TALLER DE EVALUACION DE VIABILIDAD DE POBLACIÓN Y HABITAT DE *Saimiri oerstedi citrinellus*

Costa Rica Squirrel Monkey Population & Habitat Viability Assessment

Parque Nacional Manuel Antonio, Costa Rica
4-7 Junio 1995

TALLER DE EVALUACION DE VIABILIDAD DE POBLACIÓN Y HABITAT DE *Saimiri oerstedi citrinellus*

POPULATION AND HABITAT VIABILITY ASSESSMENT WORKSHOP FOR *Saimiri oerstedi citrinellus*

Parque Nacional Manuel Antonio
Manuel Antonio National Park

Costa Rica

4-7 Junio 1995

FINAL REPORT
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A contribution of the IUCN/SSC Conservation Breeding Specialist Group

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15 December 1996

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Sección 1

RESUMEN EJECUTIVO

EXECUTIVE SUMMARY

Resumen Ejecutivo

El mono tití (**Saimiri oersterdii**) tiene dos subespecies. Una de ellas **S. o. citrinellus** es endémica del Pacífico Central de Costa Rica. Debido a la fragmentación del habitat original, se encuentran 36 subpoblaciones en el área. La mejor conocida es la que habita en el Parque Nacional Manuel Antonio (Wong, tesis, 1990).

Con el propósito de comprender los factores de riesgo que han afectado la sobrevivencia del mono tití, y que podrían afectar los programas de reintroducción, era necesario un análisis de su situación actual. La evaluación del riesgo es una de las mayores preocupaciones en el manejo de las especies amenazadas, y la meta es reducir el riesgo de extinción a un nivel aceptable. Un grupo de herramientas de software para ayudar la simulación y la evaluación cuantitativa del riesgo de extinción, está disponible y fue utilizada como parte del Taller de Evaluación de Viabilidad de Población y de Habitat. Esta técnica puede mejorar la identificación y priorización de los riesgos y puede contribuir a la evaluación de opciones de manejo. Para el éxito de estos esfuerzos de recuperación es importante la participación de instituciones e individuos con gran experiencia en la especie y su hábitat.

Treinta y cinco biólogos, manejadores, estudiantes, educadores, veterinarios y representantes de la comunidad participaron en el segundo Taller de Evaluación de Viabilidad de Población y de Habitat (EVPH) que se realizó en el Parque Nacional Manuel Antonio, Costa Rica, del 3 al 5 de junio de 1995, para reexaminar la aplicación de estos procedimientos recientemente desarrollados a las poblaciones silvestres de mono tití. La participación del Grupo de Especialistas en Reproducción en cautiverio de la Comisión de Sobrevivencia de Especies de la UICN fue solicitada para este EVPH con el fin de que colaboraran en este esfuerzo de recuperación. El objetivo era revisar la información disponible sobre las poblaciones silvestres como base para el desarrollo de modelos estocásticos de simulación y al mismo tiempo hacer recomendaciones detalladas de investigacion y manejo . Estos modelos estiman el riesgo de extinción y las tasas de pérdida genética de las interacciones de factores demográficos, genéticos y ambientales como una herramienta para el manejo actual de la subespecie. Otras metas incluían la determinación de los requisitos del habitat, tamaño de poblaciones, efecto de las amenazas directas, incluyendo la muerte de los animales por la gente como un factor de la declinación de la especie, así como el papel de amenazas indirectas como la enfermedad. Se priorizaron las necesidades de investigación.

En la tarde del primer día se realizóo una ceremonia de apertura en la Sala de Sesiones de la Municipalidad de Quepos. El día siguiente consistió de una serie de presentaciones que resumieron la información disponible sobre las poblaciones silvestres y en cautiverio, enfermedades, programas educativos y el habitat del mono titi. Se realizó una breve presentación sobre biologia de la población, el proceso de EVPH y la utilización del Vortex, como una introducción a la utilización de modelos y a los problemas relacionados con poblaciones pequeñas aisladas. La mayoría de estas presentaciones se dieron en el auditorio del Hospital de Quepos. El resto del taller se realizo en el Parque Nacional Manuel Antonio. Los participantes se dividieron en cinco grupos de trabajo (poblaciones silvestres, situación del habitat y modelado; distribución actual; manejo de poblaciones

en cautiverio; educación y acciones de la comunidad) para revisar en detalle la información disponible, para desarrollar valores a ser utilizados en los modelos de simulación, y desarrollar escenarios de manejo y recomendaciones. Modelos de simulación de poblaciones estocásticas fueron iniciadas con rangos de valores para las variables claves con el fin de estimar la viabilidad de las poblaciones silvestres utilizando el programa de software de modelado VORTEX.
Dentro del Parque Nacional Manuel Antonio viven 6 tropas, en la zona de amortiguamiento 8 tropas (Wong,1990). Fuera de este territorio viven 26 tropas que no se encuentran en comunicación (Arauz, 1993). Se conoce muy bien la ubicación de las subpoblaciones de Saimiri oerstedii citrinellus reportadas por Arauz (1993). Siete de estos sitios son áreas de manglar, tres son plantaciones de palma africana, rodeadas por angostas fajas de vegetación secundaria, y 16 sitios son parches de una combinación de bosque primario y un crecimiento secundario de vegetación en diferentes estadios de sucesión (Arauz,1993).Sin embargo, información sin publicar evidencia la existencia de por lo menos 4 o 5 subpoblaciones mas (Dario Castelfranco, pers. cmm., 1994).
En los modelos se asumió que el 100% de los machos adultos se podían reproducir. Se estableció la edad de madurez de las hembras en 3 años y la de los machos en 4 años. El período entre partos es dos años (el 50% de las hembras producen una cría por año). El riesgo de eventos de enfermedad como eventos estocásticos fueron incluidos en algunos de los modelos. La población inicial se estableció en 50, 100, 200, 300 o 500 (reflejando el rango de estimados de la posible capacidad de carga del habitat). Todos los escenarios se iniciaron con un rango igual de sexo y una distribución de edad estable. La reproducción se mantuvo constante. Los efectos de las depresiones de entrecruzamiento se incluyeron en algunos de los escenarios.

Las variables introducidas con un amplio rango de valores incluían principalmente la mortalidad de los adultos (10 o 12.5%), seguida por una variación sistemática de la capacidad de carga, catástrofes, depresión de entrecruzamiento con la opción de heterosis y 3.14 equivalentes letales, para determinar cuál combinación de condiciones produciría una población viable en términos de probabilidad de extinción, en relación a su tasa intrínseca de aumento. Se hicieron proyecciones para 100 años con reportes resumidos a intervalos de 10 años. Cada escenario fue corrido 500 veces.

Este informe del taller incluye un grupo de recomendaciones para la investigación y el manejo de las poblaciones silvestres, así como secciones sobre la historia de la población, biología de la población, la simulación de modelos de la población y las acciones que se necesitan.

Recomendaciones:

1. Verificar in situ las localidades en que se ha detectado la presencia de la subespecie, haciendo énfasis en el numero de tropas y en el numero de individuos por tropa, el área y sus características generales. Desarrollar una base de datos geográficos (mapa de uso y cobertura vegetal) para el área de distribución de la subespecie.

2. Evaluar la mortalidad femenina en las poblaciones naturales cercanas al Parque Nacional Manuel Antonio. Dar seguimiento a 30-40 hembras con collares de radio durante un ano por lo menos, preferiblemente por 3-4 anos. Esto proveerá de una gran cantidad de información sobre la

demografía de las tropas del mono titi.
Estas técnicas de investigación, adicionalmente darán información sobre la natalidad, mortalidad juvenil, y eventualmente sobre la dinámica de migración entre parches de metapoblaciones.

3. Desarrollar e implementar un plan para proteger las áreas donde habitan las subpoblaciones, incluyendo una zona de amortiguamiento alrededor. cuando sea posible establecer y mantener corredores de vegetación entre estas subpoblaciones.

4. Liberaciones, translocaciones y reintroducciones: El entrenamiento de personal calificado y el establecimiento de un equipo que efectúe las translocaciones y eventualmente las reintroducciones debe ser una prioridad. Por lo tanto, es muy importante realizar investigaciones que permitan identificar tropas que puedan ser candidatas a sufrir translocaciones.

5. Desarrollar una campana de educación ambiental e información dirigida a la comunidad local, nacional e internacional.

6. Se recomienda que un equipo de científicos busque la información existente sobre translocación y reintroducción de primates en general. Adicionalmente, se debe recopilar información sobre cría en cautiverio. Se deben seguir los señalamientos de la UICN para reintroducción, manejo en cautiverio, e investigacion sobre especies en vías de extinción.

7. Se recomienda que los Saimiri confiscados y abandonados provean la base para obtener experiencia en rehabilitación (incluyendo la adquisición de destrezas sociales, de búsqueda de alimento y antidepredadoras) así como proveer de un pie de cría del cual las crías eventualmente pudiesen ser reintroducidas al habitat natural. Esto podría realizarce en instituciones ya establecidas.

8. Se recomienda fuertemente una investigacion medica sobre los parásitos y las enfermedades naturales que existen en las poblaciones. La reaparición de la fiebre amarilla en Costa Rica obliga a que las poblaciones de monos titi sean periódicamente monitoreadas para determinar la presencia de esta enfermedad en ellas. Un programa de monitoreo de enfermedades debe ser parte de cualquier estudio o acción que involucre el manipuleo de los monos.

Executive Summary

The squirrel monkey (*Saimiri oerstedii*) has two subspecies. One of them *S. o. citrinellus* is endemic to the Central pacific of Costa Rica. Because of fragmentation of the original habitat, 36 separated subpopulations are found in the area. The best known population (Wong, Thesis, 1990) is in Manuel Antonio National Park.

In order to understand the risk factors that have affected the survival of the squirrel monkey and that may affect re-introduction programs, and analysis of its current situation was needed. Risk evaluation is a major concern in endangered species management and a goal is to reduce the risk of extinction to an acceptable level. A set of software tools to assist simulation and quantitative evaluation of risk of extinction is available and was used as part of a second Population Viability Assessment Workshop for this subspecies. This technique can improve identification and ranking of risks and can assist assessment of management options. Of importance to the success of these recovery efforts will be participation by institutions and individuals with extensive experience in the species and its habitat.

Thirty-five biologists, managers, students, educators, veterinarians, and representatives of Squirrel Monkey Foundations attended a second Population Viability Assessment (PVA) Workshop at the Manual Antonio National Park, Costa Rica on June 3-5, 1995 to re-examine the application of these recently developed procedures to the wild populations of the squirrel monkey. The Conservation Breeding Specialist Group of the IUCN/Species Survival Commission was asked to collaborate in this PHVA workshop to assist the conservation effort. The purpose was to review data from the wild population as a basis for developing stochastic population simulation models and to make detailed management and research recommendations. These models estimate risk of extinction and rates of genetic loss from the interactions of demographic, genetic, and environmental factors as a tool for ongoing management of the subspecies. Other goals included determination of habitat requirements, population sizes, role of direct threats including killing by people as a factor in the decline of the species, potential role of indirect threats such as disease, and prioritized research needs.

An opening ceremony and introduction to the problems was held in the town of Quepos in the late afternoon and evening of the first day. The next day, held in a local hospital auditorium, consisted of a series of presentations summarizing data on the wild and captive populations, disease, public education programs, and habitat for the squirrel monkey. A brief presentation on population biology, the PHVA process, and the use of VORTEX was made as an introduction to the use of the models and the problems associated with small isolated populations. The remaonder of the workshop was conducted at Manuel Antonio National park. The participants formed three working groups (wild population and habitat status and modelling; ca[tive population management, and public education) to review in detail current information, to develop values for use in the simulation models, and to develop management scenarios and recommendations. Stochastic population simulation models were initialized with ranges of values for the key variables to estimate the viability of the wild population using the VORTEX software modelling package.

Inside Manuel Antonio National Park live 6 troops, in the buffer zone 8 troops (Wong, 1990). Outside the range exist 26 troops that are not in communications (Arauz, 1993). The subpopulations of the S. oerstedi citrinellus reported by Arauz (1993) are well known ubicated. Arauz describes 26 sites with groups of squirrel monkeys. Seven of this sites are mangroove areas, three are African palm plantations, surrounded by narrow belts of second growth vegetation, and 16 sites are forest patchs of a combination of primary forest and secondary growth vegetation in different succession stages (Arauz, 1993). However, unpublished information, shows the existence of at least 4 to 5 more subpopulations (Dario Castelfranco, pers. comm., 1994).

In the models, 100% of adult males were assumed to be available for breeding. The age of maturity for females was set at 3 years and for males at 4 years. The interbirth interval was 2 years (50% of females produce a surviving litter with a mean of 1 young each year). The risk of disease events as stochastic events were included in some of the models. The initial population was set at either 50, 100, 200, 300, or 500 (reflecting the range of estimates of the possible habitat carrying capacity). All scenarios were initialized with an equal sex ratio and stable age distribution. Reproduction was held constant. Effects of inbreeding depression were included in some scenarios. Variables initialized with a range of values included mean adult mortality (either 10 or 12.5% followed by systematic variation of carrying capacity, the catastrophes, and inbreeding depression with the heterosis option and 3.14 lethal equivalents to determine what combination of conditions would produce a viable population in terms of probability of extinction in relation to the intrinsic rate of increase. Projections were done for 100 years with summary reports at 10 year intervals. Each scenario was run 500 times.

This workshop report includes a set of recommendations for research and management of the wild populations as well as sections on the history of the population, the population biology and simulation modelling of the population and actions needed.

Recommendations

1. Verify *in situ* the localities in which has been detected the presence of the subespecies, emphasizing in the number of troops and individuals by troop, the area of the patch and its general characteristics. Develop a geographic data base (map of use and vegetable coverage) for the area of the distribution of the subespecies.

2. Evaluate female mortality in natural populations near Manuel Antonio National Park. Follow a set of 30-40 radio-collared females for at least 1 year, and preferably 3-4 years, which can yield a wealth of information on the demographics of squirrel monkey troops. Additionally, these research techniques would give information on natality, juvenile mortality, and perhaps even the dynamics of migration between metapopulation patches.

3. Develop and implement a plan to protect the areas where subpopulations live including a surrounding buffer zone, and where possible establish and maintain vegetation corridors between these subpopulations.

4. Releases, translocations, and re-introductions: Priority must be placed on training qualified personnel and the establishment of a team to carry out translocations and eventually reintroductions. Therefore, it is of utmost importance to carry out research in order to identify candidate troops for translocations.

5. Develop an environmental education and information campaign directed to the local, national, and intenational communities.

6. It is recommended that a team of scientists gather the available information on translocation and re-introduction of primates in general. In addition, information about husbandry for captive breeding of *Saimiri* should also be compiled. The IUCN Re-introduction, Captive Breeding and Research on Endangered Species guidelines should be followed.

7. It is recommended that confiscated and surrendered *Saimiri* provide the basis to gather expertise on rehabilitation (including acquisition of social, foraging and anti-predatory skills), as well as to provide a breeding stock from which offspring could eventually be re-introduced into the wild. This could be done in already established facilities.

8. It is highly recommended that a medical survey of parasites and natural diseases that exist in current populations be conducted. The re-appearence of yellow fever in Costa Rica makes it very important that squirrel monkey populations be routinely monitored for the presence of this disease. A disease monitoring program should be part of any study or action that involves handling of the monkeys.

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Sección 2

BIOLOGIA DE LA POBLACION Y MODELOS

POPULATION BIOLOGY AND MODELLING

BIOLOGIA DE LA POBLACION Y MODELADO

Introducción

La necesidad y los efectos de las estrategias de manejo intensivo pueden ser modeladas con el fin de sugerir cuales practicas son las mas efectivas para conservar una población. VORTEX, un modelo de simulación escrito por Robert Lacy y Kim Hughes, fue utilizada como una herramienta para estudiar la interacción de múltiples variables estocasticas.

El paquete VORTEX es una simulación Monte Carlo de los efectos de fuerzas deterministicas así como de eventos estocásticos demográficos, ambientales, y genéticos en las poblaciones de vida silvestre. VORTEX modela la dinámica poblacional como eventos secuenciales discretos (por ejem., nacimientos, defunciones, proporciones sexuales, catástrofes, etc.) que ocurren de acuerdo con distribuciones de probabilidades definidas. Las probabilidades de los eventos son modelados como constantes, o como variables al azar que siguen distribuciones especificas.
El paquete simula una población basándose en la serie de eventos que describen el ciclo de vida típico de los organismos diploides con reproducción sexual.

VORTEX no intenta dar respuestas absolutas, debido a que esta proyectando estocasticamente la interacción de los muchos parámetros que ingresan en el modelo, y debido a los procesos al azar que intervienen en la naturaleza. La interpretación de los resultados depende de nuestro conocimiento de la biología de la especie, las condiciones que afectan la población, y los posibles cambios en el futuro.

Parámetros que se toman en cuenta en la simulación

Información basada en los estudios hechos por Grace Wong en el Parque Nacional Manuel Antonio. (Wong, 1990)

Sistema de apareamiento: poligamia

Edad promedio de la primera reproducción: VORTEX define la reproducción como el tiempo en que las crías nacen, no como la edad de madurez sexual.
Las hembras llegan a la madurez sexual a los 2.5 anos de edad. Debido a que la gestación tiene un periodo de 6 meses, la edad promedio de la primera reproducción, como se define en el contexto del modelado , es de 3 anos. Los machos se reproducen cuando alcanzan los 4 anos de edad.

Espectativa máxima de vida: VORTEX asume que los animales se pueden reproducir (según la tasas típicas de la especie) durante toda su vida adulta. La expectativa máxima de vida no se utiliza si la especie no se reproduce durante toda su vida.
No existe información especifica para las poblaciones silvestres de S. o. citrinellus. Ross (1991) informa de Harvey et. al. (1987) que individuos silvestres de Saimiri sciureus se reproducen hasta los 21 anos de edad. Larry Williams nos informó que monos titi de su criadero han vivido hasta

25 anos (las hembras se han reproducido hasta los 22 anos). Marie Zaldivar indico que los monos congo (Alouatta palliata) viven de 13 a 20 anos, lo que da una edad promedio de longevidad de 17 anos. Debido a que el mono titi tiene un tamaño corporal menor, se puede considerar su periodo de vida media mas corto. Con toda esta información, y tomando en cuenta que los animales en el bosque tienen una probabilidad menor de sobrevivencia (debido a la competencia, depredación, factores ambientales, enfermedades, carencia de alimentos, etc.) la edad máxima de vida se estimo en 10 anos.

Producción de crías: Información de Wong (1990), indica que la natalidad, definida aquí como la proporción de hembras observadas con infantes, es de un 76%. este estimado proviene de las observaciones directas de 94 hembras pertenecientes a 6 tropas que habitaban dentro del Parque Nacional Manuel Antonio, así como de 112 hembras de 8 tropas ubicadas en áreas fuera del parque. Esta información conduce a la conclusión de que las hembras de S.o. citrinellus son capaces de reproducirse anualmente, con alguna mortalidad de las crías inmediatamente después del nacimiento (véase la discusión posterior sobre mortalidad). Por lo tanto, establecemos la proporción de hembras que se reproducen cada ano en 90%, asumiendo que algunas hembras, aunque sean capaces de reproducirse, no lo harán.

La variación en la reproducción es modelada en VORTEX introduciendo una desviación standard (SD) para la proporción de hembras adultas que no producen crías. Debido a que se carecía de información empírica para esta variable, asumimos que esta variación (debido a las fluctuaciones en la abundancia de alimentos y a la variabilidad de la edad en que las hembras llegan a la madurez sexual) fue de 10% del valor promedio. VORTEX entonces determina el porcentaje de hembras que se reproducen cada ano de la simulación muestreando de una distribución binominal con la media especifica (90%) y SD (10%).

Reproducción de los machos: El sistema de reproducción modelado por VORTEX asume que los apareamientos son reorganizados al azar cada ano y que todos los animales que se pueden reproducir tienen iguales oportunidades de hacerlo. Algunos animales pueden ser excluidos del grupo reproductor si es considerado necesario. Todos los machos de S. o. citrinellus son considerados aptos para la reproducción, aunque los mas grandes, tal vez de una edad intermedia, pueden tener más éxito.

Proporción de sexos al nacimiento: No existen registros específicos para esta especie. Asumimos una proporción de sexos igual al Nacimiento basándonos en el patrón de la mayoría de los mamíferos y en las poblaciones de primates mantenidos en cautiverio.

Mortalidad: La mortalidad (y la desviación estandard) es incluida como un porcentaje para cada edad y sexo. Una vez que la edad reproductiva es alcanzada (adulto), la probabilidad anual de mortalidad permanece constante durante toda la vida del animal y se introduce solamente una vez.

No existe información sobre observaciones directas de mortalidad natural para S.o. citrinellus en

Costa Rica. Datos de Wong (1990) indican un limite bajo de la mortalidad juvenil de aproximadamente 25%, dado que las hembras se reproducen anualmente. Sus datos muestran una proporción de sexos en los adultos (hembra: macho) entre 2:1 y 3:1 en la catorce tropas en estudio. Los estimados de mortalidad que se muestran a continuación se derivaron para satisfacer estos patrones demográficos observados en las poblaciones silvestres.

Edad	Machos	Hembras
0-1	35 (10)	25 (6)
1-2	20 (6)	15 (4)
2-3	20 (6)	10 (3)
3-4	15 (4)	10 (3)
Adulto	19 (3)	10 (3)

Como se conoce poco de las tasas de mortalidad de esta especie en el medio silvestre, se realizo un análisis de sensibilidad para determinar la sensibilidad de las poblaciones de monos titi a los cambios de la mortalidad de hembras juveniles o adultas. Las tasas de mortalidad mostradas arriba se consideran valores básicos; la mortalidad juvenil se modelo también a 19, 22, 28, y 31%, mientras que la mortalidad de los adultos fue modelada a 4, 7, 13, y 16%. La mortalidad de los juveniles no fue cambiada en ningún escenario.

Depresión de entrecruzamiento: Esta es una variable importante cuando se trabaja con poblaciones pequeñas fragmentadas, como es el caso de esta subespecie de mono titi. Muchas poblaciones de S.o. citrinellus son suficientemente pequeñas como para que los efectos nocivos del entrecruzamiento jueguen un importante papel en la dinámica poblacional. Aun mas, si se dan las condiciones para que poblaciones que en este momento son relativamente grandes experimenten disminuciones significativas de tamaño en el futuro, la depresión de entrecruzamiento podría ser un factor importante en su viabilidad. Debido a esto, se ha incluido la depresión de entrecruzamiento en un subgrupo de modelos que tiene que ver con poblaciones particulares de tamaño pequeño.

El modelo de heterosis de la depresión de entrecruzamiento fue empleado en escenarios apropiados. En este modelo de depresión de entrecruzamiento, los individuos que son heterozigotas en un loci genético especifico, tienen una adaptación superior a aquellos que son homozigotas en ese loci. Debido a que los alelos particularmente dañinos no son removidos de la población por la selección natural durante el tiempo de este modelo, el modelo de heterosis puede proveer un sobreestimado de los efectos nocivos del entrecruzamiento en las poblaciones de mono titi modeladas.

La severidad de la depresión de entrecruzamiento en las poblaciones de mamíferos, se puede medir como el numero de "equivalentes letales" contenidos en el genoma de la población en estudio. Información obtenida para poblaciones en cautiverio de 12 especies de primates sugiere que las mismas encubren cerca de 4 equivalentes letales, numero un poco mayor que el valor medio obtenido en el grupo de datos de 40 especies de mamíferos analizado por Ralls et. all.

(1988). De hecho, dos especies de primates, Saginus fuscicollis illigeri y Lemur fulvus, tenían dos de las mas altas cargas genéticas de todas las especies de mamíferos analizadas. Debido a que no existe información especifica sobre la depresión de entrecruzamiento en S.o. citrinellus, el valor medio mas conservador de 3.14 equivalentes letales fue utilizado en todos los escenarios de modelado apropiados.

Tamaño poblacional inicial: Unicamente existe información especifica para el Parque Nacional Manuel Antonio. Datos recientes indican que en el Parque residen aproximadamente 260 individuos. Con el fin analizar el impacto del pequeño tamaño poblacional en la vulnerabilidad a la extinción de esta especie, se construyeron una serie de escenarios con poblaciones de 200, 100, 75, 50 y 25 individuos. En todos los escenarios, los individuos de la población fueron clasificados entre las categorías de edad y sexo de acuerdo a la distribución de edades calculada de la tabla de vida correspondiente. La depresión de entrecruzamiento se incluyo en los escenarios con un tamaño poblacional de 100 o menos individuos. El entrecruzamiento generalmente tiene un impacto insignificante en las poblaciones mayores de 100 individuos dentro de las condiciones modeladas en este caso.

Capacidad de carga: la capacidad de carga (K) define el limite superior para el tamaño poblacional, sobre esta se impone la mortalidad adicional sobre las categorías de edad y sexo por igual, con el fin de retornar la población a este valor. VORTEX utiliza la capacidad de carga para imponer al modelo un techo dependiente de la densidad, a las tasas de sobrevivencia.

Se le asigno al Parque una capacidad de carga de 300. En todos los otros escenarios con poblaciones menores, en los que estábamos modelando poblaciones fragmentadas ocupando (presumiblemente) fragmentos boscosos péquenos y aislados, la capacidad de carga era idéntica al numero original de individuos.

Catástrofes: Las catástrofes se definen como los extremos de las variaciones ambientales. Son eventos que impactan en la reproducción y/o en la sobrevivencia. Ejemplos de catástrofes son los tornados, las inundaciones, las sequías, el fuego o la enfermedad. Estos eventos suceden y se deben considerar seriamente cuando modelan el destino de las poblaciones pequeñas. Las c-atástrofes se modelan asignándoles una probabilidad anual de ocurrencia y un factor de severidad que varia entre 0.0 (efecto máximo o absoluto) a 1.0(sin efecto). La reproducción anual y las tasas de sobrevivencia durante los anos de catástrofes se obtienen multiplicando la probabilidad de reproducción o sobrevivencia normal (sin catástrofe) por estos factores.

Dos tipos de catástrofes fueron considerados inicialmente:

1) Epidémica, como la fiebre amarilla. Danilo Leandro considera que podrían haber 1 o 2 epidemias cada 60 anos, y que estas podrían causar una reducción en la reproducción y la supervivencia de un 50%.

Frecuencia: una vez cada 60 anos (1.6% anualmente).
Reproducción: reducción del 50%
Sobrevivencia: reducción del 50%.

2) Efectos climáticos, como la tormenta tropical Gert que ocurrió en 1993. Los huracanes difícilmente tocan Costa Rica directamente, aunque sus efectos secundarios afectan la zona, como sucedió con el Huracán Juana. Por lo tanto asumimos que un huracán afectara la zona cada 100 años. Una catástrofe de este tipo afectara la sobrevivencia pero no la reproducción.

Frecuencia : 10%
Reproducción: sin efecto
Sobrevivencia: reducción del 25%

Estructura de la metapoblación: Se construyo un escenario que investigo el impacto de la subestructura poblacional dentro y en los alrededores del Parque Nacional Manuel Antonio. Observaciones realizadas por Grace Wong y sus colegas señalan la existencia de dos poblaciones de mono titi fuera de los limites del Parque Nacional: una población cerca de Quepos, y otra en las afueras del parque. Estas tres poblaciones tienen la oportunidad de intercambiar individuos, aunque las tasas de migración se desconocen. Unicamente se permitió la migración de hembras entre 3 y 4 anos, con una tasa de sobrevivencia del 75% durante la migración.

La probabilidad de migración entre las poblaciones del Parque (tanto la que se encuentra dentro de el como la que esta en las inmediaciones), y la población de Quepos varia entre 0.001 a 0.005, mientras que la probabilidad de migración entre la población del parque y la que se encuentra en su limite varia de 0.03 a0.04. Los esquemas de mortalidad fueron idénticos para las tres subpoblaciones. esta suposición se basa en la información presentada por Wong (1990), en la cual indica que la estrucrura de natalidad y edad en las poblaciones fuera del parque eran muy similares a las de la población del Parque. Sin embargo, no esta claro si los monos titi tienen una mortalidad mas alta debido a la captura de individuos como mascotas, etc. Todos los otros parámetros para las poblaciones fuera del Parque fueron considerados idénticos a los de la población del dentro del mismo. A la población de Quepos se le asigno una capacidad de carga de 182 animales; adicionalmente, se estableció que la capacidad de carga disminuía en una tasa linear anual de 3.5% durante 10 anos. Esto produciría una disminución del 35% en la capacidad de carga en 10 anos, y por lo tanto la población disminuiría a 122 animales. A la población que se encuentra en los limites del parque se le asigno una capacidad de carga de 87 animales, con una tasa linear de disminución de 2% durante 10 anos. Esto resultaría en una disminución del 20%, proyectándose una población de 70 animales después de 10 años. Estas disminuciones en la capacidad de carga se incluyen para simular la degradación gradual del habitat del mono titi en áreas cercanas al Parque, debido a las presiones de la expansión humana.

