Distribution, ecology, life history, genetic variation, and risk of extinction of nonhuman primates from Costa Rica

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Abstract: We examined the association between geographic distribution, ecological traits, life history, genetic diversity, and risk of extinction in nonhuman primate species from Costa Rica. All of the current nonhuman primate species from Costa Rica are included in the study; spider monkeys (*Ateles geoffroyi*), howling monkeys (*Alouatta palliata*), capuchins (*Cebus capucinus*), and squirrel monkeys (*Saimiri oerstedii*). Geographic distribution was characterized accessing existing databases. Data on ecology and life history traits were obtained through a literature review. Genetic diversity was characterized using isozyme electrophoresis. Risk of extinction was assessed from the literature. We found that species differed in all these traits. Using these data, we conducted a Pearson correlation between risk of extinction and ecological and life history traits, and genetic variation, for widely distributed species. We found a negative association between risk of extinction and population birth and growth rates; indicating that slower reproducing species had a greater risk of extinction. We found a positive association between genetic variation and risk of extinction; *i.e.*, species showing higher genetic variation had a greater risk of extinction. The relevance of these traits for conservation efforts is discussed. Rev. Biol. Trop. 52(3): 679-693. Epub 2004 Dic 15.

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Palabras clave: monos del Nuevo Mundo, *Alouatta palliata*, *Ateles geoffroyi*, *Cebus capucinus*, *Saimiri oerstedii*, isozimas, destrucción del habitat, conservación biológica.

Forest destruction and fragmentation, agricultural practices, hunting, and extraction for pets or research purposes (Mittermeier and Cheney 1987, Rodriguez-Luna *et al.* 1996) have negatively affected nonhuman primate species in Central America. However, species differ in their responses to these factors. There are four nonhuman primate species in Costa Rica and they all show different risks of extinction. Squirrel monkeys (*Saimiri oerstedii*) are at greater risk; the IUCN lists them as

endangered, with one subspecies (*S. o. citrinellus*) listed as critically endangered (Mittermeier *et al.* 1986, Rylands *et al.* 1995, Rylands 1997, Boinski and Sirot 1997). Squirrel monkeys are the Central American nonhuman primates at greater risk of extinction. Spider monkeys (*Ateles geoffroyi*) rank second and one subspecies (*A. g. panamensis*) is considered to be endangered while the other (*A. g. ornatus*) is described as vulnerable in the IUCN red list (Rylands *et al.* 1995, Rylands

1997). Howling monkeys (*Alouatta palliata*) and capuchins (*Cebus capucinus*) have experienced recent reductions in their population sizes and their geographic distributions but they are not considered vulnerable or endangered by the IUCN specialists (Rylands *et al.* 1995, Rylands 1997).

Several factors determine the ability of a species to survive environmental disturbance. Rareness is associated with greater risks of extinction (Rabinowitz *et al.* 1986). Species rareness is determined by the geographic distribution, the diversity of habitats occupied, and population sizes (Rabinowitz *et al.* 1986, Dobson and Yu 1993). Species with broader geographic distributions, found in more types of habitats, and with larger population sizes, are at lower risks of extinction. Vulnerability is also determined by ecological and life history traits (Johns and Skorupa 1987, Arita *et al.* 1990, Sorensen and Fedigan 2000). Among nonhuman primates, a larger size and a greater proportion of fruit in the diet are believed to increase the risk of extinction; *i.e.* large bodied frugivores are more vulnerable than smaller bodied folivores (Johns and Skorupa 1987, Sorensen and Fedigan 2000). Lower fecundity and larger home ranges are also associated with greater risks of extinction (Johns and Skorupa 1987, Mc Farland 1989, Sorensen and Fedigan 2000).

Low levels of genetic diversity are also believed to increase the risk of extinction of threatened or endangered populations (O'Brien *et al.* 1985, Allendorf and Leary 1986, O'Brien and Everman 1988, Quattro and Vriejenhoek 1989, O'Brien 1994a, 1994b, Lacy 1997). Perhaps the most frequently cited example involves the cheetah; extremely small levels of genetic variation in this species have been associated with low fecundity in captivity and high offspring mortality in the wild (O´Brien *et al.* 1985, O´Brien and Evermann 1988, O´Brien 1994a, 1994b) (for a criticism of this hypothesis see Caro and Laurenson 1994, Laurenson *et al.* 1995). Data from several species show that low levels of genetic diversity do not result in low rates of population growth (Bonnel and Selander 1974, Hoelzel *et al.* 1993, Stewart *et al.* 1994, see references in Avise 1994). Also, many threatened species retain high levels of genetic diversity (Dinerstein and Mc Cracken 1990, Baker *et al.* 1993, Hartl and Hell 1994, Tomiuk *et al.* 1997, Ye *et al.* 1999, Young *et al.* 1999). Among primates, microsatellite variation in geographically restricted and endangered bonobos (*Pan paniscus*) is comparable to that of its widespread congener *P. troglodytes* (Reinartz *et al.* 2000). Therefore, there is not a clear correlation between genetic diversity and risk of extinction.

