ANÁLISIS DE VIABILIDAD DE POBLACIÓN Y HÁBITAT PARA EL MONO AULLADOR DE MANTO (*Alouatta palliata mexicana*)

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE MANTLED HOWLER MONKEY (*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 de marzo de 1995
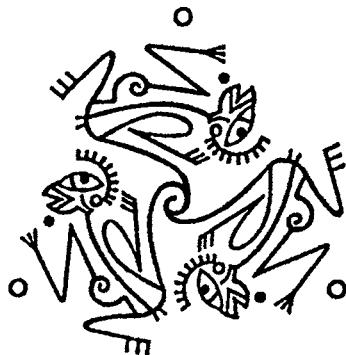
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Recopilado por los Participantes del Taller
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Rodríguez Luna, E., L. Cortés Ortiz, P. Miller, & S. Ellis (eds.). 1995. *Population and Habitat Viability Assessment for the mantled howler monkey* (Alouatta palliata mexicana). IUCN/SSC Conservation Breeding Specialist Group: Apple Valley, MN.

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24 May 1996

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Sección 1
Resumen Ejecutivo

RESUMEN EJECUTIVO

Introducción

México es considerado como uno de los países con mayor diversidad biológica a nivel mundial; sin embargo, su riqueza está siendo reducida por diversas actividades humanas a un grado en el que muchas especies se encuentran en la vía de la extinción.

Particularmente, los bosques tropicales han sufrido un gran decremento, siendo sustituidos principalmente por áreas agrícolas y ganaderas. Entre otras implicaciones, esto ha significado la reducción del hábitat para los primates mexicanos. En México se encuentra el límite norte para la distribución de los primates neotropicales, aquí se encuentran el mono aullador negro (*Alouatta pigra*), el mono aullador de manto (*Alouatta palliata mexicana*), y el mono araña con dos subespecies (*Ateles geoffroyi vellerosus* y *A. geoffroyi yucatanensis*). Estos cuatro primates han sido considerados como especies en peligro, y de manera más precisa, mediante un taller de Conservación, Análisis y Manejo Planificado (CAMP por sus siglas en inglés), realizado del 27 de febrero al 1° de marzo de este año, el primero se consideró como taxón en "Riesgo Bajo" y los tres últimos como "Vulnerables" (de acuerdo al nuevo criterio de evaluación de la IUCN, versión 2.2., 1994). Se ha estimado que la reducción del hábitat de estos animales alcanza una magnitud del 80% o más en México (Estrada, 1993), lo cual revela el nivel de amenaza en que se encuentran.

De continuar la tendencia actual de transformación de los bosques tropicales en México, estos primates deberán ser colocados pronto en las categorías superiores de Amenaza. Por tanto, es necesario desplegar una serie de acciones conservacionistas a fin de evitar la desaparición de las poblaciones silvestres de estos monos.

Evaluación de Viabilidad de Población y de Hábitat (PHVA, por sus siglas en inglés)

En el taller PHVA para *Alouatta palliata mexicana* se propuso utilizar información biológica y opiniones de expertos para estimar el riesgo de extinción en que se encuentra este taxón; considerando tamaño y distribución de sus poblaciones, así como los factores que le afectan negativamente.

Para estimar el riesgo en posibles escenarios ecológicos futuros se utilizó un modelo de simulación (VORTEX, versión 7.0) y se identificaron los factores críticos para el decremento de las poblaciones. Asimismo, se consideraron algunas alternativas de manejo que podrían mejorar la situación del primate.

Se reconoció que para esta evaluación se dispuso de datos de campo de desigual calidad, siendo necesario realizar suposiciones en algunos casos. Por tanto, muchas de las conclusiones y recomendaciones deberán ser consideradas críticamente conforme se disponga de mejor información.

Resumen de Recomendaciones
Esquema general para el estudio y conservación de *A. p. mexicana.*

Dada la acelerada perturbación, fragmentación y pérdida de hábitat de este mono, es necesario desarrollar un programa de estudio y conservación que asegure su permanencia como parte del patrimonio natural de México.

Estudios

    a) Taxonomía a nivel anatómico y genético
    b) Distribución y áreas de occupación
    c) Ocupación de distintos tipos de hábitat
    d) Densidad poblacional y estimación de ámbito hogareño en distintas condiciones ambientales
    e) Cambios en la organización social en relación a variación ambiental
    f) Crecimiento poblacional (tasas de natalidad y mortalidad)
    g) Migración entre poblaciones
    h) Cambios en las estrategias de forrajeo
    I) Efectos de la fragmentación sobre poblaciones silvestres
    j) Estudios sobre caza, captura y comercialización de animales

Acciones Conservacionistas

Mejorar manejo en áreas naturales protegidas
    a) Protección legal
    b) Vigilancia
    c) Monitoreo de poblaciones
    d) Restauración ecológica
    e) Desarrollo de programas educativos
    f) Reintroducción y/o suplementaciones (sólo en condiciones especiales y bajo estrictas medidas de seguridad)
    g) Vinculación (instituciones de investigación, dependencias gubernamentales, asentamientos humanos locales) para desarrollo de programas

Establecer nuevas áreas naturales protegidas
    a) Prospección de áreas candidatas con poblaciones silvestres de monos
    b) Identificación y planteamiento de áreas apropiadas para conservación
    c) Propuesta de plan de manejo
    d) Todos los citados para el punto anterior

Desarrollar un programa de translocaciones (programa piloto)
    a) Análisis de factibilidad (poblaciones y área de liberación)
    b) Captura
    c) Transporte

d) Evaluación clínica
e) Manejo en cautiverio
f) Liberación
g) Monitoreo

Manejo de metapoblación en hábitat fragmentado
a) Identificación de áreas fragmentadas
b) Translocaciones
c) Monitoreo
d) Manejo de población viable

Control y reducción de tráfico
a) Formulación de norma jurídica apropiada
b) Vigilancia efectiva en áreas silvestres
c) Vigilancia efectiva en zonas rurales y urbanas donde se realiza la comercialización
d) Mecanismo apropiado para la formulación de denuncias, consignaciones y decomisos.
e) Penalización debidamente tipificada para los traficantes
f) Campaña educativa para impedir el tráfico
g) Canalización de animales decomisados

Educación
a) Desarrollo de programas para lograr una actitud favorable y de colaboración hacia la conservación de los primates, utilizando diferentes medios masivos de comunicación.
b) Implementación de programas educativos en los zoológicos

Colaboración interinstitucional
a) Sociedades científicas
b) Instituciones educativas y zoológicos
c) Dependencias gubernamentales
d) Sectores de la sociedad civil
e) Organismos internacionales dedicados a la conservación

Incluir las estrategias de conservación de los primates en programas de conservación regionales.
a) Promoción de alternativas de desarrollo sustentable
b) Hacer copartícipes de los programas a los habitantes locales

Reporte de PHVA del Mono Aullador de Manto

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Sección 2
Taxonomía y Distribución
de *Alouatta palliata mexicana*
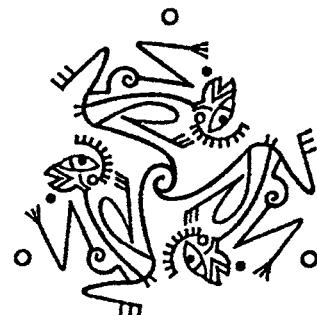
TAXONOMÍA Y DISTRIBUCIÓN DE *Alouatta palliata mexicana*

Objetivo de la Revisión

Analizar la posición taxonómica de *Alouatta palliata mexicana*, y sus áreas de distribución original, actual y potencial; estimar sus números poblacionales y detectar algunos factores que pudieran estar afectando a sus poblaciones; con la finalidad de establecer su estado de amenaza, así como proponer algunas medidas que puedan ayudarnos a su conservación.

Arreglo Taxonómico

Orden: Primates
    Familia: Cebidae
        Genero: *Alouatta*
            Especie: *Alouatta palliata*
                Subespecies: *Alouatta palliata palliata*
                              Alouatta palliata mexicana
                              Alouatta palliata aecuatorialis

       La validez taxonómica de *Alouatta palliata mexicana* es generalmente aceptada, considerándose actualmente como una de las tres subespecies que se han descrito para la especie. Si bien, acorde con Lawrence (1933) morfológicamente es muy difícil distinguir esta subespecie de *A. palliata palliata*, hasta la fecha no existe ningún reporte de estas subespecies viviendo en simpatría. Dada la gran variación individual que existe entre los caracteres diagnósticos de estas subespecies, aunque no se considera prioritario, se estima conveniente recomendar la realización de una revisión taxonómica a nivel subespecífico utilizando técnicas modernas.

Distribución Geográfica

Distribución original

La distribución original de *Alouatta palliata mexicana* comprende los Estados de Veracruz, Tabasco, Oaxaca y Chiapas, en México; aunque existen registros muy viejos y dudosos para Campeche y Quintana Roo (Elliot, 1904 ?; Díaz de León, 1905 y Villa, 1959 ?). En Centroamérica se le ha reportado para Belice y Guatemala; aunque también es requerida su confirmación.

Ocupación de distintos tipos de hábitat

Los monos aulladores de la especie *A. palliata* son adaptables a diferentes tipos de vegetación. Se pueden encontrar en: bosque maduro siempre verde (selva alta perennifolia), bosque deciduo, bosque ripario, vegetación secundaria, bosque subxérico (Neville, et. al., 1988), selva mediana

subperennifolia (Estrada, 1989). Habitan sitios que varían desde el nivel del mar hasta los 1100 m.s.n.m. aproximadamente.

Distribución actual y tamaño de la población

El cálculo de las densidades de *A. p. mexicana* y de las áreas ocupadas por esta subespecie en México se ha realizado manejando datos y estimaciones de diferentes procedencias y realizando extrapolaciones, a falta de datos más exactos. La única información relativamente detallada disponible es para la zona de Los Tuxtlas (Estrada 1982; 1989; 1994).

Estrada (1989; 1994) propone una densidad de 23 individuos por Km^2 en áreas protegidas de Los Tuxtlas y 3.6 individuos por Km^2 en las que no están protegidas. Estima una población de 1152 individuos de *A. p. mexicana* para la región de Los Tuxtlas (1994) a partir de la densidad de 3.6 individuos por Km^2. Sin embargo, en sus gráficas sobre las tropas encontradas en su sitio de estudio, presenta datos que indican una población superior (aproximadamente 1800 individuos). Estos datos corresponden al 40% de los 120 fragmentos que estudió en el área del Volcán de San Martín Tuxtla; en los cuales encontró *A. palliata mexicana*. Estos fragmentos presentan un rango de extensión de 1 a 2000 ha. Considerando los datos anteriores se estimó (redondeando) una densidad promedio de 10 individuos por Km^2. Por tratarse de una densidad intermedia entre las dos proporcionadas anteriormente, puede ser una estimación para la densidad en otras áreas ocupadas por esta subespecie en México.

Para este análisis consideramos únicamente las áreas protegidas que aún existen dentro del rango de distribución original de la especie y algunas áreas biológicas de gran extensión que no están protegidas. Para todas estas áreas no se tienen datos, pero presentan una vegetación similar y se supone que es un hábitat menos fragmentado que el de Los Tuxtlas, por lo que se podría estar subestimando a la población.

García-Orduña (1986, sin publucar) realizó una estimación del área ocupada por selva en Los Tuxtlas, obteniendo un área total de 623 Km^2. Asumiendo que las dos principales áreas protegidas en la región (Volcán de San Martín Tuxtla, 70 Km^2 y Sierra de Santa Martha, 250 Km^2; Estrada 1989) no han sufrido una deforestación significativa y ave el área ocupada por otros fragmentos en la región (303 Km^2 en 1986) presenta una tasa de deforestación del 4.2% anual (Dirzo, 1992), en la actualidad quedarían solamente 197.287 Km^2 en estos fragmentos.

Extrapolando la proporción de fragmentos ocupados por *A. p. mexicana* en el estudio de Estrada (40% del total) a toda la región de Los Tuxtlas (197.287 Km^2 de selva en fragmentos), obtenemos 78.91 Km^2 ocupados por la subespecie en fragmentos fuera de las dos áreas principales en Los Tuxtlas.

Para el cálculo del área ocupada por *A. p. mexicana* en las demás localidades de México, se ha considerado la información de Vásquez-Sánchez (1988) para la extensión de El Ocote y de Muñoz-Alonso (1994) para Manzanillar, en Chiapas; así como la de Estrada (1989) para la extensión del área Uxpanapa-Chimalapas en Veracruz-Oaxaca.

La capacidad de carga se estimó utilizando los datos de ámbito hogareño (Estrada, 1989; 1994) reportado para la especie (entre 30 y 60 ha para un grupo de 10 individuos).

La composición de los grupos en todas estas áreas se ha obtenido generalizando los datos que aporta Estrada (1989): para fragmentos protegidos un tamaño promedio de 10 individuos y una composición de 3 machos, 4 hembras, 1.5 juveniles y 1.5 infantes; para fragmentos no protegidos, la composición de 1 macho, 1.5 hembras, 1 juvenil y 1 infante (esta composición ha sido usada para los fragmentos más pequeños en Los Tuxtlas).

Volcán San Martín Tuxtla (Región de Los Tuxtlas, Veracruz)

Situación legal: Área protegida: Reserva Especial de la Biósfera
Area total: 7000 ha (Estrada, 1989)
Area ocupada: 7000 ha
Tipo de vegetación: Selva alta perennifolia y selva mediana subperennifolia.
Densidad ocupada para cálculos: 16.45 ind./Km^2 (inferida)
Proporción de edades y sexos en la población (ocupada para la estimación de la estructura):
       3♂ : 4♀ : 1.5 juv. : 1.5 inf.
Número de individuos en la población: 1152 (Estrada, 1994)
Machos: 346   Juveniles: 172
Hembras: 461   Infantes: 173
Capacidad de carga: entre 1166.66 y 2333.33 individuos

Sierra de Santa Martha (Región de Los Tuxtlas, Veracruz)

Situación legal: Área protegida: Reserva Especial de la Biósfera
Área total: 55000 ha (SEDUE, Dic. 28/4/80)
Área ocupada: Abarca alrededor de 10000 ha (Ramírez, F, y Paré, L. 1993)(3500 ha zona núcleo y 6500 ha zona de amortiguamiento, aproximadamente).
Tipo de vegetación: Selva alta perennifolia y selva mediana subperennifolia.
Densidad ocupada para cálculos: 10 ind./Km^2
Proporción de edades y sexos en la población (ocupada para la estimación de la estructura):
       3♂ : 4♀ : 1.5 juv. : 1.5 inf.
Número de individuos: 1000
Machos: 300   Juveniles: 150
Hembras: 400   Infantes: 150
Capacidad de carga: entre 1666.66 y 3333.33 individuos

Región de Uxpanapa (Veracruz)

Situación legal: Área no protegida
Área total: 165000
Área ocupada: 165000
Tipo de vegetación: Selva alta perennifolia y selva mediana subcaducifolia.
Densidad ocupada para cálculos: 10 ind./Km^2
Proporción de edades y sexos en la población (ocupada para la estimación de la estructura):
    3♂ : 4♀ : 1.5 juv. : 1.5 inf.
Número de individuos en la población: 1650
Machos: 495   Juveniles: 247
Hembras: 660   Infantes: 248
Capacidad de carga: entre 2750 y 5500 individuos

Sierra de Los Chimalapas (Oaxaca)

Situación legal: Área no protegida
Area total: 167000 ha (Wendt, 1983)
Area ocupada: 83500 ha (Estrada, 1989)
Tipo de vegetación: Selva alta perennifolia y selva mediana subcaducifolia.
Densidad ocupada para cálculos: 10 ind./Km^2
Proporción de edades y sexos en la población (ocupada para la estimación de la estructura):
    3♂ : 4♀ : 1.5 juv. : 1.5 inf.
Número de individuos: 8350
Machos: 2505   Juveniles: 1252
Hembras: 3340   Infantes: 1253
Capacidad de carga: entre 20875 y 41750 individuos.

El Manzanillar (Chiapas)

Situación legal: Área no protegida (Propuesta de Reserva Ecológica según Muñoz-Alonso, 1994)
Área total: 2493 ha (Muñoz-Alonso, 1994)
Área ocupada: 2493 ha
Tipo de vegetación: Selva alta perennifolia.
Densidad ocupada para cálculos: 10 ind./Km^2
Proporción de edades y sexos en la población (ocupada para la estimación de la estructura):
    3♂ : 4♀ : 1.5 juv. : 1.5 inf.
Número de individuos en la población: 249
Machos: 75   Juveniles: 37
Hembras: 100   Infantes: 37
Capacidad de carga: entre 416.5 y 833 individuos.

El Ocote (Chiapas)

Situación legal: Área protegida: Zona de Protección Forestal y Faunística.
Área total: 48800 (Vázquez-Sánchez, 1988)
Área ocupada: 12000 ha (zona núcleo y zona de recuperación)
Tipo de vegetación: Selva alta perennifolia y selva mediana subcaducifolia.
Densidad ocupada para cálculos: 10 ind./Km^2
Proporción de edades y sexos en la población (ocupada para la estimación de la estructura):
  3♂ : 4♀ : 1.5 juv. : 1.5 inf.
Número de individuos en la población: 1200
Machos: 360   Juveniles: 180
Hembras: 480   Infantes: 180
Capacidad de carga: entre 2000 y 4000 individuos.

Otras áreas

Para las zonas de Macuspana y Teapa en el estado de Tabasco, México y para Guatemala y Belice no se tienen datos para realizar las estimaciones.

Estado de la Especie

En el libro rojo de la IUCN, en 1990 este taxón se incluía en la categoría indeterminado, ya que estaba considerado dentro de la especie *Alouatta villosa* (que incluía a los taxa ahora definidos como *A. palliata* y *A. pigra*). Sin embargo, en 1994 se incluye la especie *A. pigra*, pero inexplicablemente se elimina de la lista la especie *A. palliata* por completo. Durante un taller de Conservación, Análisis y Manejo Planificado (CAMP por sus siglas en inglés) para los primates mexicanos, realizado del 27 de febrero al 1° de marzo de este año, esta subespecie se determinó como "vulnerable", siguiendo el nuevo criterio para evaluar el estado de las especies de la IUCN (versión 2.2, 1994). La Convención sobre el Comercio Internacional de Flora y Fauna Silvestres, en 1986 la incluye en el apéndice I (Burton y Pearson, 1987) y SEDESOL (1994) la declara como especie en Peligro de Extinción.

Recomendaciones

Con base en el análisis de la información recabada, se recomienda como prioritaria la realización de trabajo de campo para conocer con precisión el área de distribución actual de esta subespecie; así como el tamaño de sus poblaciones.

Por otro lado, se hace imprescindible conocer las tendencias actuales de fragmentación y reducción del hábitat.

Finalmente, aunque no es una acción prioritaria, se recomienda realizar estudios taxonómicos basados en técnicas modernas, que permitan hacer una diferenciación clara entre las distintas subespecies.

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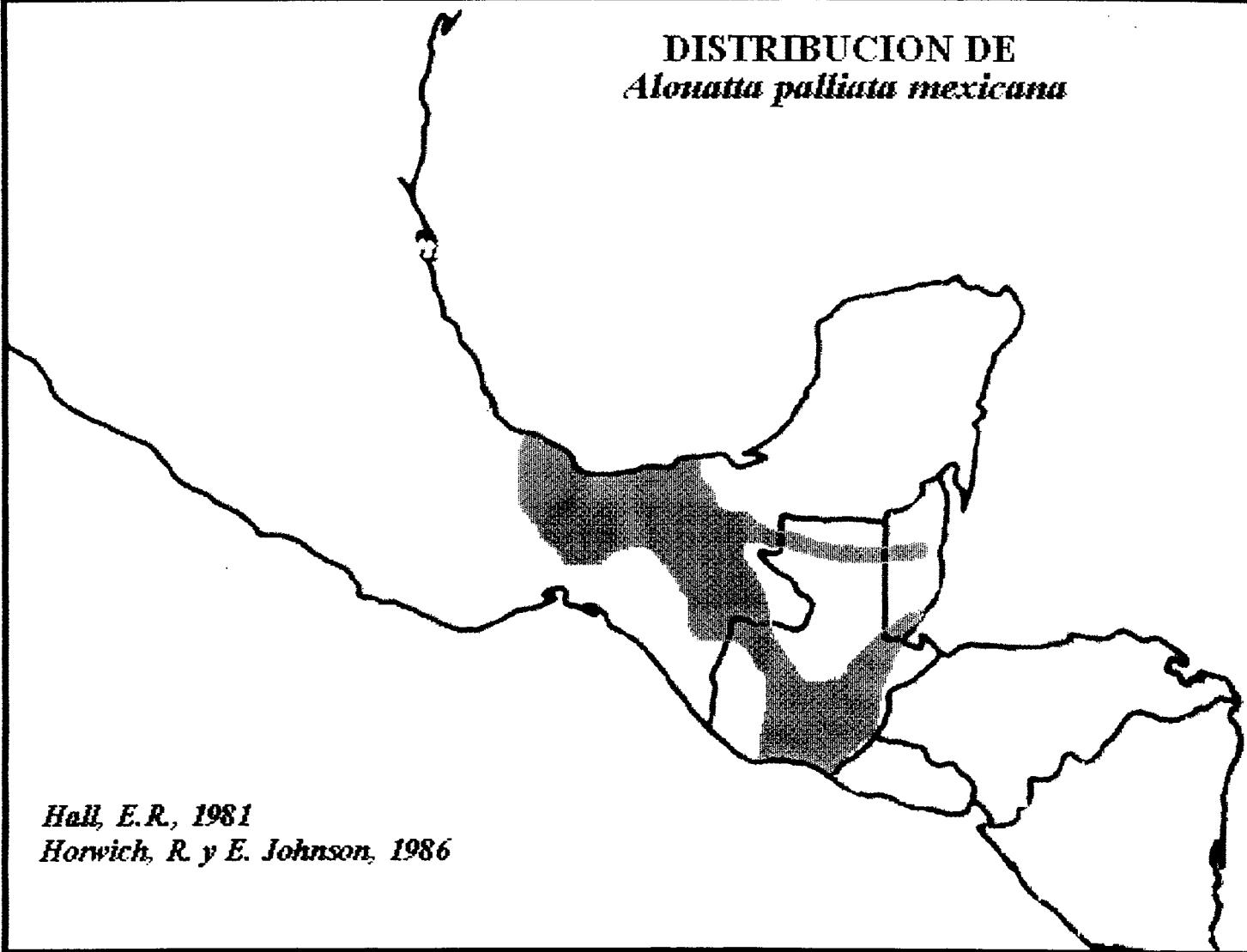
Hall, E.R., 1981
Horwich, R. y E. Johnson, 1986

Reporte de PHVA del Mono Aullador de Manto

PRINCIPALES AREAS PROTEGIDAS DE MESOAMERICA
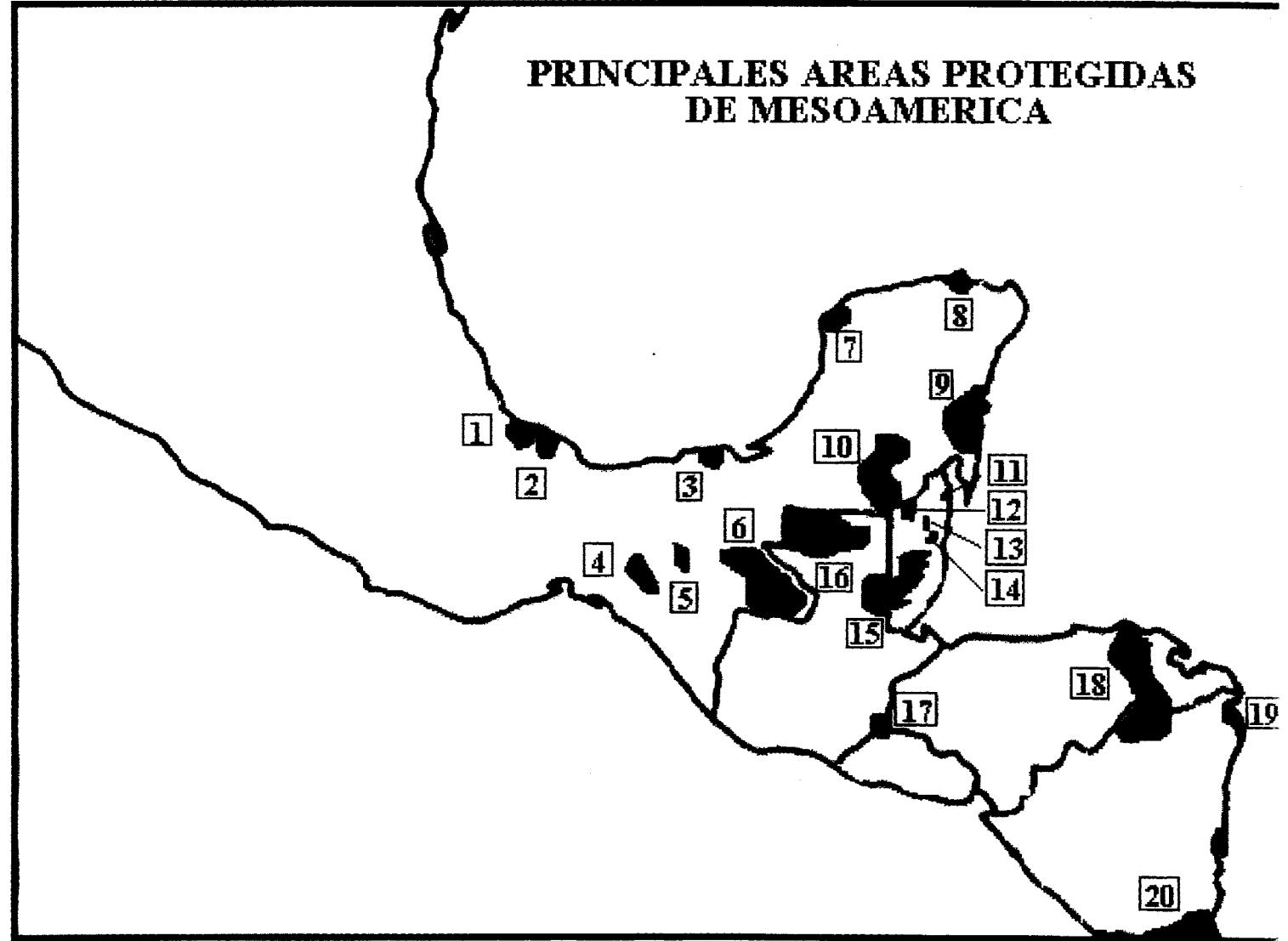
PRINCIPALES TIPOS DE CLIMAS DE MEXICO

Cálido húmedo 4.7%

Cálido subhúmedo 23%

Seco 28.3%

Muy seco 20.8%

Templado subhúmedo 20.5%

Templado húmedo 2.7%
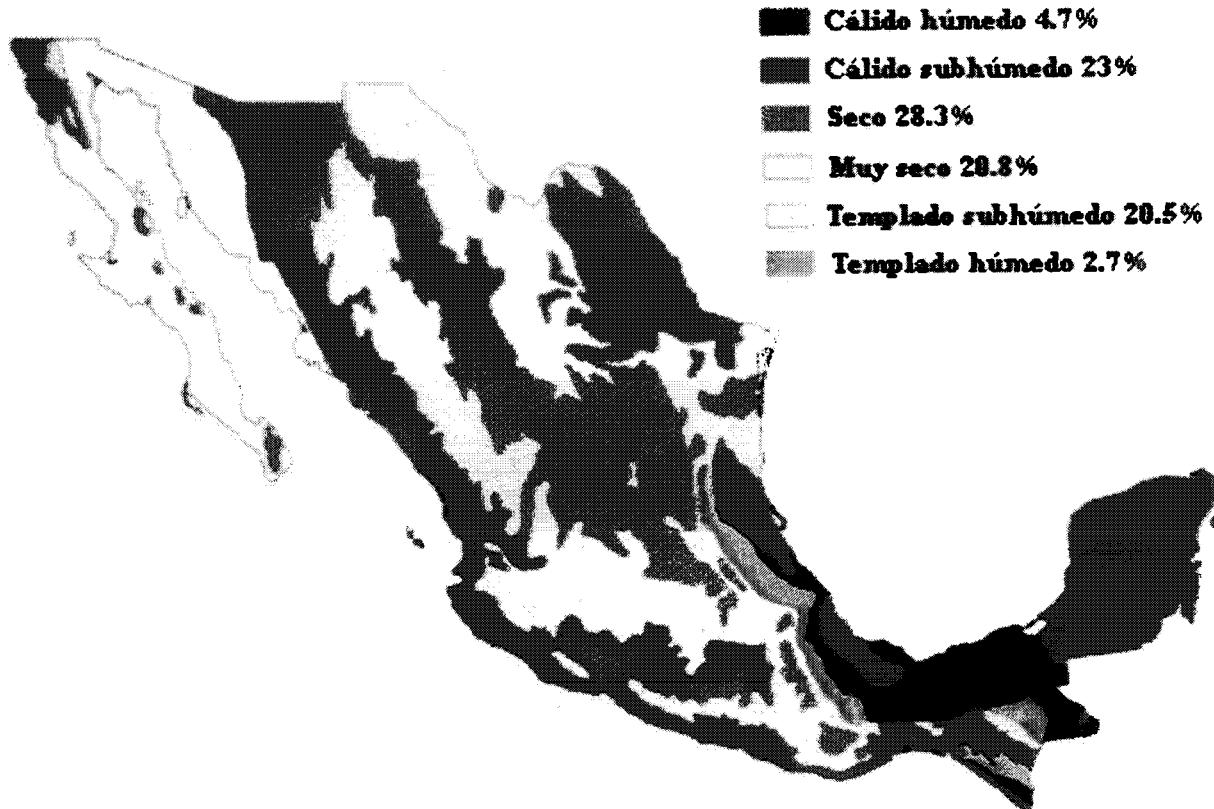
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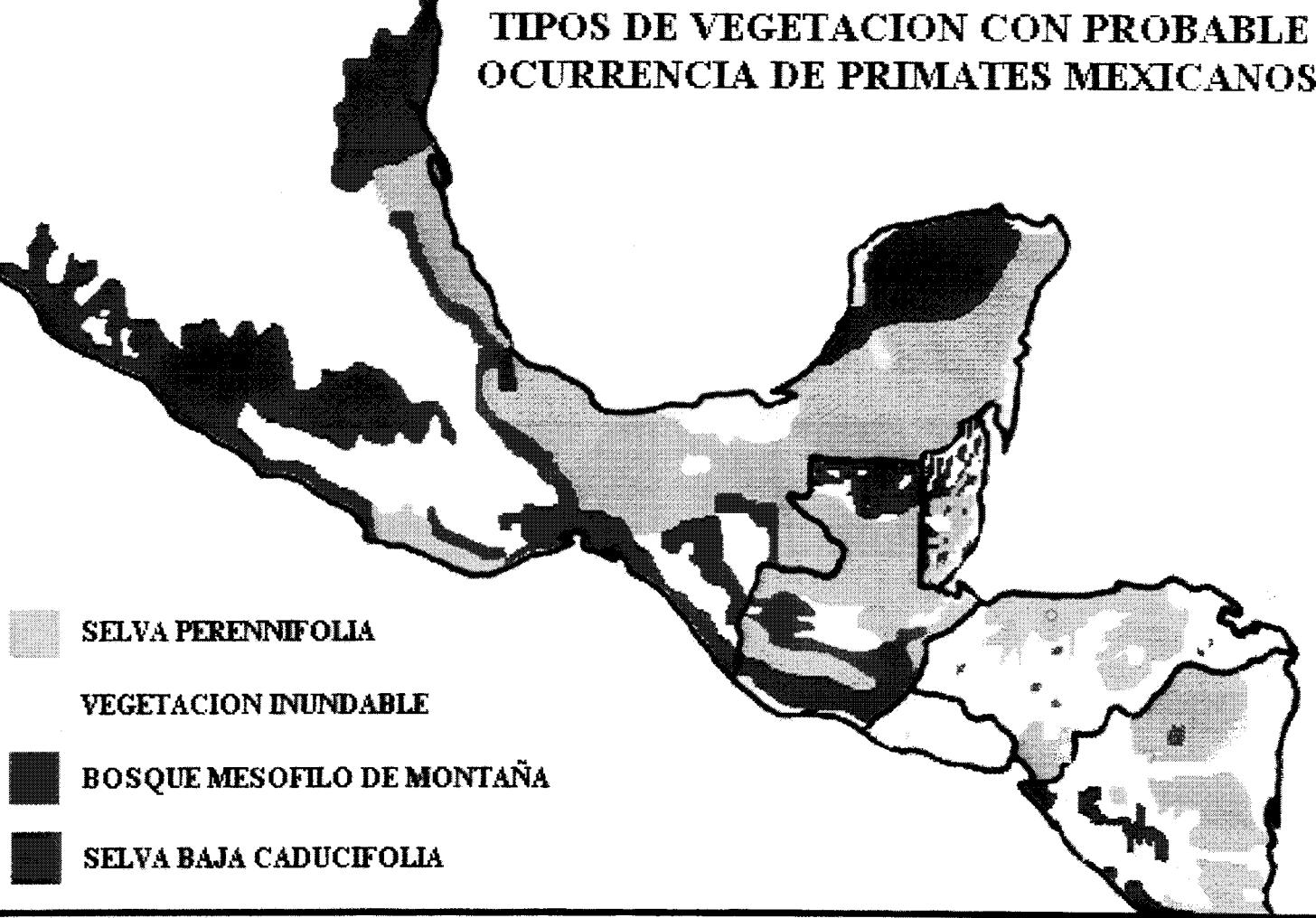
SELVA PERENNIFOLIA

VEGETACION INUNDABLE

BOSQUE MESOFILO DE MONTAÑA

SELVA BAJA CADUCIFOLIA

ANÁLISIS DE VIABILIDAD DE POBLACIÓN Y HÁBITAT PARA EL MONO AULLADOR DE MANTO
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 de marzo de 1995

Sección 3
Biológia de la Población y Modelos
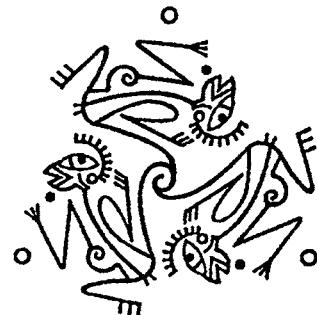
BIOLOGÍA DE POBLACIONES Y MODELAJE

Introducción

La población de monos aulladores (*Alouatta palliata mexicana*) en México, ocupa remanentes de bosque perturbado en los estados de Veracruz, Tabasco, Campeche, Oaxaca y Chiapas. No obstante, éste y los otros primates que habitan en esta área, *Alouatta pigra* y *Ateles geoffroyi*, están en peligro de extinción, como resultado de la cacería y captura ilegales, así como de la rápida destrucción de su hábitat natural.