Repeticiones y anos de proyección: Cada escenario de modelo fue repetido 500 veces, con proyecciones poblacionales extendiéndose por 100 anos. Los resultados obtenidos se resumieron en intervalos de 10 anos, para ser utilizados en las tablas y figuras que siguen. Todas las simulaciones se condujeron utilizando el paquete de software VORTEX 7.0.

Resultados del modelo de simulación

Explicación de las tablas y figuras

Los resultados numéricos de los modelos de simulación aparecen en las tablas 1 a 9. Cada tabla representa un set de condiciones especificas, por ejemplo, esquema de la mortalidad de los juveniles o adultos, suma de la depresión de entrecruzamiento, etc. En cada tabla, los resultados están organizados en una estructura de canasta: cada tamaño poblacional fue corrido con cada nivel de mortalidad juvenil o adulta en las hembras, con o sin catástrofes y depresión de entrecruzamiento.

Los encabezados de las tablas son los siguientes:

r : tasa de crecimiento poblacional deterministica, calculada por los métodos de la matriz de Leslie de la tabla de datos de vida.

r (SD): desviación estandard y promedio de la tasa de crecimiento poblacional estocastica a través de las repeticiones, calculada de la variación anual en tamaño poblacional.

P(E): Probabilidad de extinción de la población durante los 100 anos que cubren las simulaciones, calculada como la proporción de poblaciones corridas que se extinguen dentro de 100 anos;

N (SD): tamaño final de las poblaciones en existencia después de 100 anos;

H : proporción de la heterozigosis poblacional original que se espera permanezca en las poblaciones remanentes después de 100 anos;

T(E): Tiempo promedio de extinción de aquellas poblaciones que se extinguen. Este valor se da únicamente para aquellos escenarios en los cuales por lo menos el 10% de las poblaciones corridas se extinguen.

Se dan los números de los archivos producidos para cada escenario para referencias futuras y recuperación, si es necesario.

Las figuras 1 a 18 son una compilación gráfica de los resultados del modelado, intentando mostrar las relaciones entre factores específicos y su impacto en la persistencia de la población. Cada figura presenta resultados para la tasa de crecimiento estocastica, probabilidad de extinción, o tamaño poblacional final para cada uno de los seis tamaños poblacionales modelados (o cuatro poblaciones en esos escenarios incluyendo depresión de entrecruzamiento), como una función de la mortalidad de los juveniles o de los adultos. Estos datos se tomaron directamente de los resultados de 100 anos presentados en las tablas adjuntas.

Resultados de la simulación deterministica

Las tasas de crecimiento determinista de la población para cada escenario, calculadas de las tablas de vida utilizando los algoritmos matriciales de Leslie, se presentan en la quinta columna de las tablas 1-8. Estos cálculos asumen que tanto las tasas de nacimiento como las de crecimiento son constantes (sin variaciones anuales ni fluctuaciones estocásticas), no hay limitaciones en las copulas, y el entrecruzamiento no tiene impacto en la fecundación o en la viabilidad. Obsérvese que la mortalidad y la inclusión/ exclusión de catástrofes son las variables que afectan estas tasas deterministicas. Por lo tanto, la tasa de crecimiento poblacional a largo plazo, en ausencia de variaciones estocásticas, es independiente del tamaño de la población.
Nuestro escenario de modelado básico, (archivo #201), con una mortalidad juvenil femenina de 25% y adulta de 10%, da como resultado una población con un crecimiento anual mayor del 4% (r =0.042, =1.043: Tabla 1).Si la mortalidad juvenil se aumenta a 31%, la tasa de crecimiento determinista es reducida por casi 36% a 0.0027 (archivo #205). Similarmente, disminuyendo la mortalidad juvenil a 19% se obtiene un aumento del 36% en el crecimiento deterministico (r = 0.057, = 1.058: archivo #202). Si la mortalidad de las hembras adultas se aumenta a 16%, la tasa de crecimiento determinista se reduce 71% a r =0.012. Bajo condiciones de mortalidad adulta reducida, la población es capaz de crecer un 7% anual a largo plazo (r = 0.071, = 1.074: Archivo #206).

Esta información indica que un cambio en con respecto al crecimiento determinista de un 1% en la mortalidad femenina juvenil, resulta en un cambio en r de 0.0025. Sin embargo, el mismo grado de cambio en la mortalidad femenina adulta, conduce a un cambio en r de 0.0049. En otras palabras, el crecimiento poblacional determinista en esta especie, es dos veces mas sensible a la mortalidad femenina adulta en comparación con la mortalidad femenina juvenil.

Si las catástrofes son removidas de los modelos, el crecimiento determinista aumenta en un 50% (dependiendo del nivel de mortalidad) en comparación con los escenarios descritos (Tabla 4). En nuestro escenario base del modelo, en ausencia de catástrofes (Archivo #291), la población podría realizar cerca de 5.5% de crecimiento determinista al año. El aumento de la sensibilidad de la población a la mortalidad adulta se mantiene en estos escenarios sin catástrofes.

Resultados de la simulación estocásticos

Los cálculos de las tasas de crecimiento poblacional a partir de los promedios de natalidad y mortalidad en una tabla de vida, podrían sobreestimar el crecimiento poblacional a largo plazo, si existen fluctuaciones en los parámetros demográficos por alguna razón. Más aún, esta sobreestimación podría ser mas grave conforme la mortalidad aumenta y las poblaciones disminuyen. La inclusión de estas fuerzas al azar en el proceso de modelado de la población, producen tasas de crecimiento estecástico que son, en cada caso, menores que las tasas de crecimiento determinista calculadas de los parámetros promedio de la tabla de vida. Aunque esta reducción es relativamente pequeña en condiciones de baja mortalidad femenina (por ejem. ,Archivo #206), la tasa de crecimiento estecástico es reducido hasta un 50% cuando la mortalidad

de los adultos es alta, aun cuando el tamaño de la población sea relativamente grande (Archivo #209; Tabla 1).
La influencia de factores estocásticos en las poblaciones pequeñas es muy pronunciada. Las tasas de crecimiento estocástico pueden tornarse negativas a pesar de las tasas positivas de crecimiento determinista a largo plazo. (por ejem., Archivo # 245, tabla 3).

En todos los tamaños poblacionales modelados, un aumento tanto en la mortalidad juvenil como adulta, produjo un aumento en la probabilidad de extinción y a una reducción tanto del tamaño final de la población como de la proporción de la heterozigosis poblacional retenida (Figuras 3-6). Como en el caso de las tasas de crecimiento deterministas, la mortalidad de los adultos tiene una mayor influencia en la determinación de la probabilidad de extinción de la población y en el tamaño final de la población, que la mortalidad juvenil.

La interacción entre la mortalidad y la persistencia poblacional es tremendamente dependiente del tamaño de la población modelada. El riesgo de extinción bajo condiciones básicas y un tamaño poblacional alto fue cero (Archivo #201; Tabla 1), y aumento a 3.4% bajo condiciones de mortalidad alta de los adultos (Archivo #209). La probabilidad de extinción para poblaciones de 50 individuos, con niveles base de mortalidad, aumenta a 13.6%,; esta aumenta a 50% para poblaciones de 25 individuos (Archivos #237 y #246, respectivamente). Debe notarse que este riesgo de extinción esta presente aunque el promedio de crecimiento estocástico positivo sea alrededor de un 2% anual ($r = 0.019$; Archivo # 246). La interacción de una población pequeña y una mortalidad femenina alta, tanto de adultos como jóvenes, conduce a un considerable riesgo de extinción (por ejem., Archivos #245 y #254). El tiempo promedio de extinción de la población para la mayoría de estos escenarios es de aproximadamente 60 años.

Si se quita de las poblaciones modeladas la influencia de las catástrofes, la estabilidad de la mayoría de las poblaciones se aumenta (Tablas 4-6, Figuras 7-12). Todas las tasas de crecimiento estocástico son positivas, y la variación sobre estas tasas es reducida en comparación con los escenarios en los que se incluyen catástrofes. La influencia de la mortalidad femenina en el crecimiento poblacional es, sin embargo, evidente. La reducción en la variación de la tasa promedio de crecimiento conduce a una reducción del riesgo de extinción en todos los escenarios. De hecho, poblaciones de al menos 100 individuos son inmunes al riesgo de extinción bajo estas condiciones, estabilizándose los tamaños poblacionales finales muy cerca de la capacidad de carga. Poblaciones muy pequeñas (por ejem., no mas de 50 animales) se mantienen susceptibles a la extinción aun en la ausencia de catástrofes, aun cuando el riesgo sea reducido bruscamente. (compare archivos #336, Tabla 6 y #201, tabla 3).

Los efectos deletéreos del entrecruzamiento en las poblaciones pequeñas de monos titi pueden tener un impacto dramático en la viabilidad poblacional (Tablas 7 y 8, Figuras 13-18). Del 60 al 65% de las tasas de crecimiento estocástico en escenarios que incluyen la depresión de entrecruzamiento, son negativos. Adicionalmente, todas las poblaciones tienen al menos algún riesgo de extinción. Bajo condiciones básicas de modelado, el riesgo de extinción vario entre 17% ($K = 100$: Archivo #255) a 100% ($K = 25$: Archivo #282). Independientemente del nivel de mortalidad femenina adulta o juvenil, poblaciones muy pequeñas (K = 25) se extinguirán en 50-55 años (Tabla 8). Poblaciones mas grandes tienen un menor (sin embargo sustancial) riesgo de extinción en estas condiciones, sin embargo, el tamaño final de las mismas después de 100 años esta muy por debajo de la capacidad de carga aun en las condiciones de mortalidad mas optimistas.

Resultados del escenario de la metapoblación

Las tres poblaciones modeladas en el escenario de la metapoblación muestran un considerable crecimiento estocástico, variando entre 0,030 y 0.071. Los tamaños poblacionales finales para cada población estaban por debajo de la capacidad de carga. La población mas pequeña, la que se encontraba en las afueras del Parque, fue la única que tuvo un riesgo de extinción mayor de cero (P(E)= 0.016); la migración era insuficiente para recolonizar la población una vez que la extinción ocurría.

La metapoblación como un todo tenia una tasa de crecimiento estocástico de 0.0479. Durante el tiempo establecido para la simulación, no hay riesgo de extinción para la metapoblación, y el tamaño final de la misma era de 442 animales, 86% sobre la capacidad de carga de la metapoblación después de 100 años (tomando en consideración la reducción en K en aquellas poblaciones fuera del Parque). Sobre todo, esta estructura de la metapoblación aparentemente es muy estable, con el potencial de tener cerca de 500 monos titi, bajo condiciones adecuadas de manejo.

Resumen y Recomendaciones

Las siguientes recomendaciones se hacen basándose en los resultados de la simulación discutidos anteriormente:

1. Las poblaciones de monos titi en Costa Rica, bajo las condiciones modeladas utilizando el VORTEX, son mas sensibles a la mortalidad femenina adulta con respecto a su crecimiento estocástico, y al riesgo de extinción.

2. El tamaño poblacional es un factor mayor determinante en la existencia del mono titi en Costa Rica. Las poblaciones menores de 100 individuos muestran una considerable inestabilidad demográfica y riesgo de extinción. Durante los lapsos de tiempo modelados en estos escenarios, poblaciones menores de 50 animales generalmente no tienen viabilidad.

3. Catástrofes, como epidemias y huracanes, son factores importantes que influencian la viabilidad de las poblaciones de mono titi. Estos efectos son mas pronunciados en las poblaciones pequeñas, en las cuales el riesgo de extinción es mas evidente a pesar de tener tasas promedio positivas de crecimiento estocástico.

4. El efecto deletéreo del entrecruzamiento aumenta el riesgo de extinción en todas las poblaciones estudiadas. Las poblaciones deben mantenerse relativamente grandes para mantener el entrecruzamiento al mínimo. Investigaciones sobre monos titi en cautiverio (por ejem., S. sciurus)

puden dar contribuciones valiosas al conocimiento de la naturaleza y severidad de la carga genética presente en la subespecie costarricense.

5. Given the sensitivity shown by squirrel monkey populations to changes in female mortality, research should be undertaken to evaluate this parameter in natural populations near Manuel Antonio National Park. Following a set of 30-40 radio-collared females for at least 1 year, and preferably 3-4 years, can yield a wealth of information on the demographics of squirrel monkey troops. Additionally, these research techniques would give information on natality, juvenile mortality, and perhaps even the dynamics of migration between metapopulation patches.

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 species, the conditions affecting the population, and possible changes in the future.

Input Parameters for Simulations

Data based on the studies of Grace Wong in Manuel Antonio National Park (Wong 1990).

<u>Mating System</u>: Polygynous.

<u>Average Age of First Reproduction</u>: VORTEX defines breeding as the time when young are born, not the age of sexual maturity.

Females reach sexual maturity at 2.5 years of age. Coupled with a 6-month gestation period, the average age of first reproduction as defined in the context of the modelling is 3 years. Males breed when they have reached 4 years of age.

<u>Age of Senescence</u>: VORTEX assumes that animals can breed (at the species' typical rate) throughout their adult life. The maximum life expectancy is not used if the species does not reproduce throughout its entire adult lifespan.

No specific data exist for wild populations of *S. o. citrinellus*. Ross (1991) reports from Harvey et al. (1987) that non-captive individuals of *S. sciureus* reproduce up to 21 years of age. Larry Williams informed us that he has had captive squirrel monkeys live up to 25 years in captivity (with females reproducing up to 22 years). Marie Zaldivar indicated that wild howler monkeys (*Alouatta palliata*) live 13 to 20 years of age, which gives a probable mean lifespan of 17 years.

Since squirrel monkeys have a smaller body size, it is expected that their lifespan would be considerably shorter. From all this information and taking into account that animals in the wild have lower probability of survival (because of competition, predation, environmental factors, diseases, food shortages, etc) the maximum age was estimated to be 10 years.

Offspring Production: Data from Wong (1990) indicate that natality, here defined as the proportion of females observed with infants, averages 76%. This estimate comes from direct observations of 94 females among 6 troops within Manuel Antonio National Park as well as 112 females among 8 troops in areas outside the Park. These data lead to the conclusion that *S. o. citrinellus* are capable of breeding anually, with some mortality of offspring soon after birth (see discussion of mortality below). Therefore, we set the proportion of females breeding each year as 90%, assuming that some females, while capable of breeding in a given year, will in fact not reproduce.

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 approximately 10% 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 (90%) and SD (10%).

Male Breeding Pool: The breeding system modelled by VORTEX assumes that mates are randomly reshuffled each year and that all animals that can breed have an equal probability of breeding. Some animals may be excluded from the breeding pool if deemed appropriate. All *S. o. citrinellus* males are considered available for breeding, although larger males, perhaps of intermediate age, may be more successful.

Sex Ratio at Birth: No specific records exist for this species. We assumed an equal sex ratio at birth based upon the pattern in most mammals and in primates in captive populations.

Mortality: Mortality (and standard deviation) is entered as a percent for each age and sex class. Once reproductive (adult) age is reached, the annual probability of mortality remains constant over the remaining life of the animal and is entered only once.

No direct observational data exist on natural mortality rates for *S. o. citrinellus* in Costa Rica. Data from Wong (1990) indicate a lower bound on juvenile mortality of approximately 25%, given that females breed annually. Moreover, her data show an adult sex ratio (female:male) of between 2:1 and 3:1 in the fourteen study troops. The mortality estimates shown below were derived in order to satisfy these demographic patterns observed in wild populatons.

Age	Males	Females
0-1	35 (10)	25 (6)
1-2	20 (6)	15 (4)
2-3	20 (6)	10 (3)
3-4	15 (4)	10 (3)
Adult	10 (3)	10 (3)

As little is known of mortality rates in this species in the wild, a sensitivity analysis was conducted to determine the sensitivity of squirrel monkey populations to changes in either juvenile or adult mortality of females. The mortality rates shown above are considered the "base" values; juvenile mortality was also modelled at 19, 22, 28, and 31% while adult mortality was also modelled at 4, 7, 13, and 16%. Sub-adult mortality was not changed in any scenario.

Inbreeding Depression: This is an important variable any time one deals with small and fragmented populations, which seems to be the case for this species of squirrel monkey. Many populations of *S. o. citrinellus* are small enough that the deleterious effects of inbreeding may play a significant role in the dynamics of the population. Moreover, if conditions are such that populations that are now relatively large experience significant bottlenecks in population size in the future, inbreeding depression could become a prominent factor influencing populatio viability. Consequently, we have included inbreeding depression in a subset of models dealing with particularly small population sizes.

The heterosis model of inbreeding depression was employed in appropriate scenarios. In this model of inbreeding depression, 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 squirrel monkey 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 captive populations of 12 primate species suggests that these species harbor about 4 lethal equivalents, a number slightly greater than the median value obtained in the larger dataset of 40 mammalian species analyzed by Ralls et al. (1988). In fact, two primate species, Illiger's saddle-backed tamarin (*Saguinus fuscicollis illigeri*) and the brown lemur (*Lemur fulvus*), had two of the highest genetic loads of all mammal species analyzed. However, because specific data on inbreeding depression in *S. o. citrinellus* do not exist, the more conservative median value of 3.14 lethal equivalents was used in all appropriate modelling scenarios.

Initial Population Size: Specific data exist only for Manuel Antonio National Park. Recent data indicated that 260 individuals currently reside in the Park. In order to assess the impact of small population size on vulnerability to extinction for this species, a series of scenarios were constructed with population sizes of 200, 100, 75, 50, and 25 individuals. In all scenarios, individuals within the population were distributed among age and sex classes according to the stable age distribution calculated from the corresponding life table. Inbreeding depression was included in scenarios with population size of 100 or less. Inbreeding generally has a negligible impact on fitness of populations larger than about 100 individuals under the conditions modelled herein.

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. In other words, VORTEX uses the carrying capacity to impose a ceiling model of density-dependence on survival rates.

The Park was assigned a carrying capacity of 300. In all other scenarios involving smaller populations, in which we were modelling fragmented populations occupying (presumably) small, isolated forest fragements, the carrying capacity was identical to the initial number of indviduals.

Catastrophes: Catastrophes can be thought of as extremes of environmental variation. They are events that impact reproduction and/or survival. Examples of catastrophes can be tornadoes, floods, droughts, fire, or disesase. Such events do happen and are very real considerations when attemptig to model the fate of small populations. 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). Annual reproduction and survival rates during catastrophe years are then obtained by multiplying the normal (non-catastrophe) probability of reproduction or survival by these factors.

Two catastrophes were initially considered:
1) Epidemic, such as yellow fever. Danilo Leandro considered that there could be 1 or 2 epidemics every 60 years, and it would cause a reduction in reproduction and survival of 50%.

Frequency: once every 60 years (1.6% annually)
Reproduction: 50% reduction
Survival: 50% reduction

2) Hurricanes, such as the 1993 occurrence of tropical storm Gert. Hurricanes rarely hit Costa Rica (there have been two recorded events during this century, hurricanes Juana and Gert), and it would be even more improbable that hurricanes would strike the Pacific coast of the country. We therefore assumed that there would be one hurricane affecting the park every 100 years. Such a catastrophe will affect survival but will have no effect on reproduction.

Frequency: 10%
Reproduction: no effect
Survival: 25% reduction

Meta-population Structure: A scenario was constructed that investigated the impact of population substructure in and around Manuel Antonio National Park. Observations made by Grace Wong and colleagues indicate that two other squirrel monkey populations exist outside the boundaries of the National Park: one population near Quepos, and another just outside the Park. These three populations have the opportunity to exchange individuals between them, although the precies migration rates are unknown. Only females between the ages of 3 and 4 years were allowed to migrate, with a 75% survival rate during migration.

The probability of migrating between the Park populations (both within and immediately outside) and the Quepos population ranged from 0.001 to 0.005, while the probability of migrating between the Park and immediately outside ranged from 0.03 to 0.04. Mortality schedules were identical for all three subpopulations. This assumption was based on data presented in Wong (1990) in which natality and age structures in populations outside the Park were very similar to those for the Park population. Moreover, it is unclear to what extent squirrel monkeys experience higher mortality because of capture for the pet trade, etc. All other parameters for those populations outside the Park were identical to the Park population. The Quepos population was given a carrying capacity of 182 animals; in addition, the carrying capacity was set to decrease at an annual linear rate of 3.5% for 10 years. This would result in a 35% decrease in carrying capacity to 122 animals after 10 years. The population immediately outside the Park was given a carrying capacity of 87 animals, with this carrying capacity decreasing at an annual linear rate of 2% for 10 years. This would result in a 20% decrease in carrying capacity to 70 animals after 10 years. These reductions in carrying capacity are included to simulate the gradual degradation of squirrel monkey habitat in areas near the Park that are subjected to pressures imposed by human expansion.

Iterations and Years of Projection: Each modelling scenario was iterated 500 times, with population projections extending 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 7.0 software package.

Results from Simulation Modelling

Explanation of Tables and Figures

The numerical results of the simulation models appear in Tables 1 through 9. Each table represents a specified set of coditions, for example, juvenile or adult mortality schedule, addition of inbreeding depresion, etc. Within each table, the results are organized in a nested structure: each population size was run with each level of juvenile and adult female mortality, with and without catastrophes and inbreeding depression.

The headings for the tables are as follows:

r_d: deterministic population growth rate, calculated by Leslie matrix methods from life table data;

r_s (SD): mean and standard deviation of population stochastic growth rate across iterations, calculated from annual variation in population size;

P(E): probability of population extinction over the 100-year time span of the simulation, calculated as the proportion of iterated populations that become extinct within 100 years;

N_{100}(SD): final size of those populations remaining extant after 100 years;

H_{100}: proportion of the original population heterozygosity expected to remain in extant populations after 100 years;

T(E): mean time to extinction of those populations becoming extinct. This value is given only for those scenarios in which at least 10% of the iterated populations went extinct.

Note that VORTEX otput file numbers are given for each scenatio for future reference and retrieval, if necessary.

Figures 1 through 18 are a graphical compilation of the modelling results, attempting to show the relationships between specific factors and their impact on population persistence. Each figure presents results for stochastic growth rate, probability of extinction, or final population size for each of the six population sizes modelled (or four populations in those scenarios including inbreeding depression) as a function of either juvenile or adult mortality. These data are taken directly from the 100-year results presented in the accompanying tables.

Deterministic Simulation Results

The deterministic population growth rates for each scenario, calculated from the life tables using Leslie matrix algorithms, are presented in the fifth column of Tables 1-8. These calculations assume that birth and death rates are constant (no annual variations nor stochastic fluctuations), there is no limitation of mates, and inbreeding has no impact on fecundity or viability. Note that mortality and the inclusion/exclusion of catastrophes are the variables that affect these deterministic rates. Therefore, the long-term rate of population growth, in the absence of stochastoc variation, is independent of population size.

Our baseline modelling scenario (File #201), with 25% juvenile and 10% adult female mortality, results in a population with greater than 4% annual growth (r_d = 0.042, λ = 1.043: Table 1). As juvenile is increased to 31%, the deterministic growth rate is reduced by almost 36% to 0.027 (File #205). Similarly, decreasing juvenile mortality to 19% leads to a 36% increase in deterministic growth (r_d = 0.057, λ = 1.058: File #202). If adult female mortality is increased to 16%, the deterministic growth rate is reduced 71% to r_d = 0.012. Under conditions of low adult mortality, the population is capable of about 7% annual growth over the long term (r_d = 0.071, λ = 1.074: File #206).

These data indicate that, with respect to deterministic growth, a 1% incremental change in juvenile female mortality results in a change in r_d of 0.0025. However, the same degree of incremental change in adult female mortality leads to a change in r_d of 0.0049. In other words, deterministic population growth in this species is nearly twice as sensitive to adult female mortality compared to juvenile female mortality.

If catastrophes are removed from the models, deterministic growth increases by as much as 50% (depending on the level of mortality) compared to the scenarios just described (Table 4). Under our baseline modelling scenario in the absence of catastrophes (File #291), the population could realize nearly 5.5% annual deterministic growth. The enhanced sensitivity of the population to adult mortality remains in these non-catastrophe scenarios.

Stochastic Simulation Results

Calculations of population growth rates from average birth and death rates in a life table will overestimate long-term population growth if there are fluctuations in demographic parameters for any reason, even random sampling variance. Furthermore, this overestimate will be more severe as mortality increases and populations become smaller. The inclusion of these random forces in the population modelling process results in stochastic growth rates that are, in every case, lower than the deterministic growth rates calculated from the mean life table parameters. While this reduction is indeed relatively small under conditions of lower female mortality (i.e., File #206), the stochastic growth rate is reduced by as much as 50% when adult mortality is high, even when population size is relativey large (File #209; Table 1). The influence of stochastic factors on persistence of small populations is quite pronounced. Stochastic growth rates can become negative despite positive long-term deterministic growth rates (i.e., File #245; Table 3).

In all population sizes modelled, increasing both juvenile and adult female mortality led to an increase in the probability of extinction and a reduction in both the final population size and the proportion of population heterozygosity retained (Figures 3-6). As in the case of deterministic growth rates, adult mortality has a greater influence in determining the probability of population extinction and final population size than does juvenile mortality.

The interaction between mortality and population persistence is strongly dependent on the size of the modelled population. Risk of extinction under baseline conditions and higher population size was zero (File #201; Table 1), and increased to 3.4% under conditions of high adult mortality (File #209). Probability of extinction for populations of 50 individuals, under baseline mortality levels, increases to 13.6%; this risk increases to 50% for populations of size 25 (Files #237 and #246, respectively). Note that this risk of extinction is present despite positive mean stochastic growth potential of about 2% annually (r_s = 0.019; File #246). The interaction of low population size and higher female mortality, both juvenile and adult, leads to considerable risk of extinction (e.g., Files #245 and #254). The average time to population extinction for many of these scenarios is approximately 60 years.

If the influences of catastrophes are removed from the modelled populations, the stability of most of the populations is considerably increased (Tables 4-6, Figures 7-12). All stochastic growth rates are positive, and the variation about these mean rates is reduced compared to those scenarios incorporating catastrophes. The influence of female mortality on population growth is, however, still evident. The reduced variation in mean growth rate leads to a reduced risk of population extinction in all scenarios. In fact, populations of at least 100 individuals are immune from extinction risk under these conditions, with final population sizes stabilizing very near to carrying capacity. Very small populations (i.e., no more than 50 animals) remain susceptible to extinction even in the absence of catastrophes, although the risk is sharply reduced (compare Files #336 (Table 6) and #201 (Table 3)).

The deleterious effects of inbreeding in smaller populations of squirrel monkey can have a dramatic impact on population viability (Tables 7 and 8, Figures 13-18). 60-65% of the stochastic growth rates in scenarios including inbreeding depression are negative. In addition, all populations had at least some risk of extinction. Under baseline modelling conditions, extinction risk ranged from 17% (K = 100: File #255) to 100% (K = 25: File #282). Regardless of the level of juvenile or adult female mortality, very small populations (K = 25) are almost certain to become extinct within 50-55 years (Table 8). Larger populations have a lower (although still substantial) risk of extinction under these conditions, but final population sizes after 100 years are considerably below carrying capacity in all but the most optimistic mortality conditions.

<u>Metapopulation Scenario Results</u>

All three populations modelled in the metapopulation scenario show considerable positive stochastic growth, ranging from 0.030 to 0.071. Final population sizes for each population were just below carrying capacity. The smallest population, that immediately outside the Park, was the only population to have a non-zero risk of extinction (P(E) = 0.016); migration was insufficient to recolonize the population once extinction occurred.

The metapopulation as a whole exhibited a stochastic growth rate of 0.0479. There was no risk of metapopulation extinction over the time span of the simulation, and the final population size was 427 animals, over 86% of the combined metapopulation carrying capacity after 100 years (taking into account the reduction in K in those populations outside the Park). Overall, this metapopulation structure appears very stable, with the potential to support nearly 500 squirrel monkeys under suitable management strategies.

