Manage. 48:542-550.

Cancino, J. 1988. Hábitos de alimentación del berrendo peninsular (*Antilocapra americana peninsularis*). Bachelor Thesis. Universidad Autónoma Chapingo, Chapingo, Mexico. 66pp.

Cancino, J. in press. Food habits of the peninsular pronghorn.

Cancino, J., R. Rodriguez-Estrella, and A. Ortega. 1994. First aerial survey of historical range for peninsular pronghorn of Baja California, Mexico. J. Arizona-Nevada Acad. Sci 28:46-50.

Diario Oficial. 1991. Acuerdo por el que se establecen los critérios ecológicos CT-CERN-001-91 que determinan las especies raras, amenazadas, en peligro de extinctión o sujetas a protección especial y sus endemismos, de la flora y fauna terrestres y acuaticas en la Republica Méxicana. Diario Oficial de le Federación. Tomo CDLII. No. 12. pp. 7-35.

Hall, E.R. 1981. The Mammals of North America. Vol. II. 2nd Edition. John Wiley and Sons, New York.

Jaramillo, F. 1989. Contribución al conomiciento y conservación del berrendo de Baja California (*Antilocapra americana peninsularis*, Nelson 1912: Antilocapridae, Mammalia) en el Desierto de Vizcaíno, Baja California Sur, México. Tesis profesional. Universidad Nacional Autónoma de México. 140 pp.

Nelson, E.W. 1925. Status of the pronghorned antelope, 1922-1924. Bull. No. 1346. U.S. Department of Agriculture, Washington, DC. 64pp.

Ralls, K., J.D. Ballou, and A.R. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conservation Biology 2:185-193.

Ricklefs, R.E. 1979. Ecology. 2nd Edition. Chiron, New York.

SEDESOL. 1993. Secretaria de Desarrollo Social. Censo del berrendo de Baja California. Informe interno. Delegación estatal en Baja California Sur.

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 10

LISTA DE PARTICIPANTES
LIST OF PARTICIPANTS

LISTA DE PARTICIPANTES - PARTICIPANTS

Francisco Anguiano
SEDESOL
Calz. A. Olachea E/
Palacio de Justicia
La Paz, 23000, B.C.S.
México
Tel: (112) 21699

Izquierdo Apolo
Pal. Gob. 2 Nivel
Gob. Edo. I.
La Catol. E/Allende y
23075 Bravo
(112) 29477 Ext. 242

Benjamin Ballesteros
SEDESOL
Calz. A. Olachea E/
Palacio de Justicia
La Paz, 23000, B.C.S.
México
Tel: (112) 21699

Carmen Blazquez
Centro de Investigaciones Biológicas del Noroeste, S.C.
Apartado Postal 128
La Paz, 23000, B. C. S.
Tel: (112) 53633
Fax: (112) 53625

Ing. Jorge Cancino
Centro de Investigaciones Biológicas del Noroeste, S. C,
Apartado Postal 128
La Paz, 23000, B. C. S.
Tel: (112) 53633
Fax: (112) 53625

Sergio Alvarez Castañeda
Centro de Investigaciones Biológicas del Noroeste, S.C.
Apartado Postal 128
La Paz 23000, B.C.S.
Tel: (112) 53633
Fax: (112) 53625

Biol. Carlos Castillo
Centro Ecológico de Sonora
Carretera a Guaymas Km 2
Apartado Postal 1497
Guaymas, 83000, Sonora
Tel: 62-50-1034-1137
Fax: 62-50-1236-1225

Laura Colton
California Fish and Game
1416 Ninth Street
Sacramento CA 95814 USA
Tel: 916-653-6886

James DeVos Jr.
Arizona Game and Fish Department
2222 West Greenway Road
Phoenix AZ 85023 USA
Tel: (602) 942-3000

Patricia Gallina
Centro de Investigaciones Biológicas del Noroeste, S.C.
Apartado Postal 128
La Paz 23000, B.C.S.
Tel: (112) 53633
Fax: (112) 53625

Patricio Robles Gil
Agrupación Sierra Madre, S. C.
Insurgentes Sur 949-701
Col. Napoles
México, 03810, D. F.
Tel: (5) 682-8687
Fax: (5) 520-8820

Marco Antonio Giron
SEDESOL
Calz. A. Olachea E/
Palacio de Justicia
La Paz, 23000, B.C.S.
México
Tel: (112) 21699

Fernando Heredia
ESSA
Av. Baja California S/N
Gro. Negro, B.C.S.
Tel: (112) 70505 Ext. 351

Tim Hill
Minnesota Zoological Gardens
13000 Zoo Boulevard
Apple Valley, Minnesota 55124
U.S.A.
Tel: (612) 431-9272
Fax: (612) 431-9300

Jim Lewis
US Fish & Wildlife Service
500 Gold Avenue SW
Albuquerque, NM 87103
U.S.A.
Tel: 505-766-2914
Fax: 505-766-8063

Carlos Manterola
Agrupación Sierra Madre, S. C.
Insurgentes Sur 949-701
Col. Napoles
México, 03810, D. F.
Tel: (5) 682-8687
Fax: (5) 520-8820

Dr. Rodrigo Medellín
Centro de Ecología
U.N.A.M.
Apartado postal 70-275
Ciudad Universitaria
México, 04510, D.F.
Tel: 5-550-5215
Fax: 5-548-5259