Estrategias necesarias de manejo intensivo y sus efectos, se pueden modelar para sugerir cuáles prácticas serían las más efectivas para preservar a los monos aulladores en México. VORTEX, un paquete de modelaje y simulación escrito por Robert Lacy y Kim Hughes, se usó como una herramienta para estudiar la interacción de múltiples variables, tratadas estocásticamente.

El programa VORTEX es una simulación Monte Carlo de los efectos de fuerzas determinísticas y de eventos estocásticos tanto demográficos, ambientales y genéticos, sobre las poblaciones silvestres. VORTEX modela la dinámica de una población como eventos discretos y secuenciales (por ejemplo, nacimientos, muertes, catástrofes, etc.) que ocurren de acuerdo a probabilidades definidas. Las probabilidades de los eventos son modeladas como constantes o como variables aleatorias que siguen distribuciones específicas. VORTEX simula una población yendo paso a paso a través de series de eventos que describen el ciclo de vida típico de organismos diploides que se reproducen sexualmente.

VORTEX no intenta dar respuestas absolutas, ya que proyecta estocásticamente las interacciones de muchos parámetros que entran en el modelo y por la aleatoriedad de los procesos implicados en la naturaleza. La interpretación de los resultados depende de nuestro conocimiento de la biología del primate, las condiciones que afectan a la población y los posibles cambios en el futuro.

Introducción de Parámetros para las Simulaciones

Edad de la primera reproducción: VORTEX define la reproducción como nacimientos. Por ello, dado que la edad de la madurez sexual de las hembras es de 36 meses con un período de gestación de aproximadamente 6 meses (Glander, 1980), la primera reproducción para las hembras se estableció conservadoramente en 4 años. La madurez sexual para machos es alcanzada a los 42 meses, sin embargo, la estructura social en las tropas de monos aulladores generalmente prohibe que los machos menores de 5 años se reproduzcan.

Producción de descendencia: El intervalo entre nacimientos se estableció en 2 años para monos aulladores. Por ello, el 50% de las hembras reproductivas no se reproducen en un año dado. De las hembras que se reproducen, todas procrean sólo a una cría.

La variación en la reproducción es modelada en VORTEX introduciendo una desviación estándar (SD), por la proporción de hembras que fallan en producir descendencia en un año determinado. Por falta de datos empíricos, nosotros asumimos tal variación (debida a las fluctuaciones en abundancia de alimento y variaciones en la edad a la cual las hembras alcanzan la madurez sexual) en 25% de la media. VORTEX entonces determina el porcentaje reproductivo cada año de la simulación, muestreando de una distribución binomial con la media específica (50%) y SD (12.5%).

Como no existen datos que indiquen que la proporción sexual al nacer sea diferente de 50:50 en monos aulladores, nosotros usamos una tasa sexual igual para todos los escenarios.

Edad de senectud: VORTEX asume que todos los animales pueden reproducirse (en una tasa normal) a través de toda su vida adulta. Datos generales para poblaciones silvestres sugieren que los monos aulladores pueden alcanzar 20 años de edad, aunque esto probablemente es un evento raro. Froehlich, et al (1981) capturaron un macho en la Isla de Barro Colorado, en Panamá, que se estimó en 20.5 años de edad, basados en el desgaste dental.

Mortalidad: Nosotros construimos dos diferentes esquemas de mortalidad que a *grosso modo* corresponden a datos de dos poblaciones de monos aulladores separadas. El escenario de "baja" mortalidad usa datos de una población translocada a la isla Agaltepec, en el Lago de Catemaco, Veracruz, México. Esta población se presume tener una densidad muy baja con un amplio territorio y recursos alimenticios. El esquema de mortalidad de esta población (adaptado de Cortés-Ortiz et al, 1994) es el siguiente:

	% de Mortalidad (SD)	
Clase de edad	Machos	Hembras
0-1	15.0 (4.5)	10.0 (3.0)
1-2	2.0 (1.0)	0.5 (2.0)
2-3	2.0 (1.0)	0.0 (2.0)
3-4	0.0 (2.0)	0.0 (2.0)
4-5	0.0 (2.0)	4.5 (1.4)
5 en adelante	3.75 (1.1)	4.5 (1.4)

El esquema alternativo de "alta" mortalidad representa una población similar a la que ocurre en la Isla de Barro Colorado, Panamá (Froehlich et al, 1981). Se piensa que esta población está en una densidad mayor que la de la isla Agaltepec, con gran competencia por una variedad de recursos. El esquema de "alta" mortalidad es el siguiente:

	% de Mortalidad (SD)	
Clase de edad	Machos	Hembras
0-1	15.0 (4.5)	10.0 (3.0)
1-2	12.0 (3.6)	10.0 (3.0)
2-3	10.0 (3.0)	5.0 (1.5)
3-4	15.0 (4.5)	5.0 (1.5)
4-5	10.0 (3.0)	12.0 (3.6)
5 en adelante	12.0 (3.6)	12.0 (3.6)

Este esquema, de hecho, parece ser optimista comparado con la tabla actual de mortalidad presentada por Froehlich et al (1981) en la cual casi el 90% y 70% de machos y hembras respectivamente, mueren antes de alcanzar los 5 años de edad. Los participantes en el taller consideraron que este nivel de mortalidad es demasiado alto para las poblaciones de aulladores en México.

Debido a que la mortalidad de juveniles (clase de edad 0-1) fue la misma en ambos esquemas de mortalidad propuestos, se construyeron escenarios que variaran específicamente este parámetro para investigar su impacto sobre la persistencia de poblaciones. Se aumentó la mortalidad de las hembras en 15% y 20%, con la correspondiente mortalidad para machos establecida en 20% y 25%. Tal aumento en la mortalidad juvenil puede reflejar la pérdida de individuos debida a la cacería ilegal para consumo o para tráfico de mascotas, ambos de los cuales existen en México (Estrada y Coates-Estrada, 1984).

Capacidad de carga: K define un límite superior para el tamaño de la población, arriba del cual se impone una mortalidad adicional para regresar la población a K. VORTEX, por tanto, usa K para imponer la dependencia de la densidad sobre las tasas de sobrevivencia.

Alouatta palliata mexicana existe en numerosas poblaciones aisladas ubicadas en el sur de México. La densidad estimada para monos aulladores en esas áreas varía de 3.6 individuos por Km^2, en áreas no protegidas (Estrada y Coates-Estrada, 1994) a 23 individuos por Km^2, en algunas de las áreas protegidas alrededor de Los Tuxtlas (Estrada, 1989). Para calcular la capacidad de carga para nuestras simulaciones, usamos una densidad estimada de 16 individuos por Km^2, un valor consistente con un área protegida en Los Tuxtlas (Estrada y Coates-Estrada, 1994). Basados en esta densidad generalizada, las poblaciones fueron simuladas teniendo capacidades de carga de 100, 200, 400 y 1000. Estas capacidades de carga abarcan un amplio rango de fragmentos de hábitat actualmente ocupados por *A. palliata mexicana*, incluyendo pequeños fragmentos dentro del área del Volcán de San Martín Tuxtla en Veracruz, así como grandes fragmentos tales como la región de Manzanillar en Chiapas.

Tamaño de población inicial: Con datos de censos actuales limitados, nosotros usamos una estimación de densidad general de 10 individuos por Km^2, como una guía para determinar los tamaños iniciales de población. Por ello, iniciamos las simulaciones con un tamaño de población igual a la mitad de la capacidad de carga, es decir, 50, 100, 200 y 500 individuos. Estos valores para tamaño de población inicial y capacidad de carga, aunque son algo generalizados, son extremadamente útiles en nuestra evaluación del impacto de varias fuerzas estocásticas en la persistencia de poblaciones de tamaño variable.

Distribución inicial de edades: Nosotros iniciamos todas las corridas del modelo con una distribución de edades estable, que distribuye la población total en cada clase sexo-edad, de acuerdo con los esquemas existentes de reproducción y mortalidad.

Depresión por consanguinidad: No existen datos específicos sobre la prevalencia y los efectos de la consanguinidad en poblaciones silvestres de monos aulladores de manto. Sin embargo, dada la severa fragmentación de hábitat adecuado para los aulladores y a la resultante fragmentación de

las poblaciones de estos monos en tales fragmentos de bosque, puede ser razonable inferir que algún grado de consanguinidad medible esté ocurriendo en estas pequeñas poblaciones. Por ello, hemos incluido la depresión por consanguinidad específicamente en el subgrupo de escenarios modelados que tienen que ver con poblaciones pequeñas, es decir, de 50 a 100 individuos.

Nosotros usamos el modelo de heterosis de la depresión por consanguinidad, en el cual los individuos que son heterocigotos en un locus genético determinado, tienen mayor aptitud que aquellos que son homocigotos en ese mismo locus. Debido a que los alelos nocivos no son eliminados de la población por selección natural en el tiempo de este modelo, el modelo de heterosis puede dar una sobrestimación conservadora de los efectos deletéreos de la consanguinidad en las poblaciones de monos aulladores modeladas.

La severidad de la depresión por consanguinidad en poblaciones de mamíferos puede ser medida como el número de "equivalentes letales" contenidos en el genoma de la población de interés. Datos de muchas especies de mamíferos cautivos (incluyendo 12 especies de primates) sugieren que estas especies guardan alrededor de 3 equivalentes letales (Ralls et al, 1988). Consecuentemente, nosotros modelamos la depresión por consanguinidad usando este valor medio de equivalentes letales.

Catástrofes: Las catástrofes son consideradas como extremos en la variación ambiental, y son tratados de manera diferente, conceptual y operativamente en VORTEX. Tanto la frecuencia de ocurrencia de los eventos catastróficos como su impacto sobre la reproducción y la sobrevivencia, son modelados por el programa. Tres catástrofes se incluyeron en la simulación:

Incendios: Grandes incendios que generalmente ocurren en el área, más o menos una vez cada 5 años. El efecto de estos incendios es bajo, con un 5% de reducción en la reproducción y un 10% de reducción en la sobrevivencia.

Huracanes: Se piensa que fuertes tormentas golpean esta área cada 10 años. El efecto de los huracanes es ligeramente más fuerte, con un 10% de reducción en la reproducción y un 30% de reducción en la sobrevivencia durante los años en que éstos ocurren.

Enfermedades: Enfermedades epidémicas ocurren muy raramente, pero pueden tener un efecto devastador sobre la población. Las enfermedades se modelaron como si ocurrieran una vez cada 100 años con un 40% de reducción en la reproducción y un 60% de reducción en la sobrevivencia.

Iteraciones y años de proyección: Cada escenario en el cual estaba ausente la depresión por consanguinidad fue repetido 500 veces, mientras que aquellos que incorporaron la depresión por consanguinidad fueron repetidos 250 veces, debido a limitaciones computacionales. Se hicieron proyecciones para 100 años en todos los escenarios. Los resultados fueron resumidos en intervalos de 10 años en las figuras de series de tiempo. Cada escenario tabulado tiene un número de archivo correspondiente para referencia y para una recuperación futura de otros resultados, si es necesario. La simulación fue corrida usando VORTEX versión 7.0.

Resultados de la Simulación

Explicación de tablas y figuras

Los resultados numéricos de la simulación aparecen en las Tablas 3.1 a la 3.5. Cada tabla representa un grupo específico de condiciones, por ejemplo, esquema de mortalidad juvenil, tamaño de población inicial, etc. Dentro de cada tabla, los resultados se organizan en una estructura que coloca a una serie de datos dentro de la otra: cada tamaño de población inicial se corrió con cada nivel de mortalidad juvenil bajo condiciones específicas.

Los encabezados de las tablas son los siguientes:

r_d: tasa de crecimiento determinístico, calculada por los métodos de la matriz de Leslie de los datos de la tabla de vida;

r_s (SD):   media y desviación estándar de la tasa de crecimiento estocástico, a través de las iteraciones, calculada de la variación anual en el tamaño de la población;

P(E):   probabilidad de extinción en los 100 años que abarca la simulación, calculada como la proporción de poblaciones iteradas que se extinguieron en 100 años;

N_{100} (SD):   tamaño final de las poblaciones que permanecieron sin extinguirse después de 100 años;

H_{100}:   proporción de heterocigosidad que se espera permanezca en las poblaciones sobrevivientes después de 100 años;

T(E):   tiempo promedio de extinción de la población, en aquellos escenarios en los cuales cuando menos el 10% de las poblaciones simuladas llegaron a la extinción.

Note que los números de archivos de salida de VORTEX son dados para cada escenario para referencia futura y recuperación, si es necesario.

Las Figuras 3.1 a la 3.7 son una compilación gráfica de los resultados modelados, que intentan mostrar las interrelaciones entre factores específicos y su impacto sobre la persistencia de la población.

Resultados de la simulación determinística

Las tasas de crecimiento determinístico de la población para cada escenario, calculado de las tablas de vida usando los algoritmos de la matriz de Leslie, se presentan en la quinta columna de las Tablas 3.1 - 3.5. Estos cálculos asumen que las tasas de nacimientos y de muertes son constantes (no hay variaciones anuales ni fluctuaciones estocásticas), no existe limitación de parejas y la consanguinidad no tiene impacto sobre la fecundidad o la viabilidad. Note que la mortalidad, inclusión/exclusión de catástrofes y éxito reproductivo proporcional de las hembras son las únicas variables que afectan estas tasas determinísticas. Por ello, la tasa de crecimiento de esas poblaciones a largo plazo, en ausencia de variación estocástica, es independiente del tamaño de población inicial y de la capacidad de carga del hábitat.

Bajo condiciones de baja mortalidad en adultos, como aquellos que parecen predominar en la isla Agaltepec, las poblaciones de monos aulladores muestran un crecimiento determinístico positivo, sin hacer caso a la mortalidad juvenil. Por supuesto que el crecimiento determinístico se reduce conforme la mortalidad infantil aumenta de 10% a 20%. Esta tasa de crecimiento aumenta dramáticamente en la ausencia de catástrofes (r_d = 0.101-0.088; Tabla 3.2, archivos 525-527). Bajo las mismas condiciones de mortalidad de adultos, la inspección de las Tablas 3.3 y 3.4 indica que, en presencia de enfermedad, la ocurrencia de huracanes ocasionales tiene mayor impacto sobre el crecimiento de la población que los incendios forestales ocasionales. Para ilustrarlo, compare el archivo 549, en el cual tanto enfermedad como incendios fueron incluidos en la simulación y r_d = 0.074, con el archivo 573 donde enfermedad y huracanes son incluidos y r_d = 0.063.

Si las poblaciones de monos aulladores experimentan alta mortalidad, como es el caso de los de la Isla de Barro Colorado, los modelos predicen un crecimiento determinístico mucho más bajo. Por ejemplo, comparar las poblaciones que están en declive determinístico (r_d = 0.042-0.029; Tabla 3.1, archivos 501-503) cuando todas las catástrofes están presentes y la mortalidad de adultos es baja, con las tasas de crecimiento de 0.034-0.020 cuando las catástrofes están ausentes y la mortalidad de adultos es alta (Tabla 3.2, archivos 537-539). Los huracanes nuevamente se muestran como los que tienen el mayor impacto sobre las poblaciones de monos aulladores (Tablas 3.3 y 3.4) con tasas de crecimiento que varían de 0.006 a -0.018 dependiendo de la mortalidad juvenil que exista así como de cuál evento catastrófico está incluido en el modelo.

Estos resultados claramente indican que la mortalidad de adultos puede tener impactos dramáticos en la persistencia de las poblaciones. Condiciones tales como aquellas que persistieron inicialmente en la isla Agaltepec -baja densidad de población, poca competencia por alimento y otros recursos- conducen al potencial para el rápido crecimiento de la población a largo plazo. En contraste, la alta mortalidad de adultos característica de una mayor densidad de población, conduce a un crecimiento determinístico mucho más bajo, y en muchas ocasiones conduce a un declive de la población projectado a largo plazo. Además, el impacto de eventos ambientales catastróficos, y de huracanes en particular, son substanciales y necesitan ser considerados en el desarrollo de cualquier plan de manejo coordinado para monos aulladores.

Resultados de la simulación estocástica

Los cálculos de las tasas de crecimiento de la población, a partir del promedio de las tasas de nacimientos y muertes en una tabla de vida, sobrestimarán el crecimiento de la población a largo plazo si por alguna razón hay fluctuaciones estocásticas en los parámetros demográficos, aún una variación aleatoria en la muestra. Para demostrar este fenómeno, note que la inclusión de estas fuerzas aleatorias en el proceso de modelaje de la población resulta en tasas de crecimiento estocástico, que son, en cada caso, más bajos que las tasas de crecimiento determinístico calculadas de la media de los parámetros de la tabla de vida.

Por ejemplo, con un tamaño inicial de población de 50 individuos y baja mortalidad de juveniles y adultos (Tabla 3.1, archivo 501), la tasa de crecimiento estocástico (r_s) es 0.028, o

33% más baja que la tasa de crecimiento determinístico de 0.042. Conforme la mortalidad juvenil aumenta, la tasa de crecimiento estocástica se reduce en una forma similar a la observada para la tasa de crecimiento determinístico. Bajo condiciones de alta mortalidad de adultos, la variación estocástica en los parámetros de historia de vida resulta en un declive más severo en la tasa de crecimiento de la población. Bajo las mismas condiciones del archivo 501, pero con alta mortalidad de adultos (Tabla 3.1, archivo 513), la media de la tasa de crecimiento estocástico de la población es -0.052, o el doble de la tasa de declive determinístico (r_d = -0.026). Todas la otras condiciones en la presencia de alta mortalidad conducen a reducciones similares en el crecimiento estocástico.

Cuando la mortalidad en adultos es baja, bajo las condiciones modeladas en los escenarios listados en la Tabla 3.1, el riesgo de extinción de la población excede el 4% sólo bajo los tamaños de población inicial más pequeños. Si la mortalidad infantil es tan alta como 20%, la probabilidad de extinción es 12% (Tabla 3.1, archivo 503) pero se reduce rápidamente conforme la mortalidad juvenil o el tamaño inicial de la población se reducen. Es importante darse cuenta de que en estos resultados, a pesar de una media positiva de tasa de crecimiento estocástico en los primeros doce escenarios en la Tabla 3.1, el riesgo de extinción en muchos escenarios es diferente de cero. Este es un resultado directo de la variación aleatoria incluida en estas simulaciones. Después de 100 años, el tamaño final de la población en todos los escenarios con baja mortalidad de adultos es alrededor de 70-75% de la capacidad de carga del hábitat. Como un resultado, una proporción considerable de la heterocigosidad es retenida, variando desde 81.6% (archivo 503) a un máximo de 98.2% (archivo 510).

Si la mortalidad de adultos aumenta, como en aquellos escenarios listados en la mitad inferior de la Tabla 3.1, las poblaciones simuladas son desestabilizadas dramáticamente. Como un ejemplo, dando un tamaño inicial de población de 100 y una mortalidad juvenil de 15% (archivo 517), el riesgo de extinción es 82.4%; esto presenta gran contraste con la misma simulación con baja mortalidad de adultos (archivo 505), donde P(E) 0.024. Si la mortalidad juvenil es particularmente alta, poblaciones muy pequeñas tienen un riesgo de extinción muy alto (es decir, archivo 515: P(E) = 0.970). Las poblaciones que se extinguen bajo estas condiciones tienen un tiempo promedio de extinción de 50-70 años aproximadamente. Además, aquellas poblaciones simuladas que no se extinguen, tienen tamaños de población muy pequeños después de los 100 años y un alto riesgo de extinción en el periodo de tiempo inmediato al final de la simulación. Aún aquellas simulaciones que empiezan con un gran número de individuos, como en el archivo 522 (Tabla 3.1), tienen muy pocos animales que permanecen después de la duración de la simulación. Por supuesto, esta reducción dramática en el tamaño de la población conduce a que sólo una pequeña proporción de variación genética sea retenida en la población que queda.

La sensibilidad extrema de las poblaciones de monos aulladores simuladas, hacia las catástrofes identificadas durante el taller, se muestran en la Tabla 3.2. Cuando las catástrofes fueron eliminadas de los modelos, todos las tasas de crecimiento estocástico fueron positivas, la extinción de la población fue eliminada de todos los escenarios excepto uno (archivo 539), y todas la poblaciones crecieron rápidamente hasta la capacidad de carga o muy cerca de ésta. De la misma forma, todas las poblaciones retuvieron cuando menos el 85% de su heterocigosidad

inicial. De estos resultados es claro que los eventos ambientales catastróficos incluidos en estos modelos tienen efectos dramáticos sobre la viabilidad de las poblaciones de monos aulladores.

Es posible observar más de cerca el impacto relativo de estas catástrofes diseñando y comparando resultados de escenarios que incluyen solamente ciertos eventos catastróficos. Por ejemplo, la Tabla 3.3 muestra resultados de aquellos modelos que incluyen solamente epidemias e incendios (los huracanes fueron eliminados), mientras que la Tabla 3.4 muestra los resultados de modelos que sólo incluyen epidemias y huracanes (los incendios fueron eliminados). El riesgo de extinción de la población casi fue eliminado de los escenarios con baja mortalidad de adultos cuando se retiraron los huracanes del modelo y los tamaños de la población después de 100 años fueron cercanos a la capacidad de carga (mitad superior de la Tabla 3.3). Si los huracanes se incluyen en el modelo y los incendios se eliminan (Tabla 3.4), la viabilidad completa de la población es similar a los resultados presentados en la Tabla 3.3. Sin embargo, es de interés notar que estos resultados puntualizan el alto grado de interacción entre estos eventos catastróficos. A pesar del impacto relativamente bajo de los incendios sobre las poblaciones de primates, el riesgo de extinción cuando se presentan todas las catástrofes permanece mucho mayor que cuando sólo se incluyen huracanes y enfermedad, particularmente cuando la mortalidad de adultos en alta. Por ejemplo, una población de 500 individuos con alta mortalidad de adultos y 15% de mortalidad juvenil tiene una probabilidad de extinción de 0.484 (Tabla 3.1, archivo 523), mientras que la misma población sujeta solamente a enfermedades y huracanes tiene una probabilidad de extinción de sólo 0.144 (Tabla 3.4, archivo 595). Como en las simulaciones iniciales, el promedio de tiempo hacia la extinción para aquellas poblaciones en considerable riesgo, es aproximadamente de 60-70 años.

Los resultados de aquellas simulaciones que incorporan los efectos de la depresión por consanguinidad en las poblaciones más pequeñas, se muestran en la Tabla 3.5. La depresión por consanguinidad actúa incrementando la vulnerabilidad a la extinción de las poblaciones simuladas, pero los efectos de la consanguinidad en conjunto, no son tan severos como los que se relacionan a las catástrofes incluidas. Esto se muestra gráficamente en la Figura 3.1. Cuando las catástrofes son eliminadas de los modelos, aún las poblaciones con baja mortalidad en adultos sujetas a efectos deletéreos de la consanguinidad aumentan rápidamente en tamaño hasta la capacidad de carga (Figura 3.1A), idénticas a las poblaciones para las cuales la consanguinidad no tiene efecto. Cuando se suman las catástrofes a los modelos, las trayectorias de la población son muy similares para las simulaciones con o sin consanguinidad.

Estos resultados son aún más notables cuando la mortalidad de adultos es alta (Figura 3.1B). En ausencia de catástrofes, la tasa de crecimiento de la población es positiva aún cuando se considere la consanguinidad, aunque no a la misma tasa que con baja mortalidad en adultos. Sin embargo, cuando se incluyen las catástrofes, la tasa de crecimiento de la población se vuelve negativa y el tamaño final de la población se reduce de un valor inicial de 100 a aproximadamente 20. Además, estos resultados son muy similares aun cuando se consideren o no los efectos de la consanguinidad.

Conclusiones

Los resultados del modelaje de simulación de poblaciones para monos aulladores en México se resumen en las Figuras 3.2 a la 3.7. En presencia de catástrofes, el aumento en la mortalidad juvenil lleva a una gran inestabilidad de la población, pero principalmente cuando la mortalidad de adultos es alta. En conjunto, las diferencias dramáticas en la viabilidad de la población se observan cuando se comparan las dos condiciones de mortalidad de adultos, en presencia de variación ambiental catastrófica (Figuras 3.2 y 3.3). En ausencia de tal variación ambiental extrema, las diferencias en la mortalidad de adultos virtualmente no tienen impacto (Figuras 3.4 y 3.5). Estos resultados gráficamente ilustran las interacciones entre los parámetros de historia de vida de los aulladores y la naturaleza de la variación en el ambiente que habitan.

Basados en estas observaciones, es importante dedicar esfuerzos de investigación sobre las poblaciones de monos que habitan en tierra firme para determinar los esquemas de mortalidad con mayor precisión. Esto podría lograrse colocando collares con radiotransmisores a 15 ó 30 animales cuando menos y monitorearlos por un largo periodo (cuando menos de dos años). Durante este lapso, también se podrían colectar datos sobre fecundidad, así como alguna información sobre variación derivada ambientalmente en estas tasas vitales. De hecho, debido al papel que juegan los huracanes, incendios y enfermedades, en la dinámica de poblaciones de aulladores, se debe dirigir una atención cuidadosa hacia una comprensión minuciosa de la frecuencia y severidad de estos eventos. Los datos meteorológicos históricos pueden ser muy útiles en este sentido.

El impacto de la depresión por consanguinidad se resume en las Figuras 3.6 y 3.7. El aumento de la mortalidad infantil nos lleva a un ligero aumento del riesgo de extinción bajo consanguinidad, pero sólo en presencia de catástrofes. Sin embargo, la depresión por consanguinidad es más evidente cuando se considera el tamaño de la población final. Esto es más fácil de observar cuando la población inicial es de 50 individuos y las catástrofes han sido eliminadas de los modelos. Cuando la mortalidad de adultos es baja, el tamaño de la población final permanece muy cerca de 100, conforme la mortalidad juvenil se aumenta, con o sin depresión por consanguinidad (compare las curvas "$N_0 = 50$; Baja" en las Figuras 3.4B y 3.7B); sin embargo, cuando la mortalidad de adultos es alta, el tamaño de la población final es consistentemente más bajo con el aumento en la mortalidad juvenil, cuando se incluye la consanguinidad en los modelos (compare las curvas "$N_0 = 50$; Alta" en las Figuras 3.5B y 3.7B). Después de 100 años de simulación, el tamaño de la población final bajo 20% de mortalidad juvenil es de 88 cuando la depresión por consanguinidad está ausente, pero es solamente de 63 cuando ésta se incluye. Estos tamaños de población reducidos deberían conducir a niveles de consanguinidad aumentados, además de reducir el tamaño de la población y aumentar el riesgo de extinción futura de la población. Como un resultado, es importante reconocer el impacto que la consanguinidad puede tener sobre la viabilidad de poblaciones particularmente pequeñas. Por ello, se debería dirigir una atención cuidadosa a determinar los niveles de depresión por consanguinidad en poblaciones cautivas de monos aulladores, para obtener una comprensión más completa de este fenómeno en poblaciones silvestres.

Recomendaciones

Las siguientes recomendaciones se elaboraron a partir de los resultados de la simulación discutida anteriormente:

1. Las importantes interacciones entre mortalidad juvenil, mortalidad de adultos y variabilidad ambiental requieren del desarrollo de investigación sobre esquemas de reproducción y mortalidad en las poblaciones de monos aulladores en México. Esta información puede obtenerse a través de estudios de radio-telemetría en 10-20 adultos sobre un periodo no menor de 2 años. Datos como estos son de vital importancia para el refinamiento de los modelos para simular la viabilidad de las poblaciones.

2. Aunque la presencia de depresión por consanguinidad en monos aulladores no es un factor tan serio para determinar la viabilidad de la población, como lo es la variación ambiental extrema, debería ser evaluada. Esto se logra más fácilmente analizando registros detallados de pedigrí de ésta y otras especies de monos aulladores en cautiverio.

3. Debido al riesgo extremo de extinción manifestado por poblaciones con altos niveles de mortalidad de adultos, puede ser necesario considerar las acciones que deban tomarse para reducir este riesgo. Más específicamente, se deberían desarrollar y evaluar estrategias de manejo diseñadas tanto para reducir la mortalidad de adultos o para suplementar artificialmente poblaciones pequeñas en declive estocástico.

Sample VORTEX Input File

```
HOWL597.OUT       ***Output Filename***
Y       ***Graphing Files?***
N       ***Each Iteration?***
Y        ***Screen display of graphs?***
250       ***Simulations***
100       ***Years***
10      ***Reporting Interval***
1       ***Populations***
Y       ***Inbreeding Depression?***
H
3.140000
N       ***EV correlation?***
3       ***Types Of Catastrophes***
P       ***Monogamous, Polygynous, or Hermaphroditic***
4       ***Female Breeding Age***
5       ***Male Breeding Age***
20       ***Maximum Age***
0.500000        ***Sex Ratio***
1       ***Maximum Litter Size***
N       ***Density Dependent Breeding?***
50.000000       ***Population 1: Percent Litter Size 0***
50.000000       ***Population 1: Percent Litter Size 1***
12.500000       ***EV--Reproduction***
10.000000       ***Female Mortality At Age 0***
3.000000        ***EV--FemaleMortality***
0.500000        ***Female Mortality At Age 1***
2.000000        ***EV--FemaleMortality***
0.000000        ***Female Mortality At Age 2***
2.000000        ***EV--FemaleMortality***
0.000000        ***Female Mortality At Age 3***
2.000000        ***EV--FemaleMortality***
4.500000        ***Adult Female Mortality***
1.350000        ***EV--AdultFemaleMortality***
15.000000        ***Male Mortality At Age 0***
4.500000        ***EV--MaleMortality***
2.000000        ***Male Mortality At Age 1***
1.000000        ***EV--MaleMortality***
2.000000        ***Male Mortality At Age 2***
1.000000        ***EV--MaleMortality***
0.000000        ***Male Mortality At Age 3***
2.000000        ***EV--MaleMortality***
0.000000        ***Male Mortality At Age 4***
2.000000        ***EV--MaleMortality***
3.750000        ***Adult Male Mortality***
1.100000        ***EV--AdultMaleMortality***
20.000000        ***Probability Of Catastrophe 1***
0.950000        ***Severity--Reproduction***
0.900000        ***Severity--Survival***
10.000000        ***Probability Of Catastrophe 2***
0.900000        ***Severity--Reproduction***
0.700000        ***Severity--Survival***
1.000000        ***Probability Of Catastrophe 3***
0.600000        ***Severity--Reproduction***
0.400000        ***Severity--Survival***
N       ***All Males Breeders?***
Y       ***Answer--A--Known?***
70.000000       ***Percent Males In Breeding Pool***
Y       ***Start At Stable Age Distribution?***
50       ***Initial Population Size***
100       ***K***
0.000000        ***EV--K***
N       ***Trend In K?***
N        ***Harvest?***
N       ***Supplement?***
Y       ***AnotherSimulation?***
```

Sample VORTEX Output File

```
VORTEX -- simulation of genetic and demographic stochasticity

HOWL597.OUT
Tue May 23 10:08:46 1995


  1 population(s) simulated for 100 years, 250 iterations

  HETEROSIS model of inbreeding depression
    with 3.14000 lethal equivalents per diploid genome

  First age of reproduction for females: 4   for males: 5
  Age of senescence (death): 20
  Sex ratio at birth (proportion males): 0.50000


Population 1:

  Polygynous mating;
    70.00 percent of adult males in the breeding pool.

  Reproduction is assumed to be density independent.

    50.00 (EV = 12.50 SD) percent of adult females produce litters of size 0
    50.00 percent of adult females produce litters of size 1

   10.00 (EV = 3.00 SD) percent mortality of females between ages 0 and 1
    0.50 (EV = 2.04 SD) percent mortality of females between ages 1 and 2
    0.00 (EV = 2.00 SD) percent mortality of females between ages 2 and 3
    0.00 (EV = 2.00 SD) percent mortality of females between ages 3 and 4
    4.50 (EV = 1.35 SD) percent annual mortality of adult females (4<=age<=20)
   15.00 (EV = 4.50 SD) percent mortality of males between ages 0 and 1
    2.00 (EV = 1.00 SD) percent mortality of males between ages 1 and 2
    2.00 (EV = 1.00 SD) percent mortality of males between ages 2 and 3
    0.00 (EV = 2.00 SD) percent mortality of males between ages 3 and 4
    0.00 (EV = 2.00 SD) percent mortality of males between ages 4 and 5
    3.75 (EV = 1.10 SD) percent annual mortality of adult males (5<=age<=20)
    EVs may have been adjusted to closest values
         possible for binomial distribution.
    EV in mortality will be correlated among age-sex classes
         but independent from EV in reproduction.

  Frequency of type 1 catastrophes: 20.000 percent
    with 0.950 multiplicative effect on reproduction
    and 0.900 multiplicative effect on survival

  Frequency of type 2 catastrophes: 10.000 percent
    with 0.900 multiplicative effect on reproduction
    and 0.700 multiplicative effect on survival

  Frequency of type 3 catastrophes: 1.000 percent
    with 0.600 multiplicative effect on reproduction
    and 0.400 multiplicative effect on survival


  Initial size of Population 1:
    (set to reflect stable age distribution)
  Age 1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20  Total
      3  3  2  3  2  1  2  1  1  1  1  1  1  0  1  0  1  0  0  1     25  Males
      3  3  3  2  2  2  2  1  1  1  1  1  1  0  1  0  1  0  0  0     25  Females

  Carrying capacity = 100 (EV = 0.00 SD)
```

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

    r =   0.042      lambda = 1.043      R0 =      1.473
    Generation time for:  females = 9.23     males = 10.17

Stable age distribution:  Age class      females      males
                               0          0.070        0.070
                               1          0.057        0.054
                               2          0.051        0.048
                               3          0.046        0.042
                               4          0.042        0.038
                               5          0.036        0.035
                               6          0.031        0.030
                               7          0.027        0.026
                               8          0.024        0.023
                               9          0.020        0.020
                              10          0.018        0.017
                              11          0.015        0.015
                              12          0.013        0.013
                              13          0.011        0.012
                              14          0.010        0.010
                              15          0.009        0.009
                              16          0.007        0.008
                              17          0.006        0.007
                              18          0.006        0.006
                              19          0.005        0.005
                              20          0.004        0.004

Ratio of adult (>= 5) males to adult (>= 4) females: 0.845


Population 1

Year 10
       N[Extinct] =         0, P[E] = 0.000
       N[Surviving] =     250, P[S] = 1.000
       Population size =              68.52 (    1.64 SE,    25.90 SD)
       Expected heterozygosity =      0.972 (   0.001 SE,    0.012 SD)
       Observed heterozygosity =      0.997 (   0.000 SE,    0.007 SD)
       Number of extant alleles =     55.24 (    1.00 SE,    15.79 SD)

Year 20
       N[Extinct] =         1, P[E] = 0.004
       N[Surviving] =     249, P[S] = 0.996
       Population size =              72.05 (    1.78 SE,    28.12 SD)
       Expected heterozygosity =      0.955 (   0.002 SE,    0.025 SD)
       Observed heterozygosity =      0.984 (   0.001 SE,    0.023 SD)
       Number of extant alleles =     39.08 (    0.79 SE,    12.50 SD)


Year 30
       N[Extinct] =         3, P[E] = 0.012
       N[Surviving] =     247, P[S] = 0.988
       Population size =              71.86 (    1.81 SE,    28.45 SD)
       Expected heterozygosity =      0.938 (   0.003 SE,    0.040 SD)
       Observed heterozygosity =      0.970 (   0.002 SE,    0.031 SD)
       Number of extant alleles =     30.13 (    0.61 SE,     9.58 SD)

Year 40
       N[Extinct] =         5, P[E] = 0.020
       N[Surviving] =     245, P[S] = 0.980
       Population size =              72.80 (    1.83 SE,    28.63 SD)
       Expected heterozygosity =      0.923 (   0.003 SE,    0.047 SD)
       Observed heterozygosity =      0.955 (   0.003 SE,    0.041 SD)
       Number of extant alleles =     24.67 (    0.50 SE,     7.83 SD)
```

```
Year 50
     N[Extinct] =        9, P[E] = 0.036
     N[Surviving] =    241, P[S] = 0.964
     Population size =              74.10 (   1.81 SE,    28.05 SD)
     Expected heterozygosity =       0.908 (  0.004 SE,     0.063 SD)
     Observed heterozygosity =       0.940 (  0.003 SE,     0.052 SD)
     Number of extant alleles =     20.95 (   0.42 SE,     6.49 SD)

Year 60
     N[Extinct] =       10, P[E] = 0.040
     N[Surviving] =    240, P[S] = 0.960
     Population size =              70.65 (   1.87 SE,    28.96 SD)
     Expected heterozygosity =       0.891 (  0.006 SE,     0.091 SD)
     Observed heterozygosity =       0.923 (  0.006 SE,     0.088 SD)
     Number of extant alleles =     18.21 (   0.37 SE,     5.71 SD)

Year 70
     N[Extinct] =       13, P[E] = 0.052
     N[Surviving] =    237, P[S] = 0.948
     Population size =              69.64 (   1.97 SE,    30.32 SD)
     Expected heterozygosity =       0.876 (  0.006 SE,     0.095 SD)
     Observed heterozygosity =       0.905 (  0.006 SE,     0.097 SD)
     Number of extant alleles =     16.00 (   0.33 SE,     5.08 SD)

Year 80
     N[Extinct] =       15, P[E] = 0.060
     N[Surviving] =    235, P[S] = 0.940
     Population size =              69.20 (   1.98 SE,    30.35 SD)
     Expected heterozygosity =       0.865 (  0.006 SE,     0.085 SD)
     Observed heterozygosity =       0.897 (  0.005 SE,     0.082 SD)
     Number of extant alleles =     14.34 (   0.31 SE,     4.72 SD)

Year 90
     N[Extinct] =       24, P[E] = 0.096
     N[Surviving] =    226, P[S] = 0.904
     Population size =              67.07 (   2.03 SE,    30.56 SD)
     Expected heterozygosity =       0.854 (  0.006 SE,     0.087 SD)
     Observed heterozygosity =       0.885 (  0.006 SE,     0.089 SD)
     Number of extant alleles =     13.07 (   0.27 SE,     4.10 SD)

Year 100
     N[Extinct] =       29, P[E] = 0.116
     N[Surviving] =    221, P[S] = 0.884
     Population size =              64.78 (   2.02 SE,    30.06 SD)
     Expected heterozygosity =       0.845 (  0.005 SE,     0.075 SD)
     Observed heterozygosity =       0.876 (  0.006 SE,     0.083 SD)
     Number of extant alleles =     11.78 (   0.25 SE,     3.78 SD)


In 250 simulations of Population 1 for 100 years:
  29 went extinct and 221 survived.