Summary and Recommendations

The following concluding summary remarks and recommendations can be made based on the simulation results discussed above:

1. Squirrel monkey populations in Costa Rica, under the conditions modelled using VORTEX, are most sensitive to adult female mortality with respect to stochastic

population growth and risk of extinction.

2. Population size is a major determining factor in persistence of squirrel monkeys in Costa Rica. Populations of less than 100 individuals show considerable demographic instability and extinction risk. Over the time spans modelled in these scenarios, populations of less than 50 animals are generally inviable.

3. Catastrophes, such as disease epidemic and hurricanes, are important factors influencing the viability of squirrel monkey populations. These effects are most pronounced in smaller populations, where substantial risk of extinction may be evident despite positive mean stochastic growth rates. The re-appearence of yellow fever in Costa Rica makes it very important that squirrel monkey populations be routinely monitored for the presence of this disease.

4. The deleterious effects of inbreeding greatly increase the risk of extinction in all populations studied. Populations must remain relatively large for inbreeding to be kept to a minimum. Research on captive squirrel monkeys (e.g., *S. sciurus*) can make valuable contributions to our understanding of the nature and severity of the genetic load present in the Costa Rican subspecies.

5. Given the sensitivity shown by squirrel monkey populations to changes in female mortality, research should be undertaken to evaluate this parameter in natural populations near Manuel Antonio National Park. Following a set of 30-40 radio-collared females for at least 1 year, and preferably 3-4 years, can yield a wealth of information on the demographics of squirrel monkey troops. Additionally, these research techniques would give information on natality, juvenile mortality, and perhaps even the dynamics of migration between metapopulation patches.

PRIORIDADES DE INVESTIGACION

Investigación prioritaria

1. Demografía, con énfasis en la mortalidad y migración dentro y fuera del parque

Otra investigación importante:

2. Requerimientos de habitat

3. Uso y movimiento en el habitat

4. Hacer mapa de información geográfica

5. Evaluar el impacto de las actividades humanas en las áreas fuera del parque

6. Determinar el tamaño mínimo de población viable (MVP)

7. Verificar la situación actual de las poblaciones aisladas identificadas por J. Arauz (tamaño del grupo, habitat, disponibilidad de alimento, posibilidades de migración)

8. Determinar la tasa de migración entre las diferentes tropas y poblaciones

9. Evaluar la condición sanitaria de las poblaciones. En caso de necesidad de translocación de poblaciones pequeñas, dar prioridad en la determinación de sus enfermedades para saber si se puede realizar la translocación

10. Analizar la situación genética de las diferentes poblaciones del mono titi, de ser posible incluyendo también a las poblaciones de Corcovado para verificar su situación taxonómica e implementar las debidas acciones de conservación que los resultados arrojen.

11. Analizar la situación de las poblaciones de esta subespecie presentes en el área de Conservación Osa. Incluir dichas poblaciones en el plan de conservación de S. o. citrinellus.

12. Determinar las características de comportamiento de la especie, en particular las de comportamiento reproductivo.

RECOMENDACIONES DE MANEJO

Recomendación prioritaria:

1. Centrar el uso de recursos financieros y humanos y las acciones de manejo en la población de Manuel Antonio y Quepos, al tener esta una mayor probabilidad de sobrevivencia al menor costo. Esto incluiría: (a) consolidar la adquisición de tierras en el actual Parque Nacional, (b) la ampliación de este hacia el sur, y (c) el manejo de la población exterior al Parque en Manuel Antonio y Quepos

Otras recomendaciones importantes:

2. Elaborar un plan de manejo para el área fuera del parque

3. Elaborar un plan para que los guardaparques en sus recorridos por el parque colecten información sobre las tropas de los monos titi (No. de individuos según sexo y edad, movimientos entre tropas).

4. Si existen tropas de tamaño menor a 25 individuos, se intentara en primera instancia comunicarlas con tropas vecinas. De no existir estas, se trasladarían a un área adecuada

donde no existan otras poblaciones de la misma especie y se buscara adjuntarlas con otras micropoblaciones que se encuentren en la misma situación. Esta seria una alternativa de conservación e investigación siempre preferible a la cría en cautiverio.

5. Desarrollar actividades de educación ambiental a nivel nacional y local para tratar de reducir la mortalidad de infantes y hembras adultas en la zona de Quepos y Punta Quepos, debida principalmente a la captura de animales (pues normalmente se mata a la madre para poder capturar al infante y venderlo como mascota).

6. Revisar periódicamente (anualmente) los valores incluidos en este modelo de simulación.

INVESTIGATION PRIORITIES

High-priority Investigation

1. Demography with emphasis on mortality - especially of adult females - and migration into and outside of the park

Other important investigations

2. Habitat requirements.

3. Use and movements in the habitat

4. Make map of geographic distribution information.

5. Evaluate the impact of the human activities in the areas of the park

6. Determine the minimum viable popualtion size (MVP).

7. Verify the current situation of the isolated populations identified by J. Arauz (size of the group, habitat, availability of food, possibilities of migration)
   Determine the rate of migration between the different troops and populations

8. Evaluate the health condition of the populations. In the event of need of translocation of small populations, give priority in the determination of their diseases to know if the translocation can be done safely.

9. Analyze the genetic situation of the different populations of the titi, including comparison to the populations of Humpback subspecies to verify their taxonomic situation and to implement the appropriate conservation actions that the results indicate.

10. Analyze the situation of the poblations of this subspecies present in the area of Conservation Dares. Include said populations in the conservation plan of *S. o. citrinellus.*

11. Determine the characteristics of behavior of the subspecies, in particular reproductive behavior.

MANAGEMENT RECCOMENDATIONS

High-priority Reccomendation:

1. Center the use of financial and human resources and the management actions on the population in Manuel Antonio and Fit, upon having this a greater probability of survival to the smaller cost. This includes: (a) to consolidate the aquisition of lands in the current national park, (b) the expanion of the Park southward, and (c) the managing of the population foreign to the park in + +Manuel Antonio and Fit.

Other important recommendations:

2. Elaborate a managing plan for the area would be of the park

3. Elaborate a plan so that the park guards in their tours of the park collect information on the troops of the titi monkeys (Number of individuals by sex and age and movements between troops).

4. If exist of group smaller than 25 individuals attempt first to connect them with neighboring troops. If not posible, then evaluate translocation to an adequate area adequate where there no other populations of the same subspecies and combine them with other micropopulations that are found in the same situation. This series of alternatives for conservation and investigation should be given priority to placing in captivity.

5. Develop activities of education environmental at domestic level and local to reduce infant mortality and female adult in the zone of Quepos and Punta Quepos due mainly to the animalscapture (since normally the mother is killed to capture to the infant and to sell it as pet).

6. Check annually the values included in this model of simulation.

Sample VORTEX Input File

```
SAIM201.OUT     ***Output Filename***
Y     ***Graphing Files?***
N     ***Each Iteration?***
Y     ***Screen display of graphs?***
500     ***Simulations***
100     ***Years***
10     ***Reporting Interval***
1     ***Populations***
N     ***Inbreeding Depression?***
Y     ***EV correlation?***
2     ***Types Of Catastrophes***
P     ***Monogamous, Polygynous, or Hermaphroditic***
3     ***Female Breeding Age***
4     ***Male Breeding Age***
9     ***Maximum Age***
0.500000     ***Sex Ratio***
1     ***Maximum Litter Size***
N     ***Density Dependent Breeding?***
10.000000     ***Population 1: Percent Litter Size 0***
90.000000     ***Population 1: Percent Litter Size 1***
10.000000     ***EV--Reproduction***
25.000000     ***Female Mortality At Age 0***
6.000000     ***EV--FemaleMortality***
15.000000     ***Female Mortality At Age 1***
4.000000     ***EV--FemaleMortality***
10.000000     ***Female Mortality At Age 2***
3.000000     ***EV--FemaleMortality***
10.000000     ***Adult Female Mortality***
3.000000     ***EV--AdultFemaleMortality***
35.000000     ***Male Mortality At Age 0***
10.000000     ***EV--MaleMortality***
20.000000     ***Male Mortality At Age 1***
6.000000     ***EV--MaleMortality***
20.000000     ***Male Mortality At Age 2***
6.000000     ***EV--MaleMortality***
15.000000     ***Male Mortality At Age 3***
4.000000     ***EV--MaleMortality***
10.000000     ***Adult Male Mortality***
3.000000     ***EV--AdultMaleMortality***
1.600000     ***Probability Of Catastrophe 1***
0.500000     ***Severity--Reproduction***
0.500000     ***Severity--Survival***
1.000000     ***Probability Of Catastrophe 2***
1.000000     ***Severity--Reproduction***
0.750000     ***Severity--Survival***
Y     ***All Males Breeders?***
Y     ***Start At Stable Age Distribution?***
260     ***Initial Population Size***
300     ***K***
0.000000     ***EV--K***
N     ***Trend In K?***
N     ***Harvest?***
N     ***Supplement?***
Y     ***AnotherSimulation?***
```

Títulos de las Figuras

Figura 1. Tasa de crecimiento poblacional estocástico como una función de la mortalidad de hembras juveniles para la serie de tamaños poblacionales utilizados en todos los escenarios modelados. Los símbolos utilizados para delinear los tamaños poblacionales son idénticos en esta y las subsecuentes figuras.

Figura 2. Tasa de crecimiento poblacional estocásticos como una función de la mortalidad de hembras adultas para el grupo de tamaños poblacionales utilizados en todos los escenarios odelados.

Figura 3. Probabilidad de extinción de la población dentro de 100 años como una función de la mortalidad de hembras juveniles para el grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 4. Probabilidad de extinción de la población en 100 años en función de la mortalidad de hembras adultas para el grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 5. Tamaño poblacional final después de 100 años para poblaciones existentes como una función de la mortalidad de hembras juveniles para el grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 6. Tamaño poblacional final después de 100 años para poblaciones existentes como una función de la mortalidad de hembras adultas para el grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 7. Tasa de crecimiento poblacional estocástico como una función de la mortalidad de hembras juveniles luego de la eliminación de las catástrofes al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 8. Tasa de crecimiento poblacional estocástico para una función de la mortalidad de las hembras adultas luego de la eliminación de las catástrofes al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 9. Probabilidad de extinción de la población en 100 años como una función de la mortalidad de hembras juveniles luego de la eliminación de las catástrofes al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 10. Probabilidad de extinción de la población en 100 años como una función de la mortalidad de hembras adultas luego de la eliminación de las catástrofes al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 11. Tamaño poblacional final después de 100 años para las poblaciones existentes como una función de la mortalidad de hembras juveniles luego de la eliminación de las catástrofes al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 12. Tamaño poblacional final después de 100 años para las poblaciones existentes como una función de la mortalidad de hembras adultas luego de la eliminación de catástrofes al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 13. Tasa de crecimiento poblacional estocástico como una función de la mortalidad de hembras juveniles después de agregar la depresión de entrecruzamiento al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 14. Tasa de crecimiento poblacional estocástico como una función de la mortalidad de hembras adultas después de agregar la depresión de entrecruzamiento al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 15. Probabilidad de extinción de la población en 100 años como una función de la mortalidad de hembras juveniles después de agregar la depresión de entrecruzamiento al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 16. Probabilidad de extinción de la población en 100 años como una función de la mortalidad de hembras adultas después de agregar la depresión de entrecruzamiento al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 17. Tamaño poblacional final después de 100 años para las poblaciones existentes como una función de la mortalidad de hembras juveniles después de agregar la depresión de entrecruzamiento al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figura 18. Tamaño poblacional final después de 100 años para las poblaciones existentes como una función de la mortalidad de hembras adultas después de agregar la depresión de entrecruzamiento al grupo de tamaños poblacionales utilizados en todos los escenarios modelados.

Figure Legends

Figure 1. Stochastic population growth rate as a function of juvenile female mortality for the set of population sizes used in all model scenarios. The symbols used to delineate population sizes are identical in this and all subsequent figures.

Figure 2. Stochastic population growth rate as a function of adult female mortality for the set of population sizes used in all model scenarios.

Figure 3. Probability of population extinction within 100 years as a function of juvenile female mortality for the set of population sizes used in all model scenarios.

Figure 4. Probability of population extinction within 100 years as a function of adult female mortality for the set of population sizes used in all model scenarios.

Figure 5. Final population size after 100 years for extant populations as a function of juvenile female mortality for the set of population sizes used in all model scenarios.

Figure 6. Final population size after 100 years for extant populations as a function of adult female mortality for the set of population sizes used in all model scenarios.

Figure 7. Stochastic population growth rate as a function of juvenile female mortality after the elimination of catastrophes for the set of population sizes used in all model scenarios.

Figure 8. Stochastic population growth rate as a function of adult female mortality after the elimination of catastrophes for the set of population sizes used in all model scenarios.

Figure 9. Probability of population extinction within 100 years as a function of juvenile female mortality after the elimination of catastrophes for the set of population sizes used in all model scenarios.

Figure 10. Probability of population extinction within 100 years as a function of adult female mortality after the elimination of catastrophes for the set of population sizes used in all model scenarios.

Figure 11. Final population size after 100 years for extant populations as a function of juvenile female mortality after the elimination of catastrophes for the set of population sizes used in all model scenarios.

Figure 12. Final population size after 100 years for extant populations as a function of adult female mortality after the elimination of catastrophes for the set of population sizes used in all model scenarios.

Figure 13. Stochastic population growth rate as a function of juvenile female mortality after the addition of inbreeding depression for the set of population sizes used in all model scenarios.

Figure 14. Stochastic population growth rate as a function of adult female mortality after the addition of inbreeding depression for the set of population sizes used in all model scenarios.

Figure 15. Probability of population extinction within 100 years as a function of juvenile female mortality after the addition of inbreeding depression for the set of population sizes used in all model scenarios.

Figure 16. Probability of population extinction within 100 years as a function of adult female mortality after the addition of inbreeding depression for the set of population sizes used in all model scenarios.

Figure 17. Final population size after 100 years for extant populations as a function of juvenile female mortality after the addition of inbreeding depression for the set of population sizes used in all model scenarios.

Figure 18. Final population size after 100 years for extant populations as a function of adult female mortality after the addition of inbreeding depression for the set of population sizes used in all model scenarios.

Table 1. Costa Rica squirrel monkey population analysis.

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
201	260 (300)	25	10	.042	.037 (.134)	0.0	262 (60)	0.937	—
202		19	10	.057	.053 (.132)	0.0	274 (51)	0.940	—
203		22	10	.050	.045 (.134)	0.0	266 (60)	0.937	—
204		28	10	.035	.030 (.136)	0.006	246 (70)	0.933	—
205		31	10	.027	.022 (.134)	0.004	234 (78)	0.928	—
206		25	4	.071	.066 (.134)	0.0	281 (44)	0.941	—
207		25	7	.057	.053 (.132)	0.0	271 (55)	0.939	—
208		25	13	.027	.022 (.135)	0.008	234 (78)	0.925	—
209		25	16	.012	.005 (.142)	0.034	185 (93)	0.907	—
210	200 (200)	25	10	.042	.036 (.138)	0.010	171 (43)	0.907	—
211		19	10	.057	.052 (.135)	0.002	180 (36)	0.908	—
212		22	10	.050	.045 (.135)	0.004	178 (37)	0.906	—
213		28	10	.035	.030 (.135)	0.004	170 (44)	0.903	—
214		31	10	.027	.022 (.137)	0.010	155 (52)	0.897	—
215		25	4	.071	.067 (.133)	0.0	186 (29)	0.912	—
216		25	7	.057	.051 (.136)	0.0	181 (38)	0.908	—
217		25	13	.027	.021 (.141)	0.012	153 (53)	0.890	—
218		25	16	.012	.006 (.143)	0.050	126 (58)	0.866	—

Table 2. Costa Rica squirrel monkey population analysis.

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
219	100 (100)	25	10	.042	.035 (.142)	0.016	83 (24)	0.816	—
220		19	10	.057	.049 (.146)	0.022	87 (21)	0.818	—
221		22	10	.050	.042 (.142)	0.014	87 (20)	0.820	—
222		28	10	.035	.027 (.147)	0.036	80 (25)	0.808	—
223		31	10	.027	.019 (.148)	0.060	75 (26)	0.798	—
224		25	4	.071	.065 (.141)	0.010	92 (18)	0.825	—
225		25	7	.057	.050 (.141)	0.002	88 (19)	0.821	—
226		25	13	.027	.017 (.150)	0.092	77 (27)	0.798	—
227		25	16	.012	.000 (.162)	0.218	64 (31)	0.770	65
228	75 (75)	25	10	.042	.035 (.145)	0.036	63 (16)	0.765	—
229		19	10	.057	.049 (.148)	0.016	66 (15)	0.760	—
230		22	10	.050	.042 (.148)	0.038	64 (16)	0.758	—
231		28	10	.035	.025 (.155)	0.080	58 (19)	0.746	—
232		31	10	.027	.018 (.154)	0.116	56 (20)	0.745	64
233		25	4	.071	.064 (.145)	0.010	68 (13)	0.763	—
234		25	7	.057	.049 (.146)	0.014	65 (16)	0.763	—
235		25	13	.027	.016 (.160)	0.144	56 (21)	0.734	69
236		25	16	.012	-.002 (.167)	0.276	45 (23)	0.703	66

Table 3. Costa Rica squirrel monkey population analysis.

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
237	50 (50)	25	10	.042	.030 (.161)	0.136	41 (13)	0.634	64
238		19	10	.057	.046 (.158)	0.064	43 (11)	0.658	—
239		22	10	.050	.039 (.158)	0.076	42 (12)	0.662	—
240		28	10	.035	.021 (.167)	0.198	38 (14)	0.642	65
241		31	10	.027	.012 (.169)	0.282	37 (14)	0.640	63
242		25	4	.071	.063 (.152)	0.032	45 (10)	0.667	—
243		25	7	.057	.045 (.159)	0.080	44 (11)	0.661	—
244		25	13	.027	.013 (.170)	0.266	37 (14)	0.612	63
245		25	16	.012	-.006 (.180)	0.448	31 (15)	0.585	63
246	25 (25)	25	10	.042	.019 (.194)	0.504	19 (7)	0.422	52
247		19	10	.057	.035 (.191)	0.384	20 (6)	0.406	53
248		22	10	.050	.028 (.190)	0.418	19 (6)	0.423	55
249		28	10	.035	.010 (.197)	0.596	18 (7)	0.419	53
250		31	10	.027	-.002 (.209)	0.706	18 (7)	0.405	49
251		25	4	.071	.051 (.186)	0.308	21 (6)	0.437	51
252		25	7	.057	.035 (.192)	0.368	20 (6)	0.402	52
253		25	13	.027	.000 (.207)	0.698	17 (7)	0.417	52
254		25	16	.012	-.015 (.214)	0.792	16 (7)	0.371	47

Table 4. Costa Rica squirrel monkey population analysis. No catastrophes

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
291	260 (300)	25	10	.054	.053 (.080)	0.0	293 (13)	0.948	—
292		19	10	.069	.067 (.080)	0.0	296 (10)	0.946	—
293		22	10	.062	.061 (.080)	0.0	295 (12)	0.948	—
294		28	10	.047	.045 (.082)	0.0	291 (17)	0.949	—
295		31	10	.039	.037 (.083)	0.0	286 (20)	0.949	—
296		25	4	.083	.082 (.079)	0.0	298 (8)	0.947	—
297		25	7	.069	.068 (.080)	0.0	296 (11)	0.947	—
298		25	13	.040	.037 (.083)	0.0	286 (21)	0.948	—
299		25	16	.024	.022 (.086)	0.0	268 (37)	0.944	—
300	200 (200)	25	10	.054	.053 (.083)	0.0	194 (10)	0.922	—
301		19	10	.069	.067 (.083)	0.0	196 (9)	0.921	—
302		22	10	.062	.060 (.082)	0.0	196 (8)	0.922	—
303		28	10	.047	.045 (.085)	0.0	192 (12)	0.923	—
304		31	10	.039	.037 (.085)	0.0	190 (15)	0.924	—
305		25	4	.083	.082 (.081)	0.0	198 (6)	0.920	—
306		25	7	.069	.067 (.082)	0.0	196 (9)	0.922	—
307		25	13	.040	.038 (.085)	0.0	190 (16)	0.923	—
308		25	16	.024	.022 (.089)	0.0	177 (28)	0.917	—

Table 5. Costa Rica squirrel monkey population analysis. No catastrophes

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
309	100 (100)	25	10	.054	.052 (.090)	0.0	96 (7)	0.848	—
310		19	10	.069	.067 (.090)	0.0	98 (5)	0.844	—
311		22	10	.062	.059 (.091)	0.0	97 (6)	0.847	—
312		28	10	.047	.044 (.093)	0.0	94 (9)	0.846	—
313		31	10	.039	.036 (.094)	0.0	93 (11)	0.850	—
314		25	4	.083	.081 (.088)	0.0	99 (5)	0.842	—
315		25	7	.069	.066 (.090)	0.0	98 (5)	0.845	—
316		25	13	.040	.036 (.094)	0.0	93 (11)	0.844	—
317		25	16	.024	.020 (.099)	0.004	84 (18)	0.836	—
318	75 (75)	25	10	.054	.050 (.096)	0.0	72 (6)	0.802	—
319		19	10	.069	.065 (.095)	0.0	73 (5)	0.796	—
320		22	10	.062	.058 (.095)	0.0	72 (6)	0.795	—
321		28	10	.047	.043 (.098)	0.0	70 (8)	0.798	—
322		31	10	.039	.036 (.099)	0.0	68 (11)	0.796	—
323		25	4	.083	.080 (.093)	0.0	74 (4)	0.797	—
324		25	7	.069	.066 (.094)	0.0	73 (5)	0.798	—
325		25	13	.040	.035 (.099)	0.002	67 (11)	0.797	—
326		25	16	.024	.019 (.107)	0.036	61 (17)	0.774	—

Table 6. Costa Rica squirrel monkey population analysis. No catastrophes

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
327	50 (50)	25	10	.054	.050 (.106)	0.0	47 (5)	0.706	—
328		19	10	.069	.063 (.104)	0.0	48 (4)	0.691	—
329		22	10	.062	.056 (.105)	0.0	47 (6)	0.701	—
330		28	10	.047	.041 (.109)	0.004	45 (7)	0.708	—
331		31	10	.039	.034 (.111)	0.010	44 (8)	0.705	—
332		25	4	.083	.079 (.102)	0.0	49 (3)	0.711	—
333		25	7	.069	.064 (.104)	0.0	48 (4)	0.708	—
334		25	13	.040	.033 (.112)	0.024	44 (8)	0.688	—
335		25	16	.024	.016 (.123)	0.090	38 (12)	0.659	68
336	25 (25)	25	10	.054	.040 (.142)	0.154	21 (5)	0.445	55
337		19	10	.069	.057 (.137)	0.078	22 (4)	0.449	—
338		22	10	.062	.047 (.139)	0.118	22 (5)	0.453	60
339		28	10	.047	.031 (.148)	0.248	20 (6)	0.443	64
340		31	10	.039	.024 (.150)	0.294	20 (6)	0.456	60
341		25	4	.083	.071 (.131)	0.028	23 (4)	0.469	—
342		25	7	.069	.056 (.135)	0.066	22 (4)	0.472	—
343		25	13	.040	.021 (.156)	0.352	19 (6)	0.439	59
344		25	16	.024	.005 (.164)	0.512	17 (7)	0.404	57

Table 7. Costa Rica squirrel monkey population analysis. Addition of inbreeding depression: heterosis model, 3.14 lethal equivalents.

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
255	100 (100)	25	10	.042	.009 (.153)	0.170	55 (31)	0.787	80
256		19	10	.057	.023 (.151)	0.086	66 (31)	0.794	—
257		22	10	.050	.017 (.149)	0.100	63 (32)	0.795	77
258		28	10	.035	.000 (.158)	0.234	46 (30)	0.773	79
259		31	10	.027	-.009 (.161)	0.336	42 (29)	0.772	76
260		25	4	.071	.042 (.141)	0.018	80 (25)	0.823	—
261		25	7	.057	.027 (.145)	0.052	71 (28)	0.809	—
262		25	13	.027	-.009 (.160)	0.310	37 (28)	0.757	76
263		25	16	.012	-.028 (.175)	0.638	28 (24)	0.733	74
264	75 (75)	25	10	.042	.000 (.164)	0.322	34 (22)	0.726	76
265		19	10	.057	.014 (.158)	0.198	44 (23)	0.750	80
266		22	10	.050	.008 (.158)	0.246	39 (22)	0.738	77
267		28	10	.035	-.011 (.174)	0.490	30 (21)	0.721	76
268		31	10	.027	-.016 (.172)	0.530	27 (20)	0.716	72
269		25	4	.071	.034 (.149)	0.078	54 (21)	0.764	—
270		25	7	.057	.018 (.154)	0.148	45 (23)	0.747	79
271		25	13	.027	-.020 (.176)	0.596	23 (19)	0.686	73
272		25	16	.012	-.036 (.189)	0.834	16 (13)	0.638	74

Table 8. Costa Rica squirrel monkey population analysis. Addition of inbreeding depression: heterosis model, 3.14 lethal equivalents.