In this study we conducted a literature review to obtain information about the ecology and life history of the nonhuman primate species from Costa Rica. All nonhuman primate species found in Costa Rica are included in the study; *i.e.*, spider monkeys (*A. geoffroyi*), howling monkeys (*A. palliata*), capuchins (*C. capucinus*), and squirrel monkeys (*S. oerstedii*). We searched existing databases and contacted people working in protected areas to characterize their geographic distribution. In addition, we conducted red cell isozyme electrophoresis to characterize their genetic variation. Using these data, we examined the association between the risk of extinction of nonhuman primates from Costa Rica and their geographic distribution, ecology, life history, and genetic diversity.

MATERIALS AND METHODS

Study species

Geographic distribution: At a regional level, the four species differ in their geographic distribution. *Ateles geoffroyi*, *Alouatta palliata*, and *Cebus capucinus* have a wide geographic distribution (Crockett and Eisenberg 1987, Rylands *et al.* 1995, Rylands 1997, Crockett 1998, Sorensen and Fedigan 2000). *A. geoffroyi* are found from Mexico to Panama, *A. palliata* are found from Mexico to northern Ecuador, and *C. capucinus* from

Honduras to Colombia. *Saimiri oerstedii* have a very restricted geographic distribution; historically their distribution has been limited to the Pacific wet lowlands of Costa Rica and Panama at altitudes lower than 500 masl, an area smaller than 8000 km^2 (Wong 1990a, 1990b, Boinski and Sirot 1997, Crockett 1998, Boinski and Cropp 1999).

At a local level, the four species also differ in their distribution. Appendix 1 shows the presence or absence of these species within conservation areas and protected areas. Conservation areas are large administrative units that include both protected and non-protected areas. These data underestimate the distribution of these species within the country because only populations from protected areas are included. Nonhuman primates are also found outside protected areas, but it was not possible to verify their presence or absence there.

Overall, *A. geoffroyi*, *C. capucinus*, and *A. palliata* have a wide geographic distribution within the country, whereas *S. oerstedii* have a very narrow distribution (Wilson 1983, Boza 1992, Rodriguez and Chinchilla 1996, Boinski and Sirot 1997, Carrillo *et al.* 1999, Saenz *et al.* 1999, Wong *et al.* 1999, Mora 2000). *A. geoffroyi* occur principally in protected areas of larger size and extensive forest coverage. *A. geoffroyi* are not found in the Central Pacific conservation area, where the protected areas are of smaller size. *C. capucinus* and *A. palliata* are found in all conservation areas and most protected areas. *S. oerstedii* are only found in the Central Pacific and Osa conservation areas located in the central and south Pacific region.

Population sizes: We lack accurate estimates of population sizes for the whole country, but there is published data for populations within some protected areas. A census conducted in 1972 at the Santa Rosa National Park (Freese 1976) reported estimated population sizes of 110 individuals for *A. geoffroyi*, 85 *A. palliata*, and 300 *C. capucinus*. Follow up censuses show that, after almost 30 years of protection within the park and regeneration of the natural habitat, *A. palliata* and *C. capucinus* have increased their numbers to 606 and 585 individuals, respectively (Sorensen and Fedigan 2000, Fedigan and Jack 2001). We do not have figures for *A. geoffroyi* but, according to Sorensen and Fedigan (2000), the population of *A. geoffroyi* has grown at a slower rate.