Dr. Phil Miller
Conservation Breeding Specialist Group
12101 Johnny Cake Ridge Road
Apple Valley, Minnesota 55124 USA
Tel (612) 431-9325
Fax: (612) 432-2757

Fernando Jaramillo Monroy
PG 7 Consultores, S.C.
Apartado Postal 1000
Tuxtla Gutiérrez
29000 Chiapas, México
Tel/Fax: (961) 51097

J. Cesar Peralta
ESSA
Apartado Postal 1
Gro. Negro 23940 B.C.S.
Tel: (115) 70505

Felipe Ramirez
Zoologico Pachuca
Tesoreros #30
Col. Torriello Guerra
Tlalpan, 14050, Mexico D.F. C.P.
Tel: (915) 8461039

J. Carlos Ramirez
SEDESOL
Calz. A. Olachea E/
Palacio de Justicia
La Paz, 23000, B.C.S.
México
Tel: (112) 21699

Jose Maria Reyes
Dirección General de Flora y Fauna
Silvestres.
Av. Nuevo Leon 210
México, D. F.
Tel: (5) 584-7578
Fax: (5) 574-8346

M. en C. Ricardo Rodrígues-Estrella
Centro de Investigaciones Biológicas del
Noroeste, S.C.
Apartado Postal 128
La Paz 23000, B.C.S.
Tel: (112) 53633
Fax: (112) 53625

Bernardo Sanabria
SEDESOL
Gemenis 14-B Col. Fovisste
Gro. Negro 23940 B.C.S.
Tel: (112) 71380

Jose A. Sanchez
SEDESOL
Calz. A. Olachea E/
Palacio de Justicia
La Paz, 23000, B.C.S. MEXICO
Tel: (112) 21699

Victor Sánchez Sotomavor
Biocenosis, A.C.
Av. Universidad 1863
Col Oxtopulco
México, 04310, D.F.
Tel: 5-661-9186
Fax: 5-661-8699

Jose Bernal Stoopen
Texas A&M University
240 East 47th St. #22C
New York NY 10017 USA
Tel & Fax: (212) 688-9208

Gerardo Tapia-Hervert
AZCARM
11 Oriente 2407
Col. Aviacion
Puebla 72007, Pue.
Tel: (22) 358713/8
Fax: (22) 358607

Laura Thompson-Olais
Cabeza Prieta National Wildlife Refuge
1611 North Second Avenue
Ajo AZ 85321 USA
Tel: (602) 387-6483
Fax: (602) 387-5359

Gabriel Velazquez
SEDESOL
Calz. A. Olachea E/
Palacio de Justicia
La Paz, 23000, B.C.S.
México
Tel: (112) 21699

EVALUACIÓN DE VIABILIDAD DE LA POBLACIÓN Y DEL HABITAT DEL BERRENDO PENINSULAR
(*Antilocapra americana peninsularis*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE PENINSULAR PRONGHORN
(*Antilocapra americana peninsularis*)

La Paz, Baja California Sur, México
Centro de Investigaciones Biológicas del Noroeste, S.C.
16-18 de Noviembre de 1994

SECCIÓN 11

REFERENCIA TÉCNICA DE VORTEX
VORTEX TECHNICAL REFERENCE

Wildl. Res., 1993, **20**, 45–65

VORTEX: A Computer Simulation Model for Population Viability Analysis

Robert C. Lacy

Department of Conservation Biology, Chicago Zoological Society,
Brookfield, Illinois 60513, U.S.A.

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,

1035-3712/93/010045$10.00

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,

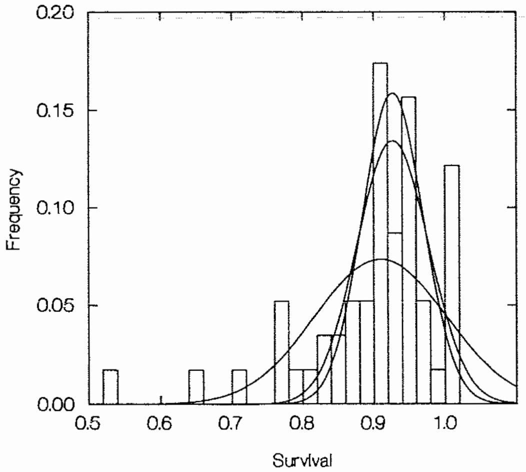


Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938–90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution 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 individual 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

$$SE(p) = \surd[p \times (1 - p)/n] \, ,$$

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

$$f_{AB}=0\cdot5\times(f_{MB}+f_{PB})$$

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 $f_{AA}=0\cdot5\times(1+F)$. [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 disequilibrium) 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 ($N \pm \text{SD} = 151 \pm 123$) 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. Continuous-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.

Acknowledgments

James W. Grier made available his simulation program, SPGPC, which provided many of the algorithms on which the first version of VORTEX (SIMPOP) was based. I thank Ulysses S. Seal, Thomas J. Foose, Jon Ballou, Nathan R. Flesness, Tim W. Clark, Gary Backhouse, David Lindenmayer, Simon Bennett, and many of the staff of the Department of Conservation and Environment, Victoria, Australia, for many helpful comments on VORTEX and PVA. Tim W. Clark, David Lindenmayer and two anonymous reviewers provided valuable critiques of drafts of this paper.

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)
```

Manuscript received 4 March 1992; revised and accepted 13 August 1992