		Female Mortality (%)							
File #	N_0 (K)	Juvenile	Adult	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
273	50 (50)	25	10	.042	-.015 (.184)	0.706	15 (11)	0.625	72
274		19	10	.057	-.001 (.176)	0.538	21 (14)	0.638	74
275		22	10	.050	-.008 (.179)	0.608	18 (13)	0.626	72
276		28	10	.035	-.023 (.193)	0.780	16 (13)	0.581	67
277		31	10	.027	-.028 (.193)	0.842	12 (10)	0.610	65
278		25	4	.071	.017 (.167)	0.314	28 (14)	0.657	77
279		25	7	.057	.002 (.172)	0.464	22 (13)	0.641	75
280		25	13	.027	-.030 (.197)	0.866	12 (9)	0.585	65
281		25	16	.012	-.045 (.204)	0.974	9 (6)	0.595	58
282	25 (25)	25	10	.042	-.032 (.220)	1.0	—	—	47
283		19	10	.057	-.022 (.216)	0.990	6 (4)	0.255	52
284		22	10	.050	-.027 (.219)	0.998	3 (0)	0.500	50
285		28	10	.035	-.034 (.218)	1.0	—	—	46
286		31	10	.027	-.042 (.227)	1.0	—	—	42
287		25	4	.071	-.010 (.211)	0.964	8 (4)	0.376	58
288		25	7	.057	-.020 (.212)	0.984	8 (5)	0.346	53
289		25	13	.027	-.042 (.219)	1.0	—	—	42
290		25	16	.012	-.053 (.229)	1.0	—	—	37

Figure 1.
Juvenile Female Mortality and Population Growth

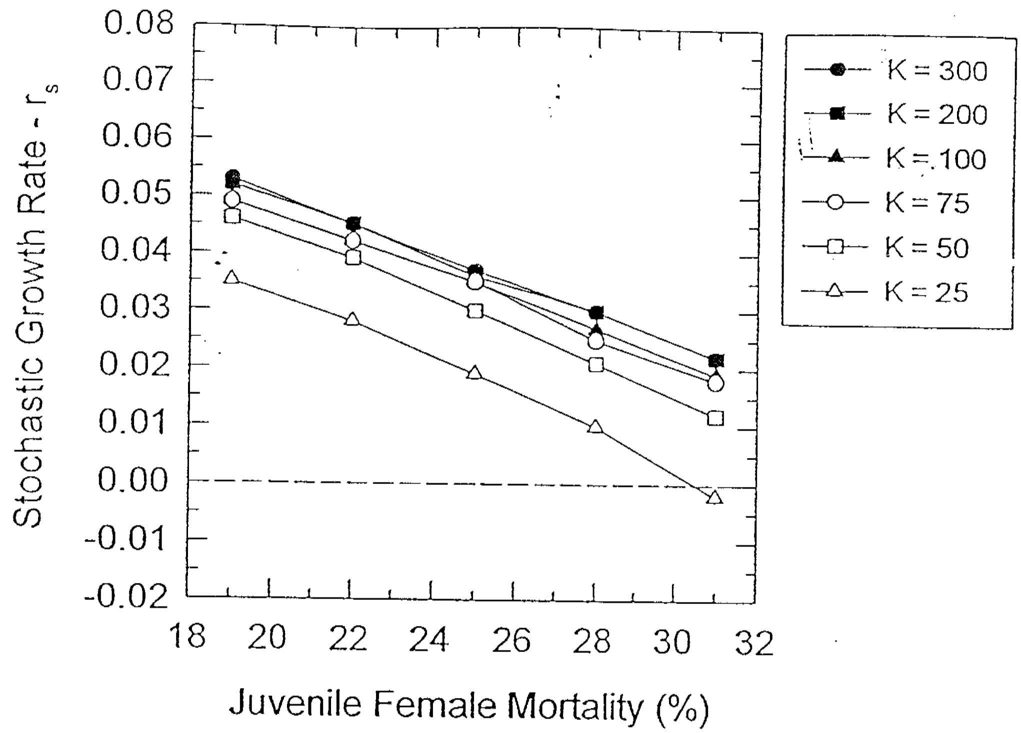


Figure 2.
Adult Female Mortality and Population Growth

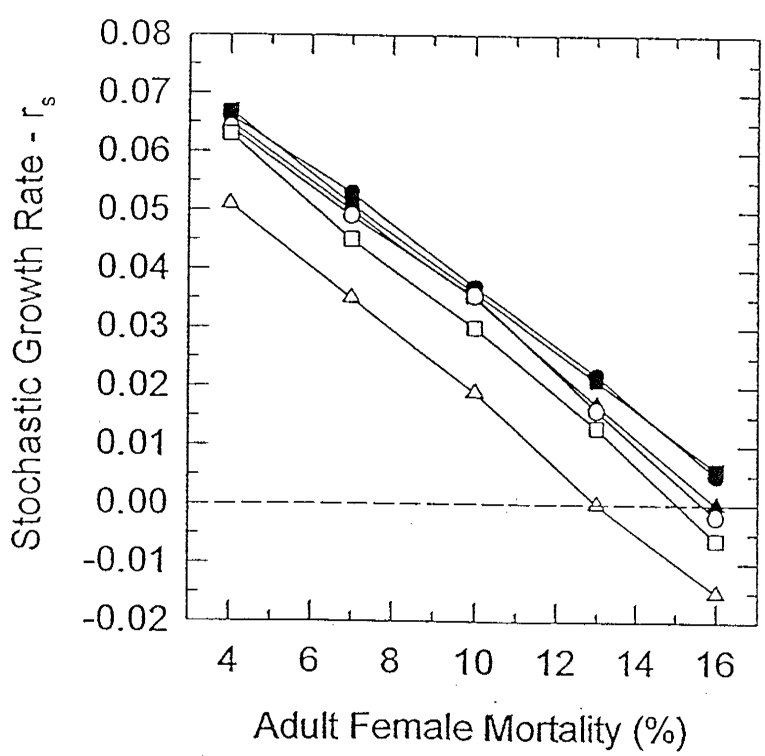


Figure 3.
Juvenile Female Mortality and Extinction Probability

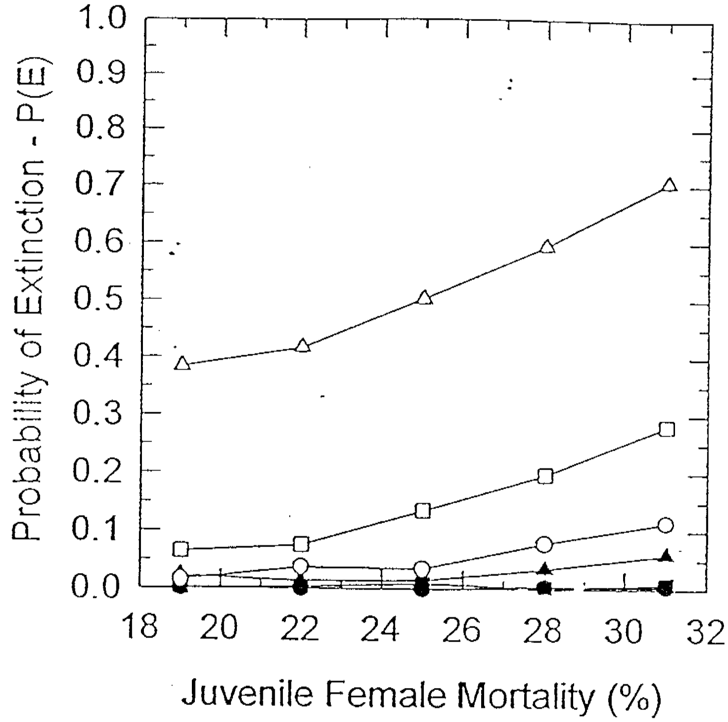


Figure 4.
Adult Female Mortality and Extinction Probability

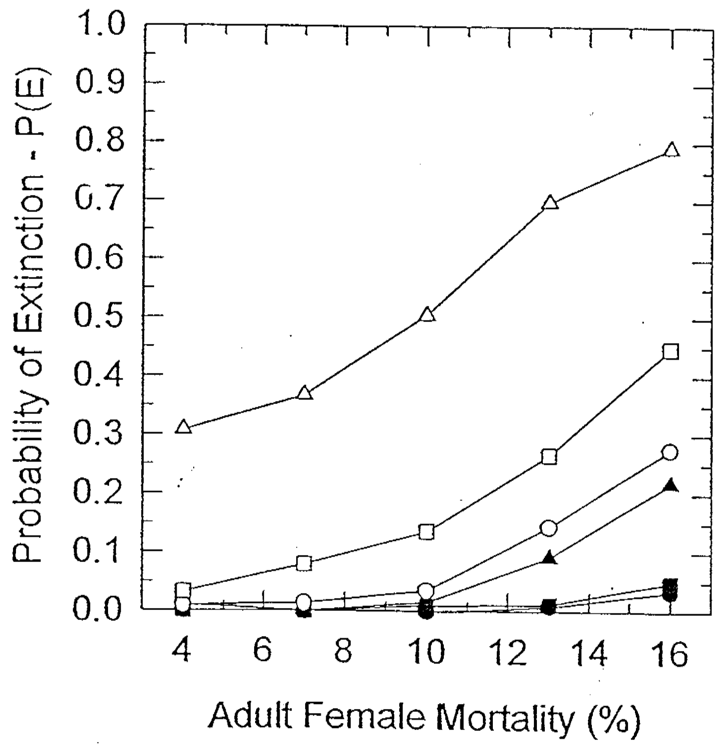


Figure 5.
Juvenile Female Mortality and Final Population Size

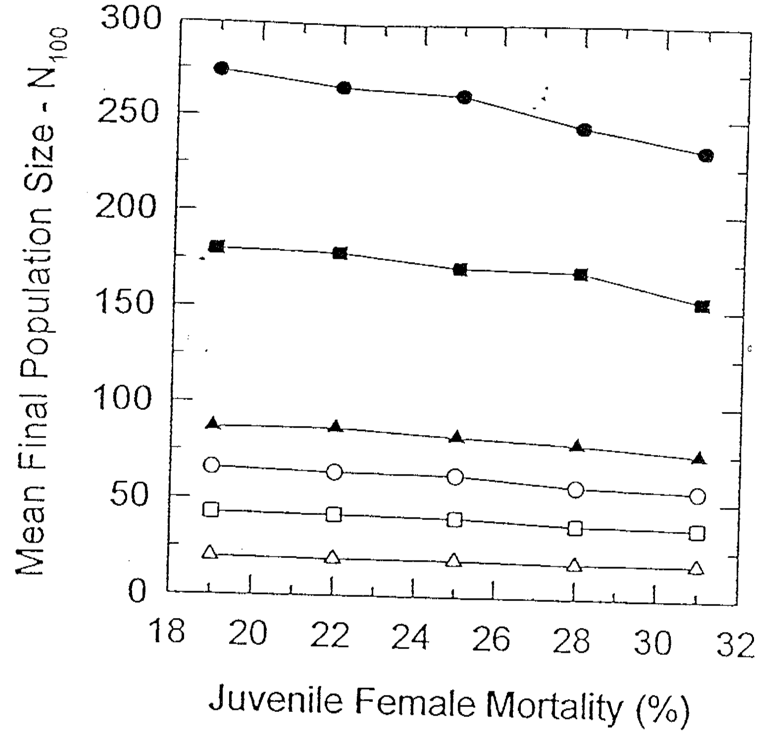


Figure 6.
Adult Female Mortality and Final Population Size

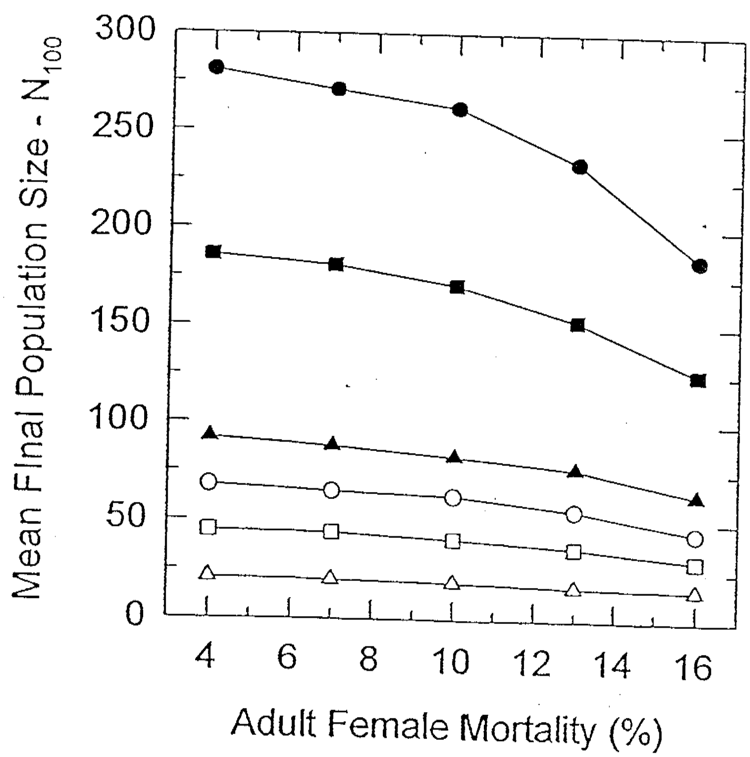


Figure 7.
Juvenile Female Mortality and Population Growth: No Catastrophes

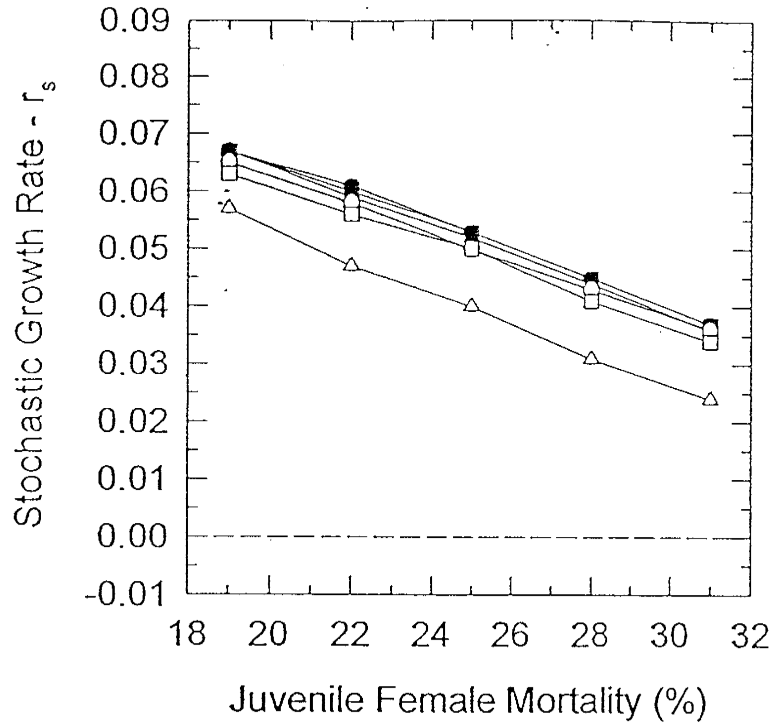


Figure 8.
Adult Female Mortality and Population Growth: No Catastrophes

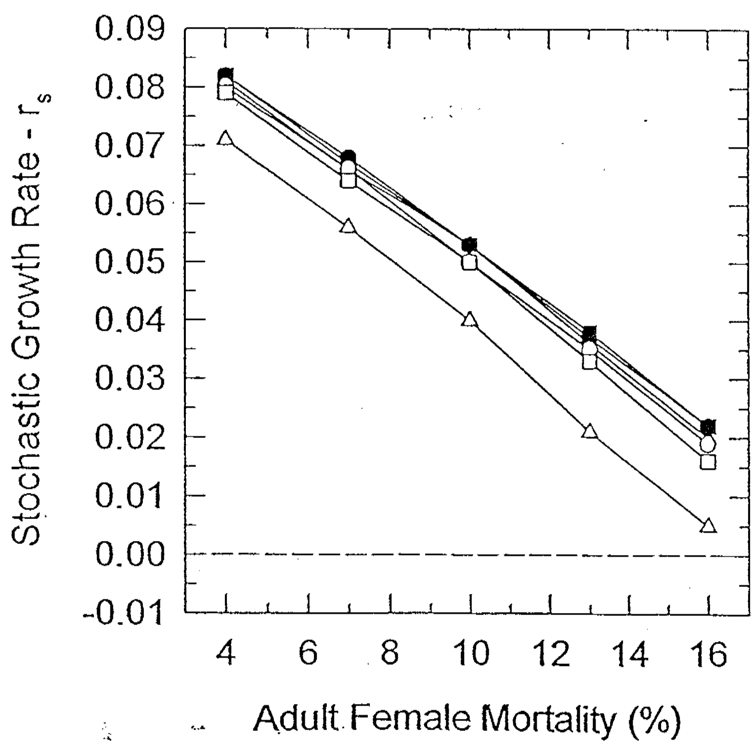


Figure 9.
Juvenile Female Mortality and Extinction Probability: No Catastrophes

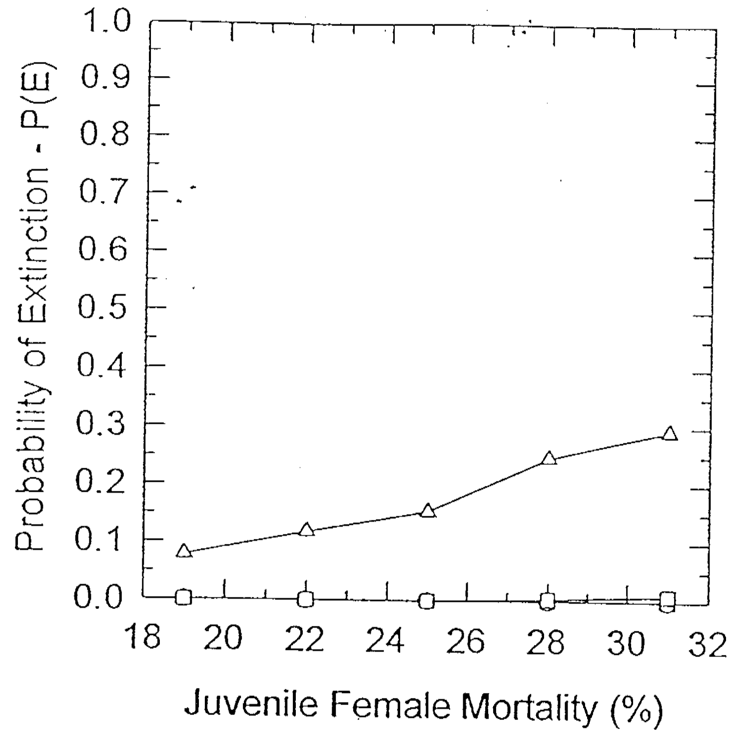


Figure 10.
Adult Female Mortality and Extinction Probability: No Catastrophes

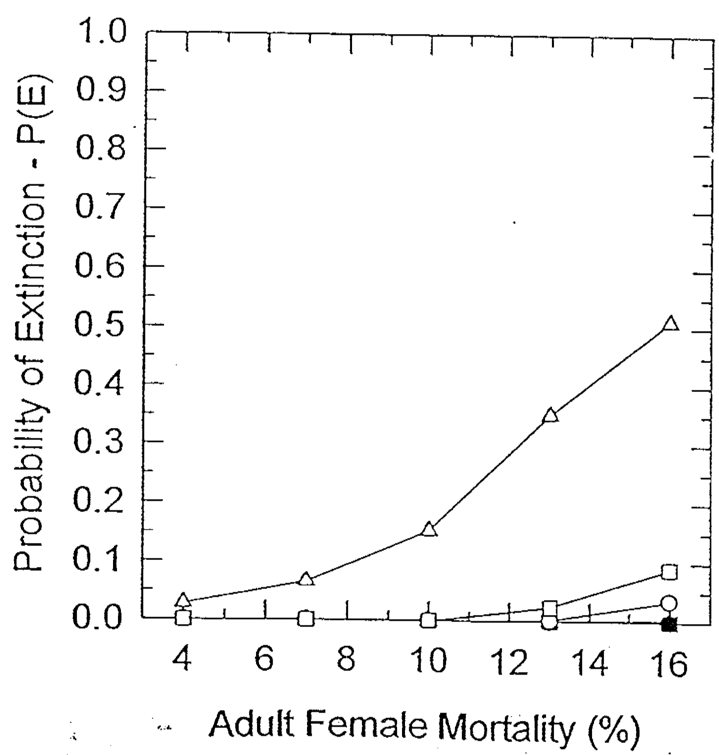


Figure 11.
Juvenile Female Mortality and Final Population Size: No Catastrophes

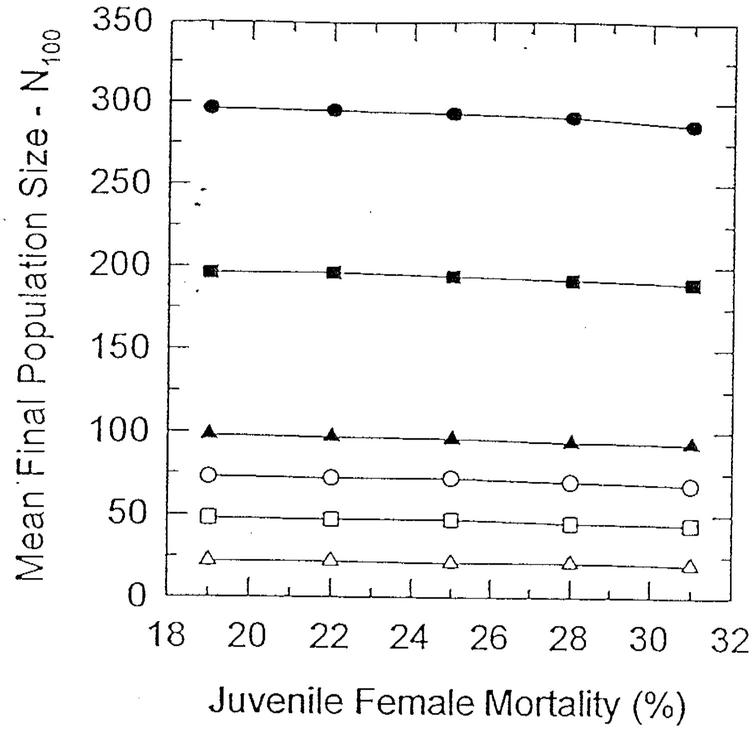


Figure 12.
Adult Female Mortality and Final Population Size: No Catastrophes

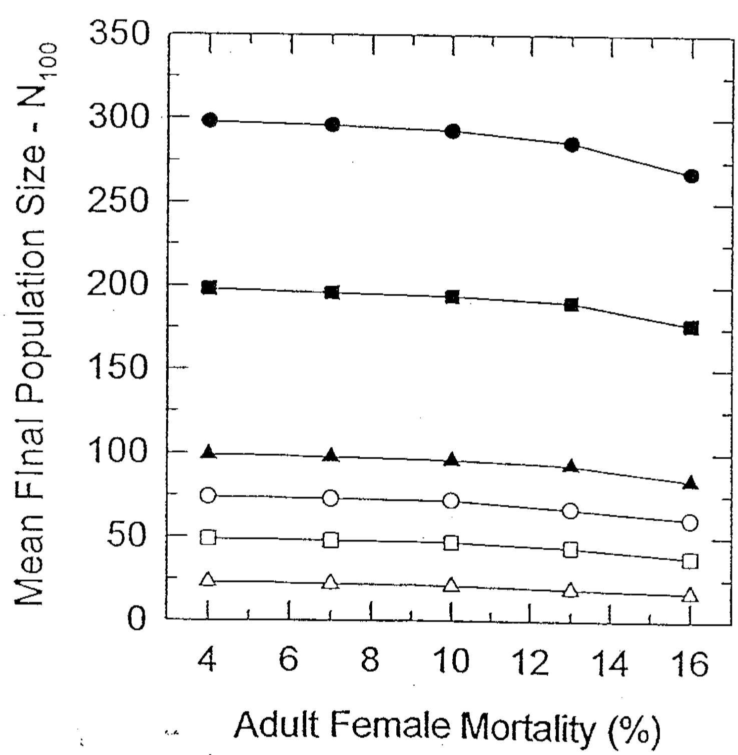


Figure 13.
Juvenile Female Mortality and Population Growth: Inbreeding Depression

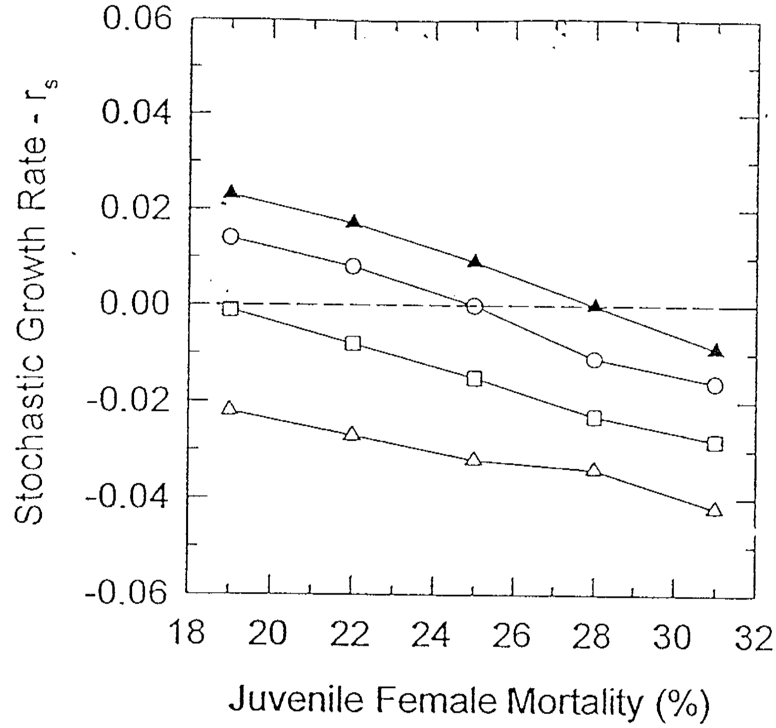


Figure 14.
Adult Female Mortality and Population Growth: Inbreeding Depression

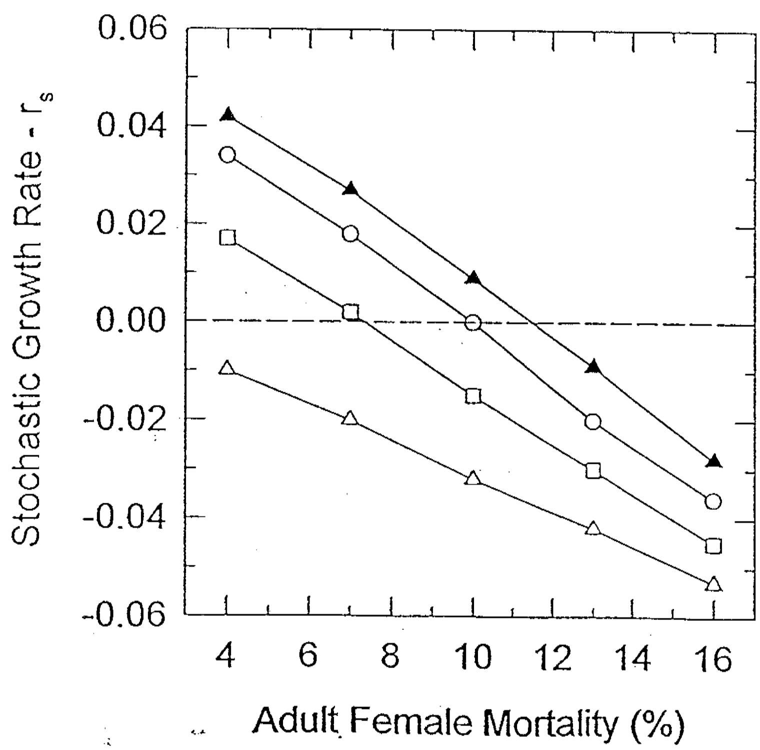


Figure 15.
Juvenile Female Mortality and Extinction Probability: Inbreeding Depression

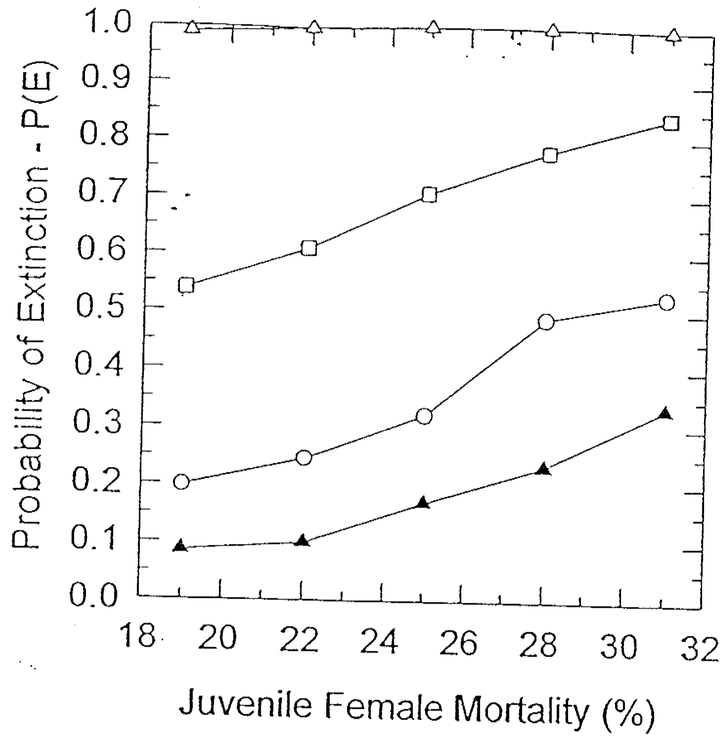


Figure 16.
Adult Female Mortality and Extinction Probability: Inbreeding Depression

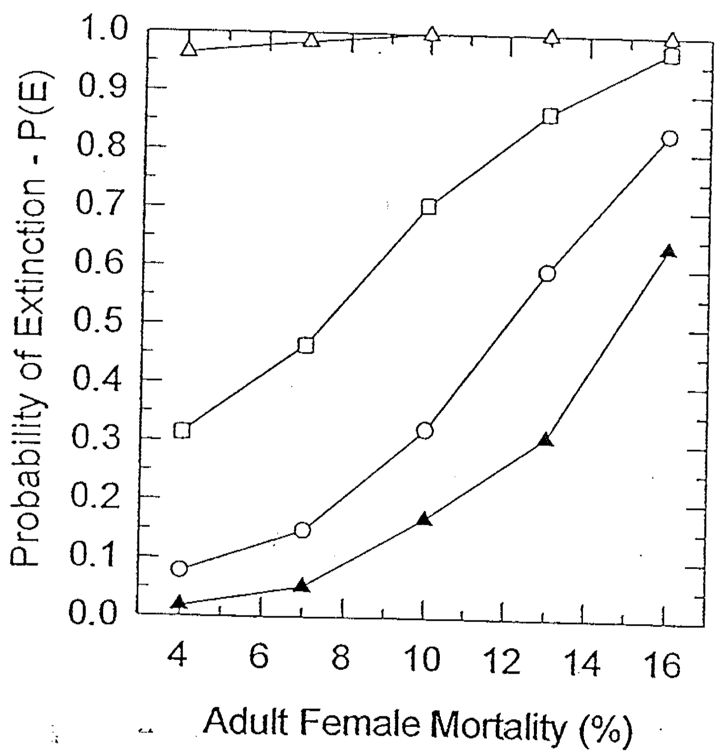


Figure 17.
Juvenile Female Mortality and Final Population Size: Inbreeding Depression

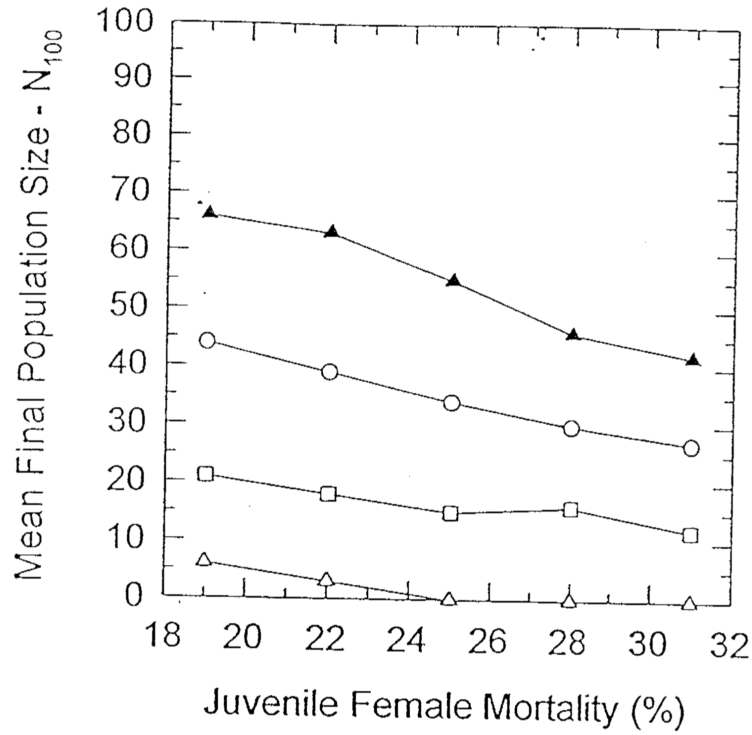
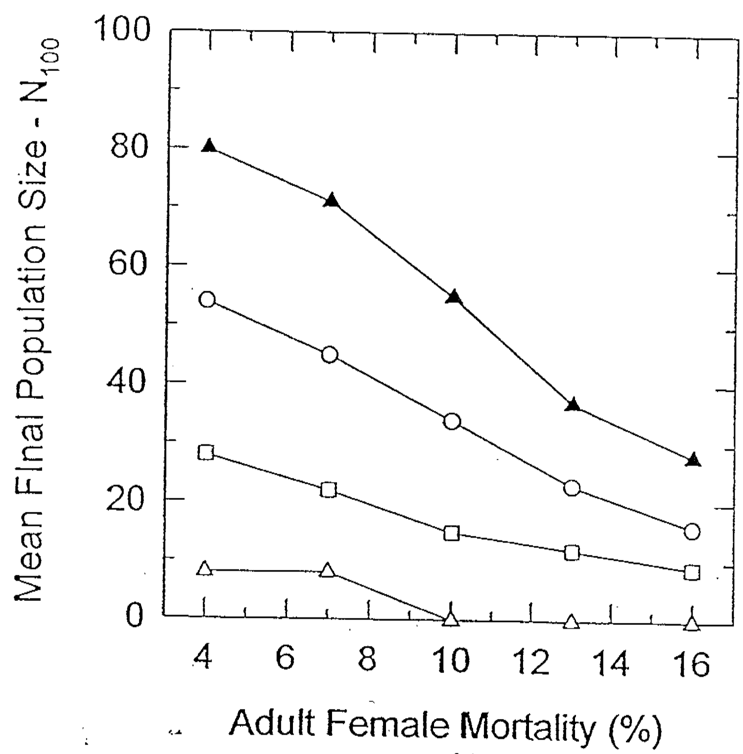


Figure 18.
Adult Female Mortality and Final Population Size: Inbreeding Depression



TALLER DE EVALUACION DE VIABILIDAD DE POBLACIÓN Y HABITAT DE *Saimiri oerstedi citrinellus*

POPULATION AND HABITAT VIABILITY ASSESSMENT WORKSHOP FOR
Saimiri oerstedi citrinellus

FINAL REPORT

Parque Nacional Manuel Antonio
Manuel Antonio National Park

Costa Rica

4-7 Junio 1995

Sección 3

Distribución y Amenazas

Subpopulation Distribution and Local Threats

DISTRIBUCION ACTUAL Y MANEJO DEL HABITAT PARA EL MONO TITI.