This gives a probability of extinction of 0.1160 (0.0203 SE),
  or a probability of success of        0.8840 (0.0203 SE).

29 simulations went extinct at least once.
Of those going extinct,
    mean time to first extinction was 68.59 years (4.62 SE, 24.85 SD).

No recolonizations.
```

```
Mean final population for successful cases was 64.78 (2.02 SE, 30.06 SD)

   Age  1      2      3      4    Adults    Total
       3.65   3.07   2.92   2.92   19.29    31.86  Males
       3.80   3.23   3.06           22.83    32.92  Females

Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was 0.0182 (0.0011 SE, 0.1684 SD)

Final expected heterozygosity was       0.8448 ( 0.0050 SE,  0.0747 SD)
Final observed heterozygosity was       0.8756 ( 0.0056 SE,  0.0834 SD)
Final number of alleles was              11.78 (   0.25 SE,    3.78 SD)

*********************************************************************
```

Tabla 3.1. Análisis de población de monos aulladores de manto.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
501	50	10	Low	.042	.028 (.174)	0.062	73 (29)	0.834	—
502		15		.036	.023 (.170)	0.070	72 (30)	0.824	—
503		20		.029	.016 (.172)	0.120	69 (31)	0.816	62
504	100	10		.042	.031 (.164)	0.010	154 (56)	0.912	—
505		15		.036	.024 (.165)	0.024	144 (57)	0.905	—
506		20		.029	.019 (.136)	0.038	137 (60)	0.898	—
507	200	10		.042	.032 (.160)	0.004	304 (108)	0.958	—
508		15		.036	.026 (.161)	0.004	290 (113)	0.951	—
509		20		.029	.018 (.160)	0.006	274 (121)	0.946	—
510	500	10		.042	.032 (.160)	0.0	763 (267)	0.982	—
511		15		.036	.026 (.158)	0.0	740 (278)	0.980	—
512		20		.029	.019 (.159)	0.002	664 (290)	0.979	—
513	50	10	High	-.026	-.052 (.223)	0.880	16 (15)	0.588	51
514		15		-.032	-.057 (.226)	0.928	16 (14)	0.602	50
515		20		-.039	-.066 (.231)	0.970	13 (15)	0.556	46
516	100	10		-.026	-.047 (.210)	0.736	27 (32)	0.694	60
517		15		-.032	-.053 (.211)	0.824	22 (23)	0.678	60
518		20		-.039	-.066 (.222)	0.926	12 (10)	0.642	55
519	200	10		-.026	-.046 (.202)	0.640	39 (46)	0.746	70
520		15		-.032	-.052 (.205)	0.702	26 (38)	0.704	66
521		20		-.039	-.061 (.208)	0.816	19 (20)	0.702	63
522	500	10		-.026	-.041 (.184)	0.366	64 (92)	0.834	77
523		15		-.032	-.048 (.191)	0.484	42 (58)	0.800	76
524		20		-.039	-.057 (.196)	0.628	28 (34)	0.750	75

Tabla 3.2. Análisis de población de monos aulladores de manto: sin catástrofes.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
525	50	10	Low	.101	.100 (.049)	0.0	100 (3)	0.897	—
526		15		.095	.093 (.050)	0.0	100 (3)	0.899	—
527		20		.088	.086 (.050)	0.0	100 (3)	0.902	—
528	100	10		.101	.100 (.043)	0.0	200 (4)	0.947	—
529		15		.095	.094 (.043)	0.0	200 (4)	0.948	—
530		20		.088	.087 (.043)	0.0	200 (4)	0.949	—
531	200	10		.101	.101 (.040)	0.0	400 (6)	0.973	—
532		15		.095	.094 (.040)	0.0	400 (6)	0.974	—
533		20		.088	.087 (.040)	0.0	400 (6)	0.974	—
534	500	10		.101	.101 (.037)	0.0	1000 (9)	0.989	—
535		15		.095	.094 (.037)	0.0	1000 (10)	0.990	—
536		20		.088	.087 (.037)	0.0	1000 (9)	0.990	—
537	50	10	High	.034	.031 (.073)	0.0	95 (9)	0.871	—
538		15		.027	.024 (.074)	0.0	93 (11)	0.867	—
539		20		.020	.017 (.077)	0.006	88 (16)	0.857	—
540	100	10		.034	.032 (.063)	0.0	195 (9)	0.937	—
541		15		.027	.025 (.064)	0.0	191 (15)	0.935	—
542		20		.020	.018 (.067)	0.0	183 (26)	0.928	—
543	200	10		.034	.033 (.058)	0.0	391 (17)	0.968	—
544		15		.027	.026 (.060)	0.0	387 (21)	0.967	—
545		20		.020	.019 (.061)	0.0	379 (29)	0.966	—
546	500	10		.034	.033 (.055)	0.0	983 (30)	0.987	—
547		15		.027	.026 (.057)	0.0	967 (49)	0.987	—
548		20		.020	.019 (.058)	0.0	952 (63)	0.987	—

Tabla 3.3. Análisis de población de monos aulladores de manto: epidemias e incendios.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
549	50	10	Low	.074	.067 (.121)	0.002	93 (15)	0.882	—
550		15		.067	.061 (.122)	0.0	94 (15)	0.883	—
551		20		.060	.054 (.120)	0.004	90 (20)	0.885	—
552	100	10		.074	.068 (.117)	0.0	188 (29)	0.940	—
553		15		.067	.062 (.117)	0.0	186 (34)	0.940	—
554		20		.060	.054 (.117)	0.0	185 (36)	0.942	—
555	200	10		.074	.069 (.114)	0.0	377 (60)	0.970	—
556		15		.067	.062 (.115)	0.0	381 (52)	0.970	—
557		20		.060	.055 (.113)	0.0	374 (63)	0.970	—
558	500	10		.074	.068 (.116)	0.0	938 (154)	0.988	—
559		15		.067	.063 (.109)	0.0	936 (167)	0.988	—
560		20		.060	.057 (.109)	0.0	936 (156)	0.988	—
561	50	10	High	.006	-.005 (.150)	0.218	55 (31)	0.751	64
562		15		-.001	-.012 (.156)	0.304	44 (30)	0.716	66
563		20		-.008	-.021 (.166)	0.468	35 (25)	0.706	61
564	100	10		.006	-.003 (.139)	0.116	106 (63)	0.857	73
565		15		-.001	-.010 (.142)	0.138	77 (58)	0.813	70
566		20		-.008	-.018 (.147)	0.254	57 (48)	0.793	73
567	200	10		.006	.000 (.127)	0.032	212 (127)	0.920	—
568		15		-.001	-.007 (.131)	0.056	162 (122)	0.900	—
569		20		-.008	-.016 (.138)	0.124	99 (92)	0.860	83
570	500	10		.006	.000 (.123)	0.004	513 (323)	0.961	—
571		15		-.001	-.006 (.123)	0.020	382 (288)	0.955	—
572		20		-.008	-.013 (.125)	0.024	241 (230)	0.933	—

Tabla 3.4. Análisis de población de monos aulladores de manto: epidemias y huracanes.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
573	50	10	Low	.063	.051 (.161)	0.014	85 (22)	0.862	—
574		15		.057	.045 (.162)	0.012	83 (23)	0.860	—
575		20		.050	.039 (.162)	0.030	81 (26)	0.856	—
576	100	10		.063	.053 (.157)	0.0	174 (41)	0.930	—
577		15		.057	.047 (.155)	0.0	167 (47)	0.930	—
578		20		.050	.041 (.155)	0.01	166 (45)	0.929	—
579	200	10		.063	.053 (.154)	0.0	346 (86)	0.965	—
580		15		.057	.047 (.155)	0.002	340 (89)	0.963	—
581		20		.050	.041 (.152)	0.002	330 (95)	0.963	—
582	500	10		.063	.055 (.152)	0.0	881 (199)	0.986	—
583		15		.057	.047 (.152)	0.0	844 (225)	0.986	—
584		20		.050	.041 (.153)	0.002	834 (227)	0.985	—
585	50	10	High	-.004	-.022 (.198)	0.538	40 (30)	0.697	61
586		15		-.011	-.032 (.204)	0.660	29 (23)	0.674	57
587		20		-.018	-.039 (.207)	0.752	24 (19)	0.662	55
588	100	10		-.004	-.019 (.182)	0.334	63 (54)	0.798	66
589		15		-.011	-.026 (.188)	0.428	49 (45)	0.761	68
590		20		-.018	-.037 (.196)	0.602	33 (36)	0.718	64
591	200	10		-.004	-.018 (.177)	0.230	112 (104)	0.853	74
592		15		-.011	-.026 (.180)	0.306	82 (90)	0.832	75
593		20		-.018	-.035 (.190)	0.48	52 (60)	0.803	70
594	500	10		-.004	-.015 (.164)	0.072	244 (253)	0.921	—
595		15		-.011	-.024 (.172)	0.144	156 (192)	0.890	79
596		20		-.018	-.032 (.178)	0.210	92 (133)	0.854	78

Tabla 3.5. Análisis de población de monos aulladores de manto: modelo de heterosis de depresión por consanguinidad, 3.14 equivalentes letales.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
Catastrophes									
597	50	10	Low	.042	.018 (.168)	0.116	65 (30)	0.845	—
598		15		.036	.009 (.177)	0.148	55 (32)	0.816	—
599		20		.029	.001 (.182)	0.232	50 (32)	0.814	64
600	100	10		.042	.025 (.162)	0.024	137 (59)	0.916	—
601		15		.036	.017 (.167)	0.060	127 (62)	0.904	—
602		20		.029	.011 (.164)	0.056	118 (67)	0.898	—
603	50	10	High	-.026	-.065 (.225)	0.988	10 (7)	0.575	49
604		15		-.032	-.071 (.228)	0.996	9 (—)	—	45
605		20		-.039	-.081 (.236)	0.992	4 (3)	—	40
606	100	10		-.026	-.060 (.216)	0.920	14 (20)	0.726	60
607		15		-.032	-.068 (.222)	0.952	12 (13)	0.686	55
608		20		-.039	-.074 (.222)	0.984	7 (1)	—	52
No catastrophes									
609	50	10	Low	.101	.091 (.049)	0.0	100 (3)	0.904	—
610		15		.095	.086 (.049)	0.0	100 (3)	0.902	—
611		20		.088	.079 (.049)	0.0	99 (3)	0.906	—
612	100	10		.101	.096 (.043)	0.0	200 (4)	0.948	—
613		15		.095	.090 (.043)	0.0	200 (4)	0.949	—
614		20		.088	.083 (.043)	0.0	200 (4)	0.950	—
615	50	10	High	.034	.020 (.073)	0.004	85 (20)	0.866	—
616		15		.027	.013 (.076)	0.0	75 (23)	0.861	—
617		20		.020	.005 (.082)	0.028	63 (27)	0.840	—
618	100	10		.034	.027 (.062)	0.0	189 (14)	0.938	—
619		15		.027	.020 (.064)	0.0	183 (23)	0.936	—
620		20		.020	.012 (.067)	0.0	165 (35)	0.928	—

Leyendas de Figuras

Figura 3.1. Tamaño de la población sobre el periodo de 100 años de simulaciones bajo diferentes condiciones ambientales y genéticas. Cats = catástrofes; Inb = Depresión por consanguinidad. Para estos escenarios particulares, la mortalidad juvenil se estableció en 15%.

Figura 3.2. Probabilidad de extinción (A) y tamaño final de la población (B) bajo condiciones de baja mortalidad de adultos, como una función de la mortalidad juvenil, para el grupo de tamaños de población inicial usados en el grupo completo de escenarios modelados.

Figura 3.3. Probabilidad de extinción (A) y tamaño final de la población (B) bajo condiciones de alta mortalidad de adultos, como una función de la mortalidad juvenil, para el grupo de tamaños de población inicial usados en el grupo completo de escenarios modelados.

Figura 3.4. Probabilidad de extinción (A) y tamaño final de la población (B) bajo condiciones de baja mortalidad de adultos y sin catástrofes, como una función de la mortalidad juvenil, para el grupo de tamaños de población inicial usados en el grupo completo de escenarios modelados.

Figura 3.5. Probabilidad de extinción (A) y tamaño final de la población (B) bajo condiciones de alta mortalidad de adultos y sin catástrofes, como una función de la mortalidad juvenil, para el grupo de tamaños de población inicial usados en el grupo completo de escenarios modelados.

Figura 3.6. Probabilidad de extinción (A) y tamaño final de la población (B) en las simulaciones que incorporaron la depresión por consanguinidad. Ver la Figura 7 para obtener la clave de los símbolos usados en las figuras.

Figura 3.7. Probabilidad de extinción (A) y tamaño final de la población (B) en las simulaciones que incorporaron la depresión por consanguinidad y sin catástrofes.

Figure 1. *Alouatta palliata mexicana:*
## Adult Mortality and Population Size
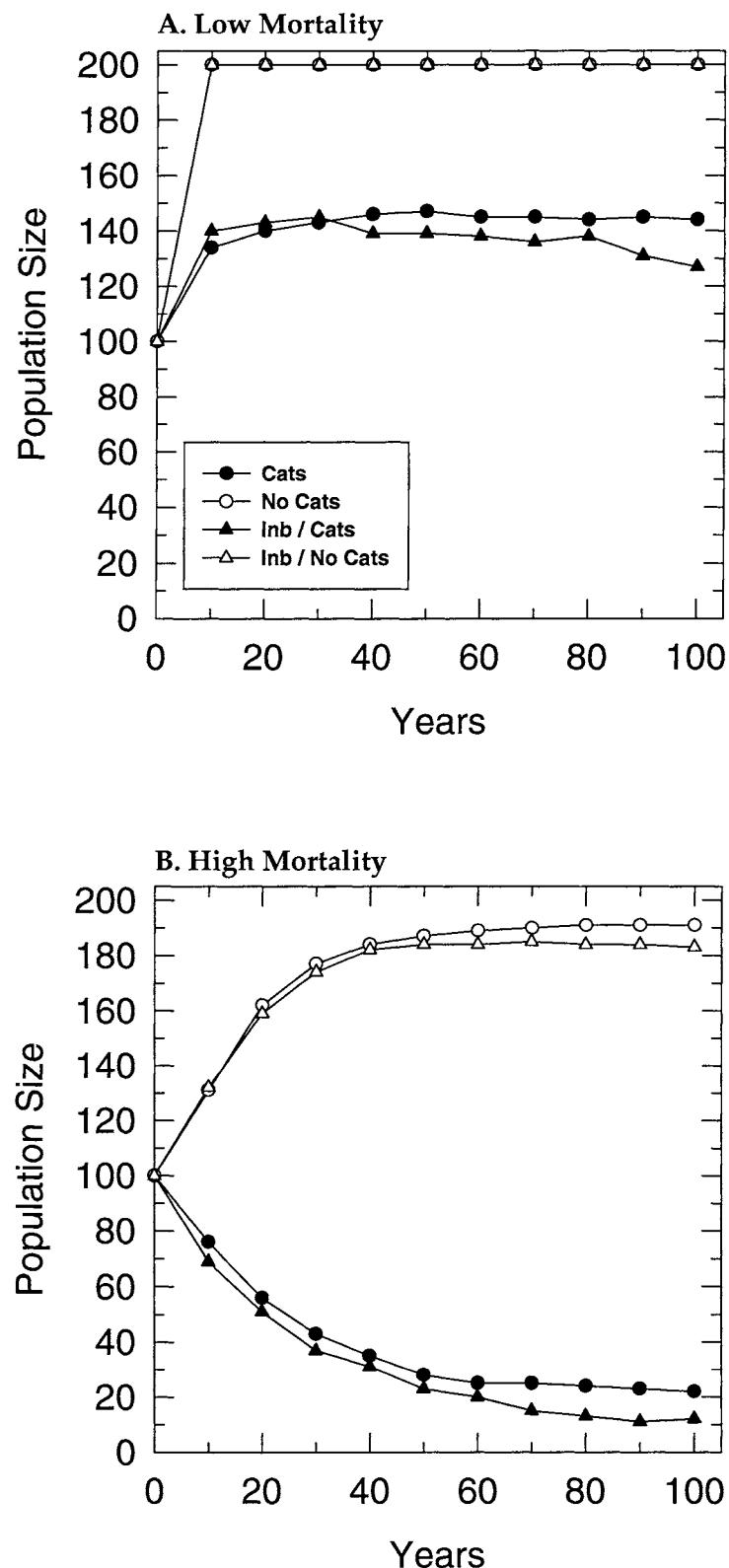
A. Low Mortality

### B. High Mortality

Figure 2. *Alouatta palliata*:
Low Adult Mortality


Figure 3. *Alouatta palliata*:
High Adult Mortality

Figure 4. *Alouatta palliata*:
Low Adult Mortality; No Catastrophes


Figure 5. *Alouatta palliata*:
High Adult Mortality; No Catastrophes

## Figure 6. *Alouatta palliata mexicana*: Inbreeding Depression

Figure 7. *Alouatta palliata mexicana*: Inbreeding Depression; No Catastrophes

Legend (Figure 7A):
- $N_0 = 50$; Low
- $N_0 = 100$; Low
- $N_0 = 50$; High
- $N_0 = 100$; High
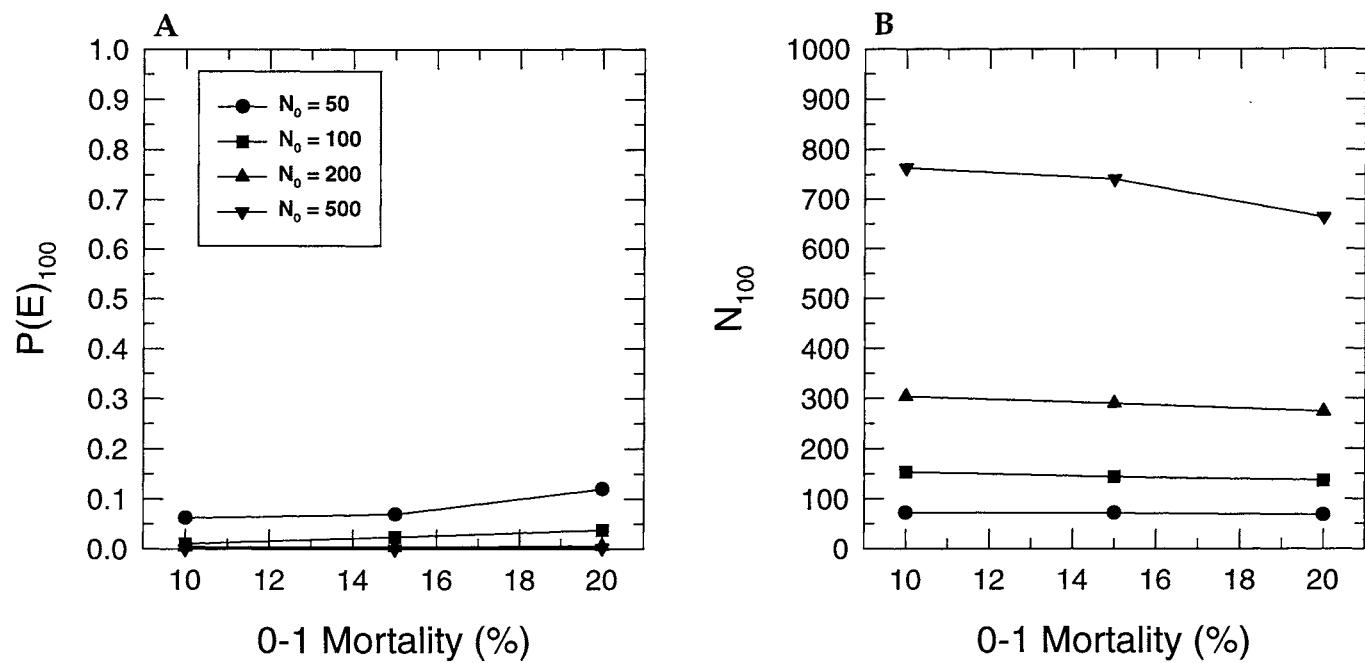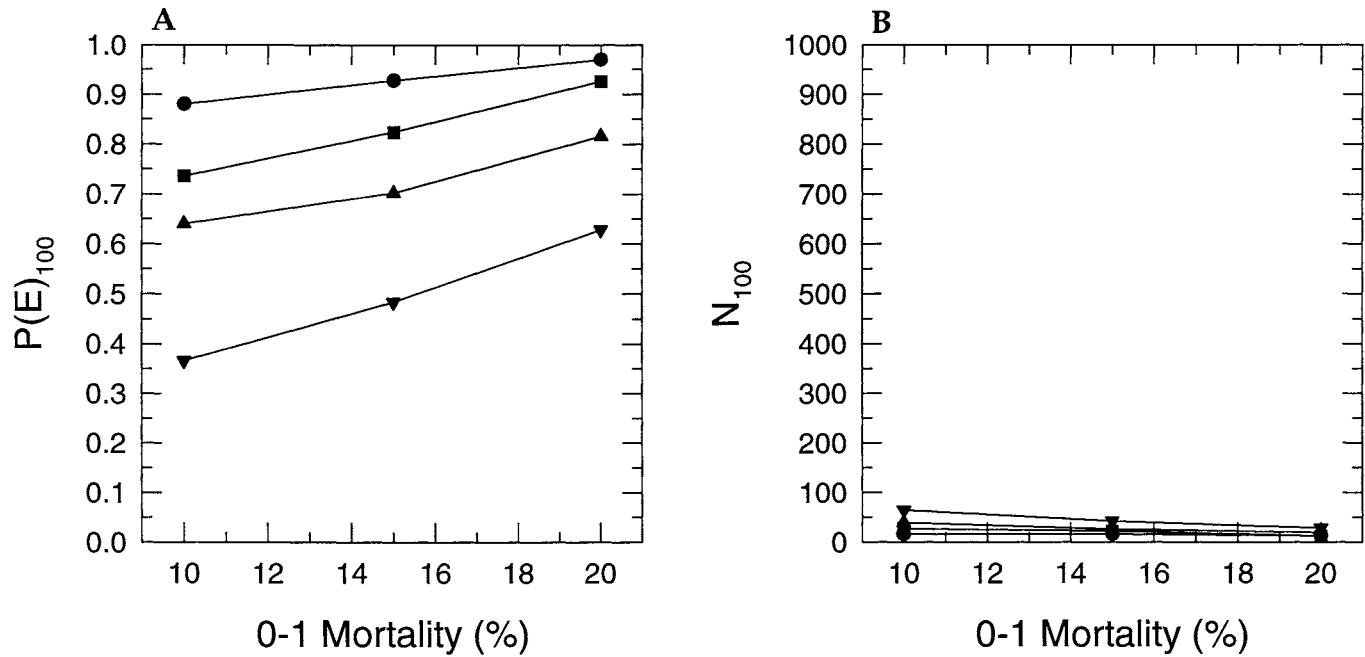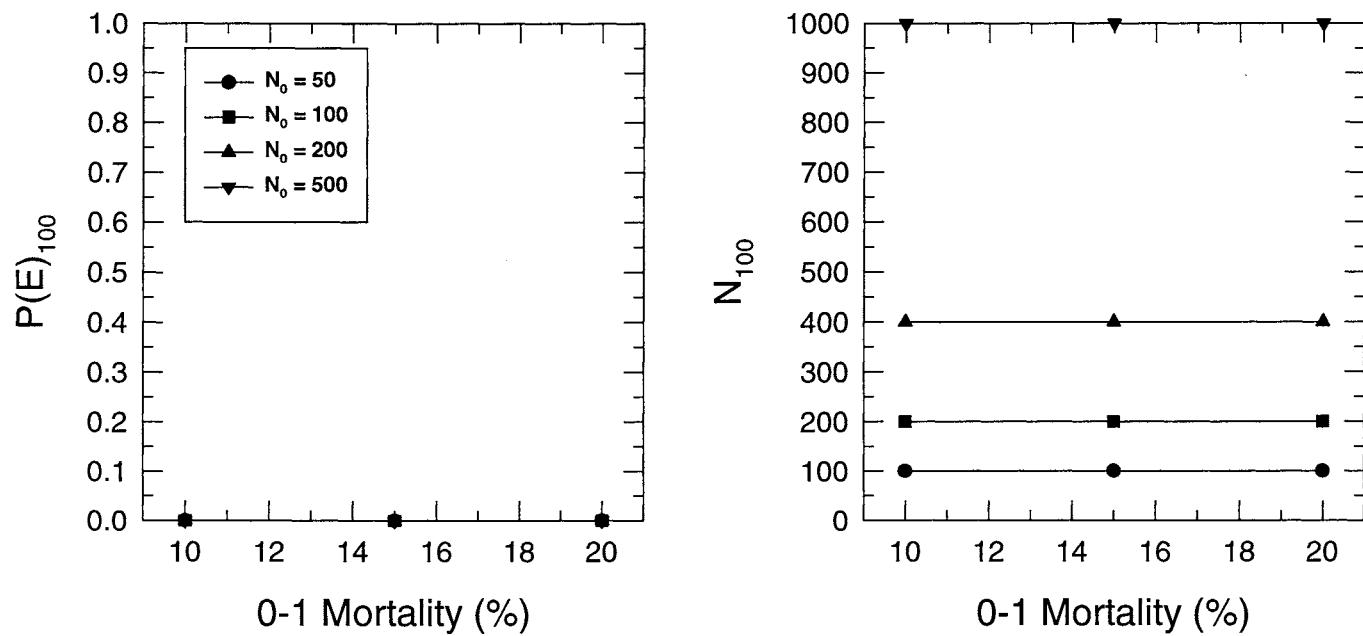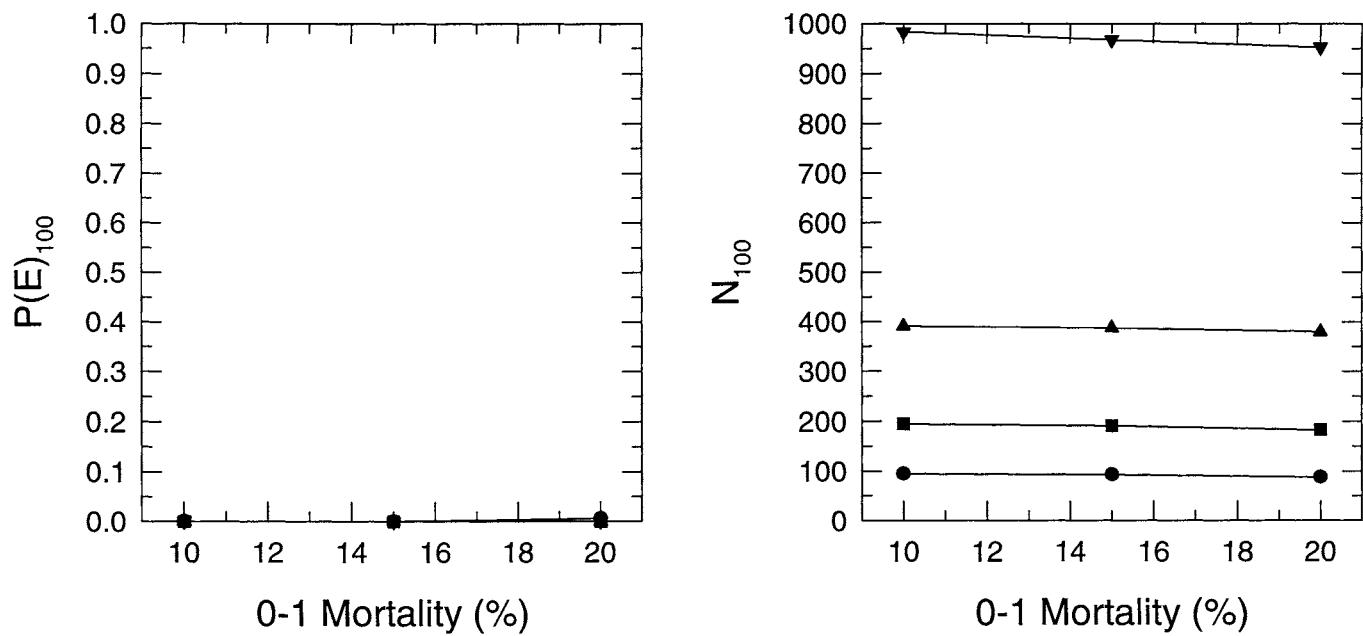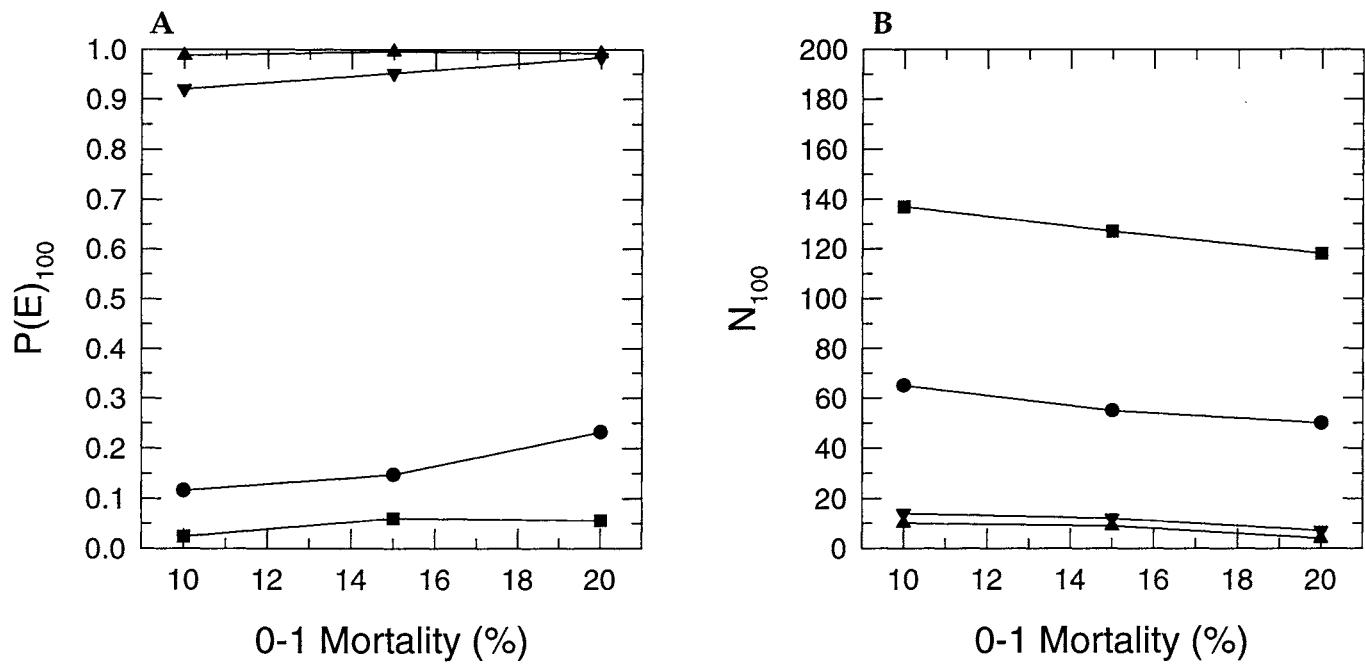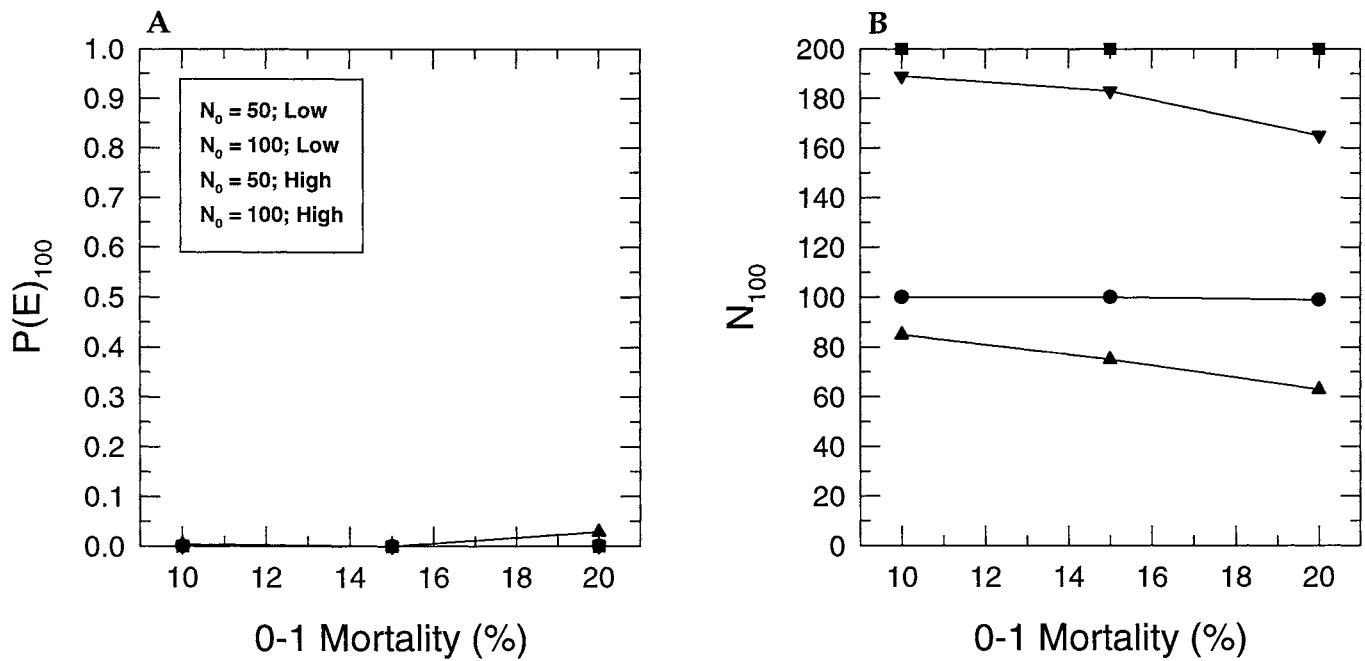
AGALTEPEC ISLAND MODELLING EXERCISE

Para probar el programa VORTEX, se escogió como primer escenario la población de la Isla de Agaltepec, ya que la dinámica de este grupo[1] se ha seguido sin interrupción desde el año de 1989 y, por tanto, se conocen varios de los parámetros necesarios para su caracterización de acuerdo al modelo.

Parámetros del Modelo

1) Las simulaciones se efectuaron en dos horizontes: 100 años y 6 años. La simulación en el horizonte de 6 años se realizó con el propósito de comparar el modelo computacional con el desarrollo de la población real en este lapso. El horizonte de 100 años se escogió para tener una idea de las tendencias de esta población en el largo plazo y estimar las probabilidades de su extinción; y así, poder evaluar los efectos de las distintas variables ambientales y demográficas.

2) Los reportes de extinción se obtuvieron en periodos de 10 años para el horizonte de 100 años y de un año para el horizonte de 6.

3) Las simulaciones no consideraron la depresión por consanguinidad, ya que no existen reportes que manifiesten algún efecto negativo de consanguinidad en esta especie; además, se ha observado que los monos aulladores no presentan gran variabilidad genética de manera natural, por lo cual consideramos que la consanguinidad podría no tener efectos nocivos importantes.

4) Se supuso que la reproducción es independiente de la densidad poblacional.

5) Se consideraron tres clases de catastrófes: incendios, ciclones y epidemias. Los parámetros correspondientes fueron estimados de la información proporcionada por conocedores de la región. Estos últimos estimaron las probabilidades correspondientes a las catástrofes de la siguiente manera:

   Incendios (0.20). Los incendios en la isla pueden ser ocasionados por pescadores de la región que algunas veces desembarcan en el lugar y encienden fogatas para preparar sus alimentos. Se estima que una vez desatado un incendio tendría un gran efecto negativo en la supervivencia y en la reproducción; dadas las dimensiones de la isla.

   Ciclones (0.05). Los vientos huracanados pueden ser un peligro para la población, aunque no ocurren con mucha frecuencia, y su impacto no sería tan grande.

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[1] el grupo fundador fue constituído por animales capturados de acuerdo a un programa de translocación con fines de estudio y conservación de la especie.

Epidemias (0.01). Aunque poco frecuente, es conocido el efecto devastador que puede tener una epidemia sobre las poblaciones de estos monos; como fue el caso de la fiebre amarilla en los años 50´s, reportada en varios lugares de Mesoamérica.

6) En 1989 se liberaron 10 monos en Agaltepec (1 infante, 1 macho adulto y 8 hembras adultas). Desde entonces el grupo se ha monitoreado ininterrumpidamente. A la fecha hay 40 individuos en la isla.

7) La información disponible sugiere que las hembras comienzan a reproducirse después de los 4 años y los machos después de los 5.

8) La proporción de sexos al nacer en Agaltepec es de 1:1.

9) Las hembras adultas producen 1 cría por camada.

10)Uno de los parámetros más difíciles de estimar para esta especie es la capacidad de carga. Para Agaltepec, se cree que el medio puede soportar una población hasta el doble de la actual. Hoy en día, la población está formada por 40 individuos, así que se escogió k=80.

Los datos anteriores fueron propuestos por Domingo Canales Espinosa; Edith Carrera Sánchez; Liliana Cortés Ortiz; Francisco García Orduña; Manuel Martínez Morales; Guadalupe Medel Palacios; Jorge Morales Mávil; Ernesto Rodríguez Luna; Oliva Rosales Rodríguez; Juan Carlos Serio Silva.

A continuación se enlistan los valores de los parámetros empleados en las simulaciones, y un resumen de los principales resultados obtenidos.

Valores Paramétricos para la Población de Agaltepec

Horizonte de 6 años.

Número de simulaciones: 100
Número de años: 6
No hay depresión por consanguinidad.
Primera edad de reproducción para hembras: 4 años
Primera edad de reproducción para machos: 5 años
Edad máxima en la que los animales mueren: 20 años
Proporción de machos al nacer: 0.5
Número de crías por camada: 1
Sistema de apareamiento: Poligínico.
Todos los machos entran en el pool reproductivo.
La reproducción es independiente de la densidad.
Porcentaje de hembras que producen camadas de tamaño 0 = 14.00
        EV = 12.27

Porcentaje de hembras que producen camadas de tamaño 1 = 86.00
Porcentaje de mortalidad de hembras de 0 y 1 año de edad: 10.00
        EV = 3.00 SD
Porcentaje de mortalidad de hembras de 1 y 2 años de edad: 0.5
        EV = 0.15 SD
Porcentaje de mortalidad de hembras de 2 y 3 años de edad: 0.00
        EV = 0.00 SD
Porcentaje de mortalidad de hembras de 3 y 4 años de edad: 0.00
        EV = 0.00 SD
Porcentaje de mortalidad de hembras adultas (4<=edad<=20): 4.5
        EV = 1.00 SD
Porcentaje de mortalidad de machos de 0 y 1 año de edad: 15.00
        EV = 4.00 SD
Porcentaje de mortalidad de machos de 1 y 2 años de edad: 2.00
        EV = 0.5 SD
Porcentaje de mortalidad de machos de 2 y 3 años de edad: 2.00
        EV = 0.50 SD
Porcentaje de mortalidad de machos de 3 y 4 años de edad: 0.00
        EV = 0.00 SD
Porcentaje de mortalidad de machos de 4 y 5 años de edad: 0.00
        EV = 0.00 SD
Porcentaje de mortalidad de machos adultos (5<=edad<=20): 3.75
        EV = 1.00 SD
Frecuencia de la Catástrofe 1 (incendios): 20%
        Efecto de la Catástrofe 1 en la reproducción: 0.5
        Efecto de la Catástrofe 2 en la sobrevivencia: 0.5
Frecuencia de la Catástrofe 2 (ciclones): 5%
        Efecto de la Catástrofe 2 en la reproducción: 0.9
        Efecto de la Catástrofe 2 en la sobrevivencia: 0.9
Frecuencia de la Catástrofe 3 (epidemias): 1%
        Efecto de la Catástrofe 3 en la reproducción: 0.4
        Efecto de la Catástrofe 3 en la sobrevivencia: 0.5
Tamaño inicial de la población: 1 macho de 1 año de edad.
        1 macho de 7 años de edad.
        2 hembras de 4 años de edad.
        2 hembras de 5 años de edad.
        1 hembra de 7 años de edad.
        1 hembra de 8 años de edad.
        1 hembra de 9 años de edad.
        1 hembra de 10 años de edad.
Tamaño inicial de la población: 10 animales.
Capacidad de carga (K) = 80
(EV = 0.00 SD).
No extracción.
No suplementación.

Resumen Final de Resultados a los 6 años

En 100 simulaciones por 6 años:
11 se extinguieron y 89 sobrevivieron.
Probabilidad de extinción: 0.1100 (0.0313 SE).
Probabilidad de sobrevivencia: 0.8900 (0.0313 SE).
11 simulaciones se extinguieron.
Tiempo promedio de la extinción: 3.55 años (0.55 SE, 1.81 SD).
Población final promedio de la población sobreviviente: 20.52 (1.46 SE, 13.76 SD).

EDAD	1	2	3	4	ADULTOS	TOTAL	
	2.01	1.55	0.85	0.99	3.39	8.80	Machos
	2.08	1.54	0.84	--	7.26	11.72	Hembras

Tasa promedio de crecimiento (r) : 0.0489 (0.0164 SE, 0.3921 SD)
Heterocigocidad final esperada: 0.8697 (0.0045 SE, 0.0426 SD).
Heterocigocidad final observada: 0.9872 (0.0027 SE, 0.0258 SD).
Número final de alelos: 13.11   (0.47 SE, 4.43 SD).

Se relizó otra simulación en el horizonte de 6 años, con la diferencia de no incluir ningún tipo de catástrofe.
Los resultados fueron los siguientes:

En 100 simulaciones, 0 poblaciones se extinguieron y 100 sobrevivieron, lo que da una probabilidad de extinción de 0.00 (probabilidad de éxito 1.00).

El tamaño promedio final de la población de los casos éxitosos fue de 43.55 (0.76 SE, 7.62 SD).

EDAD	1	2	3	4	ADULTOS	TOTAL	
	4.23	3.59	2.27	2.49	6.71	19.29	Machos
	4.65	3.67	2.20		13.74	24.26	Hembras

Tasa promedio de crecimiento (r) : 0.2424 (0.0049 SE, 0.1189 SD)
Heterocigocidad final esperada: 0.8966 (0.0013 SE, 0.0131 SD).
Heterocigocidad final observada: 0.9808 (0.0020 SE, 0.0198 SD).
Número final de alelos: 18.62   (0.11 SE, 1.13 SD).

Horizonte de 100 años.

Los datos utilizados para esta simulación fueron los mismos que para la primera simulación (incluyendo el efecto de las catástrofes), excepto en el número de años (100).

Resumen Final de Resultados a los 100 años

En 100 simulaciones por 100 años:

    79 se extinguieron y 21 sobrevivieron.

    Probabilidad de extinción: 0.79 (0.0.0407 SD).

    Probabilidad de sobrevivencia: 0.21 (0.0407 SD).

    79 simulaciones se extinguieron.

    Tiempo promedio de la extinción: 32.92 años (2.99 SE, 26.53 SD).

    Población final promedio de la población sobreviviente: 46.81 (5.81 SE, 26.64 SD).

EDAD	1	2	3	4	ADULTOS	TOTAL	
	3.43	3.95	2.76	2.38	11.00	23.52	Machos
	4.00	3.48	2.62		13.19	23.29	Hembras

    Tasa promedio de crecimiento (r) : -0.0074 (0.0055 SE, 0.3774 SD)

    Heterocigocidad final esperada: 0.5484 (0.0388 SE, 0.1779 SD).

    Heterocigocidad final observada: 0.5627 (0.0429 SE, 0.1965 SD).

    Número final de alelos: 3.95 (0.32 SE, 1.47 SD).

Comentarios

En el caso del horizonte de 6 años, en el que se consideran las catástrofes, el promedio del tamaño poblacional está por abajo del tamaño real de la población, éste se encuentra dentro del rango de variación de los tamaños poblacionales generados en la simulación. Sin embargo, para la simulación del horizonte de 6 años en el que no se consideraron las catástrofes, el número poblacional final es muy similar al real encontrado en la isla (43.55 vs. 40). Es preciso advertir que en la población real de Agaltepec no se ha presentado ningún evento catastrófico durante los seis años en que ha sido monitoreada.

    Por otra parte, la tasa promedio de crecimiento en el horizonte de 6 años sin catástrofes (0.242), es muy similar a la que se ha estimado para la población de Agaltepec (0.239).

    Estas coincidencias sugieren que el modelo (VORTEX 7.0) ha sido adecuado para simular nuestra población.

    Es importante señalar que los datos demográficos, como los porcentajes de mortalidad por sexo y clase de edad, fueron conjeturados y podría haber un error significativo que estaría amplificándose en el curso de las proyecciones poblacionales. Particularmente, para el grupo de la isla se ha observado una baja mortalidad (lo que coincide con los datos utilizados para la simulación), pero en otras condiciones naturales, estos valores seguramente son mucho más elevados para algunas clases de edad y sexo.

La estimación de la capacidad de carga fue hecha en base al reconocimiento de la tendencia de crecimiento poblacional de los animales de la isla, así como de sus patrones de ocupación de la misma y el grado de utilización de los recursos alimenticios disponibles. No obstante, es necesario considerar que esta estimación no coincide con la que se puede inferir atendiendo a los datos de densidad poblacional y ámbito hogareño reportado para la especie.

Finalmente, consideramos que los resultados de la simulación en el horizonte de 100 años (que incluye las catástrofes) puede mostrar una estimación adecuada de la posibilidad de sobrevivencia de este grupo a futuro.

ANÁLISIS DE VIABILIDAD DE POBLACIÓN Y HÁBITAT PARA EL MONO AULLADOR DE MANTO
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 de marzo de 1995

Sección 4
Amenazas a las Poblaciones Naturales
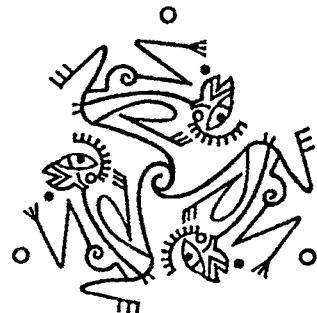
AMENAZAS A LAS POBLACIONES NATURALES DE *Alouatta palliata mexicana*

Pérdida del Hábitat

Debido al crecimiento de las poblaciones humanas, al uso intensivo y extensivo de tierras tropicales para sistemas de manejo industrial, forestal y agropecuario, la distribución original del mono aullador *Alouatta palliata* ha sido severamente fragmentada y se ha visto reducida en un 80 a 90% (Estrada, 1994).

Las poblaciones de *Alouatta palliata mexicana* se encuentran distribuidas actualmente en fragmentos boscosos de diferentes dimensiones. La tasa de deforestación anual del 4.2% reportada para el sureste mexicano (Dirzo, 1992), debida principalmente a la apertura de campos agrícolas y al desarrollo de la ganadería extensiva, genera la pérdida y fragmentación acelerada del hábitat, y por consiguiente, de sus poblaciones de monos, las cuales seguramente van a presentar en poco tiempo disminución en la variabilidad genética y aumento de homocigosis.

Algunos de los problemas que pueden sufrir estas poblaciones son alta susceptibilidad a los cambios ambientales (temperatura, precipitación, etc.) y biológicos (escasez de recursos tróficos, depredación, enfermedades epidémicas y parasitarias) lo que produce a futuro baja viabilidad y fecundidad de la población y por ende su extinción a corto plazo.

A pesar de que se han designado áreas naturales protegidas, éstas tienen fallas en su conceptualización y manejo disminuyendo su efectividad. En la mayoría de éstas no existe una vigilancia y monitoreo constantes, lo cual permite que se lleven a cabo actividades humanas que deterioran el hábitat en cuestión.

Afortunadamente existen todavía poblaciones de *Alouatta palliata mexicana* en grandes extensiones boscosas, las cuales pueden considerarse viables a futuro. Estas poblaciones pueden mantener su variación genética y adaptabilidad mejor que las pequeñas, y algunas tienen la ventaja de encontrarse en áreas protegidas presentes en su zona de distribución.

En grandes poblaciones de *A. palliata mexicana* se reducen los efectos de la consanguinidad y la pérdida a largo plazo de la variabilidad genética. Esto, aunado a la hipótesis de James y Glander (comunicación personal), de que *Alouatta palliata* es menos susceptible a los problemas de consanguinidad que otras especies de mamíferos, y al hecho de que presenta alta plasticidad ecológica y conductual, resaltando su adaptabilidad en la estructura social en relación con los cambios ambientales, nos hace pensar que estas poblaciones tienen buenas expectativas de sobrevivencia si se mantienen las condiciones actuales del hábitat de ocurrencia.

Las poblaciones de *A. palliata mexicana* presentes principalmente en las áreas naturales protegidas, pueden servir, además, como una fuente continua de material genético para las pequeñas poblaciones fragmentadas cercanas a ellas, que permitan la inmigración de por lo menos un individuo por generación para aminorar la pérdida sustancial de variabilidad genética.

Tráfico de Vida Silvestre

Debido a la problemática socioeconómica prevaleciente en casi todas las zonas tropicales, muchos de los campesinos que habitan las comunidades rurales de estas regiones, se ven presionados a buscar alternativas de subsistencia. El comercio de fauna silvestre es una de ellas.

Los primates son uno de los grupos animales con mayor demanda para venta como mascotas; el tráfico ilegal en este sentido es considerable. Al existir una gran demanda de estos mamíferos en las zonas urbanas, se presenta una fuente de ingresos a corto plazo para quienes los capturan. El costo de un ejemplar se ha reportado entre $18 a $25 U.S.D. Alternativas económicas para estas personas y programas de educación ambiental podrían ser las mejores soluciones. Sin embargo, se sospecha que existe tráfico de mascotas a mayor escala en el cual se manejan fuertes capitales y grandes cantidades de ejemplares comercializados, en donde la participación de los habitantes rurales juega un papel fundamental como colectores, encontrando como intermediarios a traficantes que exportan animales a países desarrollados.

Cacería

Otro de los factores importantes que afectan las poblaciones de monos aulladores, es la cacería, la cual se realiza en diferentes niveles: a) para la obtención de carne y, b) para trofeo de caza.

a) Obtención de carne. Habitantes de comunidades campesinas se ven en la necesidad de obtener fuentes de proteína animal para mejorar sus requerimientos nutricionales; los monos aulladores forman parte de este consumo. Sin embargo, esta no es la única utilidad, ya que en ocasiones, la carne de mono es empleada como cebo para adquirir otras presas, por ejemplo langostinos (Rodríguez-Luna et al, 1987).

No existen datos suficientes que determinen el porcentaje de monos consumidos pero se infiere que es elevado; los motivos de esta cacería se deben a costumbres arraigadas y a la carencia de recursos proteicos de origen animal en estas zonas.

b) Trofeos de caza. La cacería deportiva que se realiza en las regiones tropicales, está dirigida básicamente a grandes mamíferos como venados o jabalíes, sin embargo en ocasiones, cuando estas presas se ven disminuidas, los cazadores desvían su atención hacia animales de talla mediana como es el caso de los monos.

Recomendaciones

- Realizar estudios piloto que ayuden a obtener parámetros de consanguinidad en poblaciones fragmentadas de monos aulladores, con la finalidad de obtener información acerca de la necesidad de realizar transferencia de individuos para generar variación genética en poblaciones reducidas.
- Intensificar las investigaciones que den pauta a la búsqueda de estrategias sobre el uso de recursos naturales en comunidades humanas, que coadyuven en el aprovechamiento racional

sostenido y a la conservación del hábitat donde actualmente ocurren poblaciones silvestres de monos.

- Establecer nuevas áreas naturales protegidas y reevaluar tanto en su conceptualización como en su delimitación y efectiva protección a las que actualmente existen en el rango de distribución de *A. p. mexicana*.

ANÁLISIS DE VIABILIDAD DE POBLACIÓN Y HÁBITAT PARA EL MONO AULLADOR DE MANTO
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 de marzo de 1995

Sección 5
Ecología y Comportamiento
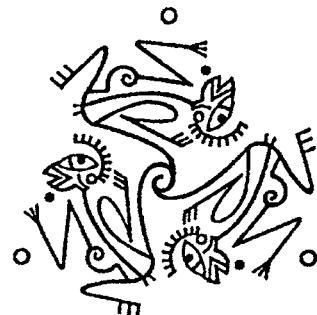
ECOLOGÍA Y COMPORTAMIENTO

Los monos aulladores (*Alouatta palliata*) constituyen una de las especies de primates con mayor conocimiento sobre su biología; sin embargo, a pesar de esta vasta información, múltiples factores están influyendo sobre sus perspectivas de sobrevivencia. La continua pérdida de hábitat y el tráfico de animales de la vida silvestre, entre otros, están determinando que las poblaciones naturales de esta especie se encuentren muy disminuidas dentro de su distribución original.

Bajo esta situación, es pertinente desarrollar estudios más amplios sobre la historia natural del mono aullador (*Alouatta palliata*), que sean la base para el diseño de programas conservacionistas. A continuación se presentan algunos aspectos relevantes.

Hábitos Alimenticos de los Monos Aulladores

Diversas lineas de investigación se han desarrollado a fin de conocer más sobre la ecología y conducta de los monos aulladores. Dentro de éstas, una de la más ampliamente investigada es la que se refiere a sus Hábitos Alimenticios.

Los monos aulladores de la especie *Alouatta palliata* han mostrado diversas facetas en su comportamiento alimenticio. Por un lado, existen estudios que muestran una marcada tendencia hacia la folivoría (Milton, 1980; Glander, 1981), mientras que otros, señalan que existe una clara inclinación hacia la frugivoría (Hladik & Hladik, 1969; Smith, 1977). Como se observa, mediante estas dos condiciones extremas, los monos aulladores pueden localizarse en un amplio rango de oportunidades alimenticias, por lo que, algunos autores han preferido señalar que *Alouatta* "Es un primate folívoro que también come frutos" (Altmann, 1959).

Se ha identificado que *Alouatta palliata* presenta rutas de forrajeo claramente definidas, las cuales le permite, localizar los recursos alimenticios en el espacio y en el tiempo. En una revisión de Estrada (1993), sobre el total de especies consumidas por Alouatta en su distribución neotropical nos indica que existen 291 especies pertenecientes a 66 familias que son explotadas como recurso alimenticio por los monos aulladores. Las Hojas jovenes y los frutos maduros han sido reportados como las partes vegetales mas ampliamente consumidas (Glander, 1975, Milton, 1980, Chapman, 1987, Estrada, 1984).

Para el nivel de cada parte vegetal consumida, se señala que 218 especies (58 familias) son usadas en el consumo de hojas y 122 especies (38 familias) para frutos y finalmente 55 especies (24 familias) en el consumo de flores. Para las familias que presentan una mayor preferencia en el consumo, se observa que las especies de las Leguminosas y las Moraceas, y este patrón de preferencias se muestra gran consistencia en todos los sitios del Neotropico donde Alouatta ha sido estudiado.

Los monos aulladores han mostrado también selección en cuanto a la ocupación de ciertos estratos arboreos con el fin de alimentarse, así, dividiendo en estratos los árboles de los que se alimentan, se observa que los monos aulladores prefieren más intensamente el estrato superior, medio e inferior respectivamente (Mendel, 1976; Serio-Silva, 1992), lo anterior se

explica señalando, que es en estos dos primeros estratos, más que en el inferior, donde se encuentran las partes vegetales que consumen ampliamente: las hojas jóvenes y los frutos maduros.

Asimismo, en diversos reportes se ha identificado que *A. palliata* selecciona especies relativamente raras dentro de su Ambito Hogareño, de esta forma, especies ampliamente consumidas presentan una densidad relativa baja, esto nos da a entender que estas especies presentan algunas propiedades nutricionales y químicas pueden estar influyendo en la selección de estas especies.

En relación a lo anterior, Estrada (1984) señala que se grupo de estudio aunque se alimento de 27 especies diferentes, solo 8 de estas alcanzaban el 89 % del total del tiempo alimenticio. Esta selección se expresa también en el estudio de Glander (1981), el cual indica que los monos ejercen una intensa selección sobre los arboles que se encuentran dentro de su ambito hogareño, consumiendo solamente el 19.5 % del total presente.

El género *Ficus* se ha considerado en diversos estudios como de gran importancia dentro del repertorio alimenticio. En la mayoría de los trabajos realizados con *A. palliata* en condiciones silvestres, *Ficus* alcanza los porcentajes más altos dentro de las especies consumidas (Estrada, 1984; Crockett & Eisemberg, 1987). Un ejemplo de esto se da en el estudio de Serio-Silva (1992), quien señala que el 56.5 % del tiempo dedicado a la alimentación se ocupó unicamente para el consumo de las especies de este género.

Como se señaló anteriormente, los monos aulladores aparte de mostrarse selectivos con las especies que consumen, también muestran una estricta selección sobre las partes vegetales ingeridas; así, mientras que existen reportes que los ubican como intensamente folívoros (Glander, 19?, Milton, 1980), para el caso de los estudios desarrollados en México con esta especie, Estrada (1984) muestra una proporción casi equivalente en cuanto al consumo de hojas y frutos, y Serio-Silva (1992) hace referencia a la marcada frugivoría que se presenta en su estudio con monos aulladores bajo condiciones de semilibertad en una isla del lago de Catemaco, Veracruz, México. Los datos anteriores parecen indicarnos la gran importancia que tienen los diferentes tipos de vegetación y sus respectivos patrones fenológicos a fin de conducir las diferentes tendencias alimenticias.

Se ha observado, que los monos aulladores pueden consumir de manera accidental larvas de insectos en el interior de algunos frutos (Milton, 1980, Serio-Silva, 1992); los cuales pueden contibuir, aunque sea mínimamente, a un incremento nutricional en su dieta, esto mediante la extracción de la proteina animal que las larvas representan.

Sin embargo, la característica más importante de este tipo de comportamiento selectivo es que los aulladores muestran una gran plasticidad en sus respuestas al medio ambiente que se encuentran ocupando, con lo que en un momento dado, ante ciertas presiones ambientales pueden estar respondiendo bajo una faceta de folívoros mientras que ante la presencia de frutos, los monos los pueden explotar con gran avidez.

Hábitos Alimenticos de *Alouatta palliata*

El avance inexorable de los asentamientos humanos hacia las áreas naturales está causando la constante modificación y disminución del hábitat de muchas especies de mamíferos mexicanos. Esta incesante transformación del hábitat, sin duda, se relaciona directamente con la disponibilidad de alimento para muchas especies.

Para el caso particular de *Alouatta palliata*, especie muy selectiva en su comportamiento alimenticio, se presenta un gran impacto en sus poblaciones, causado principalmente por la fragmentación y empobrecimiento del hábitat en el rango original de su distribución. Los monos aulladores han mostrado ser muy estrictos en la selección de las especies que consumen; éstas varían de acuerdo a los distintos ecosistemas que ocupa la especie.

Estudios sobre los hábitos alimenticios en *Alouatta palliata* alcanzan gran importancia, ya que mediante el conocimiento de éstos en ambientes estables se podrán identificar áreas potenciales para liberaciones mediante programas de translocación. Sin duda, estrategias como ésta pueden contribuir de manera determinante a la conservación de la especie, arrojándonos además datos importantes de la biología de este primate, tales como la capacidad de carga diferencial en los distintos ambientes y la influencia que tiene sobre ésta, la presencia o ausencia de ciertas especies alimenticias.

Los monos se muestran ampliamente selectivos sobre sus hábitos alimenticios a distintos niveles, desde aspectos particulares como los nutrientes y compuestos químicos que necesitan o evitan, las partes vegetales que consumen, los estratos arbóreos donde se alimentan, hasta las especies que seleccionan dentro de su dieta.

Factores como los anteriores influyen de manera importante en la dificultad de mantener bajo condiciones de cautiverio a individuos de esta especie. En base a lo anterior, es necesario determinar cuáles factores influyen de manera decisiva en las poblaciones cautivas. Asimismo, se podría elaborar una lista general de especies vegetales y compuestos químicos (tanto necesarios como nocivos) para delinear una dieta adecuada para animales cautivos.

Recomendaciones

Es necesario insistir en la elaboración, en conjunto, de un plan de estudio y conservación *in situ* para *A. palliata mexicana*, donde se contemple el desarrollo de investigaciones en torno a sus hábitos alimenticios, que como se ha manifestado son de gran complejidad.

Estas investigaciones deberán incluir:

- Desarrollar un mayor número de estudios que nos permitan dilucidar las principales tendencias alimenticias en *Alouatta palliata mexicana* en condiciones silvestres.

- Determinar qué especies vegetales destacan dentro de la selección del alimento por *A. p. mexicana*.

- Ubicar la presencia de los principales compuestos nutricionales y químicos que puedan estar influyendo en la selección del alimento por el mono aullador.

- Determinar, mediante el estudio de grupos de monos aulladores, la relación que existe entre la presencia de especies alimenticias y capacidad de carga dentro de su ámbito hogareño.

- Elaborar una dieta-patrón para grupos de monos que están bajo cautiverio, utilizando especies que consumen en su hábitat natural.

Patrón Diario de Actividades

El patrón diario de actividades para la especie *Alouatta palliata* ha sido extensamente estudiado, principalmente en la isla de Barro Colorado en Panamá. En esta área, Altmann (1959) y Bernstein (1964), realizaron estudios que brindan información sobre el patrón de actividad para esta especie. Chivers (1969) registró las variaciones en el patrón de actividades en relación con el clima durante el día y las estaciones seca y húmeda. Asimismo, Richard (1970) comparó los patrones de actividades entre *Ateles geoffroyi* y *Alouatta palliata*; Mittermeier (1975) estudió el efecto de la dinámica poblacional y el patrón de actividades y, Milton (1980) en su obra dedicó un espacio a describir el patrón diario.

Los patrones diarios de actividades reportados para esta especie no difieren considerablemente incluso para aquellas poblaciones existentes en diferentes regiones, países o tipos de vegetación.

Serio Silva (1992) y Carrera Sánchez (1993) reportan que *A. palliata mexicana* presenta en general un patrón habitual a lo largo del día. Es decir, es posible identificar un pico de alimentación al inicio de la mañana y al filo del medio día, en relación inversa a la actividad de descanso. Este patrón es observado a lo largo del año.

No se han señalado diferencias en el patrón de actividades durante las estaciones seca y húmeda. La actividad disminuye en la estación húmeda pero también durante los períodos de intenso calor. En la estación seca debido a la mayor disponibilidad de recursos alimenticios, disminuye la locomoción aumentando los períodos de alimentación y descanso.

Con relación al patrón de actividades, Milton (1980) concluye: "en relación al tiempo es notablemente uniforme día a día y mes a mes. Los saraguatos permanecen descansando una proporción de su tiempo relativamente alta. La regularidad de su conducta sugiere que los monos son capaces de evitar fluctuaciones extremas en su gasto voluntario de energía, y el bajo nivel de actividad quizá les permita mantener reservas de energía en momentos en que los frutos están disponibles en forma restringida".

Esta información acerca de los patrones de actividades nos permite conocer la respuesta conductual de la especie en términos energéticos con respecto a las fluctuaciones ambientales.

Asimismo, nos permite analizar la posible relación entre la disponibilidad de alimento, calidad del hábitat, utilización del hábitat y determinación del ámbito hogareño, con respecto a las variaciones estacionales.

Recomendaciones

A pesar de que existe información extensa sobre los patrones de actividades, consideramos que es necesario desarrollar las siguientes líneas de investigación:

- Realizar una comparación entre el patrón de actividades de grupos que habitan vegetación continua y grupos habitando fragmentos muy perturbados (reducidos).

- Comparar los patrones de actividades en grupos de esta especie con estructuras poblacionales diferentes, en relación con tamaño del grupo, diferenciación de sexos y clases de edad.

Repertorio Conductual

A pesar de la vasta información que se tiene sobre la especie no existen muchos trabajos que presenten su repertorio conductual. Sólo dos estudios presentan información detallada y suficiente sobre el género *Alouatta* (Neville, 1988; Braza, 1980) y uno sobre *Alouatta palliata mexicana* (Carrera Sánchez, 1994).

Los monos aulladores son primates sociales cuyas relaciones afectivas son muy fuertes. Sin embargo, algunas conductas de cohesión grupal, por ejemplo el aloacicalamiento, no son tan comunes en comparación con los monos del Viejo Mundo (Jones, 1977).

El agonismo intragrupal en estos animales ha sido observado entre machos, hembras y de padres a crías. La agresión entre machos adultos puede provocar en algunas ocasiones que individuos jóvenes (machos y hembras) dejen el grupo para vivir solitariamente, integrarse a uno establecido o formar una nueva tropa. En el caso de las hembras el juego rudo a menudo conduce a la agresión, la cual es limitada por el macho dominante. Entre los infantes, el juego rudo es una forma de preparación para la vida adulta. Se han reportado casos de infanticidios (Galetti, 1994) y se considera que los machos infantes reciben más agresión que las hembras infantes.

El comportamiento sexual de estos monos sigue un patrón definido por cortejo y cópula. El cortejo típico consiste en una serie de movimientos rápidos de la lengua hacia dentro y fuera de la boca. Además, pueden ocurrir, presentación de área perineal; seguimientos con huidas cortas por parte de la hembra y olfateo de genitales, quizá con fines de detección estral (Braza, 1980). Durante la cópula puede ocurrir que otra hembra, o algún infante, la interrumpa lo que representa un mecanismo social con relación a una alta densidad poblacional (Young, 1981).

Respecto al cuidado de las crías, la madre tiene un papel protagónico y por tanto mayor influencia en la socialización del infante (Clarke, 1990). Asimismo, otras hembras del grupo ejercen un papel de "tías". Estas permanecen junto a la madre, acicalando al infante y en

ocasiones provocan serios pleitos al intentar robarlo. Debido a la inexperiencia en la crianza y a las persecuciones que ocurren en esta situación, existe el riesgo de dañar al infante ya que puede llegar a caer (Serio-Silva, 1994). Otros miembros de la tropa en ocasiones cuidan del infante; el macho puede llegar a adoptar algún infante huérfano (Neville et al, 1988) y los hermanos mayores a rescatarlo cuando se atrasa en los movimientos grupales.

El estudio del comportamiento nos da la pauta para comprender cómo los individuos se desempeñan en su hábitat y así establecer programas de manejo para su conservación *in situ* y *ex situ*. Además, por ser una especie en peligro, el conocer su biología implica un apoyo para su conservación.

Recomendaciones

Consideramos necesario efectuar los siguientes estudios que reconocemos como prioritarios en este tópico:

- Conducir estudios sobre estructura social y determinación de jerarquías de dominio.

- Realizar investigación sobre las migraciones que ocurren entre los grupos, la integración de individuos solitarios y la formación de grupos nuevos.

- Desarrollar estudios sobre mecanismos de separación entre los grupos que comparten hábitats reducidos.

- Hacer comparaciones entre el comportamiento de grupos que habitan condiciones de semilibertad, fragmentos y área continua.

- Practicar el seguimiento conductual de grupos translocados o reintroducidos.

- Utilizar animales decomisados para investigación, analizar las posibilidades que tienen de ser rehabilitados para su posterior liberación o manejo.

- Realizar estudios de ecología reproductiva.

Demografía y Reproducción

Distintos aspectos de demografía y reproducción de las poblaciones de esta especie han sido reportados por algunos autores para Panamá (Isla de Barro Colorado: Altmann, 1954; Carpenter 1934; Chivers,1969; Milton 1980, 1985; Mittermeier 1973; Smith, 1970; Otis et. al. 1981; entre otros), Costa Rica (Hacienda La Pacífica: Clarke 1984; Glander 1980; Jones 1980, 1985) y México (Isla de Agaltepec: Cortés-Ortiz et. al. 1993, 1994 y Los Tuxtlas: Estrada et. al. 1982, 1984, 1989, 1994). En la mayoría de los casos se trata de poblaciones que se encuentran en condiciones especiales (confinamiento o fragmentación), lo cual puede brindar una visión que no se corresponda completamente con otras poblaciones que habiten extensiones de hábitat

mayores. Sin embargo, se muestran datos que varían entre las distintas localidades y que pueden servir para valorar la situación de las poblaciones bajo distintos escenarios ecológicos.

La densidad poblacional reportada para la especie varía de 110 ind/Km^2 en Costa Rica a 16 ind/Km^2 en la isla de Barro Colorado en Panamá. Un reporte de particular interés es el que brinda Estrada (1994) para México (Los Tuxtlas, Veracruz), donde dadas las condiciones de fragmentación existentes, reporta una densidad poblacional de 3.6 ind/Km^2. Esta es la condición de muchas áreas en México donde existen poblaciones silvestres de *A. p. mexicana*, por lo cual es de gran importancia realizar investigación en el campo que permita identificar las densidades bajo condiciones de hábitat continuo y con diferentes grados de perturbación.

En cuanto al tamaño y estructura de los grupos, el número promedio de animales varía entre 8 y 23 (pero se pueden encontrar grupos hasta de 2 a 45 individuos). La proporción sexual de adultos es de 2.5 hembras por cada macho en promedio (1.16 a 4.11). Para una población tipo de 20 individuos, podríamos encontrar una composición de 8 hembras, 4 machos, 3 juveniles (entre 14 meses y 3 años) y 4 infantes (entre 0 y 14 meses) aproximadamente.

Las tasas de natalidad, mortalidad y crecimiento poblacional han sido estimadas en tres de las localidades antes mencionadas y se puede observar que existen diferencias importantes en los valores calculados; mientras que para una población se observa r= 0.10, para otra se estimó en r= 0.29, lo que indica un crecimiento poblacional más acelerado en la última.

Los valores de mortalidad en estas poblaciones brindan tasas diferentes de acuerdo a clases de edad y sexo. Existe una mayor mortalidad para infantes (menores de 1 año) y la mayoría de los datos marcan una mortalidad más alta en machos que en hembras para diversas clases de edad; particularmente, en relación a los adultos esta diferencia puede deberse a una competencia intrasexual más intensa.

El tipo de organización social para la especie se ha reportado como sistemas poligínicos, unimacho, multimachos y de edad graduada, en los cuales no todos los machos adultos tienen igual acceso a las hembras reproductivas.

Las hembras presentan ciclos estrales que varían alrededor de 17 días, con un estro de 2 a 4 días (estas variaciones pueden ser individuales o incluso ocurrir para la misma hembra en diferentes momentos). En las poblaciones multimachos, en estos períodos de estro una hembra puede aparearse con más de un macho; aunque se ha sugerido que hay un patrón más o menos definido en el cual el macho dominante cópula preferentemente en la parte media de ese periodo, donde se presume que se presenta la ovulación. Este tipo de estudios conductuales y la determinación de su correlato fisiológico serán de suma importancia para determinar el momento en que una hembra es fértil dentro de su ciclo estral y evaluar el aporte génico de los distintos machos del grupo a la siguiente generación.

Los aulladores se reproducen todo el año. El período de gestación reportado varía de 180 a 194 días. Es conveniente realizar estudios más cuidadosos para estimar con mayor exactitud este período, ya que tal variación se presenta en un rango de valores muy amplio. El intervalo

entre nacimientos se ha reportado entre 16 y 22 meses en promedio (13-25), pero se reduce significativamente en hembras que han perdido a su cría. Se hace necesario un conocimiento más preciso sobre estos aspectos, que apoye el desarrollo programas de manejo de la especie.

Recomendaciones

En relación a la demografía de la especie se hace necasario:

- Realizar un monitoreo prolongado de poblaciones silvestres que hagan posible la elaboración de tablas de vida para conocer la dinámica poblacional que siguen tales poblaciones bajo diferentes condiciones ambientales.

- Desarrollar estudios de campo que permitan conocer las densidades poblacionales de la subespecie, tanto en ambientes contínuos como fragmentados, y bajo distintos tipos de vegetación que habitan; así como cambios en la estructura por clases de edad y sexo.

Para reproducción:

- Continuar desarrollando estudios que permitan obtener información precisa acerca de los parámetros reproductivos para la subespecie.

- Realizar estudios fisiológico-conductuales que diluciden la relación que existe en estos dos niveles, al momento de las cópulas y, por tanto, la aportación génica diferencial de los machos en el grupo.

Problemas Genéticos

Las poblaciones de *Alouatta palliata mexicana* se encuentran distribuidas actualmente en fragmentos boscosos de diferentes dimensiones. Algunos de éstos son tan reducidos que están albergando pequeñas poblaciones de monos, las cuales seguramente tienen pérdida genética en cada generación.

Las poblaciones cuando llegan a ser tan pequeñas y aisladas tienden a presentar varios riesgos demográficos y genéticos que influyen en su sobrevivencia, debido, básicamente al entrecruzamiento de individuos emparentados, lo cual produce pérdida de variabilidad y aumento de homocigosis. Algunos de los problemas que pueden sufrir estas poblaciones son: alta susceptibilidad a los cambios ambientales (climáticos, escaséz de recursos tróficos), a depredadores, a enfermedades epidémicas y parasitarias, esto produce a futuro baja viabilidad y fecundidad de la población y por ende su extinción en corto plazo.

Afortunadamente exiten también poblaciones de *Alouatta palliata maxicana* en grandes extensiones boscosas, las cuales pueden considerarse viables a futuro. Estas poblaciones pueden

mantener su variación genética y adaptabilidad mejor que las pequeñas y se encuentran en áreas protegidas presentes en su zona de distribución.

Estas grandes poblaciones de *Alouatta* evitan los efectos de la consanguinidad y la pérdida a largo plazo de la variabilidad genética. Esto, aunado a la hipótesis de James y Glander (comunicación personal), de que *Alouatta palliata* es menos susceptible a los problemas de consanguinidad que otras especies de mamíferos, y el hecho de que esta especie presenta alta plasticidad ecológica y conductual, resaltando aquí su adaptabilidad en la estructura social de acuerdo con los cambios ambientales, nos hacen pensar que estas poblaciones tienen buenas expectativas de sobrevivencia si pudiera controlarse la acelerada destrucción actual del hábitat.

Estas grandes poblaciones de *Alouatta* presentes principalmente en las áreas naturales protegidas de su rango de distribución, pueden servir, además, como una fuente continua de material genético para las pequeñas poblaciones fragmentadas cercanas a ellas, que permitan la inmigración de por lo menos un individuo por generación para aminorar la pérdida sustancial de variabilidad genética.

Para poner a prueba esta hipótesis, se propone realizar un estudio piloto en una pequeña población en semilibertad situada en la isla de Agaltepec, en el sureste de Veracruz, con la finalidad de establecer parámetros de consanguinidad. La selección de este grupo se debe al conocimiento que se tiene sobre la línea de parentesco de los individuos que conforman la población.

En el estudio consistirá básicamente en la extracción de DNA de muestras de sangre; se tratará de estandarizar la técnica molecular que nos brinde mayor información sobre la consanguinidad. Los métodos que se pueden probar son: el de "RAPD markers" (Random Amplified Polimorphic DNA), utilizado regularmente en genética de poblaciones, y la técnica por variación de DNA mitocondrial, utilizada por James y Horwich (1993) en *Alouatta pigra*.

Los resultados que se obtengan de este muestreo preliminar, podrán brindar información acerca de la mejor técnica a ser aplicada en un muestreo de poblaciones silvestres fragmentadas para conocer si existe consanguinidad en éstas, conocer su impacto, y además, paralelamente apoyar estudios de variabilidad morfológica y genética acerca de la taxonomia de la especie.