TABLE 1

Frequency of the most common allele for each red cell isozyme loci for each primate species

Locus	Species			
	Ateles geoffroyi (N=10)	*Alouatta palliata** (N=76)	*Cebus capucinus* (N=5)	*Saimiri oerstedii* (N=8)
CA2	1.0000	1.0000	1.0000	1.0000
DIA	0.6111	1.0000	1.0000	0.6250
EST-1	0.8889	1.0000	1.0000	0.8750
EST-2 Allele A	0.8333	1.0000	1.0000	0.8750
Allele B	0.1111			
GPI	1.0000	1.0000	1.0000	0.6250
LDH-1	1.0000	1.0000	1.0000	1.0000
LDH-2	1.0000	1.0000	1.0000	1.0000
MDH	1.0000	1.0000	1.0000	1.0000
PGD	1.0000	1.0000	1.0000	0.8750
PGM-1	1.0000	1.0000	1.0000	1.0000
PGM-2	1.0000	1.0000	1.0000	1.0000
SOD	1.0000	1.0000	1.0000	1.0000
TPI	1.0000	1.0000	0.8000	1.0000

* From: Zaldivar *et al.* (2003).

Censuses conducted in other areas within the Guanacaste region also show that *A. palliata* are more common, followed by *C. capucinus*. In all sites censused, *A. geoffroyi* are the least common. At Palo Verde, Massey (1987) found that the density of *A. palliata* was 59.3 ind/km², for *C. capucinus* there were about 15.4 ind/km², and for *A. geoffroyi* only 0.62 ind/km². At Cabo Blanco, Lippold (1988) found 80 *A. palliata*, and 54 *C. capucinus*. Other censuses show fairly large populations of *A. palliata*. At La Pacífica, the estimated population size has remained around 351 individuals for almost twenty years (Clarke *et al.* 1986, Clarke and Zucker 1994, Clarke *et al.* 2002a, 2002b). At La Selva, the population ranged between 105 and 225 individuals (Stoner 1994).

S. oerstedii is believed to have smaller populations than the other species. According to Boinski and Sirot (1997), the current population size of *S. o. citrinellus* within the protected area of the Manuel Antonio National Park is about 100 individuals, while the population size of *S. o. oerstedii* within the Corcovado National Park ranges between 200 and 500 individuals.

Habitats occupied: *A. geoffroyi*, *A. palliata*, and *C. capucinus* occupy a variety of altitudinal ranges and habitats, including mangroves, riparian forests, dry and humid forests, lowland, premontane, and montane forests, secondary forests, and forest edges (Eisenberg 1983, Freese 1983, Glander 1983, Sanchez 1991, Stoner 1994, Carrillo *et al.* 1999, Mora 2000, Clarke *et al.* 2002a, 2002b). *A. geoffroyi* are found at altitudes ranging from sea level to 2200 m (Carrillo *et al.* 1999), but are restricted to large forest fragments and are less common in altered environments (Estrada 1988, Estrada and Coates-Estrada 1996, Carrillo *et al.* 1999, Sorensen and Fedigan 2000). *A. palliata* and *C. capucinus* show comparable altitude ranges (between sea level and 2500 and 3000 m, respectively) (Carrillo *et al.* 1999), but they can be found in small forest patches and altered environments (Freese 1983, Wilson 1983, Crockett 1998, Horwich 1998, Carrillo *et al.* 1999). The mean size of protected areas in which *A. geoffroyi* occurs is 33 529 ha whereas *A. palliata*, and *C. capucinus* are found in areas averaging 23 906 and 23 930 ha, respectively (From the values in Appendix 1). *S. oerstedii* occupy fewer kinds of habitats. They are commonly found at altitudes below 500 m, in secondary forests and forest edges, but they can also be present in habitats showing a mosaic of forest types and in cultivated areas (Boinski 1987, Wong 1990a, 1990b, Carrillo *et al.* 1999).

Home range and diet: There is a great degree of variation in home range size within each species (Appendix 2) (Freese 1983, Boinski 1987, Fedigan *et al.* 1988, Wong 1990a, 1990b, Sanchez 1991, Clarke and Zucker 1994, Stoner 1994, Boinski and Sirot 1997, Sorensen and

TABLE 2

Indicators of genetic diversity for each primate species. Standard deviation in parentheses

Species	*Ateles geoffroyi*	*Alouatta palliata* *	*Cebus capucinus*	*Saimiri oerstedii*
Observed number of alleles	1.3077	**1.0000**	1.0769	1.3846
	(0.6304)	**(0.0000)**	(0.2774)	(0.5064)
Effective number of alleles	1.1201	**1.0000**	1.0362	1.2004
	(0.2678)	**(0.0000)**	(0.1305)	(0.3254)
Percentage polymorphic loci	23.08	**0.00**	7.69	38.46
Observed heterozygosity	0.0598	**0.0000**	0.0000	0.0962
	(0.1167)	**(0.0000)**	(0.0000)	(0.1266)
Nei's expected heterozygosity	0.0741	**0.0000**	0.0246	0.1226
	(0.1521)	**(0.0000)**	(0.0888)	(0.1727)

* From: Zaldivar *et al.* (2003)

Fedigan 2000). Overall, home range sizes vary between 25 and 100 ha.