Revisar cual fue la distribución histórica de la subespecie

De acuerdo con la información suministrada por Arauz (1993) y la extractada de las memorias del Taller de Evaluación de viabilidad de población y habitat de Saimiri oerstedi realizado en junio de 1994, se sabe que la distribución histórica de la especie era desde Herradura hasta el Río Grande de Térraba, con una variación altitudinal entre los 0 y 500 m.s.n.m.

Revisar la distribución actual de la subespecie en Costa Rica

La distribución actual comprende la misma zona pero esta se encuentra muy fraccionada y el Parque Manuel Antonio es la única área protegida. Los limites de la distribución actual son: al noroeste Río la Gloria a inmediaciones de la Quebrada Amarilla y hacia el sur los manglares ubicados en las inmediaciones de Coronado y el Río Grande de Térraba. La ubicaciones fuera del Parque son 26 sitios con grupos de monos titi; siete son zonas de manglar, tres plantaciones de palma africana rodeadas de vegetación secundaria y 16 representados por parches boscosos compuestos por una mezcla de vegetación primaria y vegetación secundaria (Arauz, 1993). De acuerdo con Castelfranco y otros pobladores del área (D. Castelfranco, com.pers. 1994) existen unas cinco subpoblaciones mas que no se mencionan en el trabajo anterior, ademas de las que existen en el Parque.

Con base en la información actual, cuales serían las acciones prioritarias a desarrollar.

A partir de la información existente sobre sitios de conservación propuestos para el Area de Conservación Pacífico Central (Proyecto GRUA, 1995) y de la información sobre ubicación de grupos de la subespecie, se presenta una clasificación de los probables sitios de ampliación del área considerando la presencia de monos en cada una de ellos. En esta área se encuentran propiedades que son del estado y propiedades particulares. Referente a las propiedades particulares hay tres tipos de incentivos que da el MIRENEM para reforestación, regeneración natural para fijación del carbono y protección de bosque natural, que se podrían utilizar para conseguir que algunos particulares protejan parte de sus propiedades para actividades de conservación.

De las áreas en donde se han observado grupos de monos de la subespecie citrinellus, mencionadas anteriormente, solo una de ellas se encuentra bajo protección (Parque Nacional Manuel Antonio), 8 están en planes futuros para protección y 23 sin ningún tipo de protección, de estas ultimas 3 se encuentran dentro de plantaciones de palma africana, 3 en manglares y 17 en parches de bosque.

A corto plazo se recomienda que se continúe con los estudios sobre las poblaciones existentes fuera del área protegida para evaluar su estado actual (poblaciones en peligro, en recuperación, etc.), la cobertura vegetal, requerimientos de habitat, requerimientos alimenticios y otros aspectos relacionados con la subespecie.

Prioridades

A. Protección Actual: Parque Nacional Manuel Antonio

1. Consolidación del Area: legalizar la propiedad de todas las tierras que conforman en Parque.

2. Protección del habitat existente y planteamiento de investigaciones referentes a: monitoreo hacia cambios de habitat con base en los estudios previos de Wong (1991), habitat y distribución de las tropas de *S. oerstedi citrinellus*, seguimiento de la sucesión vegetal, monitoreo de poblaciones, determinación del numero de individuos por tropa.

3. Evaluación del grado de fragmentaron del habitat y del aislamiento de la subespecie, incluye tamaño, tiempo de aislamiento y numero de individuos.

B. Protección futura: Areas fuera del Parque

1. Ampliación del área hacia la Boca del Río Naranjo y la Boca del Río Savegre, y zonas de propiedades privadas (incentivos).

2. Planteamiento de investigaciones referentes a: monitoreo de habitat, distribución de las tropas de S. oerstedi citrinellus, seguimiento de la sucesión vegetal, monitoreo de poblaciones, determinación del numero de individuos por tropa.

3. Isla Damas (zona de manglares), evaluar las poblaciones y el habitat del mono titi.

4. Aplicación de las leyes para protección de manglares y de la milla marítima.

5. Establecimiento de corredores biológicos que conecten el parque con las zonas de protección futuras y otras áreas de conservación.

6. Regeneración de terrenos que se encuentran en propiedades privadas a través de los incentivos que se apliquen a cada uno de los casos. El propósito de esta regeneración es mantener la continuidad de la zona de protección.

7. Protección de los cursos de agua.

8. Fomentar el uso de cercas vivas, mayormente con especies que provean cobertura vegetal,

alimento y otros recursos al mono titi.

9. Evaluación del grado de fragmentación del habitat y del aislamiento de la subespecie, incluye tamaño, tiempo de aislamiento y numero de individuos.

C. Areas sin ningún tipo de protección

1. Creación de una base de datos geográfica (realización de un mapa de cobertura y uso actual de la tierra, mapa de comunidades humanas, mapa de ubicación de la subespecie, etc).

2. Verificación de la existencia de la subespecie en estas áreas.

3. Planteamiento de investigaciones referentes a: monitoreo de habitat, distribución de las tropas de S. oerstedi citrinellus, seguimiento de la sucesión vegetal, monitoreo de poblaciones, determinación del número de individuos por tropa.

4. Estudio del efecto de la transformación del habitat de la subespecie en plantaciones de palma.

5. Estudio del efecto de la transformación del habitat de la subespecie en manglares.

6. Evaluación del grado de fragmentación del habitat y del aislamiento de la subespecie, incluye tamaño, tiempo de aislamiento y numero de individuos.

7. Evaluación de otras posibles herramientas que se puedan utilizar en la conservación de la subespecie (p.e. translocación, reintroducción).

D. Siempre partiendo de la idea de que el Parque Nacional Manuel Antonio (Pnma) es el núcleo del Area de Conservación de la subespecie, cuales cree que deberían ser las zonas que deberían estar comunicadas con el PNMA.

Reafirmar la propuesta del proyecto GRUA de la ampliación del Area de Conservación Pacifico Central, que propone la unión de los Santos con Manuel Antonio.

E. Determine cuales parches boscosos fuera del Pnma son los prioritarios para la Conservación de este primate.

Parches boscosos de la región del Río Tulin de acuerdo con las recomendaciones de Arauz (1993), los que potencialmente se pueden conectar entre si, utilizando la vegetación ribereña. Es necesario realizar estudios para determinar el estado actual de estos parches.

F. *Cuales son las acciones a corto y mediano plazo que deben ser trabajadas en este campo.*

Para poder hacer recomendaciones se requiere de generar información que permita la evaluación integral.

1. A corto plazo verificar la distribución actual de la especie con base en la información generada por Arauz (1993), Wong et al (1991) y otros autores.

2. A corto plazo diseño y puesta en marcha del plan de monitoreo de poblaciones y habitat en el PNMA.

3. Inventario de los recursos alimenticios que utiliza el mono titi (especialmente plantas e insectos).

4. A corto plazo acelerar el proceso de consolidación de las áreas de protección en la ACPC.

5. A mediano plazo elaboración de la base de datos geográfica, haciendo énfasis en el grado de fragmentación y aislamiento de las poblaciones del mono titi.

G. *Quienes deberían ser los responsables de ejecutar esas acciones.*

1. Entidades gubernamentales.

2. Gobiernos locales.

3. Universidades.

4. ONG dedicadas a actividades de conservación.

Análisis de la vulnerabilidad de las poblaciones de mono titi que se encuentran fuera del área protegida.

Considerando los 23 grupos no protegidos, se plantea cuales son las acciones necesarias para saber que es lo que hay que hacer con dichos grupos.

Se realizo una clasificación de cada uno de los grupos según su grado de vulnerabilidad teniendo en cuenta los siguientes criterios:

1. Numero de individuos
2. Area del parche
3. Tiempo de aislamiento
4. Grado de aislamiento: teniendo en cuenta las distancias hasta el parche mas cercano y distancias hacia el PNMA.

Como no se dispone de la información (numero de individuos y otros datos) se propone que esto debe ser un punto prioritario a investigar.

Con la información disponible se sabe que hay tres grupos que se ubican en plantaciones de palma africana, tres en zonas de manglar y 17 en parches de bosque. Los resultados obtenidos fueron:

<u>a. Parches de bosque:</u>

Bosque cercanos al Río Tulin: según Arauz (1993) en esta área hay dos subpoblaciones con la probabilidad de encontrar otras y muy cerca de ellas en Gamalotillo y Punta Judas se encuentran otros dos grupos. Estas corresponden a las localidades 1, 3,4 5 mencionadas por Arauz (1993).

Por el tamaño de los parches se sugiere realizar esfuerzos tendientes a lograr la mayor conectividad posible entre ellos y considerar a la zona del Río Tulin como un centro importante para la conservación de la subespecie. Según la caracterización la vulnerabilidad en estos bosques seria considerada como VULNERABILIDAD MEDIA. Esta zona tiene la posibilidad de ser conectada con las áreas propuestas para anexar a la ACPC, a través de la vegetación riberena.

Aunque cercanos al Río Tulin pero aislados se encuentran tres puntos en donde se ha detectado la presencia del mono titi. Estos corresponden con los puntos 2,6 y 7 indicados por Arauz (1993). En esto se plantea la necesidad de una evaluación inmediata del tamaño de los grupos y del tamaño de los parches. Estos son considerados como de VULNERABILIDAD MEDIA, aunque después de efectuados los estudios esta calificación puede variar.

Las localidades 9, 10 y 12 de Arauz (1993), corresponde a áreas en fincas privadas de las cuales la región Surubres (punto 12) se considera la de MAS ALTA VULNERABILIDAD por ser un parche pequeño y el uso potencial para cultivos. Las localidades 9 (La Vasconia) y 10 (El Rey), teniendo en cuenta su cercanía a las áreas de protección propuestas, se consideran de VULNERABILIDAD MEDIA.

La localidad 19 (Arauz, 1993), propiedad privada de Juan Delgado, tiene un grupo muy aislado que aunque el propietario al parecer esta interesado en la conservación, por el tamaño del parche la población esta considerada de ALTA VULNERABILIDAD.

La localidad 25 se encuentra ubicada en la Reserva Privada Ventanas de Osa. Por las características de la zona y sus objetivos se considera como una zona de BAJA VULNERABILIDAD

Las localidades 20, 21, 22a y 22b (Arauz, 1993) ubicadas de 7 a 12 Km al noreste del PNMA, se caracterizan por ser áreas de crecimiento secundario y todas están localizadas en propiedades privadas. Estos puntos se encuentran equidistantes uno del otro a una distancia aproximada a los 3 Km. Los primeros 4 a 6 Km desde el PNMA hasta estos puntos se encuentran ocupados con cultivos de palma africana, lo que demuestra una clara fragmentación del habitat para la especie. Se considera que estas están dentro de una VULNERABILIDAD MEDIA, debido a que estas poblaciones se encuentran dentro del área propuesta dentro del proyecto GRUA (zona con incentivos para conservación). Con base en lo anterior y a que estos grupos se encuentran relativamente cerca uno de otros se propone que sean manejados como un núcleo poblacional; ademas los individuos de estos sitios podrían potencialmente comunicarse con el PNMA mediante la vegetación riberena del Río Naranjo.

b. Manglares

Las localidades en manglar corresponden a los números 8, 26 y 24 (Arauz, 1993). El punto 8 esta localizado en el Estero Zapote; aunque se localiza muy cerca del Refugio de Vida Silvestre de Damas (propuesto), se encuentra aislado por el Río Parrita y en el se da una fuerte presión por turismo, calificándose como una población de ALTA VULNERABILIDAD. Para este se propone evaluar el numero se individuos existentes y su posibilidad de relación con grupos cercanos.

Localidad 26 corresponde a los manglares al sur de Coronado; por el tamaño del área y la ligera explotación de los recursos existentes se considera de VULNERABILIDAD MEDIA.

La localidad 24 corresponde a un pequeño parche de manglar en propiedad privada, con alto potencial turístico, catalogándose como de ALTA VULNERABILIDAD.

c. Cultivos de Palma Africana

Las localidades 15, 16 y 18 (Arauz, 1993) se encuentran ubicadas dentro de cultivos de Palma Africana.

El punto 15 se localiza en la Finca Pocares; las tropas han sido vista en medio de los cultivos de palma. El punto 16 con plantaciones de palma y teca, se encuentra en Finca Cerros y el punto 18 se encuentra en los palmares próximos al basurero de Quepos (Finca Anita). Todas estas se consideran como de VULNERABILIDAD ALTA.

Recomendaciones

1. Realizar una verificación in situ de las localidades en donde se ha detectado la presencia de la subespecie, enfatizando en el numero de tropas e individuos por tropa, el tamaño del parche y características generales.

2. Realizar una base de datos geográfica (mapa de uso y cobertura vegetal) para el área de la distribucion de la subespecie.

3. Diseñar una estrategia para el manejo de los núcleos poblacionales de: Río Tulin, area comprendida entre la Quebrada Sabalo y Llano Grande y el PNMA.

4. Evaluar en forma individual la situación de cada uno de los grupos que se encuentran aislados actualmente. Evaluar los factores que amenazan la estabilidad de esas tropas y tomar decisiones para su supervivencia.

5. Vincular estas recomendaciones con el proyecto GRUAS, dada la importancia que tiene esta subespecie.

6. Que se regule todo tipo de construcción o se controle en aquellas áreas que han sido o van a ser declaradas como corredores biológicos y que la subespecie utiliza en sus desplazamientos.

7. Consolidar el area: legalizar la propiedad de todas las tierras que conforman el PNMA y acelerar el proceso de implemtentación de las nuevas zonas propuestas por GRUA.

8. Tener en cuenta las prioridades propuestas en este documento.

Recomendación Prioritaria: Ampliar la base de datos digital sigpac (sistema de información geográfica del pacifico central), proveniente del proyecto: monitoreo de los recursos forestales Por satélite y manejo integrado de cuencas en Costa Rica (Universidad Nacional, universidad gante y comunidades de Europa) y la investigacion sobre la verificación de la distribución de la especie mediante el uso de gps y otros aspectos como numero de tropas, numero de individuos por tropa, aspectos demograficos de la tropa, preferencia de habitat y habitos alimenticios.

Grupo B: Distribucion actual y manejo del habitat para el Mono Titi.
Jacobo Arauz (Facilitador), Hugo Fernando Lopez (Relator), Leda Castro
Vernon Arias, Wilfredo Segura, Gustavo Vargas, Katia Gorrichategui, Geisel Mora, Belkys Jimenez, Dora Ingrid Rivera.

CURRENT DISTRIBUTION AND MANAGING OF THE HABITAT FOR THE TITI.

Historical Distribution of the Subspecies

According to the information supplied by Arauz (1993) and the summary of the report of the Workshop of Evaluation of viability of Population and Habitat of *Saimiri oerstedi* accomplished in June of 1994, it is known that the historical distribution of the species was from Herradura until the Large River of Terraba, with an altitudinal variation between 0 and 500 meters.

Current Distribution of the Subspecies in Costa Rica

The current distribution corresponds to the same zone but is found very fractioned, and Manuel Antonio National Park is the only area protected. Limits of the current distribution are: to the northwest Rio la Gloria and sorowdings of Quebrada Amarilla and southward the mangroves located near Coronado and the Rio Grande de Terraba. The locations outside the Park are 26 sites with groups of titi monkeys; seven are mangrove zones, three are plantations of African palm sorrounded of secondary vegetation and 16 are represented by forest patches compound by a mixture of primary and secondary vegetation (Arauz, 1993). According to Castelfranco and other habitants of the area (D. Castelfranco, com.pers. 1994) exist five subpopulations more that are not mentioned in the previous work, besides those that exist in the Park.

Based on the Current Information, Which Would Be the High-priority Actions to Develop.

Based on the information existing about sites of conservation proposed for the Central Pacific Conservation Area (Project GRUA, 1995) and on the information of localization of groups of the subespecies, is needed a clasification of the probable sites of enlargement of the area considering the monkeys presence in each one of them. In this area are found statal and particular properties. Referring to the particular properties there are three types of incentives that the MIRENEM gives for reforestation, for natural regeneration and carbon fixation, and protection of natural forest. This might be utilized to obtain that some particular persons protect part of their properties for activities of conservation.

Of the areas in which there have been observed groups of monkeys of the subespecies *citrinellus*, mentioned previously, only one of them is found under protection (National Park Manuel Antonio), 8 are in future plans for protection, and 23 without any type of protection; of these 3 are found within African palm plantations, 3 in swamps and 17 in forest patches.

In the short term is recommended to continue with the studies on the existing populations, to evaluate their current status (populations in danger, in recuperation, etc.), the vegetable coverage, habitat requirements, nutritional requirements and other aspects related to the subespecies.

Priorities

A. Current Protection: National Park Manuel Antonio

1. Consolidation of the Area: to legalize the property of all the lands certified in Park.

2. Protection of the existing habitat and referring investigations position to: a) monitoring habitat changes based on the previous studies of Wong (1991), b) distribution of the troops of *S. oerstedi citrinellus*, c) follow-up of the vegetable succesion, d) monitoring of populations, e) determination of the number of individuals by troop.

3. Evaluation of the degree of fragmentation of the habitat and of the isolation of the subspecies, includes size, isolation time and number of individuals.

B. Future Protection: Areas that Would Be of the Park.

1. Expansion of the area toward the Mouth of the Naranjo River and the Mouth of the River Savegre, and private property zones (incentives).

2. Research: habitat monitoring, distribution of the troops of *S. oerstedi citrinellus*, follow-up of the vegetative succession, monitoring of populations, determination of the number of individuals by troop.

3. Damas Island (mangrove zone), to evaluate the populations and the habitat of the titi.

4. Application of the laws for protetion of mangrove and of the maritime mile.

5. Establish biological corridors that connect the park with the zones of future protection and other areas of conservation.

6. Regeneration of lands that are found in properties deprive to work of the incentives that are applied to each one of the cases. The purpose of this restoration is to maintain the continuity of the zone of proteccion.

7. Protection of the water courses.

8. To encourage the use of live fences, mostly with species that provide vegetable coverage, food and other resources to the titi.

9. Evaluation of the degree of fragmentation of the habitat and of the isolation of the subespecies, includes sizes, isolation time and number of individuals.

C. Areas With No Type of Protection.

1. Creation of a geographic data base (realization of a coverage map and current use of the land, human communities map, map of distribution of the subspecies, etc).

2. Verification of the existence of the subspecies in these areas.

3. Referring research to: habitat monitoring, distribution of the troops of *S. oerstedi citrinellus*, follow-up of the succession vegetable, monitoring of populations, determination of the number of individuals by troop.

4. Study of the effect of the transformation of the habitat of the subspecies in palm plantations.

5. Study of the effect of the transformation of the habitat of the subspecies in mangrove.

6. Evaluation of the degree of fragmentation of the habitat and of the isolation of the subspecies, includes size, isolation time and number of individuals.

7. Evaluation of possible other tools that they could be used in the conservation of the subspecies (i.e. translocation, re-introduction).

Always departing of the idea of the fact that the National Park Manuel Antonio (PNMA) is the nucleus of the conservation area for the subspecies, which believes that they would have to be the zones that they would have to be connected with the PNMA.

To reaffirm the proposal of the project GRUA of the amplification of the Area of Conservation Pacific Central, that proposes the union of the Santos with Manuel Antonio.

E. Determine Which Forest Patches of the PNMA Are the High-priority for the Conservation of this Primate.

According to the recommendations of Arauz (1993), forest patches of the region of the Tulin River potentially can be connected, using the riverine vegetation. It is necessary to determine the current state of these patches.

F. What Are the Actions in the Short to Medium Term That Should Be Worked in this Field.

To be able to do recommendations is required to generate information that permit the integral evaluation.

1. Verify the current distribution based on the information generated by Arauz (1993), Wong et al. (1991) and other authors.

2. Short term design and implementation of the monitoring plan of populations and habitat in the PNMA.

3. Inventory of the nutritional resources that uses the monkey titi (especially plants and insects) .

4. Accelerate the process of consolidation of the areas of protection in the ACPC, in the short term.

5. Develop the geographic data base, emphasizing the degree of fragmentation and isolation of the populations of the titi.

G. Who Would Have to be Responsible for Executing Those Actions?

1. Governmental entities.
2. Local governments.
3. Universities.
4. NGOs devoted to activities of conservation.

Analysis of the Vulnerability of the Populations of the Titi That are Found Outside of the Protected Area.

Considering 23 groups not protected, is outlined what are the necessary actions to take with those groups.

Accomplish a clasification of each one of the isolated groups based on their degree of vulnerability taking into account the following criteria:

1. Number of individuals

2. Area of the patch

3. Isolation time

4. Degree of isolation: taking into account the distances to a neighboring patch and distances from the PNMA.

As is not available this information (on number of individuals and other data) it is proposed that this must be a high-priority point to investigate.

With the information available is known that there are three groups that are located in African palm plantations, three in swamp zones and 17 in forest patches. The obtained results were:

a. Forest patches:

Nearby forest to the River Tulin: according to Arauz (1993) in this area there are two subpopulations with the probability of finding other and near them in Gamalotillo and Punta Judas are found other two groups. Correspond this to the localities 1, 3,4 5 mentioned by Arauz (1993).

Due to size of the patches and is suggested to accomplish tending efforts to achieve as much linkage as possible between them and to consider to the zone of the River Tulin as an important center for the conservation of the subespecies. Acording to caracterization the vulnerability in these forests isconsidered as MEAN VULNERABILITY. This zone has the possibility of be connected with the areas proposad to beannex to the ACPC, through the vegetation near the rivers..

Nearby to the River Tulin but isolated are found three points in which has been detected the presence of the titi. Correspond with the points 2,6 and 7 indicated by Arauz (1993). It is outlined the need of an inmediate evaluation of the size of the groups and of the size of the patches. These are considered as of MEAN VULNERABILITY, though after of effected the studies this calification can vary.

The localities 9, 10 and 12 of Arauz (1993), corresponds to private areas Curubes regions (point 12) is considered HIGH VULNERABILITY being small patch with the potential use for cultivation. The localities 9 (The Vasconia) and 10 (The King), taking into account that they are near the protection areas proposed, are considered of MEAN VULNERABILITY.

The locality 19 (Arauz, 1993), private property of Juan Delgado has very isolated group that though the owner apparently is interested in its conservation, because thesize of the patch the poblation is considerated of HIGH VULNERABILITY.

The locality 25 is found located in the Private Reservation Ventanas de osa, because of thecaracteristics of the zone its objectives is considered as a DECREASE VULNERABILITY zone.

The localities 20, 21, 22a and 22b (Arauz, 1993) located 7 to 12 Km to the northeast of the PNMA, are characterized by secondary growth areas and all are located in private properties. These points are found equidistant one of the other at a distance approximated to 3 Km. The first 4 to 6 Km from the PNMA until these points are found occupy with African palm cultivation, what demonstrates a clear fragmentation of the habitat of the species. It is considered these within a MEAN VULNERABILITY, due to the fact that these populations are found within the area proposed to GRVA proyect (zone with incentives for conservation). Based on the foregoing and to the fact that these groups are relatively near one of others is proposed that they will be handled as a populational nucleus; also the individuals of these sites could potentially be communicated with the PNMA through the riverside vegetation of the Naranjo River.

b. Mangroves

The localities in mangroves correspond to the numbers 8, 26 and 24 (Arauz, 1993). The point 8 is in the Sapot Tideland; although is located near Wild Life Refuge of Damas (proposed), is found isolated by the Parrita River and has a fort presure because of tourism, being qualified as a HIGH VULNERABILITY population. For this is proposed to evaluate the number of existing individuals and theirelationship with nearby groups.

Locality 26 corresponds to the mangroves south of Coronado because the size of the area and the few explotacion of the existing resources is considered of MEAN VULNERABILITY.

The locality 24 corresponds to small mangrove patch in private property, with high turistc potential, being catalogued as HIGH VULNERABILITY.

c. African Palm cultivation

The localities 15, 16 and 18 (Arauz, 1993) are located within African Palm cultivation.

Locality 15 is located in the Property Pocares; the troops have been sight in the middle of the palm cultivation. The point 16 with palm and teak plantations, is found in Hills Property and the point 18 is found in the palm plantation ubicated near to the waistage places (Property Anita).

All these are considered as of HIGH VULNERABILITY.

Recommendations

1. Verify *in situ* the localities in which has been detected the presence of the subespecies emphasizing in the number of troops and individual by troop, the area of the patch and its general characteristics.

2. Develop a geographic data base (map of use and vegetable coverage) for the area of distribution of the subespecies.

3. Develop a strategy for managing the population nucleous of: River Tulin, and the area between the Quebrada Sabalo and Llano Grande and the PNMA.