Finalmente, el estudio propuesto brindará información acerca de si es necesario o no realizar tranlocaciones de individuos que generen una variación genética en estas poblaciones muy fragmentadas.

ANÁLISIS DE VIABILIDAD DE POBLACIÓN Y HÁBITAT PARA EL MONO AULLADOR DE MANTO

(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 de marzo de 1995

Sección 6
Cautiverio y Enfermedades
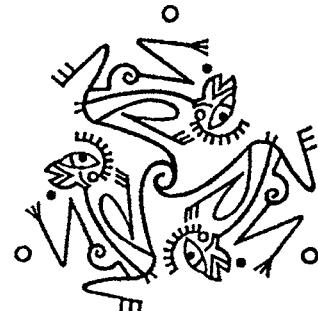
CAUTIVERIO Y ENFERMEDADES

Consideraciones Generales

Actualmente, *Alouatta palliata mexicana* no requiere un programa global de crianza y manejo en cautiverio. Sin embargo, es preciso utilizar a los individuos existentes para realizar investigación que en este momento podría generar información muy valiosa; por ejemplo, fisiología de la reproducción, genética, biomedicina, comportamiento, además de un programa de educación.

      A. palliata se ha caracterizado por ser difícil de mantener bajo condiciones de cautiverio; en México, esto es fácil de comprobar si revisamos el bajo número de colonias cautivas que actualmente existen. Esta problemática tiene su origen en los hábitos alimenticios de la especie, la cual es caracterizada como herbívoro generalista especializado y requiere por lo tanto de un alto porcentaje de hojas en la dieta. Cabe mencionar que la gran mayoría de las especies de las cuales *A. palliata* se alimenta, sólo pueden encontrarse en el área donde este primate ocurre de manera natural.

      Debido a la dificultad que representa mantener a individuos de *A. p. mexicana* bajo condiciones cautivas, resulta importante recomendar que las acciones dirigidas a la crianza y manejo sólo se efectúen en instituciones que se localicen en el área de distribución de este primate.

Acopio

Las instituciones localizadas fuera del área de distribución de *A. p. mexicana*, y que sean recipientes de donaciones de estos monos, deberán canalizar a los individuos recibidos hacia instituciones previamente seleccionadas para llevar a cabo la crianza y manejo en cautiverio, no sin antes realizar una evaluación clínica y aplicar la terapéutica apropiada en caso de que sea necesario; así, los individuos destinados al cautiverio llegarán a su destino final en un estado de salud apropiado.

Registros

Una primera necesidad para poder llevar a cabo un programa de manejo en cautiverio, es utilizar un sistema de registro que englobe identificación individual, eventos clínicos, eventos reproductivos, etc. Asimismo, se recomienda la creación de un "studbook" con fundamento genético "SPARKS" de ISIS, de esta forma se creará una línea de información común a todas las instituciones involucradas de una u otra forma en la crianza y manejo de *A. p. mexicana*.

Instalaciones y Personal Especializado

Las instituciones seleccionadas para el manejo de *A. palliata mexicana*, deben cubrir, como primera condición, estar ubicadas dentro del área de distribución natural de la especie, ya que de esta forma podrían ofrecer las condiciones ambientales requeridas por los monos aulladores.

Asimismo, deberán tener personal técnico especializado que asegure el manejo adecuado de los monos. Finalmente, contar con un soporte económico que facilite la construcción de encierros adecuados para los monos aulladores.

Alimentación

Actualmente, no se cuenta con una dieta de eficiencia reconocida para *A. palliata* en cautiverio, por lo tanto, se hace énfasis en la necesidad de realizar estudios bromatológicos y de digestibilidad, utilizando especies de plantas silvestres reportadas como alimento potencial para este primate, recomendando además el uso de frutas cultivadas como fuente de carbohidratos no estructurales.

Educación

Resulta importante establecer un programa extensivo de educación conservacionista, que enfatice que los monos aulladores no son buenas mascotas y el efecto que su uso como tal puede causar en la sobrevivencia de la especie.

Monitoreo de Enfermedades Infectocontagiosas

Debido a la escasa información de enfermedades infectocontagiosas en esta especie, tanto en vida silvestre como en cautiverio, es necesario iniciar un banco de datos que permita analizar las principales patologías que afectan a la población nacional y establecer el impacto de estas sobre la viabilidad de la subespecie.

La recopilación de datos deberá basarse en la aplicación de protocolos estandarizados que permitan la detección de las principales enfermedades, tanto en cautiverio como en vida libre. Asimismo, dadas las características particulares de esta especie, el mantenimiento en cautiverio deberá regirse por procedimientos médicos preestablecidos, que disminuyan el riesgo de enfermedades en estas poblaciones.

Se recomienda generar la siguiente información para cumplir los objetivos arriba enlistados:

- Lista de enfermedades susceptibles y/o reportadas.
  Revisión de la literatura publicada con esta especie y similares.

- Protocolos de medicina preventiva:

    Protocolo de cuarentena
    Protocolo de necropsias
    Monitoreo periódico
    Protocolo para el traslado de animales
    ****Aplicaciones en vida libre

- Protocolo de diagnóstico:
    Toma y envío de muestras
    Procesamiento de muestras
    **** Aplicaciones en vida libre

- Banco de datos.

   Una vez generados los protocolos, recomendamos su uso por los investigadores y zoológicos integrados al plan de supervivencia de esta subespecie. El material obtenido durante los estudios, deberá ser analizado en un mismo sitio de referencia para estandarizar los resultados y permitir la formación de un banco de datos.

Población en Cautiverio

Actualmente existen 7 individuos bajo condiciones de cautiverio estricto: un macho juvenil en el Zoológico de Aragón, dos machos y cuatro hembras adultos en el Parque de la Flora y Fauna Silvestre Tropical de la Universidad Veracruzana. Asimismo, existen 3 colonias en estado de semilibertad y/o semicautiverio:

   Zoológico "La Venta" en Villahermosa, Tabasco
    5 machos y 8 hembras adultos, 6 individuos inmaduros.

   En la isla Agaltepec, Catemaco, Veracruz
    12 machos, 11 hembras adultos y 17 individuos inmaduros.

   En el Zoológico Miguel Alvarez del Toro, Chiapas
    20 individuos de diferente categoría, sexo y edad.

Recomendaciones

- Determinar los centros de acopio con capacidad de recibir animales decomisados o donados, en donde se realice la crianza en cautiverio. Los individuos canalizados a los centros permanentes, deberán cumplir con ciertas características preestablecidas, que aseguren su sobrevivencia y desarrollo en cautiverio.

- Establecer un programa de educación interinstitucional que destaque los siguientes aspectos:
    a) no son buenos como mascotas
    b) es difícil satisfacer sus requerimientos naturales
    c) son trasmisores de enfermedades y agresivos hacia el ser humano
    d) la captura de estos animales ejerce un impacto negativo en la supervivencia de la especie.

- Elaborar un manual de manejo para cautiverio que incluya recomendaciones sobre:
    a) Identificación individual permanente
    b) Instalaciones
    c) Dieta
    d) Diagnóstico y tratamiento de enfermedades
    e) Taxonomía
    f) Contención
    g) Protocolos de medicina preventiva y diagnóstico

- Estas se aplicarán tanto en centros de acopio temporal como permanentes.

- Elaborar un manual de campo para la toma, manejo, envío y procesamiento de muestras.

- Establecer un centro de referencia único para el procesamiento y análisis de la información recabada.

- Reconocer las enfermedades que se presentan en esta especie.

- Crear un banco de datos.

- Formar un grupo de trabajo multidisciplinario e interinstitucional para desarrollar cada una de las recomendaciones, con reuniones anuales que tendrían como objetivo revisar la información generada y actualizar las estrategias a seguir.

Lista de Participantes y Labor a Desarrollar para le Elaboración del Manual de *A. palliata*

1. Sitios alternativos para el mantenimiento de esta especie en cautiverio (además de los ya elegidos), así como del informe de SARH de los centros de acopio o zoológicos que en determinado momento albergarían temporalmente algunos especímenes.
   MVZ. PERLA CIFUENTES CALDERON.

   Establecer un acuerdo con el Biólogo Carlos Guichard del ZOOMAT para la recepción de especímenes.
   MVZ. DOMINGO CANALES ESPINOSA

2. Guía de lugares de acopio por regiones geográficas.
   AZCARM

3. Carta a zoológicos informando destino de animales (acopio), y los requerimientos para la exhibición de *A. palliata* en un zoológico.
   LAPZ. FRANK CARLOS CAMACHO y AZCARM

4. Lista de características deseables e indeseables para los individuos destinados a mantenerse en colección, así como una alternativa para aquellos que no cumplan esos requisitos.
   MVZ. DOMINGO CANALES E.

5. Elaboración de un manual de manejo para cautiverio que incluirá diversos tópicos en relación al cuidado de estos individuos.
   MVZ. CLAUDIA LEWY, MVZ.ENRIQUE YARTO, MVZ. DULCE BROUSSET, MVZ. IVONNE RUIZ Y MVZ.GUSTAVO RAMIREZ

6. Elaboración de un manual de campo para la toma, envío y procesamiento de muestras de *A. palliata*.
   MVZ.MARCO A. BENITEZ, MVZ. ALBERTO PARAS, MVZ ABEL CONTRERAS (zoológico de Morelia)

7. Establecer un centro de referencia único para el procesamiento y análisis de muestras para las especies de primates mexicanos.
   MVZ ALBERTO PARAS, MVZ. DOMINGO CANALES, UNAM

8. Reconocer las enfermedades que se presentan en esta especie y comunicar resultados a los elaboradores del manual.
   MVZ. JORGE PAREDES P.

9. Creación de un banco de datos
   UV, UNAM

10. Carta de solicitud de apoyo a los laboratorios de la UNAM para el procesamiento de las diferentes muestras anotando el objetivo del (los) muestreo (s) y la importancia de estos resultados.
AZCARM y ASOCIACION MEXICANA DE PRIMATOLOGIA

El bosquejo de cada uno de los trabajos será entregado al MVZ DOMINGO CANALES E. para la revisión pertinente en el próximo Simposio Nacional de Primatología, a celebrarse en la ciudad de Puebla en mayo de 1995 (las fechas exactas serán confirmadas y comunicadas a los participantes de este grupo próximamente).

ANÁLISIS DE VIABILIDAD DE POBLACIÓN Y HÁBITAT PARA EL MONO AULLADOR DE MANTO
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 de marzo de 1995

Sección 7
Educación
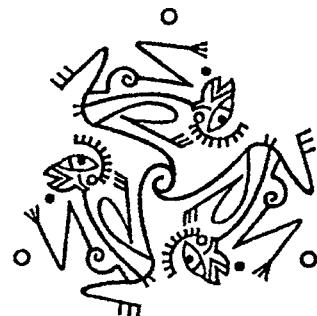
EDUCACIÓN

El éxito de los esfuerzos de conservación para *Alouatta palliata* depende fuertemente de una ciudadanía sensibilizada y conciente de la problemática en cuestión a nivel local, regional, estatal y nacional. Para lograr este punto es necesario crear programas de educación dirigidos a diversos públicos específicos; cada uno de los cuales tiene características particulares que deberán ser consideradas para obtener el máximo impacto posible con estos programas. Podemos dividir el desarrollo de dichos programas en 2 categorías: educación a nivel local y educación a nivel general.

Programa a nivel local

Estos programas pretenden tener un impacto directo sobre las poblaciones humanas que interactúan de una manera directa o indirecta con *A. p. mexicana* con regularidad. El desarrollo de estos programas debe considerar los siguientes puntos:
- Estudios socio-económicos de la localidad.
- Entendimiento de las tradiciones locales.
- Inclusión de la gente en el proceso de conservación.
- Ofrecer y explicar los beneficios y opciones que ofrece el programa de conservación.
- Generar material de apoyo y divulgación específico a cada localidad.
- Crear un entendimiento de la necesidad de proteger el hábitat y por lo tanto, respetar las áreas naturales ya sea que hayan sido decretadas como protegidas o no.
- Elaborar material que motive a las personas a coexistir con el mono aullador y ponga en claro la realidad de la historia natural del animal rompiendo con supersticiones y desinformación.

De ser necesario se elaborarán documentos en lenguajes autóctonos en las comunidades que así lo requieran.

Educación a nivel general

Por medio de estos programas se pretende concientizar y sensibilizar a la ciudadanía, tanto a nivel local como regional, nacional e internacional; ya sea que interactúen o no directamente con el mono aullador.

POPULATION AND HABITAT VIABILITY ASSESSMENT
FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 March 1995

Section 8
Executive Summary
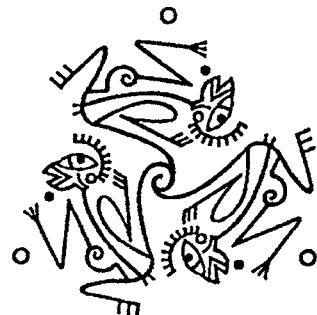
EXECUTIVE SUMMARY

Introduction

Mexico is considered to be one of the world's countries with the greatest biodiversity; however, its wealth is being reduced by a number of human activities which may contribute to the potential extinction of a number of species.

In particular, tropical forests have declined greatly as they are replaced by agricultural areas and livestock farming. This has led to a reduction in habitat for Mexican primates. Mexico is marked as the northern limit of distribution for neotropical primates, and is home to the black howler monkey *(Alouatta pigra)*, the mantled howler monkey *(Alouatta palliata mexicana)*, and two subspecies of spider monkey *(Ateles geoffroyi vellerosus* and *A. g. yucatanensis)*. These four primates were evaluated at a Conservation Assessment and Management Plan (CAMP) workshop held from 27 February to 1 March 1996. At this workshop, the black howler was assessed as being "Lower Risk" and the latter three taxa as "Vulnerable" (according to the new IUCN Red List categories of threat, version 2.2., 1994). It has been estimated that the reduction of the habitat of these animals is on the order of magnitude of 80% or more in Mexico (Estrada, 1993), which indicates the seriousness of the situation facing the taxa.

With continuation of the current trend of degradation of tropical forests in Mexico, these primate species all soon will be considered threatened. In light of this, it is crucial to develop a series of conservation actions so that the wild populations of these monkeys will not disappear.

Population and Habitat Viability Assessment (PHVA)

In the PHVA workshop for *Alouatta palliata mexicana,* biological information and expert opinion of participants was used to estimate the taxon's risk of extinction, considering also the size and distribution of its populations, and factors that may affect it negatively.

To estimate the risk in possible future ecological scenarios, the simulation model VORTEX (version 7.0) was used, identifying critical factors contributing to the decline of the populations. Alternative management strategies were considered that might improve the future of the species.

It was recognized that this evaluation would have to use field data of unequal quality, with generalizations and extrapolations being made in some cases. In light of this, many of the conclusions and recommendations should be critically examined as better information becomes available.

Summary of Recommendations

General plan for the study and conservation of *A. p. mexicana.*

Given the accelerated disturbance, fragmentation and loss of habitat faced by this taxon, it is necessary to develop a research and conservation program that will assure its permanent place in the natural wild animal populations of Mexico.

Studies

a) Taxonomy (at the anatomic and genetic levels)
b) Distribution and areas of occupation
c) Occupation of different types of habitat
d) Population density and home range area estimates under different environmental conditions
e) Changes in social organization in relation to environmental variation
f) Population growth (birthrate and mortality rates)
g) Migration between populations
h) Changes in foraging strategies
I) Effects of the fragmentation on wild populations
j) Studies on hunting, capture and commercial trade

Conservation Actions

To improve management in protected natural areas
a) Legal protection
b) Patrolling/vigilance
c) Monitoring of populations
d) Ecological restoration
e) Education programs
f) Reintroduction and/or supplementation (only under special conditions and under strict safety measures)
g) Linking (research institutions, governmental agencies, local human groups) for program development

To establish new protected natural areas
a) Exploration of areas that might be candidates to hold wild populations
b) Identification and positioning of appropriate areas for conservation
c) Proposal of a management plan
d) All cited above for the previous point

To develop a translocation program (pilot program)
a) Feasibility analysis (populations and release area)
b) Collection
c) Transport

d) Clinical evaluation
e) Captive management
f) Release
g) Monitoring

Managing of the metapopulation in fragmented habitat
a) Identification of fragmented areas
b) Translocations
c) Monitoring
d) Management of a viable population

Control and trade reduction
a) Formulation of appropriate legal norms
b) Effective Patrolling in wild areas
c) Effective Patrolling in rural and urban areas where commercial trade takes place
d) Appropriate mechanism for formulating accusations, consignations and confiscations
e) Penalties for dealers
f) Anti-trade educational campaign
g) Channeling of confiscated animals

Education
a) Program development with the aim of achieving a favorable attitude toward primates and collaboration toward their conservation, using different mass media communication techniques
b) Implementation of educational programs in zoos

Inter-institutional Collaboration
a) Scientific societies
b) Educational and zoological institutions
c) Governmental agencies
d) Sectors of the civil society
e) International organizations dedicated to conservation

The conservation strategies for primates in regional conservation programs
a) Promote development sustainable alternatives
b) Make local residents program partners

POPULATION AND HABITAT VIABILITY ASSESSMENT
FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 March 1995

Section 9
Taxonomy and Distribution of
Alouatta palliata mexicana
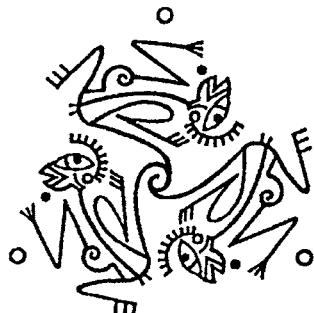
TAXONOMY AND DISTRIBUTION OF *Alouatta palliata mexicana*

Revision Objectives

To analyze the taxonomic position of *Alouatta palliata mexicana*, its original, current and potential distribution area, and to estimate its populations and detect some of the factors which may be affecting them, in order to establish its degree of threat and propose some measures which may help us in their conservation.

Taxonomic Classification

Order: Primates
   Family: Cebidae
      Genus: Alouatta
         Species: *Alouatta palliata*
            Subspecies: *Alouatta palliata palliata*
                        Alouatta palliata mexicana
                        Alouatta palliata aecuatorialis

The taxonomic validity of *Alouatta palliata mexicana* is generally accepted as one of the three subspecies described for the species. Although Lawrence (1933) established that it is very difficult to morphologically destinguish between this subspecies and *Alouatta palliata palliata*, there have been no reports of a simpatric existence between the two. Although it is not a priority, in light of the great individual variation present in the diagnostic characteristics of these subspecies, we reccommend a taxonomic revision at the subspecies level be conducted using modern techniques.

Geographic Distribution

Original distribution

Alouatta palliata mexicana's original distribution includes the states of Veracruz, Tabasco, Oaxaca and Chiapas in Mexico although there have been some very old and unreliable reports in the states of Campeche and Quintana Roo (Elliot, 1904 ?; Diaz de León, 1905 and Villa, 1959 ?). In Central-America it has been reported in Belize and Guatemala but these reports also neeed to be confirmed.

Occupation of different habitat types

The howler monkey (Alouatta palliata) is adaptable to different vegetation types. It can be found in: mature evergreen forest, deciduous forest, riparian forest, secondary forest, subxeric forest (Neville et al. 1988), and medium sub-perennial rain forest (Estrada 1989). They live in an elevation range from sea level to 1100m.

<u>Current distribution and population size</u>

The calculations of density of *Allouatta palliata* and the areas of the zones occupied by *Allouatta pilliata mexicana* in Mexico has been realized by using data and estimations from different procedures to produce extrapolations and generalizations in hopes of obtaining more exact data. The only sufficient available detailed information is for the zone of Los Tuxtlas (Estrada, 1982, 1989, 1994).

Estrada estimates a density of 23 *Allouatta palliata mexicana*/Km^2 in the protected areas of Los Tuxtlas and 3.6 *Allouatta palliata mexicana*/ Km^2 in unprotected areas. Using the figure of 3.6 *Allouatta palliata mexicana*/ Km^2, he estimates a population of 1152 *Allouatta palliata mexicana* in Los Tuxtlas (1994). However, he presents data that indicate a larger population in 40% of the 120 occupied fragments studied in the area of Volcan San Martin, with a total of 1800 individuals. These fragments represent a range in area of 1-2000 Ha. The larger fragments were as follows: 1 of 1000 Ha, 3 of 1250 Ha, 1 of 1500, 1 of 1600 Ha, 1 of 1800 Ha, and 1 of 2000 Ha. The subpopulations of *Allouatta palliata mexicana* in these fragments have an average density (rounding) of 10 individuals/Km^2. In terms of the question of an intermediate density between the above mentioned proportions, we think there can be an estimation of density of the other large protected areas occupied by *Allouatta palliata mexicana* in Mexico. In these areas, there is no data, but the vegetation is the same or appears to be, and the habitat is less fragmented, so this could an underestimation of the truth.

Francisco Garcia (1986) estimated a total area of 623 Km^2 for the area occupied by forest in Los Tuxtlas. Assuming that the two largest protected areas in the region (Volcan San Martin 70 Km^2 and Sierra de Santa Martha 250 Km^2 (Estrada, 1989)) have not suffered significant deforestation, the area occupied by other fragments will be 303 Km^2 in 1986, but with a current rate of deforestation of 7% (1995) 146 Km^2 will remain, distributed in fragments. Extrapolating from the 40% of the fragments occupied by *Allouatta palliata mexicana* of the 120 areas studied (Estrada 1994) to the whole region of Los Tuxtlas (146 Km^2 of forest fragments), we obtain 58.4 Km^2 occupied by *Allouatta palliata mexicana* in fragments outside of the two principal areas (Volcan San Martin and Sierra de Santa Martha) en Los Tuxtlas. For the calculation of the area occupied by *Allouatta palliata mexicana* in the remaining areas outside of Los Tuxtlas, the information was obtained from Alejandro Hernandez (personal communication) for the Ocote and Manzanillal and from Estrada (1989) for Uxpanapa-Chimalapas. The composition of the groups in all of these areas was obtained by extrapolating Estrada's (1989) data taken for the groups in protected fragments.
> average size of group: n=10
> composition: 3 ♂:4 ♀:1.5 Juvenile (J):1.5 Infant (I).

For the unprotected fragments the given composition is
> 1♂:1.5♀:1J:1I.

(This composition has been used for the smallest fragments in Los Tuxtlas).

San Martín Volcano Area (Los Tuxtlas, Veracruz)

The type of vegetation of this area corresponds to that of a high perene rainforest and mid subperene rainforest. The area occupied by *Alouatta palliata mexicana* encompasses about 70 Km², ranging from sea level to 1,200 meters above sea level. The population size is estimated at 1,085 individuals (based on information from Estrada, 1989; 1994)

> Population size: 1,085
> Age/Sex distribution based on an average group of 10 individuals: Males 3
>> Females   4
>> Juveniles   1.5
>> Infants   1.5

Sierra de Santa Martha (Los Tuxtlas, Veracruz)

The type of vegetation of this area corresponds to that of a high perene rainforest and mid subperene rainforest. The area occupied by *Alouatta palliata mexicana* encompasses about 250 Km², ranging from sea level to 1,100 meters above sea level. The population density is estimated at 10 individuals per Km² (based on information from Estrada, 1989; 1994)

> Population size: 2,500
> Age/Sex distribution based on an average group of 10 individuals: Males 3
>> Females   4
>> Juveniles   1.5
>> Infants   1.5

Uxpanapa Region (Veracruz)

The type of vegetation of this area corresponds to that of a high perene rainforest and mid subdecidous rainforest. The area occupied by *Alouatta palliata mexicana* encompasses about 165 Km², ranging from sea level to 1,100 meters above sea level. The population density is estimated at 10 individuals per Km² (based on information from Estrada, 1989; 1994)

> Population size: 1,650
> Age/Sex distribution based on an average group of 10 individuals:
>> Males   3
>> Females   4
>> Juveniles   1.5
>> Infants   1.5

Sierra de Los Chimalapas (Oaxaca)

The type of vegetation of this area corresponds to that of a perene rainforest. The area occupied by *Alouatta palliata mexicana* encompasses about 835 Km², ranging from sea level to 1,100 meters above sea level. The population density is estimated at 10 individuals per Km² (based on information from Estrada, 1989; 1994)

        Population size: 8,350

        Age/Sex distribution based on an average group of 10 individuals: Males 3

Females	4
Juveniles	1.5
Infants	1.5

El Manzanillar (Chiapas)

The type of vegetation of this area corresponds to that of a perene rainforest. The area occupied by *Alouatta palliata mexicana* encompasses about 70 Km², ranging from sea level to 1,100 meters above sea level. The population density is estimated at 10 individuals per Km² (based on information from Estrada, 1989; 1994)

        Population size: 700

        Age/Sex distribution based on an average group of 10 individuals: Males 3

Females	4
Juveniles	1.5
Infants	1.5

El Ocote (Chiapas)

The type of vegetation of this area corresponds to that of a high perene rainforest and mid sub-decidous rainforest. The area occupied by *Alouatta palliata mexicana* encompasses about 400 Km², ranging from sea level to 1,100 meters above sea level. The population density is estimated at 10 individuals per Km² (based on information from Estrada, 1989; 1994)

        Population size: 4,000

        Age/Sex distribution based on an average group of 10 individuals: Males 3

Females	4
Juveniles	1.5
Infants	1.5

Other Areas

There isn't enough information to estimate populations for Macuspana and Teapa in the state of Tabasco, Mexico or for Guatemala and Belize.

Species Evaluation

According to IUCN standards the classification of Vulnerable is proposed for this sub-species. Mace-Lande (classified as *A. villosa*, 1990) insufficiently known and inexplicably excluded from the list in 1994. Included in appendix I of CITES (1986) and declared by SEDESOL as in danger of extinction (1994).

Recommendations

Based on the analysis of gathered information, a primary recommendation is to carry out field studies to determine precisely the current distribution area for this subspecies as well as the size of its populations.

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 March 1995

Section 10
Population Biology and Modelling
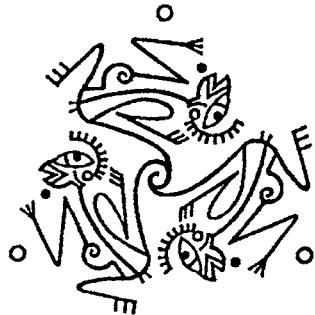
POPULATION BIOLOGY AND MODELLING

Introduction

The Mexican population of the mantled howler monkey (*Alouatta palliata mexicana*) occupies remaining forested habitat distributed in the southern states of Veracruz, Tabasco, Campeche, Oaxaca, and Chiapas. However, *Alouatta palliata mexicana* and the other primates inhabiting this area, *Alouatta pigra* and *Ateles geoffroyi*, are in danger of extinction as a result of illegal hunting and the rapid destruction of their natural rain forest habitat.

The need for and effects of intensive management strategies can be modelled to suggest which practices may be the most effective in preserving the mantled howler monkey in Mexico. VORTEX, a simulation modeling package written by Robert Lacy and Kim Hughes, was used as a tool to study the interaction of multiple variables treated stochastically.

The VORTEX program 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 (e.g., births, deaths, catastrophes, etc.) that occur according to defined probabilities. The probabilities of events are modeled as constants or as random variables that follow specified distributions. VORTEX 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 primate, the conditions affecting the population, and possible changes in the future.

Input Parameters for Simulations

Age of First Reproduction: VORTEX defines reproduction as birth. Therefore, given the age of female sexual maturity set at 36 months with a gestation period of approximately 6 months (Glander 1980), first reproduction for females was set conservatively at 4 years. Sexual maturity for males is reached at 42 months; however, social structure in howler troops generally prohibits breeding by males younger than 5 years of age.

Offspring Production: Interbirth interval was set at 2 years in howler monkeys. Therefore, 50% of adult females do not reproduce in a given year. Of those females that do reproduce, all give birth to only one offspring.

Variation in reproduction is modelled in VORTEX by entering a standard deviation (SD) for the proportion of females failing to produce offspring in a given year. Lacking empirical data,

we assumed that such variation (due to fluctuations in food abundance and variations in the age at which females reach sexual maturity) was 25% of the mean. VORTEX then determines the percent breeding each year of the simulation by sampling from a binomial distribution with the specified mean (50%) and SD (12.5%).

As no data exist indicating other than a 50:50 sex ratio at birth for mantled howler monkeys, we used an equal sex ratio for all scenarios.

Age of Senescence: VORTEX assumes that animals can breed (at the normal rate) throughout their adult life. General data for wild primate populations suggests that mantled howlers may reach 20 years of age, although this is probably a rare event. Froehlich et al. (1981) captured a male on Panama's Barro Colorado Island that was estimated to be 20.5 years of age, based on tooth wear.

Mortality: We constructed two different mortality schedules that roughly correspond to data from two separate howler populations. The "low" mortality scenario uses data from a translocated population of mantled howler monkeys on Agaltepec island at Catemaco Lake, Veracruz, Mexico. This population is presumed to be at very low density, with ample food and territory resources. The mortality schedule for this population (adapted from Cortés-Ortiz et al. 1994) is shown below:

% Mortality (SD)

Age Class	Males	Females
0-1	15.0 (4.5)	10.0 (3.0)
1-2	2.0 (1.0)	0.5 (2.0)
2-3	2.0 (1.0)	0.0 (2.0)
3-4	0.0 (2.0)	0.0 (2.0)
4-5	0.0 (2.0)	4.5 (1.4)
5-Ad	3.75 (1.1)	4.5 (1.4)

The alternative "high" mortality schedule is representative of a population similar to that on Barro Colorado Island, Panama (Froehlich et al. 1981). This population is thought to be at a higher density than the Agaltepec population, with greater competition for a variety of resources. The "high" mortality schedule is shown below:

Age Class	Males	Females
0-1	15.0 (4.5)	10.0 (3.0)
1-2	12.0 (3.6)	10.0 (3.0)
2-3	10.0 (3.0)	5.0 (1.5)
3-4	15.0 (4.5)	5.0 (1.5)
4-5	10.0 (3.0)	12.0 (3.6)
5-Ad	12.0 (3.6)	12.0 (3.6)

This schedule, in fact, is considered to be optimistic compared to the actual mortality table presented by Froehlich et al. (1981) in which almost 90% and 70% of males and females,

respectively, die before the age of five. This level of mortality was considered by the workshop participants to be too high for howler populations in Mexico.

Because the juvenile (0-1 year age class) mortality was the same in both "low" and "high" mortality schedules, scenarios were constructed that specifically varied this parameter in order to investigate its impact on population persistence. Female mortality was increased to 15% and 20% with the corresponding male mortality set at 20% and 25%. Such increases in juvenile mortality can reflect the loss of individuals resulting from illegal hunting for food or the pet trade, both of which exist in Mexico (Estrada and Coates-Estrada 1984).

Carrying Capacity: K defines an upper limit for the population size, above which additional mortality is imposed in order to return the population to K. VORTEX, therefore, uses K to impose density-dependence on survival rates.

Alouatta palliata mexicana exists in a number of isolated populations throughout southern Mexico. Density estimates for mantled howler monkeys in these areas range from 3.6 individuals per km^2 in unprotected areas (Estrada 1994) to 23 individuals per km^2 in some of the protected areas around Los Tuxtlas (Estrada 1989). To calculate carrying capacity for our simulations, we used an estimated density of 16 individuals per km^2, a value consistent with a protected area like Los Tuxtlas (Estrada 1994). Based on this generalized density, populations were simulated that had carrying capacities of 100, 200, 400, and 1000. These carrying capacities span a wide range of habitat fragments currently occupied by *A. p. mexicana* including small fragments within the Volcan San Martin Tuxtla region in Veracruz as well as larger patches such as the Manzanillar region of Chiapas.

Starting Population Size: With limited current census data, we used a general density estimate of 10 individuals per km^2 as a guide to determining initial population sizes. We therefore initialized the simulations with a population size equal to half the carrying capacity, i.e., 50, 100, 200, and 500 individuals. These values for initial population size and carrying capacity, while somewhat generalized, are extremely useful in our evaluation of the impact of various stochastic forces on the persistence of populations of variable size.

Starting Age Distribution: We initialized all of the model runs with a stable age distribution that distributes the total population among each sex-age class in accordance with the existing mortality and reproductive schedules.

Inbreeding Depression: Specific data do not exist on the prevalence and effects of inbreeding in wild mantled howler monkey populations. However, given the severe fragmentation of suitable howler habitat and resultant fragmentation of howler populations within those forest patches, it may be reasonable to infer that some measurable degree of inbreeing is occurring in these small populations. Therefore, we have included inbreeding depression in that subset of modelling scenarios specifically dealing with very small populations, i.e., 50 to 100 individuals.

We employed the heterosis model of inbreeding depression, in which individuals that are heterozygous at a given genetic locus have superior fitness to those that are homozygous at that

locus. Because detrimental alleles are not removed by natural selection from the population over time in this model, the heterosis model may provide a conservative overestimate of the deleterious effects of inbreeding in the howler monkey populations modelled below.

The severity of inbreeding depression in mammalian populations can be measured as the number of "lethal equivalents" contained in the genome of the population of interest. Data for a number of captive mammal species (including twelve species of primates) suggests that these species harbor about 3 lethal equivalents (Ralls et al. 1988). Consequently, we have modelled inbreeding depression using this median lethal equivalent value.

Catastrophes: Catastrophes are thought of as extremes in environmental variation, and are treated differently conceptually and operationally in VORTEX. Both the frequency of occurrence and the impact on reproduction and survival of the catastrophic event is modelled by the program. Three catastrophes were included in the simulations:

Fire: Large fires generally occur in the area about once every five years. The effect of these fires is small, with a 5% reduction in reproduction and a 10% reduction in survival.

Hurricane: It is thought that strong storms hit this area every ten years. The effect of hurricanes is slightly more severe, with a 10% reduction in reproduction and a 30% reduction in survival during those years in which a hurricane occurs.

Disease: Epidemic diseases occur quite rarely, but can have a devastating effect on a population. Disease was modelled as occurring once every 100 years with a 40% reduction in reproduction and a 60% reduction in survival.

Iterations and Years of Projection: Each scenario in which inbreeding depression was absent was iterated 500 times, while those scenarios incorporating inbreeding depression were interated 250 times due to computational limitations. Projections were made for 100 years for all scenarios. Output results were summarized at 10-year intervals in the time series figures. Each tabulated scenario has a corresponding file number for reference and future retrieval of other results, if necessary. The simulations were run using VORTEX version 7.0.

Results from Simulation Modelling

Explanation of Tables and Figures

The numerical results of the simulation models appear in Tables 10.1 through 10.5. Each table represents a specified set of conditions, for example, juvenile mortality schedule, initial population size, etc. Within each table, the results are organized in a nested structure: each initial population size was run with each level of juvenile mortality under specified conditions.

The headings for the tables are as follows:

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

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

P(E): probability of extinction over the 100-year time span of the simulation, calculated as the proportion of iterated population 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 heterozygosity expected to remain in extant populations after 100 years;

T(E): mean time to population extinction for those scenarios in which at least 10% of the simulated populations became extinct.

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

Figures 10.1 through 10.7 are a graphical compilation of the modelling results, attempting to show the relationships between specific factors and their impact on population persistence.

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 10.1 - 10.5. 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, inclusion/exclusion of catastrophes and proportional female reproductive success are the only variables that affect these deterministic rates. Therefore, the long-term rate of growth of these populations, in the absence of stochastic variation, is independent of initial population size and habitat carrying capacity.

Under conditions of low adult mortality, like those that appear to predominate on Agaltepec Island, howler monkey populations show positive deterministic growth, regardless of the level of juvenile mortality. Of course, deterministic growth is reduced as juvenile mortality is

increased from 10% to 20%. This rate of growth is increased dramatically in the absence of catastrophes (r_d = 0.101-0.088; Table 10.2, Files 525-527). Under these same conditions of adult mortality, inspection of Tables 10.3 and 10.4 indicate that, in the continued presence of disease, the occurrence of occasional hurricanes has a greater impact on population growth than does occasional forest fire. For illustration, compare File #549, in which disease and fire are included in the simulation and r_d = 0.074 with File #573, where disease and hurricane are included and r_d = 0.063.

If howler monkey populations experience high mortality, such as those on Barro Colorado Island, the models predict much lower deterministic growth. For example, populations are in deterministic decline (r_d = 0.042-0.029; Table 10.1, Files 501-503) when all catastrophes are present, and growth rates are reduced to 0.034-0.020 when catastrophes are absent (Table 10.2, Files 537-539). Hurricanes are again shown to be of greater impact to howler populations (Tables 10.3 and 10.4), with growth rates ranging from 0.006 to -0.018 depending on the extent of juvenile mortality as well as which particular catastrophic event is included in the models.

These results clearly indicate that adult mortality can have dramatic impacts on population persistence. Conditions such as those that initially appear to persist on Agaltepec Island—low population density, little competition for food and other resources—lead to the potential for rapid long-term population growth. On the other hand, high adult mortality characteristic of higher population densities leads to much lower deterministic growth, and in many instances leads to long-term projected population decline. Furthermore, the impact of catastrophic environmental events, and hurricanes in particular, are substantial and need to be considered in the development of any coordinated howler monkey management plan.

Stochastic Simulation Results

Calculations of population growth rates from average birth and death rates in a life table will over-estimate long-term population growth if there are stochastic fluctuations in demographic parameters for any reason, even random sampling variation. To demonstrate this phenomenon, note that 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.

For example, with an initial population size of 50 individuals and low juvenile and adult mortality (Table 10.1, File #501), the stochastic growth rate (r_s) is 0.028, or 33% lower than the deterministic growth rate of 0.042. As juvenile mortality increases, the stochastic growth rate declines in a manner similar to that observed for the deterministic growth rate. Under conditions of high adult mortality, stochastic variation in life-history parameters results in a more severe decline in the population growth rate. Under the same conditions as those in File #501 but with high adult mortality (Table 10.1, File #513), the mean stochastic population growth rate is -0.052, or double the rate of deterministic decline (r_d = -0.026). All other conditions in the presence of high mortality lead to similar reductions in stochastic growth.

When adult mortality is low under the conditions modelled in the scenarios listed in Table 10.1, the risk of population extinction exceeds 4% only under the smallest initial population sizes. If juvenile mortality is as high as 20%, the probability of extinction is 12% (Table 10.1, File #503) but declines rapidly as either juvenile mortality or initial population size is decreased. It is important to realize in these results that, despite a mean positive stochastic growth rate in the first twelve scenarios in Table 10.1, the risk of extinction in many scenarios is non-zero. This is a direct result of the random variation included in these simulations. After 100 years, the final population size in all low-adult mortality scenarios is about 70-75% of the habitat carrying capacity. As a result, a considerable proportion of the original population heterozygosity is retained, ranging from a low of 81.6% (File #503) to a maximum of 98.2% (File #510).

If adult mortality is increased, as in those scenarios listed in the bottom half of Table 10.1, the simulated populations are dramatically destabilized. As an example, given an initial population size of 100 and juvenile mortality of 15% (File #517), the risk of extinction is 82.4%; this is in great contrast to the same simulation with low adult mortality (File #505), where P(E) = 0.024. If juvenile mortality is particularly high, very small populations have a very high risk of extinction (i.e., File #515: P(E) = 0.970). Populations that become extinct under these conditions have an average time to extinction of approximately 50-70 years. In addition, those simulated populations that do not become extinct have very small population sizes after 100 years and a high risk of extinction in the immediate time period following the end of the simulation. Even those simulations starting out with a large number of individuals, as in File #522 (Table 10.1), have very few animals remaining after the duration of the simulation. Of course, this dramatic reduction in population size leads to a small proportion of genetic variation retained in the extant population.

The extreme sensitivity of simulated howler monkey populations to the catastrophes identified during the workshop is shown in Table 10.2. When catastrophes were removed from the models, all stochastic growth rates were positive, population extinction was eliminated from all but one scenario (File #539), and all populations grew very rapidly to carrying capacity or just below K. Likewise, all populations retained at least 85% of their initial population heterozygosity. It is clear from these results that the catastrophic environmental events included in these models have dramatic effects on howler monkey population viability.

It is possible to look more closely at the relative impacts of these catastrophes by designing and comparing output from scenarios that include only certain catastrophic events. For example, Table 10.3 shows results from those models that included only epidemic disease and wildfires (hurricanes removed), while Table 10.4 shows results from models that included only epidemic disease and hurricanes (wildfires removed). The risk of population extinction was nearly eliminated from low-adult mortality scenarios when hurricane was removed from the model and population sizes after 100 years were very near carrying capacity (top half of Table 10.3). Extinction risk was substantially decreased when hurricanes were removed from the model even under conditions of high adult mortality (bottom half of Table 10.3). If hurricanes are included in the model and wildfires are removed (Table 10.4), overall population viability is compromised compared to the same results presented in Table 10.3. It is of interest to note, however, that these results point to the high degree of interaction among these catastrophic

events. Despite the relatively low impact of wildfires on these primate populations, the risk of extinction when all catastrophes are present remains significantly higher than when only hurricanes and disease are included, particularly when adult mortality is high. For example, a population of 500 individuals with high adult mortality and 15% juvenile mortality has a probability of extinction of 0.484 (Table 10.1, File #523), whereas the same population subjected to only disease and hurricanes has an extinction probability of just 0.144 (Table 10.4, File #595). As in earlier simulations, the average time to extinction for those populations at considerable risk is approximately 60-75 years.

The results of those simulations incorporating the effects of inbreeding depression in the smallest populations are shown in Table 10.5. Inbreeding depression acts to increase the vulnerability of the simulated populations to extinction, but overall the effects of inbreeding are not nearly as severe as those related to the included catastrophes. This is shown graphically in Figure 10.1. When catastrophes are removed from the models, even low-adult mortality populations subjected to the deleterious effects of inbreeding increase rapidly in size to carrying capacity (Figure 10.1A), identical to those populations for which inbreeding has no effect. When catastrophes are added to the models, the population trajectories are very similar for those simulations with and without inbreeding.

These results are even more striking when adult mortality is high (Figure 10.1B). In the absence of catastrophes, population growth rate is positive even with inbreeding, although not at the rate seen with low adult mortality. However, when catastrophes are included, population growth rate becomes negative and final population size declines from an initial value of 100 to approximately 20. Moreover, these results are very similar with and without the effects of inbreeding.

Conclusions

The results of the population simulation modelling for mantled howlers in Mexico are summarized in Figures 10.2 through 10.7. In the presence of catastrophes, increases in juvenile mortality lead to greater population instability, but primarily when adult mortality is high. Overall, dramatic differences in population viability are observed when comparing the two adult mortality conditions in the presence of catastrophic environmental variation (Figures 10.2 and 10.3). In the absence of such extreme environmental variation, the differences in adult mortality have virtually no impact (Figures 10.4 and 10.5). These results graphically illustrate the interactions between howler life history parameters and the nature of the variation within the environment they inhabit.

Based on these observations, it is important to devote research effort on mainland Mexico howler populations to determine mortality schedules more precisely. This could be accomplished by radio-collaring at least 15-30 animals and monitoring them for an extended period of time (at least two years). During this period, data on fecundity could also be collected, as well as some information on environmentally-derived variation in these vital rates. In fact, because of the role that hurricanes, fire, and disease play in howler population dynamics, careful attention must be

directed towards a more thorough understanding of the frequency and severity of these events. Historical meteorological data can be very useful in this regard.

The impact of inbreeding depression is summarized in Figures 10.6 and 10.7. Increasing juvenile mortality leads to a slightly higher risk of extinction under inbreeding, but only in the presence of catastrophes. Inbreeding depression is more evident, however, when considering final population size. This is easiest to see when the initial population size is 50 and catastrophes have been removed from the models. When adult mortality is low, final population sizes remain very near 100 as juvenile mortality is increased with and without inbreeding depression (compare "$N_0 = 50$; Low" curves in Figures 10.4B and 10.7B); however, when adult mortality is high, final population size is consistently lower with increasing juvenile mortality when inbreeding is included in the models (compare "$N_0 = 50$; High" curves in Figures 10.5B and 10.7B). After 100 years of the simulation, final population size under 20% juvenile mortality is 88 when inbreeding depression is absent, but is only 63 when inbreeding depression is included. These decreased population sizes would lead to increased levels of inbreeding, further reducing population size and increasing the risk of future population extinction. As a result, it is important to recognize the impact that inbreeding may have on viability of particularly small populations. Careful attention should therefore be directed to determining levels of inbreeding depression in captive populations of howler monkeys in order to more fully understand this phenomenon in wild populations.

Recommendations

The following recommendations are made based on the simulation results discussed above:

1. The important interactions between juvenile mortality, adult mortality, and environmental variability necessitate the development of research on reproductive and mortality schedules in mantled howler monkey populations in Mexico. This information can be obtained through radio-telemetry studies on 10-20 adults over a period of at least two years. Data such as these are vital for the refinement of population viability simulation models.

2. While not as serious a factor as extreme environmental variation in determining population viability, the extent of inbreeding depression in mantled howler populations should be assessed. This is most easily accomplished by analyzing detailed pedigree records of this and related howler monkey species in captivity.

3. Because of the extreme risk of extinction experienced by populations with higher levels of adult mortality, it may become necessary to consider actions to be taken to reduce this extinction risk. More specifically, management strategies designed to either reduce adult mortality or artificially supplement small populations in stochastic decline should be developed and evaluated.

Sample VORTEX Input File