4. Evaluate individually the situation of each of the groups that are currently isolated. Evaluate the factors that threaten the stability of those troops and take decisions for their survival.

5. Link these recommendations with the GRVAS project, given the importance of this subespecies.

6. Regulate and control all types of construction in those areas that are or might serve as natural corridors between isolated subpopulations.

7. Consolidate the area by legalizing the ownership of all the lands that certify the PNMA and accelerate the process of implemtentacion of the new zones proposed by CRYING.

8. To implement the priorities proposed in this document.

High-priority Recommendation:

Widen the digital data base Sigpac (geographical information system of the Central Pacific) originating from the project: monitoring of the forest resources by satellite and integrated basins managing in rich coast (National University, University Ghent and Europe Communities) and the investigation on the monitoring of the distribution of the species through the use of GPS for precise locations and other aspects such as numbers of troops, numbers of individuals by troop, demographic aspects of the troop, preference of habitat and nutritional habits.

Distribución del SAIMIRI OERSTEDI CITRINELLUS

La distribución original del Saimiri oerstedi citrinellus, según Alfaro (1897) era desde el Cerro Herradura (9°40'N, 84°35'W) y las montañas de Dota (9°37'N, 84°9'W) hasta el río Grande de Térraba (8°25'N, 84°25'W) que se consideraba el límite sur de la distribución. La distribución actual comprende el mismo rango pero está fraccionado, quedando pequeñas poblaciones de esta subespecie. El Parque Nacional Manuel Antonio es el único hábitat protegido.

Dentro del Parque Manuel Antonio existen 6 tropas, mientras que en el área de amortiguamiento existen 8 tropas. Y en el resto de su rango hay 26 tropas que no están en comunicación (Arauz, 1993). Wong (1990) reporta que hay 6 tropas que el parque y 8 afuera del mismo.

Las ubicaciones fuera del Parque de las subpoblaciones de S. oerstedi citrinellus están señaladas por Arauz (1993). El autor localizó 26 sitios con grupos de monos titi. Siete de estas localidades son zonas de manglar, tres son plantaciones de palma africana rodeadas parcialmente por franjas angostas de vegetación secundaria y 16 sitios están representados por parches boscosos compuestos por una mezcla de vegetación primaria y vegetación secundaria en diversos estadíos sucesionales (Arauz, 1993). Sin embargo la información no publicada revela la existencia de por lo menos 4-5 subpoblaciones más (Dario Castelfranco, com. pers., 1994).

Tamaño de Tropa

Bajo condiciones naturales las tropas están formadas por 15-68 individuos siendo el promedio 30 individuos (Wong, 1990). Sin embargo dentro del ámbito de distribución actual, se han reportado grupos que están compuestos por uno a tres individuos que luego han desaparecido de la zona (Arauz 1993).

Según Wong (1990) las tropas dentro de la zona están compuestas por un 36% de hembras adultas, un 27% de infantes, un 25% de juveniles y un 12% de machos adultos. Además aclara que la composición de las tropas existentes dentro y fuera del parque presentaron una tendencia muy similar.

Los porcentajes de natalidad de la zona de Manuel Antonio variaron entre un 57% y un 89%. No hubo diferencia significativa entre las tasas de nacimiento de las tropas residentes dentro y fuera del parque (Wong 1990).

Distancia Entre Subpoblaciones

Además de las localidades conocidas en el Parque Nacional Manuel Antonio, (Wong, 1990) , Arauz (1993) señala 26 localidades adicionales y los vecinos de la zona 4 más (D. Castelfranco, com. per. 1994) . A pesar de que se puede proponer una comunicación entre algunas de las tropas y por ende un intercambio genético se considerará cada una de las localidades una subpoblación. Las localidades y la distancia entre ellas se presentan en el Cuadro 1.

Cuadro 1: Ubicación, presencia de barreras geográficas (PB), área y distancia entre localidades de *S. o. citrinellus* según Wong (1990), Arauz (1993) y vecinos de la zona, observaciones sobre las localidades y posibles localidades para translocación.

Localidad	Ubicación	Distancia	PB	Observaciones	Translocation	Area
1 Río La Gloria	9°36'N,84°32'W	7.0 km a pto 3	Deforest ,camino	Pie de monte, Q. Amarilla	Buena*	Indefinida
2 Punta Judas	9°31'N,84°32'W	5.5 km a pto 3	Deforest,camino	Costa, Bosque, Reserva privada	Buena*	Indefinida
3 Fila San Julián	9°34'N,84°31'W	3.0 km a pto 4	No hay	Pie de monte, Río Tulín	Buena*	Indefinida
4 Fila Chires	9°35'N,84°28'W	3.0 km a pto 3	No hay	Pie de monte, Río Tulín		Indefinida
5 Finca D.Rubí	9°37'N,84°28'W	5.0 km a pto 4	Deforestación	Pie de monte, Q. Bonita		Indefinida
6 Estero Tigre	9°32'N,84°28'W	5.0 km a pto 7	Desarrol.Urbano	Costa, Estero, Desarrollo habitacional, Perdida Habitat		Indefinida
7 Estero Bejuco	9°31'N, 84°26'W	5.0 km a pto 6	Desarrol.Urbano	Costa, Manglar, Q. Visita Perdida de habitat, Desarrl Urbano		Indefinida
8 Estero Zapote	9°30'N, 84°21'W	4.5 km a pto 11	D.Urbano, río	Costa, Manglar, Río Zapote Perdida de habitat		Indefinida
9 La Vasconia	9°38'N, 84°19'W	2.0 km a pto 10	Deforestación	Pie de Monte, Desarrl Urbano		Indefinida
10 El Rey	9°39'N,84°20'W	2.0 km a pto 9	Deforestación	Pie de Monte, Río Rey, Boscosa		Indefinida
11 PaloSeco,Damas Chanchera,etc.	9°30'N,84°12'-20'W	4.5 km a pto 8	Desarrol.Urbano Río Parrita	Manglar, Río Barbudal, Riesgos Menores		Indefinida
12 Filia Godínez	9°37'N,84°21'W	1.0 km a pto 13	No hay	Pie de Monte, Bosque		Indefinida
13 Filia Mora	9°38'N,84°18'W	1.0 km a pto 12	No hay	Pie de Monte, Q. Tigrilla		Indefinida
14 Bambú	9°38'N,84°16'W	1.5 km a pto 13	No hay	Pie de Monte, Bosque		Indefinida
15 Finca Pocares	9°32'N,84°15'W	6.5 km a pto 16	Deforest,Carretr	Tierras bajas, Río Seco, Palma Aficana, carretera		Indefinida
16 Finca Cerros	9°32'N,84°11'W	5.0 km a pto 18	Río Paquita, Urb	Zona baja, Cana de riego, Palma Africana		Indefinida

17 Fila del Nene	9°31'N,84°08'W	3.0 km a pto 29	No hay	Pie de Monte, Q. Huacal, Bosque	Indefinida
18 Finca Anita	9°28'N,84°09'W	3.0 Km a pto 19	Desarrol Urbano	Tierra Baja, Canal de riego,Palma Africana, Basurero	Indefinida
19 Pro.Juan Delgado	9°26'N,84°09'W	2.5 km a pto 36	Desarrl.Urbano	Tierra Baja, Canal de riego, Bosque Reserva Privada, Introd Fauna nativa sin control	Indefinida
20 Villa Nueva	9°29'N,84°04'W	3.0 km a pto 27	Desarrol. Urbano	Tierra Baja, Q. Guapinol	Indefinida
21 Cerro Nene	9°29'N,84°03'W	1.5 km a pto 22	No hay	Pie de Monte, Río Naranjo, Bosque	Indefinida
22 Salitrillos, Londres	9°26'N,84°05'W-9°28'N,84°03'W	1.5 km a pto 21	No hay	Pie de Monte, Q. Salitrillo, Bosque	Indefinida
23 Laguna Negra,	9°22'N,84°05'W	4.5 km a pto 30	No hay	Costa, Manglar, Zona de expansión del Parque	Indefinida
24 Al Sur,Portalón	9°21'N,84°00'W	7.5 km a pto 23	R.Savegre,Urban	Costa, Boca Río Savegre, Manglar	Indefinida
25 Ventanas de Osa	9°05'N,83°40'W	?	?		Indefinida
26 Río G.T-Coronad	9°02'N,83°37'W	?	?		Indefinida
27 Villa Nueva 2	9°29'N,84°4'W	2.5 km a pto 21	No hay	Pie de Monte, Q. Tocolí, Urbanismo	Indefinida
28 Paso Real	9°30'N,84°5'W	3 km a pto 29	No hay	Pie de Monte, Q. Tocolí, Bosque	Indefinida
29 Q. Calicanto	9°31'N,84°7'W	2.5 km a pto 17	No hay	Pie de Monte, Q. Calicanto, Bosque	Indefinida
30 B.R. Naranjo	9°23'N,84°7'W	3 km a pto 31	R. Naranjo	Costa, Boca Río Naranjo, Manglar	Indefinida
31 Finca Q.Azul	9°23'30"N,84°8'20"W	1 km a pto 32	No hay	Costa, Parque N.Ml Ant.	Indefinida
32 Q. Camaronera	9°24'N,84°9'W	1 km a pto 31	No hay	Costa, Borde PNMA, Urbanismo	Indefinida
33 Pta Quepos	9°24'N,84°10'20"W	2 km a pto 34	Carretera Defor.	Costa, Pta Quepos, Desarrollo turístico Urbanismo	Indefinida
34 1km C.Ml.Ant	9°24'40"N,84°9'20"W	1 km a pto 35	Deforestacion	Costa, Desarrollo turístico, Pérdida de hábitat, Carretera, Urbanismo	Indefinida

35	2km C.Ml.Ant	9°25'N,84°9'W	1 km a pto 34	Deforestacion	Costa, Desarrollo turístico, Pérdida de hábitat, Urbanismo.	Indefinida
36	Queb. Grande	9°25'20"N,84°9' 30"W	1.5 km a pto 34	Desarr. Urbano	Costa, Desarrollo turístico, Pérdida de hábitat, Carretara, Urbanismo	Indefinida

* Posibles sitios de reintroducción con gran potencialidad de protección y con animales reportados.

NOTA: Las localidades 27, 28, 29, 30 son reportes de vecinos. Las localidades 31-36 están incluidas dentro de la población Manuel Antonio.

Distribution of *Saimiri oersterdii citrinellus*

The original distribution of Saimiri oersterdii citrinellus , according to Alfaro (1897) was from Herradura hill (9 40'N, 84 35'W) and Dota mountains (9 37'N, 84 9'W) up to Rio Grande de Terraba (8 25'N, 84 25'W), which was considered the southern distribution limit. The actual distribution has the same range, but is fragmented, remaining small populaations of this subespecies. Manuel Antonio National Park is the only protected habitat.

Inside Manuel Antonio National Park live 6 troops, in the buffer zone 8 troops (Wong, 1990). Outside the range exist 26 troops that are not in communications (Arauz, 1993).

The subpopulations of the S. oerstedi citrinellus reported by Arauz (1993) are well known ubicated. The author define 26 sites with groups of squirrel monkeys. Seven of this sites are mangroove areas, three are african palm plantations, surrounded by narrow belts of second growth vegetation, and 16 sites are forest patch of a combination of primary forest and second growth vegetation in different succession stages (Arauz, 1993). However, information not published yet, show the existence of at least 4 to 5 more subpopulations (Dario Castelfranco, pers. comm., 1994).

Troops size: Under natural conditions, the troops are formed by 15 to 68 individuals, been the average of 30 individuals (Wong, 1990). However, inside the actual distribution range are been reported groups forms by 1 to 3 individuals that later had been dissapear from the zone (Arauz, 1993).

According to Wong (1990) the troops are formed by a 36% of adults females, 27% of infants, 25% of juveniles and a 12% of adults males. Besides she say that the troops composition inside and outside the park, presents a similar tendency.

The natality percentage in Manuel Antonio zone varied between 57% and 89%. There was not a significant difference in the birth rate between the recidents troops inside or outside the park (Wong 1990).

Distance between subpopulations: In spite of the provability of communications between some subpopulations therefore genetic interchange, each of the 26 troops located are considered subpopulations. Table 1 shows the localities and the distance between them.

Table 1: Location with coordinates, presence of geographic barriers, distance to nearest troop of _S. o. citrinellus_ according to Wong (1990), Arauz (1993) and neighbors in the area, observations about the localities and posible localities for translocations.

LOCALITY	COORDINATES	DISTANCE TO NEAREST TROOP	GEOGRAPHIC BARRIERS	DESCRIPTION OF AREA	TRANSLOCACION	AREA
1 Río La Gloria	9°36'N,84°32'W	7.0 k to pt 3	Deforestation, unpaved road	Mountain slope, Quebrada Amarilla, Rio La Gloria		Indefinite
2 Punta Judas	9°31'N,84°32'W	5.5 km to pt 3	Deforestion, unpaved road	Coast, Forest, Private reserve		Indefinite
3 Fila San Julián	9°34'N,84°31'W	3.0 km to pt 4	None	Mountain slope, Río Tulín	Good*	Indefinite
4 Fila Chires	9°35'N,84°28'W	3.0 km to pt 3	None	Mountain slope, Rio Chires	Good*	Indefinite
5 Finca D.Rubí	9°37'N,84°28'W	5.0 km to pt 4	Deforestation	Quebrada Bonita	Good*	Indefinite
6 Estero Tigre	9°32'N,84°28'W	5.0 km to pt 7	Urban development	Coast, estuary, housing development, habitat loss		Indefinite
7 Estero Bejuco	9°31'N, 84°26'W	5.0 km to pt 6	Urban development	Coast, mangrove, Quebrada Visita, habitat loss, urban development		Indefinite
8 Estero Zapote	9°30'N, 84°21'W	4.5 km to pt 11	Urban development, river	Coast, mangroves, Río Zapote, habitat loss		Indefinite
9 La Vasconia	9°38'N, 84°19'W	2.0 km to pt 10	Deforestation	Mountain slope, urban development		Indefinite
10 El Rey	9°39'N,84°20'W	2.0 km to pt 9	Deforestation	Mountain slope, Río Rey, forest		Indefinite
11 PaloSeco,Damas Chanchera,etc.	9°30'N,84°12'-20'W	4.5 km to pt 8	Urban development, Río Parrita	Mangrove, Río Barbudal, low risk		Indefinite
12 Filia Godínez	9°37'N,84°21'W	1.0 km to pt 13	None	Mountain slope, forest		Indefinite
13 Filia Mora	9°38'N,84°18'W	1.0 km to pt 12	None	Mountain slope, Quebrada Tigrilla		Indefinite
14 Bambú	9°38'N,84°16'W	1.5 km to pt 13	None	Mountain slope, forest		Indefinite

15 Finca Pocares	9°32'N,84°15'W	6.5 km to pt 16	Deforestation, paved road	Low lands, Río Seca, African Palm, paved road	Indefinite
16 Finca Cerros	9°32'N,84°11'W	5.0 km to pt 18	Río Paquita, village	Low lands, irrigation canal, African palm	Indefinite
17 Fila del Nene	9°31'N,84°08'W	3.0 km to pt 29	None	Mountain slope, Quebrada Huacal, forest,	Indefinite
18 Finca Anita	9°28'N,84°09'W	3.0 km to pt 19	Urban development	Low lands, irrigation canal, African palm, garbage dump	Indefinite
19 Pro.Juan Delgado	9°26'N,84°09'W	2.5 km to pt 36	Urban development	Low lands, irrigation canal, forest, private reserve, release of native animals without control	Indefinite
20 Villa Nueva	9°29'N,84°04'W	3.0 km to pt 27	Urban development	Low lands, Quebrada Guapinol	Indefinite
21 Cerro Nene	9°29'N,84°03'W	1.5 km to pt 22	None	Mountain slope, Río Naranjo, forest	Indefinite
22 Salitrillos, Londres	9°26'N,84°05'W-9°28'N,84°03'W	1.5 km to pt 21	None	Mountain slope, Qebrada Salitrillo, forest	Indefinite
23 Laguna Negra	9°22'N,84°05'W	4.5 km to pt 30	None	Coast, mangrove, possible expansion zone for Parque Manuel Antonio	Indefinite
24 Al Sur, Portalón	9°21'N,84°00'W	7.5 km to pt 23	Rio Savegre, village	Coast, mouth of Río Savegre, mangrove	Indefinite
25 Ventanas de Osa	9°05'N,83°40'W	?	?		Indefinite
26 Río G.T-Coronad	9°02'N,83°37'W	?	?		Indefinite
27 Villa Nueva 2	9°29'N,84°4'W	2.5 km to pt 21	None	Mountain slope, Qebrada Tocorí, urbanization	Indefinite
28 Paso Real	9°30'N,84°5'W	3 km to pt 29	None	Mountain slope, Quebrada Tocorí, forest	Indefinite
29 Q. Calicanto	9°31'N,84°7'W	2.5 km to pt 17	None	Mountain slope Quebrada Calicanto, forest	Indefinite

30 B.R. Naranjo	9°23'N,84°7'W	3 km to pt 31	Rio Naranjo	Coast, mouth of Río Naranjo, mangrove	Indefinite
31 Finca Q.Azul	9°23'30"N,84°8'20"W	1 km to pt 32	None	Coast, National Park Manuel Antonio	Indefinite
32 Q. Camaronera	9°24'N,84°9'W	1 km to pt 31	None	Coast, bordering National Park Manuel Antonio, urbanization	Indefinite
33 Pta. Quepos	9°24'N,84°10'20"W	2 km to pt 34	Defoestation, paved road	Coast, Punta Quepos, Turism, urban development	Indefinite
34 1km C.Ml.Ant	9°24'40"N,84°9'20"W	1 km to pt 35	Deforestation	Coast, turist development, habitat loss, paved road, urbanization	Indefinite
35 2 km C.Ml.Ant	9°25'N,84°9'W	1 km to pt 34	Deforestation	Coast, turism, habitat loss, urbanization	Indefinite
36 Queb. Grande	9°25'20"N,84°9'30"W	1.5 km to pt 34	Urban development	Coast, turist development, habitat loss, paved road, urbanization	Indefinite

*Possible sites for reintroduction recommended by Arauz (1993)
Observations 27-30 are by neighbors, not scientists and localities 31-36 are included in Manuel Antonio population.

TALLER DE EVALUACION DE VIABILIDAD DE POBLACION Y HABITAT DE *Saimiri oerstedi citrinellus*

POPULATION AND HABITAT VIABILITY ASSESSMENT WORKSHOP FOR *Saimiri oerstedi citrinellus*

FINAL REPORT

Parque Nacional Manuel Antonio
Manuel Antonio National Park

Costa Rica

4-7 Junio 1995

Sección 4

TRANSLOCACIONES, REINTRODUCCIONES Y MANEJO EN CAUTIVERIO

TRANSLOCATION, RE-INTRODUCTION AND CAPTIVE BREEDING

TRANSLOCACIONES, REINTRODUCCIONES Y MANEJO EN CAUTIVERIO

La prioridad debe estar en el entrenamiento de personal calificado y en el establecimiento de un equipo capaz de realizar translocaciones y eventualmente reintroducciones. Por lo tanto, es de gran importancia realizar investigaciones con el fin de identificar tropas que sean candidatas para ser traslocadas.

La falta de experiencia en el campo de la traslocación y reintroducción de la subespecie, hace urgente que se desarrolle esta experiencia en Costa Rica tan rápido como sea posible. Actualmente hay gran experiencia en el manejo en cautiverio del genero Saimiri en otros países. Por lo tanto, no hay urgencia en establecer un programa de reproducción en cautiverio para desarrollar las técnicas necesarias de manejo en cautiverio.

Es recomendable que un grupo de científicos busque la información disponible (Publicaciones, reportes, guías, etc.) sobre translocaciones y reintroducciones sobre primates en general. Adicionalmente se debe recopilar información general sobre el Saimiri. Se debe seguir las guías para la reintroducción, reproducción en cautiverio, e investigacion sobre especies en peligro de extinción de la UICN.

Se recomienda que como parte del esquema de entrenamiento para la translocación y reintroducción, sean invitados expertos en estas áreas, sobre todo al inicio del programa.

Se recomienda que el proceso de toma de decisiones sobre el uso de la traslocación, reintroducción y manejo en cautiverio incluya referencias a las guías de la UICN sobre estos temas.

Se recomienda realizar una investigacion medica sobre parásitos y enfermedades naturales presentes en las poblaciones silvestres.
Esto permitiría documentar los valores normales, medidas, información fisiológica y relación de sexo de las tropas existentes. Este proyecto podría estar diseñado para entrenar médicos veterinarios especialistas en vida silvestre, tanto en Costa Rica como en otros países. Esta coordinación entre Costa Rica y otros países seria beneficioso en el tanto que se solicite a los veterinarios visitantes traer su material y equipo. Esto podría coordinarse entre ZCOG, el FIG para Mesoamerica de la AZA y la Escuela de Medicina Veterinaria de la Universidad Nacional. Esta colaboración estimularía el interés sobre la conservación de la vida silvestre al reportarse los resultados en charlas en diferentes universidades.

Si se toma la decisión de translocar, reintroducir y/o establecer una colonia de monos titi en cautiverio, sugerimos seguir las siguientes recomendaciones:

TRANSLOCACION

Se recomienda que un equipo de científicos y personas de la localidad identifique tropas candidatas a ser translocadas, como tropas aisladas que no tienen oportunidades de contactar otros conespecificos debido a restricciones del habitat. Tropas que pueden ser buenas candidatas son aquellas con alto riesgo de extinción.

El equipo encargado de las translocaciones debe estar compuesto como mínimo de un veterinario, un biólogo con grandes conocimientos en la ecología del Saimiri, y una persona de la localidad familiarizada con los sitios en los cuales se hará la translocación.

Las técnicas de captura que se utilizaran en la translocación se escogerán de la lista siguiente, dependiendo de la localización del sitio, el terreno, los materiales disponibles y el veterinario.

a. dardos
b. redes
c. trampas

A. Dardos- la ventaja de esta técnica es que es rápida, y si se utiliza correctamente disminuye los problemas relacionados con el estres de captura. La desventaja es que se pueden utilizar los dardos inicamente individualmente. No recomendamos esta escogencia para capturar tropas enteras. Refiéranse a los métodos usados por el Dr. Ken Glander para monos congo y por el Lic. Ronald Sánchez de la Universidad de Costa Rica.

B. Redes-Aunque se han utilizado redes para capturar algunas especies de primates, no la recomendamos para el mono titi dado que es dificil de implementar y aumentaría los niveles de stress.

C. Trampas- Esta técnica se ha utilizado con el mono titi en Peru con gran éxito. Se pueden capturar topas enteras de una vez. Una trampa grande se coloca en el sitio de captura con comida como sebo para atraer los monos. Si la tropa es grande, varias trampas se distribuyen alrededor del sitio (hay una publicación sobre este ejemplo). El plan incluye mover las trampas al sitio, cebarlas con comida y permitir que los animales se aclimaten a la trampa, de 7 a 10 dais antes de atraparlos. Una vez que el animal cae en la trampa se anestesia usando una jeringa de extensión y el veterinario toma muestras.

Todos los animales capturados, independientemente del método utilizado, serán examinados por el veterinario y el biólogo, quienes registrarán los siguientes datos: peso, sexo y medidas generales. Muestras de sangre de heces y de orina, serán tomas en este momento. Se realizarán exámenes para determinar la presencia de parásitos externos y todos los animales serán marcados permanentemente (ejemplo, tatuaje) para la identificación en el futuro. Sería preferible que los animales se identificaran además con collares o que se les pusieran collares de radio-telemetría. El Dr. K. Glander y otros científicos, le han puesto collares a monos congos y monos araña en el norte de Costa Rica con gran éxito. Un método alternativo, es tatuar todo el grupo y después teñir todo el grupo, utilizando un tinte para pelo (como Nyasol D, que dura hasta 6 meses) para permitir la identificación a distancia. Seria importante colectar semen en ese momento. Para la translocación de animales silvestres, se recomienda una liberación rápida de los mismos (un tiempo de cautiverio máximo de 36 horas). Sin embargo, los animales que han estado en cautiverio y que van a ser reintroducidos, serán liberados en un período de tiempo más prolongado (refiérase a la sección de manejo en cautiverio)

¿Hay modelos de otras translocaciones?
¿Usan ellos cuarentena?
¿Cómo hacen ellos esto para los otros modelos?

TRANSPORTE

Las opciones de transporte comprenden jaulas de diferentes tamaños y material, su escogencia dependerá de la duración del viaje y lo que esté disponible. Los animales se transportarán individualmente, por razones médicas relacionadas a los riesgos asociados con la recuperación de la anestesia, que involucran la agresión hacia compañeros de jaula. Adicionalmente, es más fácil monitorear la condición de los individuos cuando se encuentran solos en las jaulas. Sin embargo, puede ser posible transportar dos hembras juntas sin problemas.

Los monos tití nunca se deben transportar con otras especies de primates, ni con otros mamíferos que les pudieran transmitir enfermedades. Los monos tití capturados en un sitio, se pueden transportar juntos, pero no se deben mezclar con otras tropas de mono tití capturadas en otros sitios.

Se recomienda que los monos tití capturados, no sean vacunados, debido a que pueden transmitir la enfermedad y afectar la inmunidad natural.

Se debe restringir el contacto con humanos durante el período de transferencia. Es preferible que los animales se mantengan bajo anestesia durante el transporte, por ejemplo, sulementar con inyecciones de ketamina.

LIBERACION

Dependiendo de donde procedan los animales (de cautiverio o translocaión de otro sitio) así será el tipo de liberación. Una liberación rápida se recomienda si los animales están siendo translocados de otro sitio, con un tiempo de captura máximo de 36 horas. Si los animales proceden del cautiverio, se recomienda una liberación en un período más prolongado, para permitir la aclimatación al área de liberación, por ejemplo, sonidos, olores, alimentos, nuevos animales, etc. Se recomienda usar una trampa para captura grande, para aclimatar los animales al sitio de liberación, alimentándolos en la jaula, de 4 a 10 día antes de liberarlos. Después de la liberación, se recomienda poner afuera de la jaula comida por una semana, para incrementar la fidelidad al sitio y darle a los animales tiempo para que se habitúen a él. Se recomienda dar un seguimiento después de la liberación, ya sea a través de collares de radio o marcas, por un mínimo de 6 meses o realizar un trampeo, para conocer la condición de los animales.

Existe información y publicaciones sobre la liberación de monos congos (Fred Koonz y Bob Horowitz, Zoológico del Bronx), la liberación de tamarines leonados (Ben Beck del Zoológico Nacional). Los babunes han sido liberados en Africa con mucha dificultad.

MANEJO EN CAUTIVERIO

Se recomienda que los *Saimiri* que sean confiscados y donados, sean la base para desarrollar experiencia en rehabilitación (incluyendo la adquisición de habilidades sociales, de forrajeo y anti depredatorias), así como proveer de un grupo que se reproduzca en cautiverio cuyas crías puedan ser reintroducidas en el bosque nuevamente. Esto se puede hacer en instalaciones actualmente establecidas.

Si se llegara a recomendar un programa de reproducción en cautiverio, sugerimos el siguiente diseño del recinto y el siguiente manejo.

El recinto a utilizar consistiría de varios encierros grandes y naturalísticos con una red por techo y un piso de arena o grava para facilitar el drenaje y reducir la posibilidad de enfermedades. Adicionalmente, la rotación entre los tres encierros, reducirían la reinfección con parásitos. El tamaño mínimo del encierro debe ser de 15 X 15 metros; de manera que se necesitarán tres o cuatro encierros de esas dimensiones para realizar las rotaciones. Esto también permitiría el crecimiento de la vegetación. Se les debe adicionar mecates y ramas, siempre y cuando las mismas se puedan reemplazar cuando se llenan de barro o se puedan limpiar. Se recomienda tener una tropa de 10 monos por recinto. Se recomienda proveer de una jaula para la socialización de nuevos miembros del grupo, para formar tropas más grandes, o en la que se puedan poner animales juntos para que aprendan comportamientos de compañeros de la tropa.

El Zoológico de Whipsnade en Inglaterra mantienen los monos titís en condiciones sucias naturales. Más información sobre manejo y programas de control de enfermedades, se puede obtener de ellos.

La dieta deberá incluir frutos nativos, vegetales, insectos, lombrices de tierra y animales vivos. Esta dieta ha sido exitosa en un sitio de manejo en cautiverio en Costa Rica.