```
HOWL597.OUT      ***Output Filename***
Y       ***Graphing Files?***
N       ***Each Iteration?***
Y        ***Screen display of graphs?***
250       ***Simulations***
100       ***Years***
10       ***Reporting Interval***
1       ***Populations***
Y       ***Inbreeding Depression?***
H
3.140000
N       ***EV correlation?***
3       ***Types Of Catastrophes***
P       ***Monogamous, Polygynous, or Hermaphroditic***
4       ***Female Breeding Age***
5       ***Male Breeding Age***
20        ***Maximum Age***
0.500000      ***Sex Ratio***
1       ***Maximum Litter Size***
N       ***Density Dependent Breeding?***
50.000000      ***Population 1: Percent Litter Size 0***
50.000000      ***Population 1: Percent Litter Size 1***
12.500000      ***EV--Reproduction***
10.000000      ***Female Mortality At Age 0***
3.000000     ***EV--FemaleMortality***
0.500000     ***Female Mortality At Age 1***
2.000000     ***EV--FemaleMortality***
0.000000     ***Female Mortality At Age 2***
2.000000     ***EV--FemaleMortality***
0.000000     ***Female Mortality At Age 3***
2.000000     ***EV--FemaleMortality***
4.500000     ***Adult Female Mortality***
1.350000     ***EV--AdultFemaleMortality***
15.000000      ***Male Mortality At Age 0***
4.500000     ***EV--MaleMortality***
2.000000     ***Male Mortality At Age 1***
1.000000     ***EV--MaleMortality***
2.000000     ***Male Mortality At Age 2***
1.000000     ***EV--MaleMortality***
0.000000     ***Male Mortality At Age 3***
2.000000     ***EV--MaleMortality***
0.000000     ***Male Mortality At Age 4***
2.000000     ***EV--MaleMortality***
3.750000     ***Adult Male Mortality***
1.100000     ***EV--AdultMaleMortality***
20.000000      ***Probability Of Catastrophe 1***
0.950000     ***Severity--Reproduction***
0.900000     ***Severity--Survival***
10.000000      ***Probability Of Catastrophe 2***
0.900000     ***Severity--Reproduction***
0.700000     ***Severity--Survival***
1.000000     ***Probability Of Catastrophe 3***
0.600000     ***Severity--Reproduction***
0.400000     ***Severity--Survival***
N      ***All Males Breeders?***
Y       ***Answer--A--Known?***
70.000000      ***Percent Males In Breeding Pool***
Y       ***Start At Stable Age Distribution?***
50      ***Initial Population Size***
100       ***K***
0.000000      ***EV--K***
N       ***Trend In K?***
N        ***Harvest?***
N       ***Supplement?***
Y       ***AnotherSimulation?***
```

Sample VORTEX Output File

```
VORTEX -- simulation of genetic and demographic stochasticity

HOWL597.OUT
Tue May 23 10:08:46 1995


  1 population(s) simulated for 100 years, 250 iterations

  HETEROSIS model of inbreeding depression
    with 3.14000 lethal equivalents per diploid genome

  First age of reproduction for females: 4    for males: 5
  Age of senescence (death): 20
  Sex ratio at birth (proportion males): 0.50000


Population 1:

  Polygynous mating;
    70.00 percent of adult males in the breeding pool.

  Reproduction is assumed to be density independent.

    50.00 (EV = 12.50 SD) percent of adult females produce litters of size 0
    50.00 percent of adult females produce litters of size 1

   10.00 (EV = 3.00 SD) percent mortality of females between ages 0 and 1
    0.50 (EV = 2.04 SD) percent mortality of females between ages 1 and 2
    0.00 (EV = 2.00 SD) percent mortality of females between ages 2 and 3
    0.00 (EV = 2.00 SD) percent mortality of females between ages 3 and 4
    4.50 (EV = 1.35 SD) percent annual mortality of adult females (4<=age<=20)
   15.00 (EV = 4.50 SD) percent mortality of males between ages 0 and 1
    2.00 (EV = 1.00 SD) percent mortality of males between ages 1 and 2
    2.00 (EV = 1.00 SD) percent mortality of males between ages 2 and 3
    0.00 (EV = 2.00 SD) percent mortality of males between ages 3 and 4
    0.00 (EV = 2.00 SD) percent mortality of males between ages 4 and 5
    3.75 (EV = 1.10 SD) percent annual mortality of adult males (5<=age<=20)
   EVs may have been adjusted to closest values
       possible for binomial distribution.
   EV in mortality will be correlated among age-sex classes
       but independent from EV in reproduction.

  Frequency of type 1 catastrophes: 20.000 percent
    with 0.950 multiplicative effect on reproduction
     and 0.900 multiplicative effect on survival

  Frequency of type 2 catastrophes: 10.000 percent
    with 0.900 multiplicative effect on reproduction
     and 0.700 multiplicative effect on survival

  Frequency of type 3 catastrophes: 1.000 percent
    with 0.600 multiplicative effect on reproduction
     and 0.400 multiplicative effect on survival

  Initial size of Population 1:
   (set to reflect stable age distribution)
  Age 1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20  Total
      3  3  2  3  2  1  2  1  1  1  1  1  1  0  1  0  1  0  0  1     25  Males
      3  3  3  2  2  2  2  1  1  1  1  1  1  0  1  0  1  0  0  0     25  Females


  Carrying capacity = 100 (EV = 0.00 SD)
```

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

    r =   0.042     lambda = 1.043     R0 =     1.473
    Generation time for:   females = 9.23     males = 10.17

Stable age distribution:  Age class     females     males
                              0          0.070       0.070
                              1          0.057       0.054
                              2          0.051       0.048
                              3          0.046       0.042
                              4          0.042       0.038
                              5          0.036       0.035
                              6          0.031       0.030
                              7          0.027       0.026
                              8          0.024       0.023
                              9          0.020       0.020
                             10          0.018       0.017
                             11          0.015       0.015
                             12          0.013       0.013
                             13          0.011       0.012
                             14          0.010       0.010
                             15          0.009       0.009
                             16          0.007       0.008
                             17          0.006       0.007
                             18          0.006       0.006
                             19          0.005       0.005
                             20          0.004       0.004

Ratio of adult (>= 5) males to adult (>= 4) females: 0.845


Population 1

Year 10
      N[Extinct] =         0, P[E] = 0.000
      N[Surviving] =     250, P[S] = 1.000
      Population size =            68.52 (   1.64 SE,    25.90 SD)
      Expected heterozygosity =    0.972 (  0.001 SE,    0.012 SD)
      Observed heterozygosity =    0.997 (  0.000 SE,    0.007 SD)
      Number of extant alleles =   55.24 (   1.00 SE,    15.79 SD)

Year 20
      N[Extinct] =         1, P[E] = 0.004
      N[Surviving] =     249, P[S] = 0.996
      Population size =            72.05 (   1.78 SE,    28.12 SD)
      Expected heterozygosity =    0.955 (  0.002 SE,    0.025 SD)
      Observed heterozygosity =    0.984 (  0.001 SE,    0.023 SD)
      Number of extant alleles =   39.08 (   0.79 SE,    12.50 SD)

Year 30
      N[Extinct] =         3, P[E] = 0.012
      N[Surviving] =     247, P[S] = 0.988
      Population size =            71.86 (   1.81 SE,    28.45 SD)
      Expected heterozygosity =    0.938 (  0.003 SE,    0.040 SD)
      Observed heterozygosity =    0.970 (  0.002 SE,    0.031 SD)
      Number of extant alleles =   30.13 (   0.61 SE,     9.58 SD)

Year 40
      N[Extinct] =         5, P[E] = 0.020
      N[Surviving] =     245, P[S] = 0.980
      Population size =            72.80 (   1.83 SE,    28.63 SD)
      Expected heterozygosity =    0.923 (  0.003 SE,    0.047 SD)
      Observed heterozygosity =    0.955 (  0.003 SE,    0.041 SD)
      Number of extant alleles =   24.67 (   0.50 SE,     7.83 SD)
```

```
Year 50
     N[Extinct] =           9, P[E] = 0.036
     N[Surviving] =    241, P[S] = 0.964
     Population size =                74.10 (    1.81 SE,    28.05 SD)
     Expected heterozygosity =         0.908 (   0.004 SE,     0.063 SD)
     Observed heterozygosity =         0.940 (   0.003 SE,     0.052 SD)
     Number of extant alleles =       20.95 (    0.42 SE,     6.49 SD)

Year 60
     N[Extinct] =          10, P[E] = 0.040
     N[Surviving] =    240, P[S] = 0.960
     Population size =                70.65 (    1.87 SE,    28.96 SD)
     Expected heterozygosity =         0.891 (   0.006 SE,     0.091 SD)
     Observed heterozygosity =         0.923 (   0.006 SE,     0.088 SD)
     Number of extant alleles =       18.21 (    0.37 SE,     5.71 SD)

Year 70
     N[Extinct] =          13, P[E] = 0.052
     N[Surviving] =    237, P[S] = 0.948
     Population size =                69.64 (    1.97 SE,    30.32 SD)
     Expected heterozygosity =         0.876 (   0.006 SE,     0.095 SD)
     Observed heterozygosity =         0.905 (   0.006 SE,     0.097 SD)
     Number of extant alleles =       16.00 (    0.33 SE,     5.08 SD)

Year 80
     N[Extinct] =          15, P[E] = 0.060
     N[Surviving] =    235, P[S] = 0.940
     Population size =                69.20 (    1.98 SE,    30.35 SD)
     Expected heterozygosity =         0.865 (   0.006 SE,     0.085 SD)
     Observed heterozygosity =         0.897 (   0.005 SE,     0.082 SD)
     Number of extant alleles =       14.34 (    0.31 SE,     4.72 SD)

Year 90
     N[Extinct] =          24, P[E] = 0.096
     N[Surviving] =    226, P[S] = 0.904
     Population size =                67.07 (    2.03 SE,    30.56 SD)
     Expected heterozygosity =         0.854 (   0.006 SE,     0.087 SD)
     Observed heterozygosity =         0.885 (   0.006 SE,     0.089 SD)
     Number of extant alleles =       13.07 (    0.27 SE,     4.10 SD)

Year 100
     N[Extinct] =          29, P[E] = 0.116
     N[Surviving] =    221, P[S] = 0.884
     Population size =                64.78 (    2.02 SE,    30.06 SD)
     Expected heterozygosity =         0.845 (   0.005 SE,     0.075 SD)
     Observed heterozygosity =         0.876 (   0.006 SE,     0.083 SD)
     Number of extant alleles =       11.78 (    0.25 SE,     3.78 SD)


In 250 simulations of Population 1 for 100 years:
  29 went extinct and 221 survived.

This gives a probability of extinction of 0.1160 (0.0203 SE),
  or a probability of success of           0.8840 (0.0203 SE).

29 simulations went extinct at least once.
Of those going extinct,
    mean time to first extinction was 68.59 years (4.62 SE, 24.85 SD).

No recolonizations.
```

Mean final population for successful cases was 64.78 (2.02 SE, 30.06 SD)

```
Age 1      2      3      4    Adults   Total
   3.65   3.07   2.92   2.92  19.29    31.86   Males
   3.80   3.23   3.06         22.83    32.92   Females
```

Without harvest/supplementation, prior to carrying capacity truncation,
  mean growth rate (r) was 0.0182 (0.0011 SE, 0.1684 SD)

```
Final expected heterozygosity was      0.8448 ( 0.0050 SE,  0.0747 SD)
Final observed heterozygosity was      0.8756 ( 0.0056 SE,  0.0834 SD)
Final number of alleles was            11.78 (   0.25 SE,    3.78 SD)
```

****

Table 10.1. Mantled howler monkey population analysis.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
501	50	10	Low	.042	.028 (.174)	0.062	73 (29)	0.834	—
502		15		.036	.023 (.170)	0.070	72 (30)	0.824	—
503		20		.029	.016 (.172)	0.120	69 (31)	0.816	62
504	100	10		.042	.031 (.164)	0.010	154 (56)	0.912	—
505		15		.036	.024 (.165)	0.024	144 (57)	0.905	—
506		20		.029	.019 (.136)	0.038	137 (60)	0.898	—
507	200	10		.042	.032 (.160)	0.004	304 (108)	0.958	—
508		15		.036	.026 (.161)	0.004	290 (113)	0.951	—
509		20		.029	.018 (.160)	0.006	274 (121)	0.946	—
510	500	10		.042	.032 (.160)	0.0	763 (267)	0.982	—
511		15		.036	.026 (.158)	0.0	740 (278)	0.980	—
512		20		.029	.019 (.159)	0.002	664 (290)	0.979	—
513	50	10	High	-.026	-.052 (.223)	0.880	16 (15)	0.588	51
514		15		-.032	-.057 (.226)	0.928	16 (14)	0.602	50
515		20		-.039	-.066 (.231)	0.970	13 (15)	0.556	46
516	100	10		-.026	-.047 (.210)	0.736	27 (32)	0.694	60
517		15		-.032	-.053 (.211)	0.824	22 (23)	0.678	60
518		20		-.039	-.066 (.222)	0.926	12 (10)	0.642	55
519	200	10		-.026	-.046 (.202)	0.640	39 (46)	0.746	70
520		15		-.032	-.052 (.205)	0.702	26 (38)	0.704	66
521		20		-.039	-.061 (.208)	0.816	19 (20)	0.702	63
522	500	10		-.026	-.041 (.184)	0.366	64 (92)	0.834	77
523		15		-.032	-.048 (.191)	0.484	42 (58)	0.800	76
524		20		-.039	-.057 (.196)	0.628	28 (34)	0.750	75

Table 10.2. Mantled howler monkey population analysis: no catastrophes.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
525	50	10	Low	.101	.100 (.049)	0.0	100 (3)	0.897	—
526		15		.095	.093 (.050)	0.0	100 (3)	0.899	—
527		20		.088	.086 (.050)	0.0	100 (3)	0.902	—
528	100	10		.101	.100 (.043)	0.0	200 (4)	0.947	—
529		15		.095	.094 (.043)	0.0	200 (4)	0.948	—
530		20		.088	.087 (.043)	0.0	200 (4)	0.949	—
531	200	10		.101	.101 (.040)	0.0	400 (6)	0.973	—
532		15		.095	.094 (.040)	0.0	400 (6)	0.974	—
533		20		.088	.087 (.040)	0.0	400 (6)	0.974	—
534	500	10		.101	.101 (.037)	0.0	1000 (9)	0.989	—
535		15		.095	.094 (.037)	0.0	1000 (10)	0.990	—
536		20		.088	.087 (.037)	0.0	1000 (9)	0.990	—
537	50	10	High	.034	.031 (.073)	0.0	95 (9)	0.871	—
538		15		.027	.024 (.074)	0.0	93 (11)	0.867	—
539		20		.020	.017 (.077)	0.006	88 (16)	0.857	—
540	100	10		.034	.032 (.063)	0.0	195 (9)	0.937	—
541		15		.027	.025 (.064)	0.0	191 (15)	0.935	—
542		20		.020	.018 (.067)	0.0	183 (26)	0.928	—
543	200	10		.034	.033 (.058)	0.0	391 (17)	0.968	—
544		15		.027	.026 (.060)	0.0	387 (21)	0.967	—
545		20		.020	.019 (.061)	0.0	379 (29)	0.966	—
546	500	10		.034	.033 (.055)	0.0	983 (30)	0.987	—
547		15		.027	.026 (.057)	0.0	967 (49)	0.987	—
548		20		.020	.019 (.058)	0.0	952 (63)	0.987	—

Table 10.3. Mantled howler monkey population analysis: disease and fire.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
549	50	10	Low	.074	.067 (.121)	0.002	93 (15)	0.882	—
550		15		.067	.061 (.122)	0.0	94 (15)	0.883	—
551		20		.060	.054 (.120)	0.004	90 (20)	0.885	—
552	100	10		.074	.068 (.117)	0.0	188 (29)	0.940	—
553		15		.067	.062 (.117)	0.0	186 (34)	0.940	—
554		20		.060	.054 (.117)	0.0	185 (36)	0.942	—
555	200	10		.074	.069 (.114)	0.0	377 (60)	0.970	—
556		15		.067	.062 (.115)	0.0	381 (52)	0.970	—
557		20		.060	.055 (.113)	0.0	374 (63)	0.970	—
558	500	10		.074	.068 (.116)	0.0	938 (154)	0.988	—
559		15		.067	.063 (.109)	0.0	936 (167)	0.988	—
560		20		.060	.057 (.109)	0.0	936 (156)	0.988	—
561	50	10	High	.006	-.005 (.150)	0.218	55 (31)	0.751	64
562		15		-.001	-.012 (.156)	0.304	44 (30)	0.716	66
563		20		-.008	-.021 (.166)	0.468	35 (25)	0.706	61
564	100	10		.006	-.003 (.139)	0.116	106 (63)	0.857	73
565		15		-.001	-.010 (.142)	0.138	77 (58)	0.813	70
566		20		-.008	-.018 (.147)	0.254	57 (48)	0.793	73
567	200	10		.006	.000 (.127)	0.032	212 (127)	0.920	—
568		15		-.001	-.007 (.131)	0.056	162 (122)	0.900	—
569		20		-.008	-.016 (.138)	0.124	99 (92)	0.860	83
570	500	10		.006	.000 (.123)	0.004	513 (323)	0.961	—
571		15		-.001	-.006 (.123)	0.020	382 (288)	0.955	—
572		20		-.008	-.013 (.125)	0.024	241 (230)	0.933	—

Table 10.4. Mantled howler monkey population analysis: disease and hurricane.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
573	50	10	Low	.063	.051 (.161)	0.014	85 (22)	0.862	—
574		15		.057	.045 (.162)	0.012	83 (23)	0.860	—
575		20		.050	.039 (.162)	0.030	81 (26)	0.856	—
576	100	10		.063	.053 (.157)	0.0	174 (41)	0.930	—
577		15		.057	.047 (.155)	0.0	167 (47)	0.930	—
578		20		.050	.041 (.155)	0.01	166 (45)	0.929	—
579	200	10		.063	.053 (.154)	0.0	346 (86)	0.965	—
580		15		.057	.047 (.155)	0.002	340 (89)	0.963	—
581		20		.050	.041 (.152)	0.002	330 (95)	0.963	—
582	500	10		.063	.055 (.152)	0.0	881 (199)	0.986	—
583		15		.057	.047 (.152)	0.0	844 (225)	0.986	—
584		20		.050	.041 (.153)	0.002	834 (227)	0.985	—
585	50	10	High	-.004	-.022 (.198)	0.538	40 (30)	0.697	61
586		15		-.011	-.032 (.204)	0.660	29 (23)	0.674	57
587		20		-.018	-.039 (.207)	0.752	24 (19)	0.662	55
588	100	10		-.004	-.019 (.182)	0.334	63 (54)	0.798	66
589		15		-.011	-.026 (.188)	0.428	49 (45)	0.761	68
590		20		-.018	-.037 (.196)	0.602	33 (36)	0.718	64
591	200	10		-.004	-.018 (.177)	0.230	112 (104)	0.853	74
592		15		-.011	-.026 (.180)	0.306	82 (90)	0.832	75
593		20		-.018	-.035 (.190)	0.48	52 (60)	0.803	70
594	500	10		-.004	-.015 (.164)	0.072	244 (253)	0.921	—
595		15		-.011	-.024 (.172)	0.144	156 (192)	0.890	79
596		20		-.018	-.032 (.178)	0.210	92 (133)	0.854	78

Table 10.5. Mantled howler monkey population analysis: heterosis model of inbreeding depression, 3.14 lethal equivalents.