Los procedimientos veterinarios deberían incluir:

La cuarentena para animales que vienen de vida silvestre a cautiverio, deberá de ser de 6 semanas como mínimo, lo que incluye tres exámenes de heces limpios y dos exámenes para tuberculosis negativos con una semana de diferencia (regulaciones de la AAZV).

Análisis parasitarios bi anuales en conjunto con un examen veterinario general, que incluya perfiles hematológicos, se deben realizar. Uno de estos exámenes podría ser programado cuando las hembras pudieran estar preñadas, de manera que se puedan palpar.

A los cuidadores se deben someter a pruebas de tuberculina cada 6 meses. La desinfección de calzado a la entrada del área de los recintos y vestimenta especial quedan a discreción del veterinario.

REINTRODUCCION

El equipo encargado de las reintroducciones, debe de tener como mínimo un veterinario, un biólogo con buen conocimiento de la ecología del *Saimiri* y una persona de la localidad familiarizada con los sitios de reintroducción. La rehabilitación debe ser supervisada por un etólogo.

Durante el esquema de reintroducción, el contacto con los humanos, debe ser reducido al mínimo.

Un programa para preparar los animales a ser reintroducidos, debe de incluir oportunidades para aprender habilidades que les permitan vivir en el bosque, tales como, alimentarse de comidas naturales, comportamiento de defensa ante depredadores y comportamiento social. Se recomienda referirse a los lineamientos del grupo de especialistas en reintroducción de la UICN y a los protocolos de reintroducción de los tamarines leonados dorados y del urón de patas negras. (ver apéndices).

Se recomienda que si el sitio de reintroducción contiene otras especies de primate, se debe asesorar sobre las enfermedades que las otras especies tienen y que pudieran ser transmitidas a los *Saimiri*.

NOTA:

Se recomienda actualizar esta información cada dos años con nueva literatura o datos de campo.

EXPERTOS QUE PUEDEN ASESORAR

Dr. Larry Williams - tiene una colonia de más de 300 monos titís en la Universisdad del Sur de Alabama, Estados Unidos.

Dr. Ken Glander - tiene experiencia capturando por medio de dardos especies de primates en Costa Rica.

Dr. Danilo Leandro - veterinario del Zoológico Simón Bolívar en San José, Costa Rica.

TRANSLOCATION, RE-INTRODUCTION AND CAPTIVE BREEDING

The priority must be placed on beginning to train qualified personnel and the establishment of a team to carry out translocations and eventually reintroductions. Therefore, it is of utmost importance to carry out research in order to identify candidate troops for translocations.

The lack of expertise in the fields of translocation, and re-introduction of the subspecies dictates the urgent need to develop this expertise in Costa Rica as soon as possible. There is already ample expertise in the captive husbandry of the genus Saimiri, in other countries. Therefore, there is no urgency to prioritized the establishment of a captive breeding program to develop the relevant husbandry techniques.

It is recommended that a team of scientists gather the available information (e.g., publications, reports, guidelines) on translocation and re-introduction of primates in general. In addition, information about husbandry for captive breeding of Saimiri should also be compiled. The IUCN Re-introduction, Captive Breeding and Research on Endangered Species guidelines (see appendices) should be followed.

It is recommended that, as part of the training scheme for translocation and re-introduction, experts in these areas be invited to act as instructors during the initial attempts.

It is recommended that the decision-making process about the use of translocation, re-introduction and captive breeding includes reference to the established IUCN guidelines on re-introduction and captive breeding.

It is highly recommended that a medical survey of parasites and natural diseases that exist in current populations be conducted. This would allow the documentation of "normal" values, measurements, physiological states and sex ratio from existing troops. This project could be designed to promote training of new wildlife veterinarians, both from Costa Rica and other countries. This coordination between Costa Rica and other countries would be beneficial as the visiting veterinarians could be required to bring the supplies. This could be coordinated through the Zoo Conservation Outreach Group and the AZA's Meso American Fauna Interest Group and the School of Veterinary Medicine in San Jose, Costa Rica. This collaboration could further stimulate interest in wildlife conservation by having the results reported in talks at various universities.

If the decision is made to translocate, re-introduce and / or create a captive colony of Squirrel Monkeys, these are the recommendations that we suggest be followed:

TRANSLOCATION

It is recommended that a team of scientists and local people should seek to identify candidate troops for translocation such as crop raiding or single troops with no obvious opportunity to contact other conspecifics due to habitat constraints. Good candidate troops are those with high risk of extinction.

The team in charge of translocations should be composed of (at minimum) a veterinarian, a biologist with good working knowledge of Simiri ecology and a local person familiar with the translocation sites concerned.

The capture techniques used for the translocation to be chosen from the following list, depending on the site location, terrain, supplies and the veterinarian

a. darting

b. nets

c. live trapping

A. Darting- The advantage of this technique is that it is quick and if done correctly decreases the problems related to the stress of the capture. The disadvantage is that it is only possible to dart animals individually. Therefore, we recommend that this technique only be used for individual animals. We do not recommend this choice as a way to capture entire troops. Refer to methods used by Dr. Ken Glander for Howler Monkeys and Dr. Ronald Sanchez from the School of Veterinary Medicine in Costa Rica.

B. Nets - Although netting have been used in capturing some species of primates, we do not recommend this for the Squirrel Monkey as it is difficult to implement and would increase stress levels.

C. Live Trapping - This technique has been used with Squirrel Monkeys in Peru with great success. It is possible to capture entire troops at once. A large trap is placed at the designated capture site with food bait inside to attract the monkeys. If the troop is large, several traps can be distributed around the site. (there is a publication on this method) The plan involves moving the traps to the site, baiting them with food and allowing the animals 7 to 10 days to acclimate to the trap before the actual trapping occurs. Once the trap is triggered the animals will be anesthetized using a pole syringe and samples will be taken by the Veterinarian.

All captured animals, regardless of choice of methods, will be examined by the veterinarian and biologists the following data will be recorded: weight, sex, and general measurements. Blood, fecal and urine samples will also be taken at this time. Examination for external parasites will be conducted and the animals will be permanently marked (e.g., tattoo) for future identification purposes. It would be preferable if animals also would be fitted with identification or radio transmitter collars. Dr. K. Glander and others have collared Howler Monkeys and Spider Monkeys in northern Costa Rica with much success. An alternative method, is to tattoo the whole group and then dye the whole group using an hair dye (such as Nyazol D that will last 6 mo.) to allow identification from a distance. It may also be possible to collect semen at time. Hard releases (36 hour maximum holding time) are recommended for translocation for wild animals. However captive animals that are being re-introduced should be soft-released (see captive breeding section).

? are there models on other translocation models?

? Do they use quarantine?

? How do they do this for the other models?

TRANSPORT:

The choices for transport are carrying cases or crates, this depends on the duration of the trip and what is available. The animals will be transported individually, for medical reasons related to risks associated with recovery from anesthesia involving aggression toward cage mates. In addition, it is easier to monitor the condition of the individuals when crated singly. However, it may be possible to transport two females together without problems.

Squirrel Monkeys must never be transported with other primate species or mammals with diseases that could transfer. Squirrel Monkeys from the same capture sites can be transported together but there must be no mixing of Squirrel Monkey troops from other capture sites.

It is recommended that captured Squirrel Monkeys not be vaccinated, since that can actually transmit the disease and affect natural immunity.

We MUST restrict the contact with humans during the transfer period. It is preferable that animals be maintained under anesthesia during transport, e.g., supplemental ketamine injections.

RELEASE:

Depending on where the animals are being released from (i.e., from captivity or translocated from another site) determines the type of release. Hard release is recommended if the animals are being translocated from another site with a 36 hour maximum holding time. It is recommended to do a soft release if the animals are coming from captivity to allow for acclimation to the release area, i.e., noises, smells, food, new animals, etc. It is recommended to use the large capture trap to acclimate the animals to the release site and feed them in the cage for 4 to 10 days before release. After the release, it is recommended to put out food for 1 week or so to increase site fidelity and give animals time to habituate to the site. Follow up after release either from radio collars or marking for a minimum of 6 months, or one trapping to access condition, is advised.

Information and publications are available on Howler Monkey release (Bronx Zoo, Fred Koonz) and Bob Horowitz; golden lion tamarin releases (Ben Beck, National Zoo). Baboons have been released hard in Africa.

CAPTIVE MANAGEMENT:

It is recommended that confiscated and surrendered *Saimiri* provide the basis to gather expertise on rehabilitation (including acquisition of social, foraging and anti-predatory skills), as well as to provide a breeding stock from which offspring could eventually be re-introduced into the wild. This could be done in already established facilities.

Should a captive breeding program be recommended, we suggest the following facility design and husbandry.

The cage used should consist of several large naturalistic enclosures with a net top and a sand or gravel bottom to facilitate drainage and reduce chances of diseases. In addition, rotating among 3 enclosures would reduce reinfection with parasites that would otherwise result from the use of natural substrate. The minimum size of the enclosure should be about 15 meters by 15 meters; therefore 3 or 4 15 X 15 meters enclosures would be needed to allow for rotations. This will also allow vegetation regrowth. Ropes and branches should be added, providing they can be replaced when soiled or can be sanitized. It is recommended that an average troop size of 10 monkeys be maintained per enclosure. It is also recommended that a cage be provided for socialization of new group members into the larger troops or in which to place animals with others to learn what to do from troop mates.

Whipsnade Zoo in England keeps squirrel monkeys on dirt in natural settings. More information about management and disease control programs should be obtained from them.

The diet should include native fruits, vegetables, insects, mealworms, and live animals. This diet has proven successful at a captive breeding facility in Costa Rica.

Veterinary procedures should include:
Quarantine from wild sites to captivity should be a minimum of six weeks, which includes 3 clean fecal exams and 2 negative TB tests one week apart (as per AAZV regulations).

Bi-annual parasite analysis along with a general veterinary exam including blood profiles should be conducted. One of these examinations could be scheduled when the females might be pregnant so they can be palpated.

Caretakers should have TB tests every 6 months and foot baths and special clothing must be at the discretion of the veterinarian.

RE-INTRODUCTION:

The team in charge of re-introductions should be composed of (at minimum) a veterinarian, a biologist with good working knowledge of Simiri ecology and a local person familiar with the re-introduction sites concerned. The rehabilitation should be supervised by an ethologist.

Contact with humans must be minimized for animals scheduled for re-introduction.

A program to prepare animals for re-introduction (re-habilitation) should include opportunities to learn skills to cope with life in the wild, such as feeding on natural foods, anti-predator behaviors and social skills. It is recommended to refer to the IUCN re-introduction Specialist Group Guidelines and to the Golden Lion Tamarin and Black-footed Ferret re-introduction protocols (see appendices).

It is recommended that if the re-introduction site contains other species of primate (which is likely), that we need to assess the diseases that the other species currently have that could be transferred to Saimiri.

NOTE:

It is recommended that this information be updated every two years with new literature or field data.

EXPERTS TO SEEK ADVICE FROM:

Dr. Larry Williams - runs the colony of 300+ Squirrel Monkeys at the breeding colony at University of Southern Alabama USA

Dr. Ken Glander - has experience darting primate species in Costa Rica

Dr. Danilo - Veterinarian for Simon Bolivar Zoo in San Jose, Costa Rica.

TALLER DE EVALUACION DE VIABILIDAD DE POBLACION Y HABITAT DE *Saimiri oerstedi citrinellus*

POPULATION AND HABITAT VIABILITY ASSESSMENT WORKSHOP FOR
Saimiri oerstedi citrinellus

FINAL REPORT

Parque Nacional Manuel Antonio
Manuel Antonio National Park

Costa Rica

4-7 Junio 1995

Sección 5

ACCIONES NECESARIAS

ACTIONS NEEDED

Educación Ambiental

1. Grupos Metas:

   Hoteleros
   Sector educativo - Centros Educación
   Comunidades

2.

2a. Hoteleros:
   Información sobre la problemática
   Concientización (Involucrar al sector en la problemática)

2b. Comunidades locales:
   Información sobre la problemática
   Concientización (niños, jóvenes, Adultos)

2c. Sector Educativo:
   Información
   Conciantización
   Participación activa del sector en la problemática

3. Zonas:

   1era Etapa; Aledañas al Parque
   Hoteles
   Escuelas
   Comunidades

4a. Hoteleros
   Manejo de desechos
   Mantenimiento de áreas boscosas alrededor
   Peligro y consecuencia de enfermedades producidas por animales (zoonosis).

4b. Comunidades:
   Afectación de la población por la alteración del habitat y extinción de la especie.
   Importancia de la conservación ligada al turismo y los beneficios que genera
   Importancia de los ecosistemas naturales (Manglares).

4c. Sector Educativo
   Participación activa de maestros(as) y estudiantes en programas de conservación de la especie, desarrollando actividades de orden cultural y recreativo.

Programa de capacitación a maestros

5. Empleo de medios de comunicación social

   Actividades dirigidas a las comunidades, sector educativo y Hoteleros
   Necesidad de apoyo económico por parte de empresas regionales

6. Acciones inmediatas:

   Diagnóstico de la situación
   Planificación de los programas de Educación Ambiental a implementar

7. Consideramos que los procesos educativos son continuos, ademas se debe continuar las actividades ya iniciadas en la materia, sin embargo el inicio de los trabajos con cada grupo meta deba ser inmediato.

8. Instituciones publicas: MIRENEM, ICT, MEP, Salud, Municipalidad,
   Instituciones privadas Iglesia

9. MIRENEM
   Municipalidad
   M.E.P.
   Org. Comunales

Recomendaciones

Hoteleros:

1. Campaña informativa

1.1 Organizar una reunión informativa sobre la problemática general (puede ser en uno de los hoteles). La organización de la reunión. La invitación debe hacerla la mono Tití (recorrido por el parque).

1.2 Involucrar a los hoteles

1.2.1 Regulación eficiente y objetiva de las actividades hoteleras por parte del gobierno local.

Comunidades Locales

* Organizar una reunión en cada comunidad (líderes comunales) informarle igualmente incluyendo gira por el parque, invitación a través de la radio local principalmente.

* Organizar reuniones a nivel docente para proporcionar información básica necesaria sobre el tema a fin de involucrar a este sector en la organización de planes de trabajo orientados a iniciar un cambio de actitud positiva en forma progresiva a nivel de estudiantes de la localidad.

* Para la implementación del programa en la zona de manera de cubrir los diferentes sectores sociales.

Dicho programa se desarrollará por etapas:

1 Etapa:

- Pobladores aledaños al parque.
- Hoteleros/Hoteles aledaños al parque.

Poblaciones: Manuel Antonio, Londres, Santo Domingo, Savegre y Quepos.

2 Etapa:

* Sector Educativo: escuelas, universidades, liceos, colegios técnicos y kinder más cercanos al parque.

Elementos Modulares del Programa Educativo

- Conservación del habitat
- Especies en peligro de extinción (especie Saimiri)
- Contaminación de cuerpos de agua
- El hombre como parte del medio ambiente
- Causas de extinción de especies de la zona
- Ventajas desde el punto de vista económico de la conservación de recursos.

5. A través de programas de Educación Formal hacia los grupos estudiantiles de todos los niveles y de manera no formal hacia las comunidades y sector hotelero.

Aumentando la cantidad de información interpretativa al sector ecoturístico en general.

a. Educación formal: Apoyando los programas educativos establecidos con material didáctico (folletos, guía didáctica, material biológico, panfletos, etc.) orientados hacia el tema.

b. Educación Informal: Organizar charlas, talleres "Semana de la Conservación del Mono Tití".

- Actividades desarrolladas por los grupos ecológicos de la zona sobre el tema a los pobladores.

- Día Nacional del Mono Tití.

- A través de la Iglesia (homilía de la conservación).

- Establecer un Centro de Visitantes (educativo e informativo) dentro del parque, el dinero para el establecimiento y desarrollo de dicho centro provendría de las donaciones de los turistas en los hoteles. (Se propone edificio anexo a nuestra área de trabajo).

- Mensajes a la comunidad (micros radiales) cuñas, etc. También artículos en la prensa, afiches, folletos.

- Colecta-Donación por parte de los turistas para la conservación del parque y del Mono Tití.

- Establecer una vez al mes (por los menos) que el dinero por concepto de hospedaje de los turistas en los hoteles pase directamente a los programas y actividades en pro de la conservación de la especie.

- Solicitar apoyo financiero a las empresas para cubrir gastos necesarios en la realización de actividades conservacionistas en la zona. Igualmente pedir apoyo a organizaciones conservacionistas tanto nacionales como extranjeras no solo financieramente sino con apoyo en material didáctico, capacitación a educadores y al recurso humano necesario para llevar a cabo estos programas.

Environmental Education

Target Groups:

Tourists
Educational sector
Communities

2a.
Hotels:

Information about the problem
Raising Consciousness

2b.
Local communities:

Information about the problem
Raising consciousness (children, young people, Grown-ups)

2c.
Educational sector:

Information
Concentization
Active participation of the sector in the problem.

Zones:

Surroundings of the Park

Hotels
Schools
Communities

Hotels

Handling of wastage
Maintenance of forest around
Danger and consequence of illness produced by animals ([zoonosis])

Communities:

Affecting the population through habitat alteration and extinction of the species.
Importance of conservation attached to tourism and the benefits that generates
Importance of the natural ecosystems (mangroves)

Educational sector

Active participation of teachers and students in programs of conservation of the species, developing cultural and recreative activities.
Capacitation program to teachers

Use of social communication
Activities addressed to the communities, educational sector and Hotels.
Necessity of economic support from regional business.

Immediate actions:
Diagnostic of the situation
Planning of programs of environmental Education

We consider that the educational processes are continuous, it should continue the activities already initiated, however the beginning of the works with each group goal should be immediate.

Public Institutions:
ICT, MEP, Health, Municipality, MINAE, Church, private sector, communal organizations.

Recommendations

Hotels

Informative campaign
1.1 Organize an informative meeting on the general problem
(could be in one of the hotels)
The organization of the meeting.

The invitation should be done by the Municipality, Tourism Chamber and Squirrel monkey conservation Foundation

1.2.1 Efficient and objective regulation of hotels by the local government.

Local communities

* Organize a meeting in each community (communal leaders) to inform them about the titi monkey including a tour through the park. Invitation through the local radio mainly.

* Organize meetings at educational level in order to give basic information on the topic to this sector, to help them in the organization of plans of work guided to begin a progressive change of positive attitude of the students of the location.

* The program should cover the different social sectors of the zone

This program will be developed by stages:

1 Stage:

* People who live near the park .
* Hotels who are near the park

Populations:
Manuel Antonio, London, Santo Domingo, Savegre and Quepos.

2 Stage:

* Educational Sector:

Preschool, schools, universities, high school, technical schools which are near

Elements of the Educational Program
- Conservation of the habitat - endangered species (Saimiri)/ Contamination of bodies of water- Man like part of the environment- Causes of extinction] of species of the zone/ Advantages from the point economical point of view of the conservation of resources.

The collegiate groups of all the levels should be approached through formal education programs. No formal education toward the communities and tourism sector.

Increasing the quantity of interpretative information to the ecotouristic sector, in general.

a.
Formal education:

Supporting established educational programs with material (pamphlets, guide, biological material, etc.) guided toward the topic.

Informal education:

Organizing chats, shops "Week of the Conservation of the Squirrel Monkey".

- Activities developed by the ecological groups of the zone on the topic to the citizens
- National Day of the Squirrel Monkey.

- through the Church (homily of the conservation)
- Establish a Center of Visitors (educational and informative) within the park, the money for the establishment and development of this center would come from the donations of the tourists and the hotels (annexed building proposed to our area of work).
- Messages to the community (radial); also articles in the press, posters, pamphlets.
- Donations by the tourists for the conservation of the park and of the titi monkey.
- Establish once a month (at least) that the money for concept of lodging of the tourists in the hotels pass directly to the programs and activities toward conservation of the species.
- Solicit financial support to the business sector in order to cover expenses necessary in the realization of conservationist activities in the zone.

Same request to conservationist organizations national like foreign, not only money but also educative material, capacitation to educators and to the human resource necessary in order to carry out these programs.

ACTOR	ROL ACTUAL	ROL ESTRATEGIA
Municipalidades	Conservación del manglar. Refugio V.S. mixto Damas-Palo Seco	Iniciar un papel más activo en coordinación con el Area de Conservación. Ordenamiento territorial de las zonas.
- Parrita - Aguirre	Pasivo Activo	
	- Comisión de Recursos Naturales.	Debe continuar incentivando el monitoreo (taller seguimiento) mono tití.
	- Acuerdo prohibición tránsito de madera.	
	- Milla marítima	Actualización Planes reguladores (1989).
	- Prohibición extracción materiales de ríos y plazas.	Mayor control sobre construcciones.
	- Declaratoria áreas protegidas: * Playa Rey * Cuevas de Damas	Actualización del impuesto territorial.
Hoteleros	Lucro	- Respetar Planes reguladores. - Dejar áreas verdes con especies nativas para el tránsito del mono tití. - % ganancia para la conservación. - Tratamiento aguas negras y servidas. - Financiamiento y distribución de panfletos y

		desplegables con información sobre el parque, su vida silvestre y la biodiversidad del Area de Conservación. - Colaboración con los talleres de seguimiento.
Asociaciones de Desarrollo y Cooperativas. Aguirre: Manuel Antonio. Quepos Coopefruta Sto. Domingo Savegre Silencio Otras de Asoc. de Desarrollo de otras municipalidades Unión Cantonal Asociaciones Desarrollo.	- Luchas por superar problemas de la comunidad. - 1 representante en la Comisión RN de la Municipalidad.	Promover desarrollos ecoturísticos en su comunidad para liberar la presión turística sobre el Parq. Nl.
Cámara Turismo Quepos.	Proteger los intereses de los asociados.	Saneamiento ambiental. Ordenamiento territorial. Embellecimiento Ej: Impulso construcción aceras entre Quepos y Ml. Antonio. Construcción puente para acceso parque. Cent. información (Quepos).

Sociedad civil	Pasivo	- Mayor concient. e información sobre problema - Mantenerse vigilantes y monitorear el proceso. - Aporte económico al proceso.
Palma Tica	Ninguno	Colaborar con el proceso de recuperación de habitat.
Cuerpos protección		
Guardaparques	- Muy activo: capacitado para real protección. - Incorporación reciente al proceso vigilancia, prevención y control.	- Denunciar atentados contra la especie. - Establecer programas capacitación para los guardias rurales para realizar protección.
OIJ	- Actúa cuando deben investigar denun.	Reforzar con cuerpo de voluntarios entrenados para protec.
Educ. Formal		
Preescolar		
Escolar	- Temas educ. ambiental	- Capacitación a maestros para utilizar el parque como aula abierta.
Universitaria Investigación	TCU	- Promover TCU, voluntariado e investigaciones.
AyA	- Construcción Acueductos vecinales	- Manejo y protección de cuencas.
ICE	- ICE 3 proyectos	

	Pirris Savegre Naranjito Papel pasivo Institución de apoyo	
ICE	Los proyectos se van a ejecutar después del año 2.000. Los estudios que realiza actualmente son de factibilidad de impacto ambiental y estudios básicos.	
Jardí Gaia	Centro oficial de rescate de vida silvestre del Pacífico Central. Tiene decomisadas, 95% heridos y devueltos por campañas y educa. ambiental. Tiene Convenio con MIRENEM -Dir. VS que no se está cumpliendo por falta de recursos económ. y humanos	Cerrar por falta de recursos econ. y humanos. Si no cierra servir como filtro y distribuidor de anim. decomisados. Establec. 3 centros de pre reintroducción manejados por pobladores locales en dif. zonas de vida (Cerro Nava, Sábalo, Desemb. Savegre). Entrenamiento veter., voluntarios. Centro Cons. orquídeas
Area Conserv. Pacífico Cent. (ACOPAC) Parq. Ncnal Ml. Ant.	Prevención, protección y "manejo" de la especie.	Implementación de la estrategia de conserv. de la especie (en coordinación con otras instituciones.
	Area núcleo de la protección del mono Tití.	Parque: Interpretación de senderos.
	Proomotor de acciones que se hagan en pro de la conservación de la especie.	Contratación de personal de mantenimiento para que los guardaparques tengan más

tiempo de realizar sus funciones conservacionistas.

Compra tierras para consolidar habitat tití.

Incentivar otros inves tigadores a realizar monitoreo sobre la especie.

Tener un banco de datos completo para poder tomar decisiones de manejo.

ACTOR CURRENT	**ROLE STRATEGY**	**ROLE**
Municipalities	Conservation of the swamp. Refuge V.S. mixed Ladies - Dry Stick	To begin a more active in coordination with the Conservation Area. Territorial classification of the zones.
-Parrita -Aguirre	Passive Active	
	Natural resources commission Coordination with the MINAE for an effective prohibition of wood transport.	Must continue the pursuit of goals of this workshop.
	Maritime mile Plans	Update of regulation (1989).
	Prohibition extraction material of rivers and squares.	Greater control over constructions.
	Areas declaration protected: King Beach Lady caves	Update of the territorial tax.
Hotel	Profit	To observe regulatory plans. Leave green areas with indigenous species for the traffic of the tití monkey.

ACTOR CURRENT	ROLE STRATEGY	ROLE
		Donate % of profit for conservation. Respect instructions on the treatment black and served waters. Financing and distribution of pamphlets and brochures with information on the park, its wildlife and the biodiversity of the Conservation Area. Collaboration with follow-up workshops.
Associations of Development and Cooperative.	Fight to overcome problems of the community.	Promote ecotouristic developments in their community in order to remove tourist pressure on Manuel Antonio National Park.
Aguirre: Manuel Antonio. Coopefruta Sto. Savegre Silence	1 representative in the Commission Sunday RN of the Municipality.	
Other of Assoc. of Development of others municipalities		
Union Cantonal Development Associations.		

ACTOR CURRENT	ROLE STRATEGY	ROLE
Tourism chamber	To protect the interest of the associates. Landscaping	Environmental Territorial classification. Construction of arial bridges for passage of monkeys on the highway. Bridge construction for park access. Construction of the tourism information center in Quepos.
Civil society	Passive	Greater concentration and information on problem Maintain vigilant monitoring of the process. Economic contribution to the process.
Palma Tica	None	Collaborate with the habitat recovery process.
Protection bodies		
Forest Guards	Very active: trained for protection.	Teach to denounce attacks against the species. Support of authorities in order for guards to fulfill their work.
	Establish programs of prevention and control.	To establish training programs for the guards so they can carry out protection.

ACTOR CURRENT	ROLE STRATEGY	ROLE
OIJ	Acts when they should to investigate denun.	Reinforce with body of volunteers trained for protection.
Formal education		
Preschool and	Topics of enviromental education in curriculum.	Training Secondary teachers/professors to use the park as opened classroom.
University		To promote communal work to favor the park, the species and their conservtion.
AYA	Construction of rural aqueducts ICE has 3 projects Pirris, Savegre Naranjito Passive paper Support institution The projects are going to be executed after the year 2000. The studies that are carried out currently are of feasibility of environmental and other basic studies.	Managment and protection of basins.
Gaia Garden	Official center for rescue of wildlife of the Central Pacific. Have confiscated injured animals and returned them to wild because of campaigns of environmental education. Has an agreement with MIRENEM that is not being completed due to lack of economic and human support.	Center to close due to lack of resources both econ. and human. If it does not close it could serve as filter and distributor of confiscated animals. Establish 3 reintroduciton centers managed by local people in different zones of life: Cerro Nara, Sabalo, Desembocadura of the Savegre. Training of volunteer veterinarians at Conservation orchids Cent.

ACTOR CURRENT	ROLE STRATEGY	ROLE
Central Pacific Conservation Area (ACOPAC) Manuel Antonio NP	Prevention, protection and managment of the species. of the kind	Implementation of the conservation strategy for the species (in coordination with other institutions).
	Nucleus area for the protection of the tití monkey.	Interpretation of trails In the park.
	Promotor of social actions toward conservation of the species.	Hire maintainence personnel so that park guards may have more time to accomplish their conservation functions.
		Purchase lands to consolidate tití habitat.
		Promote research on monitoring the species.
		To have a complete database in order to make informed management decisions.