File #	N_0	0-1 Mort. (%)	Mort.	r_d	r_s (SD)	P(E)	N_{100}(SD)	H_{100}	T(E)
Catastrophes									
597	50	10	Low	.042	.018 (.168)	0.116	65 (30)	0.845	—
598		15		.036	.009 (.177)	0.148	55 (32)	0.816	—
599		20		.029	.001 (.182)	0.232	50 (32)	0.814	64
600	100	10		.042	.025 (.162)	0.024	137 (59)	0.916	—
601		15		.036	.017 (.167)	0.060	127 (62)	0.904	—
602		20		.029	.011 (.164)	0.056	118 (67)	0.898	—
603	50	10	High	-.026	-.065 (.225)	0.988	10 (7)	0.575	49
604		15		-.032	-.071 (.228)	0.996	9 (—)	—	45
605		20		-.039	-.081 (.236)	0.992	4 (3)	—	40
606	100	10		-.026	-.060 (.216)	0.920	14 (20)	0.726	60
607		15		-.032	-.068 (.222)	0.952	12 (13)	0.686	55
608		20		-.039	-.074 (.222)	0.984	7 (1)	—	52
No catastrophes									
609	50	10	Low	.101	.091 (.049)	0.0	100 (3)	0.904	—
610		15		.095	.086 (.049)	0.0	100 (3)	0.902	—
611		20		.088	.079 (.049)	0.0	99 (3)	0.906	—
612	100	10		.101	.096 (.043)	0.0	200 (4)	0.948	—
613		15		.095	.090 (.043)	0.0	200 (4)	0.949	—
614		20		.088	.083 (.043)	0.0	200 (4)	0.950	—
615	50	10	High	.034	.020 (.073)	0.004	85 (20)	0.866	—
616		15		.027	.013 (.076)	0.0	75 (23)	0.861	—
617		20		.020	.005 (.082)	0.028	63 (27)	0.840	—
618	100	10		.034	.027 (.062)	0.0	189 (14)	0.938	—
619		15		.027	.020 (.064)	0.0	183 (23)	0.936	—
620		20		.020	.012 (.067)	0.0	165 (35)	0.928	—

Figure Legends

Figure 10.1. Population size over the 100-year time frame of the simulations under different different genetic and environmental conditions. Cats = catastrophes; Inb = inbreeding depression. For these particular scenarios, juvenile mortality was set at 15%.

Figure 10.2. Probability of extinction (A) and final population size (B) under conditions of low adult mortality as a function of juvenile mortality for the set of initial population sizes used in the complete set of modelling scenarios.

Figure 10.3. Probability of extinction (A) and final population size (B) under conditions of high adult mortality as a function of juvenile mortality for the set of initial population sizes used in the complete set of modelling scenarios.

Figure 10.4. Probability of extinction (A) and final population size (B) under conditions of low adult mortality and no catastrophes as a function of juvenile mortality for the set of initial population sizes used in the complete set of modelling scenarios.

Figure 10.5. Probability of extinction (A) and final population size (B) under conditions of high adult mortality and no catastrophes as a function of juvenile mortality for the set of initial population sizes used in the complete set of modelling scenarios.

Figure 10.6. Probability of extinction (A) and final population size (B) in those simulations incorporating inbreeding depression. See Figure 7 for a key to the symbols used in the figures.

Figure 10.7. Probability of extinction (A) and final population size (B) in those simulations incorporating inbreeding depression and without catastrophes.

Figure 1. *Alouatta palliata mexicana*: Adult Mortality and Population Size
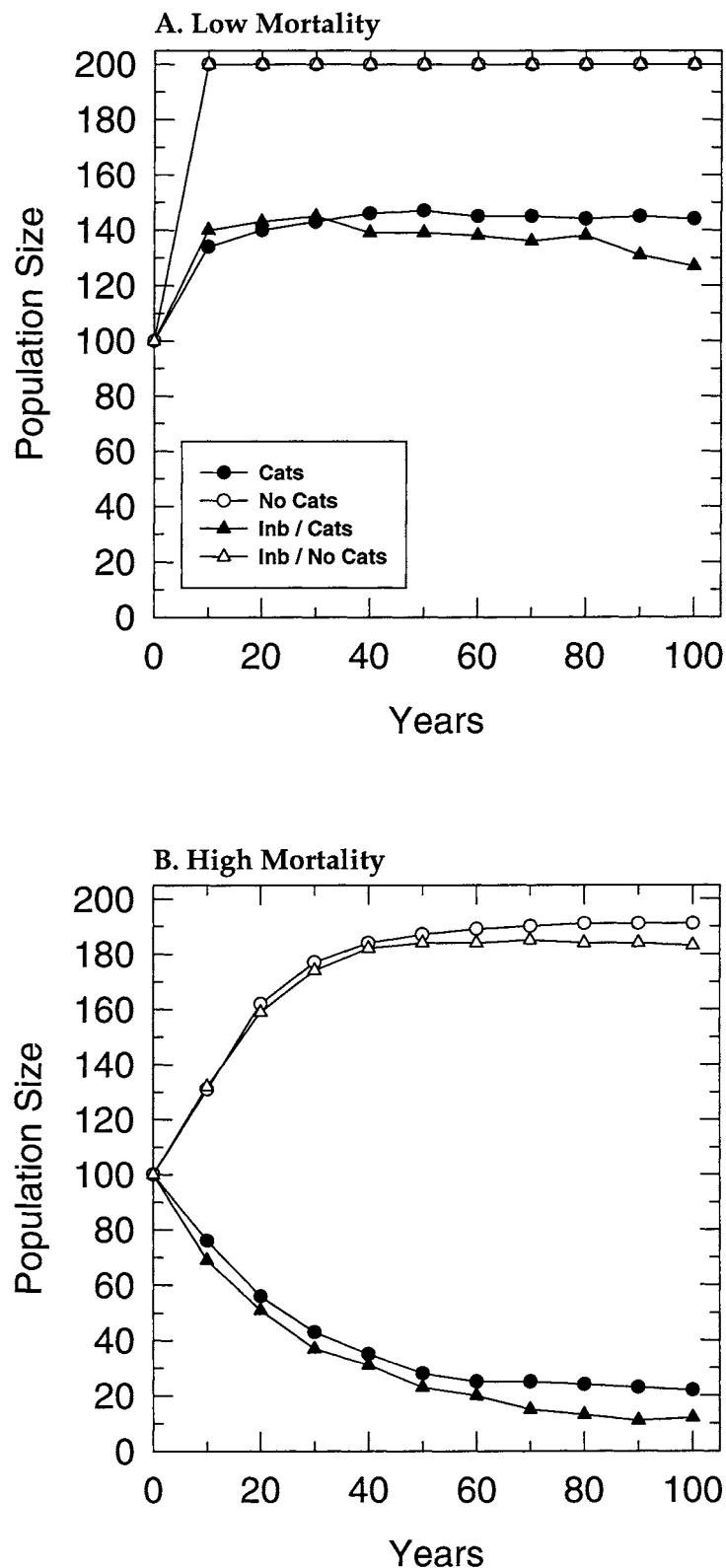
A. Low Mortality

B. High Mortality

Figure 2. *Alouatta palliata*:
Low Adult Mortality
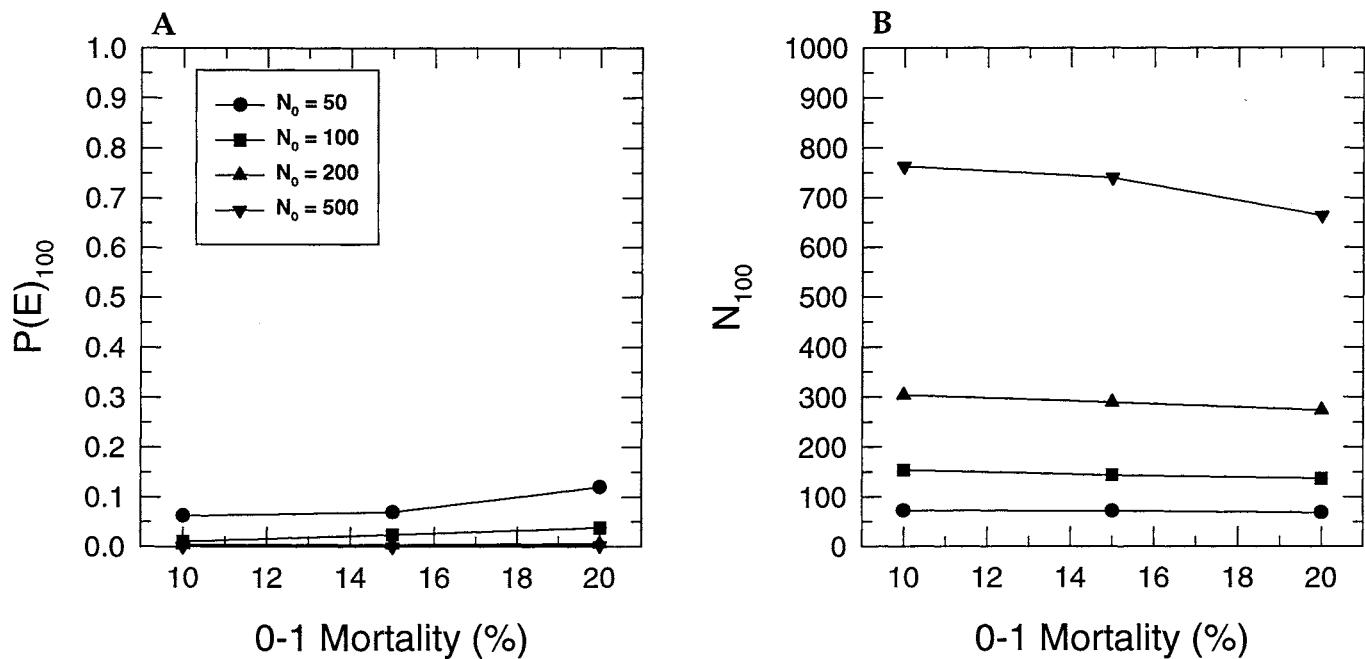
Figure 3. *Alouatta palliata*:
High Adult Mortality
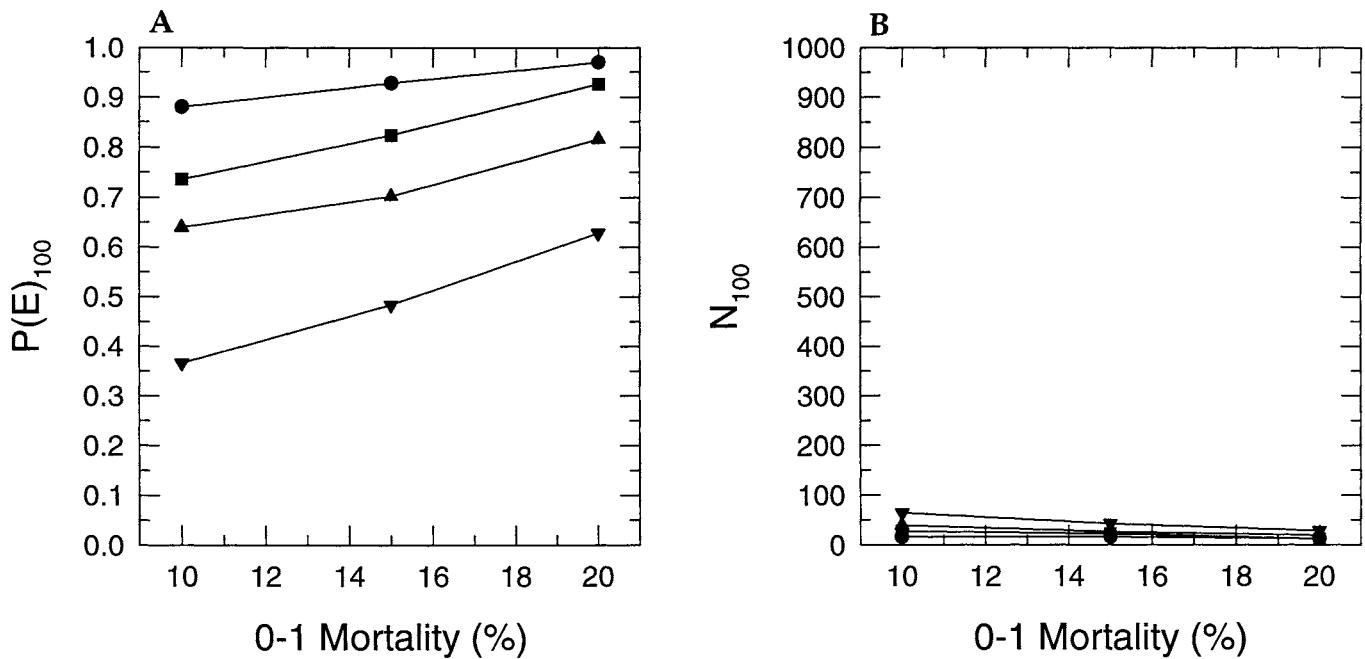
**Figure 4.** *Alouatta palliata:*
Low Adult Mortality; No Catastrophes
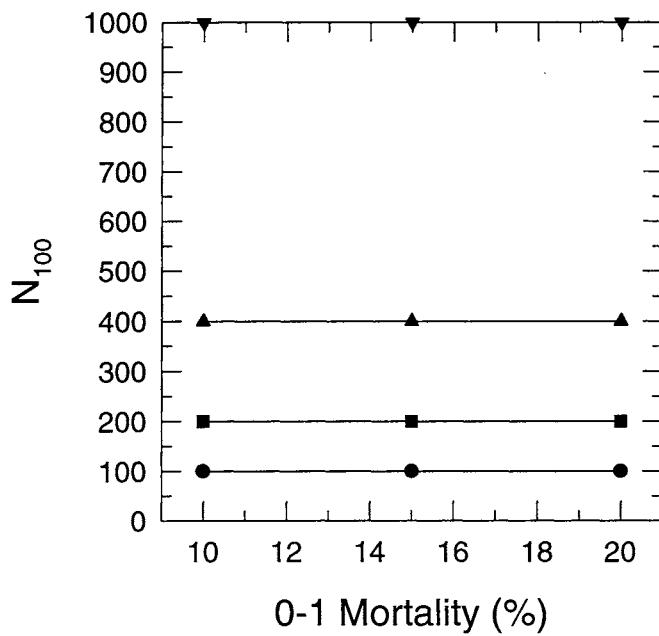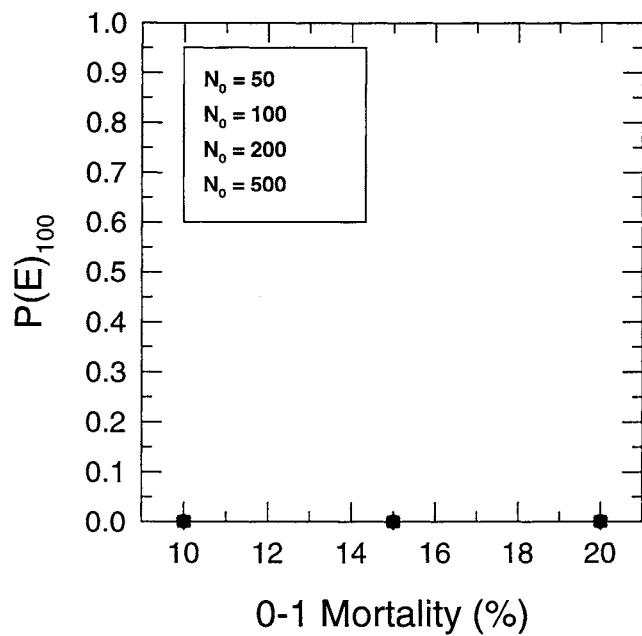
Figure 5. *Alouatta palliata:*
High Adult Mortality; No Catastrophes
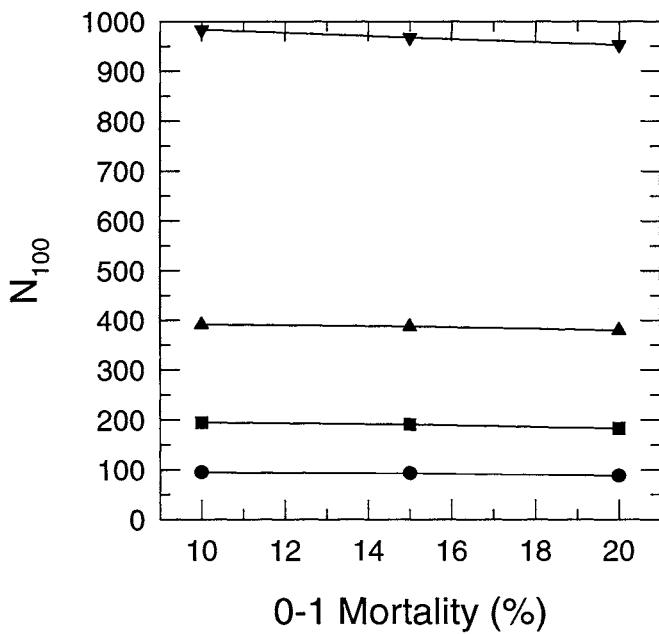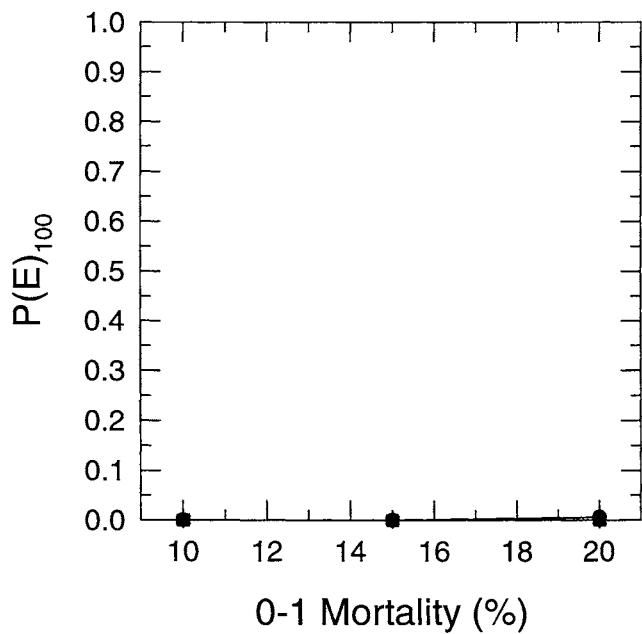
Figure 6. *Alouatta palliata mexicana*: Inbreeding Depression
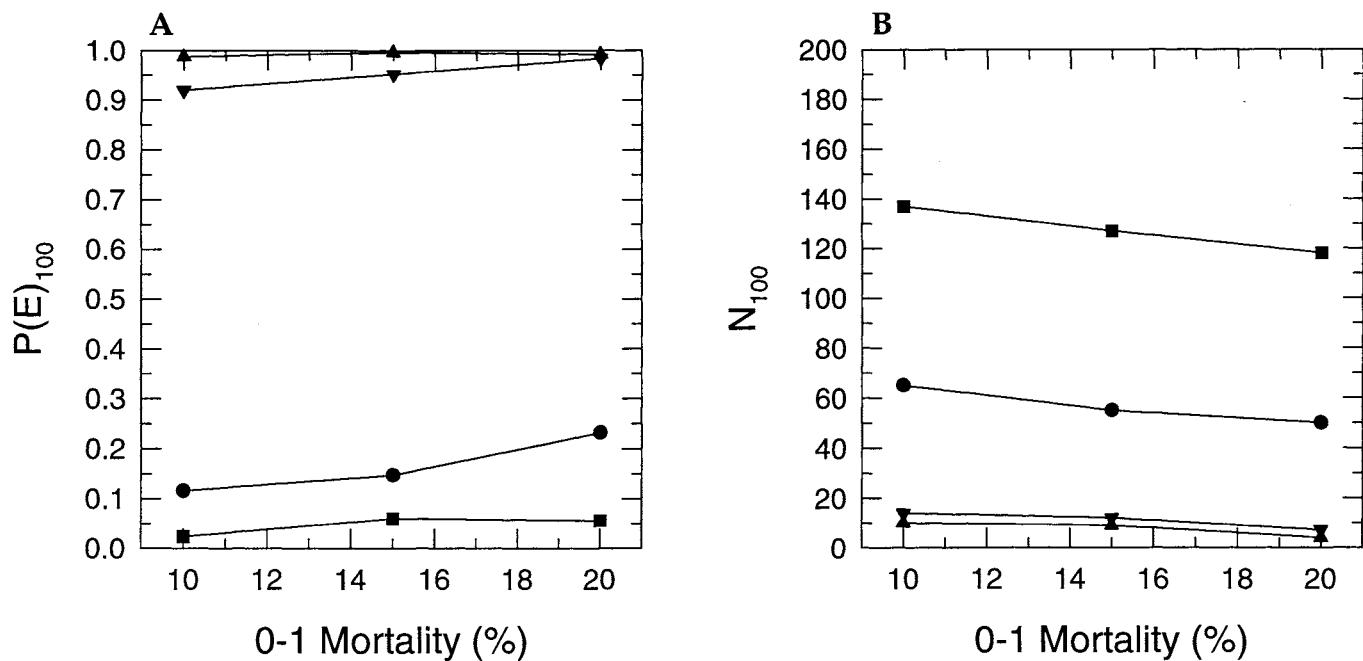
Figure 7. *Alouatta palliata mexicana*: Inbreeding Depression; No Catastrophes
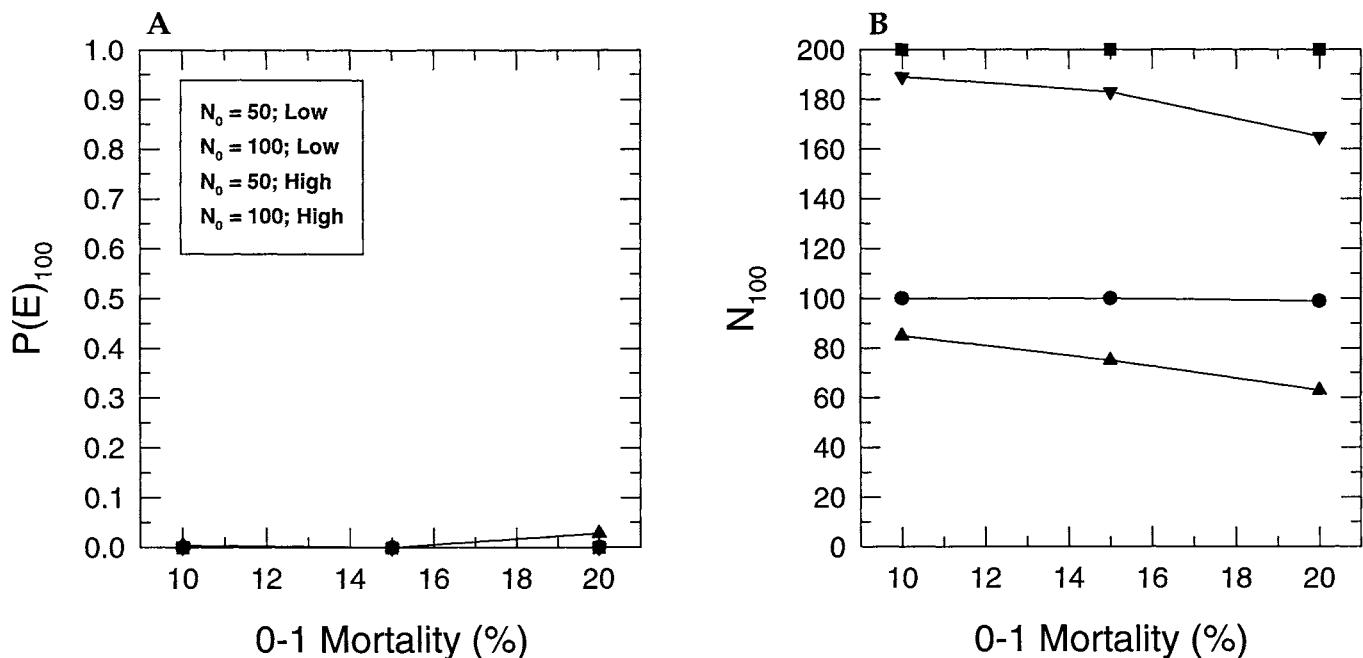
AGALTEPEC ISLAND MODELLING EXERCISE

To examine the usefulness of the VORTEX program, the first population modeled was the population of the Agaltepec Island. This group has been observed consistently since 1989; hence, many of the pertinent parameters needed for the modeling were available.

Model Parameters

1) The simulations were run in two time frames: 100 years and 6 years. The simulation in the 6-year-old time frame was run to compare the computer model with the actual population history during this span of time. The time frame of 100 years was chosen to investigate the long-term trends of this population and to estimate its probability of extinction, thus providing a means to evaluate the effects of different environmental and demographic variables.

2) The extinction reports were made for 10 year periods for the 100 year time frame and one year for the 6 year time frame.

3) The simulations did include inbreeding depression, since reports do not exist indicating negative effects of inbreeding in this species. Further, howler monkeys do not have a large amount of natural genetic variability and this is not thought to have important negative effects.

4) Reproduction was assumed to be independent of population density.

5) Three types of catastrophes were considered: fires, cyclones and disease epidemics. The corresponding parameters were estimated using the information provided by those workshop participants with knowledge of the region. The probability of these catastrophes was estimated in the following way:

   Fires (0.20). The fires on the island can be caused by fishermen who sometimes light bonfires to prepare their food. Once unleashed a fire it is estimated that a fire would affect survival and reproduction negatively, given the island dimensions.

   Cyclones (0.05). Hurricane winds can be a danger for the population, though they do not occur with great frequency, and their impact would not be great.

   Epidemics (0.01). Though not predicted to be frequent, a disease epidemic on the populations of these monkeys would be devastating, as was the case of the yellow fever epidemic reported in several Mesoamerican areas in the 1950's.

6) In 1989 10 monkeys were released in Agaltepec (1 infant, 1 adult male and 8 adult female). Since then the group has been monitored continuously. There are now 40 individuals on the island.

7)   Available information suggests that females begin to be reproduce at 4 years and the males at 5 years of age.

8)   A 1:1 sex ratio at birth is found at Agaltepec.

9)   Adult females produce 1 offspring per litter.

10) One of the most difficult parameters to estimate for this taxa is carrying capacity. For Agaltepec, it is believed that sustain a population twice the size as the current population. Today, the population is comprised of 40 individuals; the carrying capacity modeled was K=80.

The previous data were developed by Domingo Canales Espinosa; Edith Carrera Sánchez; Liliana Cortés Ortiz; Francisco García Orduña; Manuel Martínez Morales; Guadalupe Medel Palacios; Jorge Morales Mávil; Ernesto Rodríguez Luna; Oliva Rosales Rodríguez; Juan Carlos Serio Silva.

Listed below are the values used in the simulations and a summary of the preliminary results.

Parameter Values for the Agaltepec Population

6 year time frame.

Number of simulations: 100
Number of years: 6
There is no inbreeding depression.
Age of first reproduction for females: 4 years
Age of first reproduction for males: 5 years
Maximum age above which all animals die: 20 years
Proportion of males at birth: 0.5
Number of offspring by litter: 1
Mating system: Polygynous
All the males are in the breeding pool.
Reproduction is independent of density.
Percent of females that produce litters size 0 = 14.00
      EV = 12.27
Percent of females that produce litters size 1 = 86.00
Percent female mortality between 0 and 1 year old: 10.00
      EV = 3.00 SD
Percent female mortality between 1 and 2 years old: 0.5
      EV = 0.15 SD
Percent female mortality between 2 and 3 years old: 0.00
      EV = 0.00
Percent females mortality between 3 and 4 years old: 0.00
      EV = 0.00 SD

Percent mortality of adult females (4<=age<=20): 4.5
    EV = 1.00 SD
Percent male mortality between 0 and 1 year old: 15.00
    EV = 4.00 SD
Percent male mortality between 1 and 2 years old: 2.00
    EV = 0.5 SD
Percent male mortality between 2 and 3 years old: 2.00
    EV = 0.50 SD
Percent male mortality between 3 and 4 years old: 0.00
    EV = 0.00 SD
Percent male mortality between 4 and 5 years old: 0.00
    EV = 0.00 SD
Percent mortality of adult males (5<=age<=20): 3.75
    EV = 1.00 SD
Frequency of Catastrophe 1 (fires): 20%
    Effect of catastrophe 1 on reproduction: 0.5
    Effect of catastrophe 2 on survival: 0.5
Frequency of the Catastrophe 2 (cyclones): 5%
    Effect of catastrophe 2 on reproduction: 0.9
    Effect of catastrophe 2 on survival: 0.9
Frequency of the Catastrophe 3 (epidemics): 1%
    Effect of catastrophe 3 on reproduction: 0.4
    Effect of catastrophe 3 on survival: 0.5
Initial size of the population: 1 1-year-old male.
    1 7-year-old male.
    2 4-year-old females.
    2 5-year-old females.
    1 7-year-old female.
    1 8-year-old female.
    1 9-year-old female.
    1 10-year-old female.
Initial size of the population: 10 animals.
Carrying capacity (K) = 80
(EV = 0.00 SD).
No harvesting
No supplementation

Final Summary of Results for 6 years

In 100 simulations for 6 years:
        11 went extinct and 89 survived.
        Extinction probability: 0.1100 (0.0313 SE).
        Probability of survival: 0.8900 (0.0313 SE).
        11 simulations went extinct.
        Average time to extinction: 3.55 years (0.55 SE, 1.81 SD).
        Average size of the surviving population: 20.52 (1.46 SE, 13.76 SD).

AGE 1	2	3	4	TOTAL	ADULTS	
2.01	1.55	0.85	0.99	3.39	8.80	Males
2.08	1.54	0.84	--	7.26	11.72	Female

        Average population growth rate (r): 0.0489 (0.0164 SE, 0.3921 SD)
        Expected Heterozygosity: 0.8697 (0.0045 SE, 0.0426 SD).
        Observed Heterozygosity: 0.9872 (0.0027 SE, 0.0258 SD).
        Final number of alleles: 13.11   (0.47 SE, 4.43 SD).

In another simulation with a 6-year time frame, without the inclusion of catastrophes, the results were the following:

In 100 simulations, 0 populations went extinct and 100 survived, which produces a probability of extinction of 0.00 (probability of survival 1.00).

The final average size of the successful populations were 43.55 (0.76 SE, 7.62 SD).

AGE 1	2	3	4	TOTAL	ADULTS	
4.23	3.59	2.27	2.49	6.71	19.29	Males
4.65	3.67	2.20		13.74	24.26	Female

        Population growth rate average (r) : 0.2424 (0.0049 SE, 0.1189 SD)
        Expected heterozygosity: 0.8966 (0.0013 SE, 0.0131 SD).
        Observed heterozygosity: 0.9808 (0.0020 SE, 0.0198 SD).
        Final number of alleles: 18.62   (0.11 SE, 1.13 SD).

100 year time frame.

The data used for this simulation were the same as those for the first simulation (including the effect of the catastrophes), except the simulations ran over a 100 year time span.

Final Summary of Results for 100 Years

In 100 simulations for 100 years:

79 populations went extinct and 21 survived.

Probability of extinction: 0.79 (0.0.0407 SD).

Probability of survival: 0.21 (0.0407 SD).

79 populations went extinct.

Average time to extinction: 32.92 years (2.99 SE, 26.53 SD).

Average size of the surviving population: 46.81 (5.81 SE, 26.64 SD).

AGE 1	2	3	4	TOTAL	ADULTS	
3.43	3.95	2.76	2.38	11.00	23.52	Males
4.00	3.48	2.62		13.19	23.29	Female

Average population growth rate (r): - 0.0074 (0.0055 SE, 0.3774 SD)

Expected heterozygosity: 0.5484 (0.0388 SE, 0.1779 SD).

Observed heterozygosity: 0.5627 (0.0429 SE, 0.1965 SD).

Final number of alleles: 3.95 (0.32 SE, 1.47 SD).

Comments

In 6-year time frame model that considered catastrophes, the average population size is lower than the actual size of the population, although the latter is within the range of variation sizes generated in the simulation. However, for the 6-year time frame simulation not including catastrophes, the final population number is close to that found on the island (43.55 vs. 40). It should be noted that the existing population of Agaltepec has not encountered a catastrophic event during the six years it has been monitored.

The average growth rate for the 6-year time frame simulation without catastrophes (0.242) is very similar to the one which has been estimated for the actual population of Agaltepec (0.239).

The agreement of these simulations suggest that the VORTEX 7.0 model adequately simulates the population.

It is important to note that the demographic data, as percentages of mortality by sex and age class were conjectures and had they been in significant error would have been amplified in the course of the population projections. In particular, for the island group a lower mortality ha been observed (agreeing with the data used for the simulation), but in other natural conditions, these values certainly may be higher for some age and sex classes.

The estimate of carrying capacity was made based on the recognition of the growing population trend for the monkeys on the island, as well as in recognition of their patterns of occupation of the island and the degree of utilization of the available nutritional resources. Nevertheless, it

should be noted that this estimate does not coincide with the one which can be deduced solely by using population density data and home range, as previously reported for the taxon.

Finally, we consider that the results of the 100-year time frame simulation (the one including catastrophes) can show a reliable prediction of the possibility of survival of this group in the future.

POPULATION AND HABITAT VIABILITY ASSESSMENT
FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 March 1995

Section 11
Threats to Natural Populations
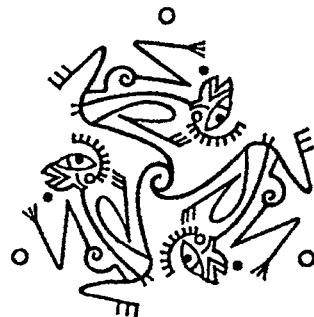
THREATS TO THE NATURAL POPULATIONS OF *Alouatta palliata mexicana*

Habitat Loss

Because of the growth of human populations and extensive and intense use of tropical lands for industrial and agricultural use and forestry, the original distribution of the mantled howler monkey *Alouatta palliata* has been severely fragmented and reduced by an estimated 80 to 90 percent (Estrada, 1994).

The populations of *Alouatta palliata mexicana* are currently distributed in fragment forests of different dimensions. The annual 4.2 percent deforestation rate reported for southeastern México (Dirzo, 1992), attributed mainly to new agricultural fields and cattle farms contributed to the accelerated loss and fragmentation of habitat. Consequently, monkey populations also decrease; accompanying the loss in habitat in a short time will be a decrease in genetic variability and an increase in homozygosity.

Some of the problems that these populations face are high susceptibility/sensitivity to environmental changes (temperature, rainfall, etc.) and biological (trophic resource shortage, predation, disease epidemics and parasites). This susceptibility leads to low future viability and low fecundity that can contribute their extinction in a short period of time.

Even though protected natural areas have been designated, conceptual and management defects reduce efficiency. In most protected areas there is no patrolling or continuous monitoring, which does not prevent negative human activities that contribute to habitat deterioration.

Fortunately, populations of *Alouatta palliata mexicana* still exist in large forest extensions that can be considered viable in the future. These populations can maintain genetic variation and adaptability better than the small, fragmented populations and some have the advantage of having established protected areas in their distribution.

In large populations of *A. p. mexicana* the effects of inbreeding and the long-term loss of genetic variability are reduced. This ties into the hypothesis of James and Glander (personal communication) that *Alouatta palliata* is less susceptible to inbreeding than other mammals, and that it shows high ecological and behavioral plasticity which leads to its adaptable social structure in relationship to the environmental changes. This plasticity leads us to believe that these populations can be expected to survive if maintained in the current habitat conditions.

The populations of *A. p. mexicana* present primarily in the protected natural areas can serve as a continuous source of genetic material for the small nearby fragmented populations. Immigration of at least one individual per generation would lessen a substantial loss of genetic variability.

Wildlife Traffic

Because of prevailing socioeconomic problems in nearly all tropical zones, many of the rural peasants are pressed to seek alternative means of subsistence, including wildlife trade.

Primates are one of the animal groups in great demand as pets; illegal traffic is considerable. There is a great demand for primates as pets in urban areas; this provides a source of short-term income for those able to capture and sell them. The cost of a single animal has been reported to be between $18 to $25 US. Economic alternatives for wildlife traders and environmental education programs could be one solution to the illegal trade problem. However, it is suspected pet trade traffic exists to an even greater scale than just in urban areas, involving large quantities of money and animals. In this market, rural inhabitants play a fundamental role as collectors, selling to intermediary dealers that export animals to developed countries.

Hunting

Another important factor affecting howler monkey populations is hunting on several levels: a) for food; and b) for trophies.

a) Hunting for food. Campesino communities need to obtain animal protein to improve their nutrition; howler monkeys are part of this protein consumption. However, monkey meat is not only used for food; it also is used as bait to catch other prey such as prawns (Rodríguez Luna et al., 1987).

Sufficient data determining the percentage of consumed monkeys does not exist but it can be inferred that it is high. This hunting in part reflects an established custom and also the lack of protection of endemic animals in these zones.

b) Hunting for trophies. Sports hunting that is accomplished in tropical regions is directed primarily at large mammals such as deer or boar, however on occasion when these prey are reduced, hunters turn their attention toward smaller mammals such as monkeys.

Recommendations

Develop pilot studies that help to obtain inbreeding parameters in fragmented populations of howler monkeys with the aim of obtaining information about the need for translocating individuals to increase genetic variation in reduced populations.

Intensify investigations that give may lead to useful strategies for the use of natural resources in human communities, providing for rational use as well as habitat conservation where wild populations of primates are currently found.

Establish new protected natural areas and re-evaluate their conceptualization with respect to effective protection that can be provided in the current distribution range of *A. p. mexicana*.

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

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Section 12
Ecology and Behavior
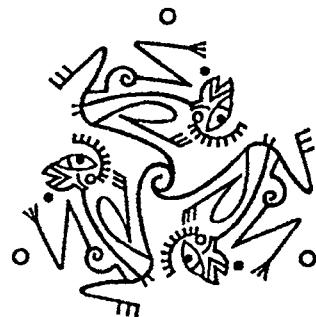
ECOLOGY AND BEHAVIOR

A great deal is known about the biology of howler monkeys. In spite of this vast knowledge, multiple factors influence its prospects for survival. The incessant loss of habitat and live animal trade are contributing to the disminution of natural populations from the original distribution.

Given this situation, relevant, wider studies should be developed on the natural history of the howler monkey, which should form the basis of for the design of conservation programs. Several relevant aspects are presented below.

Feeding Habits of Howler Monkeys

Many methods of investigation have been developed with the goal of knowing more about the ecology and behavior of Howler monkeys. Within these, one of the increasing areas of investigation is in reference to their feeding habits.

Howler monkeys, *Alouatta palliata,* have demonstrated diverse facets in their feeding behavior. On one hand, there exist studies that show a strong tendency for them to be folivorous (Milton, 1980; Glander, 1981), while others indicate that there is a clear trend towards frugivory (Hladik & Hladik, 1969; Smith, 1977). As behaviors between these two extremes have also been observed, howler monkeys can utilize a wide range of food possibilities, and for this reason, some authors have preferred to indicate that *Alouatta* "is a folivorous primate that also eats fruit" (Altmann, 1959).

It has been shown that *Alouatta palliata* has well-defined foraging routes, which permit the localization of food resources in the space and time. In a summary article by Estrada (1993), it was shown that howler monkeys utilize 291 of the neotropical species found in their distributions in 66 families as food. Young leaves and mature fruits have been reported as the plant parts most often consumed (Glander, 1975; Milton, 1980; Chapman, 1987; Estrada, 1984).

At the level of each plant part consumed, it has been shown that 218 species (58 families) are used for the leaves and 122 species (38 families) for fruit, and finally 55 species (24 families) for flowers. The families which are most preferred in terms of food are Leguminosas and Moraceas; these preferences are consistent in all the Neotropical sites in which *Alouatta* has been studied.

Howler monkeys have also demonstrated a preference in regards to the layer of trees in which it feeds. They greatly prefer the highest layer, then the middle and lowest layers respectively (Mendel, 1976; Serio-Silva, 1992). Mendel indicated that the two preferred parts are young leaves and mature fruit.

At the same time, many reports have noted that *A. palliata* selects species that are relatively rare and have a low density within its home range, which leads us to believe that these species have nutritional and chemical properties that can influence their selection by this species.

In relation to the above, Estrada (1994) indicates that although the study group fed on 27 different species, 89% of the feeding time was spent feeding on 8 of these. This selection was also expressed in a study by Glander (1981), which indicates that the primates exert an intense selection on the trees which are found within their home range, consuming only 19.5% of the total present.

In many studies, the genus *Ficus* is considered as being of great important in the feeding repertoire. In the majority of studies with *A. palliata* in wild conditions, *Ficus* comprises a high percentage among the species consumed (Estrada, 1984; Crockett & Eisenberg, 1987). An example of this is give in Serio-Silva (1992), showing that 56.5 percent of time is dedicated to eating species in this genus.

As shown previously, howler monkeys, in addition to being selective consumers show a strict preference over the parts of vegetation ingested; thus, some reports say the species is an intense folivore (Glander, 19?; Milton, 1980). Estrada (1984) showed that nearly equal proportions of fruit and leaves were consumed in Mexico, and Serio-Silva (1992) made reference to the marked frugivory of semi-free-ranging howler monkeys in the island of Lake Catemaco, Veracruz, Mexico. The data above appear to indicate the great importance of different types of vegetation and their respective phenological patterns in determining different feeding tendencies.

It has been observed that when howler monkeys accidentally consume insect larvae in fruit (Milton, 1980; Serio-Silva, 1992); these can contribute, albeit minimally, to a nutritional addition to the diet in terms of the protein source the larvae represent.

Without doubt, the most important characteristic of this type of selective behavior is that the howler monkeys show great plasticity in their response to the environment, and when certain environmental pressures arise, they are able to respond below a facet of folivory and when fruit is present to exploit it avidly.

Feeding Habits of *Alouatta palliata*

The inexorable advance of human settlements have caused constant modification and decline of habitat for Mexican mammals. In many cases, these species are listed as being in danger of extinction. This incessant transformation of habitat without doubt is directly related to food availability on which many species rely.

Mexican primates are intensely affected by this situation; this certainly is the case with *Alouatta palliata*, which is very selective in its feeding habits. Population of this species have been impacted greatly by fragmentation and impoverishment of their habitat within the natural range of distribution. Howler monkeys have been shown to be very selective feeders, based on nearly 300 species of vegetation in different ecosystems which range from tropical forests to regions with great perturbation.

Studies on the feeding habits of *Alouatta palliata* are important because they provide knowledge of the species in stable environments which can help lead to identification of potential

areas for translocation program releases. No doubt strategies like this can contribute a great deal to the conservation of the species, also providing important biological information such as the differential carrying capacity of potential environments, and the influence that this has over the present or absence of certain food species.

Primates are very selective in their feeding habits at different levels, from particular aspects such as nutrients and chemical compounds that they need or want to avoid, vegetation parts that they consume, arboreal stati of their favorite foods, to the species that they are able to select for their diet.

Factors such as those above are important to consider with respect to the difficulty of maintaining the species in captivity. Based on this, it is necessary to determine which factors may have the greatest influence on captive populations. A general list of the species and/or compounds would be useful in developing a diet for animals in captive conditions.

In light of this, it is possible that a "National Plan for the Conservation of Primates" should include: the selection of potential areas for the development of translocation or release programs; and support for *ex situ* conservation programs, which is important for the elaboration of dietary supplements that can help captive diets more closely approximate those in nature.

In summary, an *in situ* and *ex situ* conservation plan should be developed together, with the priority of investigation into the complicated feeding habits of the species.

These studies should include:

Development of a number of studies to elucidate the main feeding tendencies of *Alouatta palliata* in the wild.

Determine which food species within the diet of *Alouatta palliata* stand out.

Determine the presence of the principal nutritional and chemical compounds that can influence food selection in *Alouatta palliata*.

Carry out botanical studies in potential re-location sites for monkeys now affected in fragmented habitat.

Determine, with "pilot" groups of howler monkeys, the relation between the presence of food species and carrying capacity within the home range area.

Promote captive programs that involve the use of the food species on which howler monkeys feed in the wild, attempting to develop a model diet for captive animals.

Implement a "National Plan for the Conservation of Primates" that includes, in addition to the above points, strong directives to spread the information that it is very difficult to provide an adequate diet and maintain the animals as pets.

Daily Activity Patterns

The daily activities patterns for *Alouatta palliata* have been extensively studied, mainly on Barro Colorado island in Panama (Altmann, 1959; Bernstein, 1964). Chivers (1969) noted variations in activity patterns in relationship to the climate during the day and dy and wet seasons. Richard (1970) also compared patterns of activity between *Ateles geoffroyi* and *Alouatta palliata*; Mittermeier (1975) studied the effect of population dynamics on activity patterns and, Milton (1980) described daily patterns.

The daily activity patterns for the species do not differ considerably even for those populations existing in different regions, countries or vegetation types.

Serio Silva (1992) and Carrera Sánchez (1993) report that *A. p. mexicana* usually shows a general pattern of activity over the day. It is possible to identify a peak in foraging at the beginning of the day to mid-day, in inverse relationship to resting activity. This pattern is observed year-long.

Differences have not been shown in the pattern of activities during the dry or wet season. Activity diminishes during the wet season and also during periods of intense heat. In the dry season this is because of better availability of food resources, which decreases movement during periods of feeding and resting.

To relationship to patterns of activities, Milton (1980) concludes: "In relation to time, it is notably uniform from day to day and month to month. The monkeys rest a relatively high proportion of time. The regularity of their behavior suggests that the monkeys are capable of avoiding extreme fluctuations in their energetic costs, and a lower level of activity perhaps permits the maintenance of energy reserves at times when the fruits are available in a restricted manner."

This information about patterns of activity allows us to know the behavioral response of the species in energetic terms with respect to environmental fluctuations. It also permits analysis of the possible relation between food availability, quality of habitat, use of habitat and determination of home range limits, with respect to the seasonal variation.

Recommendations

Despite the availability of vast information on activity patterns, it is suggested that the following research directions be developed:

Comparison between the activity patterns of groups inhabiting continuous habitat and those inhabiting fragmented, disturbed habitat.

Comparison of activity patterns in groups with different population structures, in relationship to size of the group, and different age classes and sex.

Behavioral Repertoire

In spite of the vast information that exists on the species, there are not many studies that describe the behavioral repertoire. Only two studies present detailed and sufficient information on the genus *Alouatta* (Neville, 1988; Fathom, 1980) and one on *A. p. mexicana* (Carrera Sánchez, 1994).

Howler monkeys are social primates whose affective relationships are very strong. However, some group cohesion behavior are not as common in comparison with Old World primates (Jones, 1977).

Intergroup agonism in howler monkeys has been observed between males, females y animals with neonates. Aggression between adult males occasionally can lead to individual juveniles (males and female) leaving the group to live solitarily or to integrate into an established group or to form a new group. In the case of females these interactions sometimes lead to aggression, which is limited by the dominant male. Between the infants, these interactions are preparation for adult life. Cases of infanticide have been reported (Galetti, 1994); infant males are thought to receive more aggression than the female infants.

The sexual behavior of howler monkeys follows a pattern defined by courting and copulation. Typical courtship behavior consists of a series of rapid movements of the tongue in and out of the mouth. Additionally, the following behaviors may occur: perineal presentation; following short pursuits of females by males and sniffing of genitalia, perhaps to detect estrous (Fathom, 1980). During copulation, occasionally another female or infant may interrupt which may represent a social mechanism in pace at high population densities (Young, 1981).

Mothers are protagonistic with respect to the care of their infants and have a major influence on their socialization (Clarke, 1990). Other females may serve as "aunts." Females may stay near the mother, grooming the infant and occasionally try to steal it. Because of inexperience with offspring and problems that may occur in this situation, infants are at risk of falling (Serio-Silva, 1994). Other members of the group also occasionally will care for an infant; a male on occasion will adopt an orphan (Neville et al., 1988); its older siblings may recapture it during group movements.

Behavioral research give us a means of understanding how individuals behave in their habitat and may be useful in developing *in situ* and *ex situ* conservation programs. Further, for an endangered species, knowledge of biology provides a strong basis for conservation.

<u>Recommendations</u>

As priorities for behavioral studies we recommend:

Carry out studies on social structure and dominance hierarchies.

Investigate inter-group migration, integration of solitary individuals into existing groups, and formation of new groups.

Study mechanisms of separation between groups that share reduced habitats.

Compare behavior of groups that live under conditions of semi-captivity, fragmented, and continuous habitat.

Follow behavior or translocated or reintroduced groups.

Use confiscated animals for research, analyzing the possibilities that they can be rehabilitated for subsequent release or management.

Carry out ecological studies.

Demography and Reproduction

Distinct aspects of demography and reproduction have been reported for this species by researcher working in Panama (Barro Colorado Island: Altmann, 1954; Carpenter 1934; Chivers,1969; Milton 1980, 1985; Mittermeier 1973; Smith, 1970s; Otis et. al., 1981; among others), Costa Rica (Hacienda la Pacifica: Clarke 1984; Glander 1980; Jones 1980, 1985) and Mexico (Agaltepec Island: Cortés-Ortiz et al., 1993, 1994 and Los Tuxtlas: Estrada et al., 1982, 1984, 1989, 1994). In most cases the populations were found in specialized conditions (confined or fragmented), which offers a perspective that may not correspond completely with those populations that are found in larger expanses of habitat. Nevertheless, data are shown to vary between the different locales and can serve to validate the populations examined under different ecological scenarios in the modeling.

The reported population density for the species varies between 110 individuals/Km^2 in Costa Rica to 16 individuals/Km^2 on Barro Colorado island in Panama. Of particular interest is Estrada's report (1994) for Mexico (Las Tuxtlas, Veracruz), where given the existing fragmented conditions, population density is reported to be 3.6 individuals/Km^2. This is similar to many areas in Mexico where wild populations of A. p. mexicana exist, and is important with respect to field research that permits identification of density under different habitat conditions and different gradations of perturbation.

With respect to size and structure of the groups, the mean number of animals varies between 8 and 23 (groups range from 2 to 45 individuals). The proportion of sexually mature adults is 2.5 females per each male on average (1.16 to 4.11). For a typical population of 20

individuals, the group likely would be comprised of 8 females, 4 males, 3 juveniles (between 14 months and 3 years) and 4 infants (between 0 and 14 months).

The birth rate, mortality and rate of population growth have been estimated in three locations mentioned above and important differences in the calculated values exist. One population showed an observed r of 0.10, while for another r was estimated at 0.29, indicating a more accelerated population growth rate.

Mortality values in these populations are different, according to age classes and sex. Infants have higher mortality (1-year-old and below) and most data show higher mortality in males that in females for various age classes. This difference may attributable to intense intrasexual competition.

Howler monkeys have been reported to have a variety of social systems including polygynous, single-male, multi-male, and graduated age systems (not all adult males have equal access to reproductive females).

Females have estrous cycles of about 17 days, with an estrus peak of 2 to 4 days (these variations can be individual or may vary within a single female). In multi-male populations, a female may pair with more than one male, although it has been suggested that there is one dominant male that copulates preferentially in the middle of this period, which may be presumed to coincide with ovulation. Behavioral studies and determination of physiological correlates will be important to determine fertility within the estrous cycle and to evaluate the genetic contribution of distinct males to the following generation.

Howler monkeys breed year-round. Gestation varies from 180 to 194 days. It would be valuable to carry out careful research to determine gestation more accurately because current data presents such a wide range. The inter-birth interval has been reported to be between 16 and 22 months on average (13-25), but is reduced considerably in females that have lost their offspring. It is necessary to determine these factors more precisely for management programs.

Recommendations

With respect to demography, we recommend:

Extended monitoring of wild populations to elaborate life tables, including population dynamics that populations show under different environmental conditions.

Field studies should be developed to determine population densities of the subspecies, in continuous and fragmented habitat, and under different types of vegetation conditions. Studies also should be undertaken to determine changes in age class and sex.

For reproduction:

Continue developing studies to obtain precise information on reproductive parameters.

Carry out physiological-behavioral studies that elucidate the relations between these two factors with respect to copulation and therefore the genetic contribution of males in the groups.

Genetic Problems

The populations of *Alouatta palliata mexicana* are currently distributed in forest fragments of various sizes. Some of the very reduced fragments are housing small primate populations, which are certainly loosing genetic variability every generation.

When the populations become small and isolated they are faced with various demographic and genetic problems which influence their survival. The crossing of related individuals produces a loss of variability and an increase in inbreeding. Some of the problems from which these populations may suffer are: higher susceptibility to environmental changes (climatic, lack of essential resources), predation, epidemic diseases and parasites. These factors produce a future reduced viability and fecundity, which leads to extinction in the short term.

Fortunately, populations of *Alouatta palliata mexicana* also exist in large forested areas, and are considered viable in the future. These populations can maintain their genetic variation and adaptability better than the small populations, and they are found in protected areas within their distribution.

These large populations of *Alouatta* avoid the effects of inbreeding and the loss in the long-term of genetic variability. The fact that, given the hypothesis of James and Glander (personal communication), *Alouatta palliata* is less susceptible to the problems of inbreeding than other mammalian species, and the fact that this species has an ecological and behavioral adaptability, resulting in a social structure which adapts with environmental changes, leads us to believe that these populations have a good chance of surviving if the current accelerated destruction of habitat could be controlled.

These large populations of *Alouatta* occurring principally in natural protected areas within its distribution range can serve, more over, as a continuous source of genetic material for the small fragmented populations near them. The immigration of at least one individual per generation can minimize the substantial loss of genetic variability.

In order to test this hypothesis, we propose a pilot study on a small population in a semi free-ranging situation on the island of Agaltepec, in the Southeast of Veracruz, with the goal of establishing the parameters of inbreeding. In selecting a group, the parental lines of the individuals making up the population should be known.

This study basically will consist of the extraction of DNA from blood samples and the standardization of a molecular technique that provides the best information on inbreeding. The methods that can be tried are: RAPD markers (Random Amplified Polymorphic DNA), used

regularly in population genetics, and the technique of variation in mitochondrial DNA, used by James and Horwich (1993) in *Alouatta pigra*.

The results obtained from these preliminary studies can offer information about the best technique to be applied to a sample of fragmented wild populations to see if inbreeding exists in these, as well as its impact; and they can support, in parallel, studies of morphologic and genetic variability concerning the taxonomy of the species.

Finally, the proposed study will offer information about the necessity of translocating individuals with genetic variation into the very fragmented populations.

POPULATION AND HABITAT VIABILITY ASSESSMENT FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 March 1995

Section 13
Captivity and Diseases
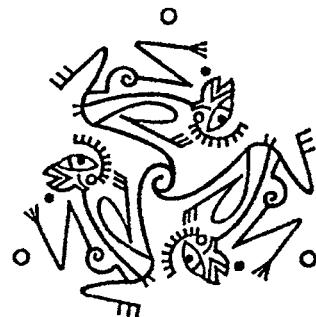
CAPTIVITY AND DISEASE

General Considerations

Currently, *Alouatta palliata mexicana* does not require a global captive breeding and management program. However, individuals already in captivity would be good candidates for investigations, for example on reproductive physiology, genetics, biomedicine, behavior, and education.

     A. palliata has been characterized as being difficult to maintain in captivity; in Mexico, this is verifiable by examining the current colonies. Most difficulties can be attributable to nutritional problems as the species is characterized as a specialized herbivore and requires therefore of a high percentage of leaves in the diet. The majority of the food species on which *A. palliata* feeds are found only in the areas in which the primate naturally occurs.

     Because of the difficulty in maintaining *A. p. mexicana* in captivity, it is recommended that captive programs and management only should be undertaken in the areas in which the primate is naturally distributed.

Collection

The local institutions outside of the distribution area of *A. p. mexicana*, and which are recipient of donated monkeys, out to channel those individuals to institutions previously selected to breed and manage them in captivity. This should not occur without a clinical evaluation and application of any appropriate treatment necessary.
This will ensure that individuals destined for captivity will arrive at their final destination in good health.

Records

A priority in developing a captive program is to use a record system that includes individual identification, clinical events, reproductive events, etc. It is further recommended that a "studbook" be created using the ISIS program "SPARKS." This will lead to sharing of information among all institutions involved in breeding or managing *A. p. mexicana*.

Facilities and Specialized Personnel

The institutions selected for managing *A. p. mexicana* should, firstly, be located within the natural distribution area of the subspecies, so that environmental conditions needed by the howler monkeys can be offered. Staff will have to have special technical training to adequately manage the monkeys. Finally, economic support must be ensured to facilitate the construction of adequate housing for the monkeys.

Nutrition

Currently, an efficient diet for *A. palliata* in captivity does not exist. Therefore, studies on digestibility and food items, using wild plant species is recommended. We also recommend using cultivated fruits as a source of non-structural carbohydrates.

Education

It is important to establish an extensive conservation education program, emphasizing that howler monkeys are not good pets and that their use as such affects the survival of the species.

Monitoring of Infectious Diseases

Because of the scant amount of information on diseases for the species, in the wild and in captivity, it is necessary to implement a data base that permits analysis of the infectious diseases that affect the national population and to determine the impact of these on the viability of the subspecies.

The data base will have to be based on standardized protocols that permit the detection of principal diseases, in captivity as well as in the wild. Also, given the particular characteristics of the taxon, maintenance in captivity should be regimented by established medical procedures that will reduce the risk of disease in these populations.

It is recommended to that the following objectives be met:

Listing of diseases reported in howler monkeys or to which they may be susceptible.

Review published literature on infectious diseases in this and related taxons.

Preventive medicine protocols:
    Quarantine protocol
    Necropsy protocol
    Periodic monitoring
    Transportation protocol
    ****Application for free-living populations

Diagnosis protocol:
    Collection and shipment of samples
    Processing of samples
    **** Application for free-living populations

Data base

Once protocols are generated, we recommend their use by researchers and zoos integrated with a survival plan for this subspecies. Biomaterials obtained during the studies should be analyzed at the same location to standardize results and to permit the formation of the data base.

Captive Population

Currently 7 individuals exist in captive conditions: a juvenile male in the Zoo of Aragon, 2 males and 4 adult females in Parque de la Flora y Fauna Silvestre Tropical de la Universidad Veracruzana. There also are 3 semi-free-ranging/semi-captive colonies:

Zoológico "La Venta" in Villahermosa, Tabasco
5 males and 8 adult females, 6 immature individuals.

Agaltepec Island, Catemaco, Veracruz
12 males, 11 adult females and 17 immature individuals.

Zoológico Miguel Alvarez del Toro, Chiapas
20 individuals of different categories of sex and age.

Recommendations

Determine captive breeding centers with the capacity for receiving confiscated or donated animals. Individuals channeled to the centers permanently should meet certain pre-established criteria that will assure their survival and development in captivity.

Establish an inter-institutional education program that emphasize the following:
   a) primates are not good pets
   b) it is difficult to satisfy their natural requirements
   c) primates transmit diseases and are aggressive toward humans
   d) collection of these animals has a negative impact on the species' survival

A handbook for managing *A. p. mexicana* in captivity should include recommendations on:
a) permanent individual identification
b) housing facilities
c) diet
d) diagnosis and treatment of diseases
e) taxonomy
f) containment
g) preventive medicine protocols and diagnostic tools

These will be applied both in temporary collection centers and permanent centers.

To elaborate a field handbook for the takes, managing, shipment and samples processing.

Develop a manual for collection, management, transportation, and processing of specimens.

Establish a reference center only for the processing and analysis of the information requested.

Recognize diseases that are presented in the taxon.

Create a data base.

Form an inter-disciplinary and inter-institutional working group to develop each of the recommendations, with annual meetings that would have as objective checking the information generated and update strategies.

List of Participants and Labor to Develop the Revised Manual for *A. palliata*

1. Alternative sites for the maintenance of this species in captivity (in addition to those already eligible), as well as of the report of SARH on collection centers or zoos that could temporarily house some specimens on short notice.
    MVZ. PERLA CIFUENTES CALDERON.

    Establish an agreement with Carlos Guichard of the ZOOMAT for receiving specimens.
    MVZ. DOMINGO CANALES ESPINOSA

2. Guide of collection centers by geographic region.
    AZCARM

3. Letter to zoos informing them of destination for animals and the requirements for the exhibition of *A. palliata* in zoos.
    LAPZ. FRANK CARLOS CAMACHO and AZCARM

4. List of desirable and undesirable characteristics for the individuals intended to be maintained in a collection, as well as an alternative for those that do not fulfil those requirements.
    MVZ. DOMINGO CANALES ESPINOSA

5. Development of handbook for managing the taxon in captivity that will include various topics on the care of the taxa.
    MVZ. CLAUDIA LEWY, MVZ. ENRIQUE YARTO, MVZ. DULCE BROUSSET, MVZ. IVONNE RUIZ AND MVZ. GUSTAVO RAMIREZ

6. Development of field handbook for the collection, shipment and processing of samples from *A. palliata*.
    MVZ. MARCO A. BENITEZ, MVZ. ALBERTO PARAS, MVZ ABEL CONTRERAS (Morelia Zoo)

7. Establish a reference center only for the processing and sample analysis for the Mexican primates.
    MVZ ALBERTO PARAS, MVZ. DOMINGO CANALES ESPINOSA, UNAM

8. Recognize the diseases presented by the taxon and communicate results to those individuals developing the manual.
    MVZ. JORGE PAREDES

9. Creation of a data base
    University of Veracruz, UNAM

10.   Letter requesting support from the laboratories of UNAM for the processing of the different samples noted above and noting the objective and the importance of these results.
AZCARM and MEXICAN ASSOCIATION OF PRIMATOLOGISTS

An outline for each of the projects will be delivered to the MVZ DOMINGO CANALES ESPINOSA for the review at the next National Symposium of Primatology, to be held in Puebla in May of 1995 (the exact dates will be confirmed and communicated to the participants of this group).

POPULATION AND HABITAT VIABILITY ASSESSMENT
FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 March 1995

Section 14
Education
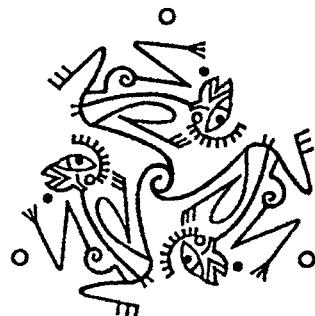
EDUCATION

The success of the conservation efforts for *Alouatta palliata* depends strongly on a sensitizing citizens and informing them of the problems in question at local, regional, state and national levels. To achieve this, it will be necessary to create education programs directed to various specific audiences, each with particular characteristics that will need to be considered in order to obtain maximum possible impact. We can divide the education into two categories: education at the local level and education at the general level.

Programs at the Local Level

These programs are intended to have a direct impact on the human populations that regularly interact directly or indirectly with *A. p. mexicana*. Developing these programs must take into account:

- Socio-economic studies of the locale
- Understanding of local traditions
- Incorporating local people in the conservation process
- Offering and explaining the benefits and options that the conservation program offers
- Generating support material and specific publications for each locale
- Creating an understanding of the need for habitat protection and to respect natural areas whether officially protected or not
- Developing material so that local people are motivated to coexist with the howler monkey and elucidate the natural history of the species to dispel superstitions and clarify misinformation.

It will be necessary to develop materials in local dialects in communities in which it is required.

Education at a General Level

Programs intended to inform and sensitize citizens, as much at the local level as the regional, national and international. These programs are targeted either at people that interact with or do not interact directly with the howler monkeys.

POPULATION AND HABITAT VIABILITY ASSESSMENT
FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
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Section 15
Referencias
References
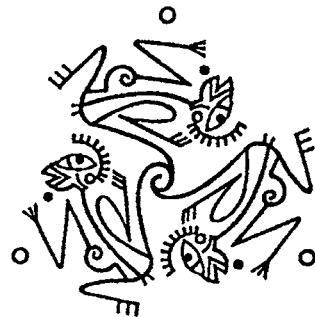
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Puebla, Pue., México
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Section 16
Lista de Participantes
List of Participants
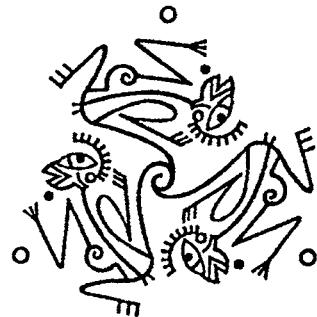
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POPULATION AND HABITAT VIABILITY ASSESSMENT
FOR THE MANTLED HOWLER MONKEY
(*Alouatta palliata mexicana*)

Puebla, Pue., México
2-4 March 1995

Section 17
Referencia Técnica de VORTEX
VORTEX Technical Reference
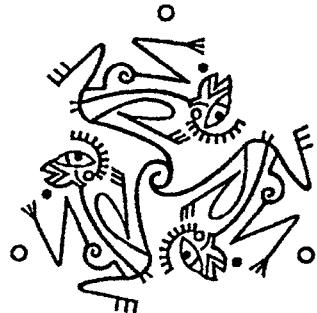
VORTEX: A Computer Simulation Model for Population Viability Analysis

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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,

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,
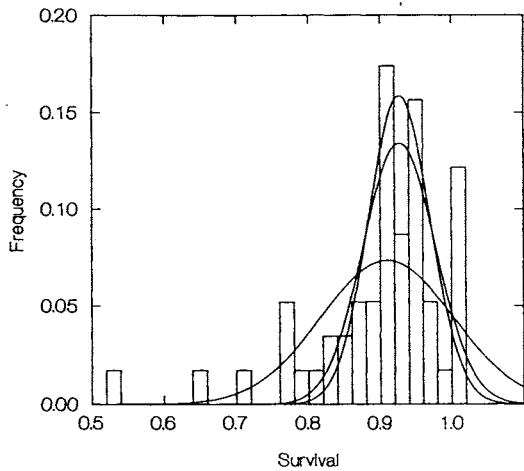
Fig. 1. Frequency histogram of the proportion of whooping cranes surviving each year, 1938–90. The broadest curve is the normal distribution that most closely fits the overall histogram. Statistically, this curve fits the data poorly. The second highest and second broadest curve is the normal distribution 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 1980a, 1980b), 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 $1 \cdot 0$ 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 $0 \cdot 040$, with annual fluctuations in the growth rate, SD (r), of $0 \cdot 141$ (Mirande *et al*. 1993). Life-table analysis predicted an r of $0 \cdot 052$. Simulations using VORTEX predicted an r of $0 \cdot 046$ into the future, with a SD (r) of $0 \cdot 081$. 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 confir-

mation 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)