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FINAL REPORT

Parque Nacional Manuel Antonio
Manuel Antonio National Park

Costa Rica

4-7 Junio 1995

Sección 6

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TALLER DE EVALUACION DE VIABILIDAD
DE POBLACIÓN Y HABITAT
DE *Saimiri oerstedi citrinellus*

POPULATION AND HABITAT VIABILITY ASSESSMENT
WORKSHOP FOR
Saimiri oerstedi citrinellus

FINAL REPORT

Parque Nacional Manuel Antonio
Manuel Antonio National Park

Costa Rica

4-7 Junio 1995

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APENDICE

APPENDIX

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VORTEX: A Computer Simulation Model for Population Viability Analysis

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Abstract

Population Viability Analysis (PVA) is the estimation of extinction probabilities by analyses that incorporate identifiable threats to population survival into models of the extinction process. Extrinsic forces, such as habitat loss, over-harvesting, and competition or predation by introduced species, often lead to population decline. Although the traditional methods of wildlife ecology can reveal such deterministic trends, random fluctuations that increase as populations become smaller can lead to extinction even of populations that have, on average, positive population growth when below carrying capacity. Computer simulation modelling provides a tool for exploring the viability of populations subjected to many complex, interacting deterministic and random processes. One such simulation model, VORTEX, has been used extensively by the Captive Breeding Specialist Group (Species Survival Commission, IUCN), by wildlife agencies, and by university classes. The algorithms, structure, assumptions and applications of VORTEX are described in this paper.

VORTEX models population processes as discrete, sequential events, with probabilistic outcomes. VORTEX simulates birth and death processes and the transmission of genes through the generations by generating random numbers to determine whether each animal lives or dies, to determine the number of progeny produced by each female each year, and to determine which of the two alleles at a genetic locus are transmitted from each parent to each offspring. Fecundity is assumed to be independent of age after an animal reaches reproductive age. Mortality rates are specified for each pre-reproductive age–sex class and for reproductive-age animals. Inbreeding depression is modelled as a decrease in viability in inbred animals.

The user has the option of modelling density dependence in reproductive rates. As a simple model of density dependence in survival, a carrying capacity is imposed by a probabilistic truncation of each age class if the population size exceeds the specified carrying capacity. VORTEX can model linear trends in the carrying capacity. VORTEX models environmental variation by sampling birth rates, death rates, and the carrying capacity from binomial or normal distributions. Catastrophes are modelled as sporadic random events that reduce survival and reproduction for one year. VORTEX also allows the user to supplement or harvest the population, and multiple subpopulations can be tracked, with user-specified migration among the units.

VORTEX outputs summary statistics on population growth rates, the probability of population extinction, the time to extinction, and the mean size and genetic variation in extant populations.

VORTEX necessarily makes many assumptions. The model it incorporates is most applicable to species with low fecundity and long lifespans, such as mammals, birds and reptiles. It integrates the interacting effects of many of the deterministic and stochastic processes that have an impact on the viability of small populations, providing opportunity for more complete analysis than is possible by other techniques. PVA by simulation modelling is an important tool for identifying populations at risk of extinction, determining the urgency of action, and evaluating options for management.

Introduction

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat, have been reduced to one or more small, isolated populations. The causes of the original decline are often obvious, deterministic forces, such as over-harvesting,

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habitat destruction, and competition or predation from invasive introduced species. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990). Of particular impact on small populations are stochastic processes. With the exception of aging, virtually all events in the life of an organism are stochastic. Mating, reproduction, gene transmission between generations, migration, disease and predation can be described by probability distributions, with individual occurrences being sampled from these distributions. Small samples display high variance around the mean, so the fates of small wildlife populations are often determined more by random chance than by the mean birth and death rates that reflect adaptations to their environment.

Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The use of simulation modelling, often in conjunction with other techniques, to explore the dynamics of small populations has been termed Population Viability Analysis (PVA). PVA has been increasingly used to help guide management of threatened species. The Resource Assessment Commission of Australia (1991) recently recommended that 'estimates of the size of viable populations and the risks of extinction under multiple-use forestry practices be an essential part of conservation planning'. Lindenmayer *et al.* (1993) describe the use of computer modelling for PVA, and discuss the strengths and weaknesses of the approach as a tool for wildlife management.

In this paper, I present the PVA program VORTEX and describe its structure, assumptions and capabilities. VORTEX is perhaps the most widely used PVA simulation program, and there are numerous examples of its application in Australia, the United States of America and elsewhere.

The Dynamics of Small Populations

The stochastic processes that have an impact on populations have been usefully categorised into demographic stochasticity, environmental variation, catastrophic events and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate and sex ratio of a population even if the probabilities of birth and death remain constant. On the assumption that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be important to population viability only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means. The distribution of annual adult survival rates observed in the remnant population of whooping cranes (*Grus americana*) (Mirande *et al.* 1993) is shown in Fig. 1. The innermost curve approximates the binomial distribution that describes the demographic stochasticity expected when the probability of survival is 92·7% (mean of 45 non-outlier years).

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The second narrowest curve on Fig. 1 shows a normal distribution that statistically fits the observed frequency histogram of crane survival in non-outlier years. The difference between this curve and the narrower distribution describing demographic variation must be accounted for by environmental variation in the probability of adult survival.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analysed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease,

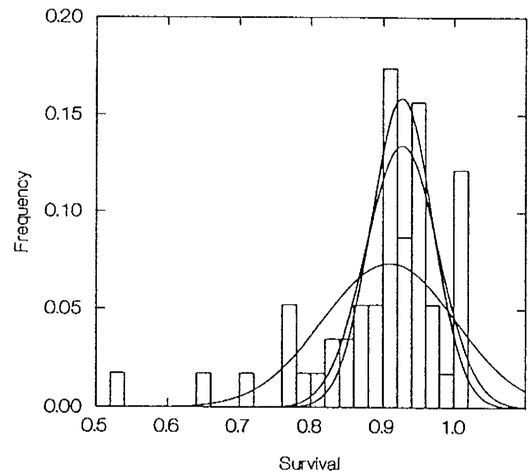

Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938–90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution that most closely fits the histogram, excluding the five leftmost bars (7 outlier 'catastrophe' years). The narrowest and tallest curve is the normal approximation to the binomial distribution expected from demographic stochasticity. The difference between the tallest and second tallest curves is the variation in annual survival due to environmental variation.

hurricanes, large-scale fires, and floods are outliers in the distribution of environmental variation (e.g. five leftmost bars on Fig. 1). As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls *et al.* 1988; Lacy *et al.* 1993). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations have a negative impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerate genetic drift (Crow and Kimura 1970). These synergistic destabilising effects of stochastic process on small populations of wildlife have been described as an 'extinction vortex' (Gilpin and Soulé 1986). The size below which a population is likely to be drawn into an extinction vortex can be considered a 'minimum viable population' (MVP) (Seal and Lacy 1989), although Shaffer (1981) first defined a MVP more stringently as a population that has a 99% probability of persistence for 1000 years. The estimation of MVPs or, more generally, the investigation of the probability of extinction constitutes PVA (Gilpin and Soulé 1986; Gilpin 1989; Shaffer 1990).

Methods for Analysing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction–recolonisation dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991). Because demographic and genetic processes in small populations are inherently unpredictable, the expected fates of wildlife populations can be described in terms of probability distributions of population size, time to extinction, and genetic variation. These distributions can be obtained in any of three ways: from analytical models, from empirical observation of the fates of populations of varying size, or from simulation models.

As the processes determining the dynamics of populations are multiple and complex, there are few analytical formulae for describing the probability distributions (e.g. Goodman 1987; Lande 1988; Burgmann and Gerard 1990). These models have incorporated only few of the threatening processes. No analytical model exists, for example, to describe the combined effect of demographic stochasticity and loss of genetic variation on the probability of population persistence.

A few studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g. Belovsky 1987; Berger 1990; Thomas 1990), but presently only order-of-magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). Threatened species are, by their rarity, unavailable and inappropriate for the experimental manipulation of population sizes and long-term monitoring of undisturbed fates that would be necessary for precise empirical measurement of MVPs. Retrospective analyses will be possible in some cases, but the function relating extinction probability to population size will differ among species, localities and times (Lindenmayer *et al.* 1993).

Modelling the Dynamics of Small Populations

Because of the lack of adequate empirical data or theoretical and analytical models to allow prediction of the dynamics of populations of threatened species, various biologists have turned to Monte Carlo computer simulation techniques for PVA. By randomly sampling from defined probability distributions, computer programs can simulate the multiple, interacting events that occur during the lives of organisms and that cumulatively determine the fates of populations. The focus is on detailed and explicit modelling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations. Computer programs available to PVA include SPGPC (Grier 1980*a*, 1980*b*), GAPPS (Harris *et al.* 1986), RAMAS (Ferson and Akçakaya 1989; Akçakaya and Ferson 1990; Ferson 1990), FORPOP (Possingham *et al.* 1991), ALEX (Possingham *et al.* 1992), and SIMPOP (Lacy *et al.* 1989; Lacy and Clark 1990) and its descendant VORTEX.

SIMPOP was developed in 1989 by converting the algorithms of the program SPGPC (written by James W. Grier of North Dakota State University) from BASIC to the C programming language. SIMPOP was used first in a PVA workshop organised by the Species Survival Commission's Captive Breeding Specialist Group (IUCN), the United States Fish and Wildlife Service, and the Puerto Rico Department of Natural Resources to assist in planning and assessing recovery efforts for the Puerto Rican crested toad (*Peltophryne lemur*). SIMPOP was subsequently used in PVA modelling of other species threatened with extinction, undergoing modification with each application to allow incorporation of additional threatening processes. The simulation program was renamed VORTEX (in reference to the extinction vortex) when the capability of modelling genetic processes was implemented in 1989. In 1990, a version allowing modelling of multiple populations was briefly named VORTICES. The only version still supported, with all capabilities of each previous version, is VORTEX Version 5.1.

VORTEX has been used in PVA to help guide conservation and management of many species, including the Puerto Rican parrot (*Amazona vittata*) (Lacy *et al.* 1989), the Javan rhinoceros (*Rhinoceros sondaicus*) (Seal and Foose 1989), the Florida panther (*Felis concolor coryi*) (Seal and Lacy 1989), the eastern barred bandicoot (*Perameles gunnii*) (Lacy and Clark 1990; Maguire *et al.* 1990), the lion tamarins (*Leontopithecus rosalia* ssp.) (Seal *et al.* 1990), the brush-tailed rock-wallaby (*Petrogale penicillata penicillata*) (Hill 1991), the mountain pygmy-possum (*Burramys parvus*), Leadbeater's possum (*Gymnobelideus leadbeateri*), the long-footed potoroo (*Potorous longipes*), the orange-bellied parrot (*Neophema chrysogaster*) and the helmeted honeyeater (*Lichenostomus melanops cassidix*) (Clark *et al.* 1991), the whooping crane (*Grus americana*) (Mirande *et al.* 1993), the Tana River crested mangabey (*Cercocebus galeritus galeritus*) and the Tana River red colobus (*Colobus badius rufomitratus*) (Seal *et al.* 1991), and the black rhinoceros (*Diceros bicornis*) (Foose *et al.* 1992). In some of these PVAs, modelling with VORTEX has made clear the insufficiency of past management plans to secure the future of the species, and alternative strategies were proposed, assessed and implemented. For example, the multiple threats to the Florida panther in its existing habitat were recognised as probably insurmountable, and a captive breeding effort has been initiated for the purpose of securing the gene pool and providing animals for release in areas of former habitat. PVA modelling with VORTEX has often identified a single threat to which a species is particularly vulnerable. The small but growing population of Puerto Rican parrots was assessed to be secure, except for the risk of population decimation by hurricane. Recommendations were made to make available secure shelter for captive parrots and to move some of the birds to a site distant from the wild flock, in order to minimise the damage that could occur in a catastrophic storm. These recommended actions were only partly implemented when, in late 1989, a hurricane killed many of the wild parrots. The remaining population of about 350 Tana River red colobus were determined by PVA to be so fragmented that demographic and genetic processes within the 10 subpopulations destabilised population dynamics. Creation of habitat corridors may be necessary to prevent extinction of the taxon. In some cases, PVA modelling has been reassuring to managers: analysis of black rhinos in Kenya indicated that many of the populations within sanctuaries were recovering steadily. Some could soon be used to provide animals for re-establishment or supplementation of populations previously eliminated by poaching. For some species, available data were insufficient to allow definitive PVA with VORTEX. In such cases, the attempt at PVA modelling has made apparent the need for more data on population trends and processes, thereby helping to justify and guide research efforts.

Description of VORTEX

Overview

The VORTEX computer simulation model is a Monte Carlo simulation of the effects of deterministic forces, as well as demographic, environmental and genetic stochastic events, on wildlife populations. VORTEX models population dynamics as discrete, sequential events that occur according to probabilities that are random variables, following user-specified distributions. The input parameters used by VORTEX are summarised in the first part of the sample output given in the Appendix.

VORTEX simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. The program was designed to model long-lived species with low fecundity, such as mammals, birds and reptiles. Although it could and has been used in modelling highly fecund vertebrates and invertebrates, it is awkward to use in such cases as it requires complete specification of the percentage of females producing each possible clutch size. Moreover, computer memory limitations often hamper such analyses. Although VORTEX iterates life events on an annual cycle, a user could model 'years' that are other than 12 months' duration. The simulation of the population is itself iterated to reveal the distribution of fates that the population might experience.

Demographic Stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination and death with a pseudo-random number generator. The probabilities of mortality and reproduction are sex-specific and pre-determined for each age class up to the age of breeding. It is assumed that reproduction and survival probabilities remain constant from the age of first breeding until a specified upper limit to age is reached. Sex ratio at birth is modelled with a user-specified constant probability of an offspring being male. For each life event, if the random value sampled from the uniform 0–1 distribution falls below the probability for that year, the event is deemed to have occurred, thereby simulating a binomial process.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), according to the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value, according to

$$N = p(1-p)/s^2 .$$

N binomial trials are then simulated by sampling from the uniform 0–1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

The 'carrying capacity', or the upper limit for population size within a habitat, must be specified by the user. VORTEX imposes the carrying capacity via a probabilistic truncation whenever the population exceeds the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation.

Environmental Variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modelled as binomial distributions. Environmental variation in carrying capacity is modelled as a normal distribution. The variance across years in the frequencies of births and deaths resulting from the simulation model (and in real populations) will have two components: the demographic variation resulting from a binomial sampling around the mean for each year, and additional fluctuations due to environmental variation and catastrophes (see Fig. 1 and section on The Dynamics of Small Populations, above).

Data on annual variations in birth and death rates are important in determining the probability of extinction, as they influence population stability (Goodman 1987). Unfortunately, such field information is rarely available (but see Fig. 1). Sensitivity testing, the examination of a range of values when the precise value of a parameter is unknown, can help to identify whether the unknown parameter is important in the dynamics of a population.

Catastrophes

Catastrophes are modelled in VORTEX as random events that occur with specified probabilities. Any number of types of catastrophes can be modelled. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors by 50% for the year. Such a catastrophe would be modelled as a random event with 0·02 probability of occurrence each year, and severity factors of 0·75 for survival and 0·50 for reproduction.

Genetic Processes

Genetic drift is modelled in VORTEX by simulation of the transmission of alleles at a hypothetical locus. At the beginning of the simulation, each animal is assigned two unique alleles. Each offspring is randomly assigned one of the alleles from each parent. Inbreeding depression is modelled as a loss of viability during the first year of inbred animals. The impacts of inbreeding are determined by using one of two models available within VORTEX: a Recessive Lethals model or a Heterosis model.

In the Recessive Lethals model, each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. This model approximates the effect of inbreeding if each individual in the starting population had one recessive lethal allele in its genome. The fact that the simulation program assumes that all the lethal alleles are at the same locus has a very minor impact on the probability that an individual will die because of homozygosity for one of the lethal alleles. In the model, homozygosity for different lethal alleles are mutually exclusive events, whereas in a multilocus model an 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

$$SE(p) = \sqrt{[p \times (1-p)/n]}\ ,$$

in which the frequency of extinction was p over n simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Availability of the VORTEX Simulation Program

VORTEX Version 5.1 is written in the C programming language and compiled with the Lattice 80286C Development System (Lattice Inc.) for use on microcomputers using the MS-DOS (Microsoft Corp.) operating system. Copies of the compiled program and a manual for its use are available for nominal distribution costs from the Captive Breeding Specialist Group (Species Survival Commission, IUCN), 12101 Johnny Cake Ridge Road, Apple Valley, Minnesota 55124, U.S.A. The program has been tested by many workers, but cannot be guaranteed to be error-free. Each user retains responsibility for ensuring that the program does what is intended for each analysis.

Sequence of Program Flow

(1) The seed for the random number generator is initialised with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for input and output devices, population parameters, duration of simulation, and number of interations.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as

$$N_{max} = (K + 3s) \times (1 + L)$$

in which K is the maximum carrying capacity (carrying capacity can be specified to change linearly for a number of years in a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), s is the annual environmental variation in the carrying capacity expressed as a standard deviation, and L is the specified maximum litter size. It is theoretically possible, but very unlikely, that a simulated population will exceed the calculated N_{max}. If this occurs then the program will give an error message and abort.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning it has been adjusted downward because of limiting memory often will not hamper the analyses. Except for limitations imposed by the size of the computer memory (VORTEX can use extended memory, if available), the only limit to the size of the analysis is that no more than 20 populations exchanging migrants can be simulated.

(5) The expected mean growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also estimated. Life-table estimations assume no limitation by carrying capacity, no limitation of mates, and no loss of fitness due to inbreeding depression, and the estimated intrinsic growth rate assumes that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life-table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7–26 below. For exploratory modelling, 100 iterations are usually sufficient to reveal gross trends among sets of simulations with different input parameters. For more precise examination of population behaviour under various scenarios, 1000 or more simulations should be used to minimise standard errors around mean results.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age–sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table. Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. VORTEX therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy–Weinberg equilibrium, is given by

$$H_e = 1 - \Sigma(p_i^2)\,,$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1·0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity by means of random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (assuming that the initial value was not zero) (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by VORTEX is the mean inbreeding coefficient of the population.

(9) The user specifies one of three options for modelling the effect of inbreeding: (a) no effect of inbreeding on fitness, that is, all alleles are selectively neutral, (b) each founder individual has one unique lethal and one unique non-lethal allele (Recessive Lethals option), or (c) first-year survival of each individual is exponentially related to its inbreeding coefficient (Heterosis option). The first case is clearly an optimistic one, as almost all diploid

populations studied intensively have shown deleterious effects of inbreeding on a variety of fitness components (Wright 1977; Falconer 1981). Each of the two models of inbreeding depression may also be optimistic, in that inbreeding is assumed to have an impact only on first-year survival. The Heterosis option allows, however, for the user to specify the severity of inbreeding depression on juvenile survival.

(10) Years are iterated via steps 11–25 below.

(11) The probabilities of females producing each possible litter size are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percentage of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates for their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) of the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for linear changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of breeding-age males specified to be breeding.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified sex ratio at birth. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) If the Heterosis option is chosen for modelling inbreeding depression, the genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between a new animal, A, and another existing animal, B is

$$f_{AB} = 0 \cdot 5 \times (f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals i and j, M is the mother of A, and P is the father of A. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_{AA} = 0 \cdot 5 \times (1 + F)$. [See Ballou (1983) for a detailed description of this method for calculating inbreeding coefficients.]

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If the Heterosis model of inbreeding depression is used and an individual is inbred, the survival probability is multiplied by e^{-bF} in which b is the number of lethal equivalents per haploid genome.

If the Recessive Lethals model is used, all offspring that are homozygous for a lethal allele are killed.

(18) The age of each animal is incremented by 1, and any animal exceeding the maximum age is killed.

(19) If more than one population is being modelled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age–sex class, VORTEX continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age class are created. Each immigrant is assigned two unique alleles, one of which will be a recessive lethal in the Recessive Lethals model of inbreeding depression. Each immigrant is assumed to be genetically unrelated to all other individuals in the population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N-K)/N$, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported. A simulated population is determined to be extinct if one of the sexes has no representatives.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate, are calculated across iterations and printed out.

Assumptions Underpinning VORTEX

It is impossible to simulate the complete range of complex processes that can have an impact on wild populations. As a result there are necessarily a range of mathematical and biological assumptions that underpin any PVA program. Some of the more important assumptions in VORTEX include the following.

(1) Survival probabilities are density independent when population size is less than carrying capacity. Additional mortality imposed when the population exceeds K affects all age and sex classes equally.

(2) The relationship between changes in population size and genetic variability are examined for only one locus. Thus, potentially complex interactions between genes located on the same chromosome (linkage 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 ($N \pm SD = 151 \pm 123$) 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 $(r) = 0{\cdot}112$ *v.* actual SD $(r) = 0{\cdot}141$]. 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.

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Appendix. Sample Output from VORTEX

Explanatory comments are added in italics

VORTEX—simulation of genetic and demographic stochasticity

TEST — *Simulation label and output file name*

Fri Dec 20 09:21:18 1991

2 population(s) simulated for 100 years, 100 runs

VORTEX first lists the input parameters used in the simulation:

HETEROSIS model of inbreeding depression
with 3·14 lethal equivalents per diploid genome

Migration matrix:

	1	2
1	0·9900	0·0100
2	0·0100	0·9900

i.e. 1% probability of migration from Population 1 to 2, and from Population 2 to 1

First age of reproduction for females: 2 for males: 2
Age of senescence (death): 10
Sex ratio at birth (proportion males): 0·5000

Population 1:

Polygynous mating; 50·00 per cent of adult males in the breeding pool.
Reproduction is assumed to be density independent.
50·00 (EV = 12·50 SD) per cent of adult females produce litters of size 0
25·00 per cent of adult females produce litters of size 1
25·00 per cent of adult females produce litters of size 2
EV is environmental variation
50·00 (EV = 20·41 SD) per cent mortality of females between ages 0 and 1
10·00 (EV = 3·00 SD) per cent mortality of females between ages 1 and 2
10·00 (EV = 3·00 SD) per cent annual mortality of adult females (2<=age<=10)
50·00 (EV = 20·41 SD) per cent mortality of males between ages 0 and 1
10·00 (EV = 3·00 SD) per cent mortality of males between ages 1 and 2
10·00 (EV = 3·00 SD) per cent annual mortality of adult males (2<=age<=10)

EVs have been adjusted to closest values possible for binomial distribution.
EV in reproduction and mortality will be correlated.
Frequency of type 1 catastrophes: 1·000 per cent
with 0·500 multiplicative effect on reproduction
and 0·750 multiplicative effect on survival
Frequency of type 2 catastrophes: 1·000 per cent
with 0·500 multiplicative effect on reproduction
and 0·750 multiplicative effect on survival

Initial size of Population 1: (set to reflect stable age distribution)

Age	1	2	3	4	5	6	7	8	9	10	Total	
	1	0	1	1	0	1	0	0	1	0	5	Males
	1	0	1	1	0	1	0	0	1	0	5	Females

Carrying capacity = 50 (EV = 0·00 SD)
with a 10·000 per cent decrease for 5 years.

Animals harvested from population 1, year 1 to year 10 at 2 year intervals:
1 females 1 years old
1 female adults (2<=age<=10)
1 males 1 years old
1 male adults (2<=age<=10)

Animals added to population 1, year 10 through year 50 at 4 year intervals:
1 females 1 years old
1 females 2 years old
1 males 1 years old
1 males 2 years old

Input values are summarised above, results follow.

VORTEX now reports life-table calculations of expected population growth rate.

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

r = −0·001 lambda = 0·999 RO = 0·997

Generation time for: females = 5·28 males = 5·28

Note that the deterministic life-table calculations project approximately zero population growth for this population.

Stable age distribution:

Age class	females	males
0	0·119	0·119
1	0·059	0·059
2	0·053	0·053
3	0·048	0·048
4	0·043	0·043
5	0·038	0·038
6	0·034	0·034
7	0·031	0·031
8	0·028	0·028
9	0·025	0·025
10	0·022	0·022

Ratio of adult (>=2) males to adult (>=2) females: 1·000

Population 2:

Input parameters for Population 2 were identical to those for Population 1. Output would repeat this information from above.

Simulation results follow.

Population1

Year 10

N[Extinct] = 0, P[E] = 0·000
N[Surviving] = 100, P[S] = 1·000
Population size = 4·36 (0·10 SE, 1·01 SD)
Expected heterozygosity = 0·880 (0·001 SE, 0·012 SD)
Observed heterozygosity = 1·000 (0·000 SE, 0·000 SD)
Number of extant alleles = 8·57 (0·15 SE, 1·50 SD)

Population summaries given, as requested by user, at 10-year intervals.

Year 100

N[Extinct] = 86, P[E] = 0·860
N[Surviving] = 14, P[S] = 0·140
Population size = 8·14 (1·27 SE, 4·74 SD)
Expected heterozygosity = 0·577 (0·035 SE, 0·130 SD)
Observed heterozygosity = 0·753 (0·071 SE, 0·266 SD)
Number of extant alleles = 3·14 (0·35 SE, 1·29 SD)

In 100 simulations of 100 years of Population1:
86 went extinct and 14 survived.
This gives a probability of extinction of 0·8600 (0·0347 SE),
or a probability of success of 0·1400 (0·0347 SE).
99 simulations went extinct at least once.
Median time to first extinction was 5 years.
Of those going extinct,
mean time to first extinction was 7·84 years (1·36 SE, 13·52 SD).
123 recolonisations occurred.
Mean time to recolonisation was 4·22 years (0·23 SE, 2·55 SD).
110 re-extinctions occurred.
Mean time to re-extinction was 54·05 years (2·81 SE, 29·52 SD).

Mean final population for successful cases was 8·14 (1·27 SE, 4·74 SD)

Age 1	Adults	Total	
0·14	3·86	4·00	Males
0·36	3·79	4·14	Females

During years of harvest and/or supplementation
mean growth rate (r) was 0·0889 (0·0121 SE, 0·4352 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
mean growth rate (r) was −0·0267 (0·0026 SE, 0·2130 SD)

Population growth in the simulation (r = −0·0267) was depressed relative to the projected growth rate calculated from the life table (r = −0·001) because of inbreeding depression and occasional lack of available mates.

Note: 497 of 1000 harvests of males and 530 of 1000 harvests of females could not be completed because of insufficient animals.

Final expected heterozygosity was 0·5768 (0·0349 SE, 0·1305 SD)
Final observed heterozygosity was 0·7529 (0·0712 SE, 0·2664 SD)
Final number of alleles was 3·14 (0·35 SE, 1·29 SD)

Population2

Similar results for Population 2, omitted from this Appendix, would follow.

******** Metapopulation Summary ********

Year 10

N[Extinct] = 0, P[E] = 0·000
N[Surviving] = 100, P[S] = 1·000
Population size = 8·65 (0·16 SE, 1·59 SD)
Expected heterozygosity = 0·939 (0·000 SE, 0·004 SD)
Observed heterozygosity = 1·000 (0·000 SE, 0·000 SD)
Number of extant alleles = 16·92 (0·20 SE, 1·96 SD)

Metapopulation summaries are given at 10-year intervals.

Year 100

N[Extinct] = 79, P[E] = 0·790
N[Surviving] = 21, P[S] = 0·210
Population size = 10·38 (1·37 SE, 6·28 SD)
Expected heterozygosity = 0·600 (0·025 SE, 0·115 SD)
Observed heterozygosity = 0·701 (0·050 SE, 0·229 SD)
Number of extant alleles = 3·57 (0·30 SE, 1·36 SD)

In 100 simulations of 100 years of Metapopulation:
79 went extinct and 21 survived.
This gives a probability of extinction of 0·7900 (0·0407 SE),
or a probability of success of 0·2100 (0·0407 SE).
97 simulations went extinct at least once.
Median time to first extinction was 7 years.
Of those going extinct,
mean time to first extinction was 11·40 years (2·05 SE, 20·23 SD).
91 recolonisations occurred.
Mean time to recolonisation was 3·75 years (0·15 SE, 1·45 SD).
73 re-extinctions occurred.
Mean time to re-extinction was 76·15 years (1·06 SE, 9·05 SD).

Mean final population for successful cases was 10·38 (1·37 SE, 6·28 SD)

Age 1	Adults	Total	
0·48	4·71	5·19	Males
0·48	4·71	5·19	Females

During years of harvest and/or supplementation
mean growth rate (r) was 0·0545 (0·0128 SE, 0·4711 SD)
Without harvest/supplementation, prior to carrying capacity truncation,
mean growth rate (r) was −0·0314 (0·0021 SE, 0·1743 SD)

Final expected heterozygosity was 0·5997 (0·0251 SE, 0·1151 SD)
Final observed heterozygosity was 0·7009 (0·0499 SE, 0·2288 SD)
Final number of alleles was 3·57 (0·30 SE, 1·36 SD)

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