These species also show variation in the proportion of time spent eating fruits, flowers, leaves, or insects (Appendix 2). Within species, the proportion of time eating each kind of fruit item varies spatially and temporally, depending on their availability. *A. geoffroyi* consume primarily fruits and some leaves and flowers (Chapman 1987, Chapman and Chapman 1991, Strier 1992, Sorensen and Fedigan 2000). *A. palliata* spend most of their time eating leaves and fruits (Glander 1981, Chapman 1987, Sanchez 1991, Strier 1992, Stoner 1996, Sorensen and Fedigan 2000). *C. capucinus* eat mostly fruits and insects and sometimes small vertebrates (Chapman 1987, Chapman and Fedigan 1990, Sorensen and Fedigan 2000). *S. oerstedii* eat mostly insects and some fruits (Schultz 1940, Baldwin and Baldwin 1972, Robinson and Janson 1987, Wong 1990a, 1990b).

Life history traits: The four species differ in their life history traits. Appendix 2 shows that *A. geoffroyi* and *A. palliata* are the largest, *C. capucinus* is intermediate, and *S. oerstedii* is the smallest (Baldwin and Baldwin 1972, Glander *et al.* 1991, Boinski and Cropp 1999). It also shows that *A. geoffroyi* has the lowest reproductive rates (Fedigan and Rose 1995, Ross and Jones 1999, Fedigan and Jack 2001). *A. palliata* and *C. capucinus* show higher reproductive rates than *A. geoffroyi* (Glander 1980, 1992, Clarke and Glander 1984, Crockett and Eisenberg 1987, Robinson and Janson 1987, Fedigan and Rose 1995, Fedigan and Jack 2001). We did not find accurate estimates of reproductive rates for *S. oerstedii*. Data on *S. sciureus*, other species in the same genus with similar life history and behavior traits, reveals the highest values for all parameters determining reproductive rates (Boinski and Cropp 1999, Ross and Jones 1999).

Genetic analysis

Sample collection: Samples of *S. oerstedii* were collected in the Central Pacific Region. All the samples collected belonged to the *S. o. citrinellus* subspecies. Two samples were collected at the Manuel Antonio National Park and six samples were collected at Jardin Gaia, a wildlife rehabilitation center next to the park, which receives animals confiscated by the Wildlife Service. The Manuel Antonio National Park has the largest extant population of *S. o. citrinellus*. Samples of *A. geoffroyi* and *C. capucinus* were obtained at the Parque Zoológico Nacional Simón Bolívar, San José, during their annual physical examination. All the animals also had been confiscated by the Wildlife Service and came from various regions within the country. The exact location of origin was not known for most of the animals. Animals born in captivity (only one) were not included in this study. We analyzed nine samples of *A. geoffroyi* and five of *C. capucinus*.

Field samples were collected using standard dart gun capture techniques (Glander *et al.* 1991). Samples from captive animals did not require darting. In all cases animals were anesthetized with Telazol (Tilethamine hydrochloride and zolazepam hydrochloride) and blood was drawn from their femoral vein using a Vacutainer with EDTA as an anticoagulant. Darted animals were allowed to recover and then released at the site of capture.

In a previous study we examined blood samples from *A. palliata* from several sites in Costa Rica (Zaldivar *et al.* 2003). A total of 76 samples were analyzed. Most samples come from the Guanacaste region, located on the Northern Pacific side of the country (61 samples), eight samples were collected in the Atlantic Region and seven samples in the Central Pacific region. Elsewhere we provide the exact location of the sites in which the samples were collected (Zaldivar *et al.* 2003) . The Atlantic and Pacific Regions are separated by a mountain range running along the center of the country in a North-South direction.

The blood samples were kept cold until processing in the laboratory. Once in the laboratory, they were centrifuged at low speed for about 15 minutes to separate plasma, white cells, and red cells. The red cells were washed

twice with isotonic 9% saline solution. Each fraction was stored separately at -20 ℃.

Isozyme analyses: In order to examine the level of genetic variation in each species, we performed electrophoresis of red cell enzymes following the methods described by Harris and Hopkinson (1978), Richardson *et al.* (1986), and Lima *et al.* (1990). Electrophoresis was conducted on 9 to 11% starch gels. Electrophoresis was run overnight at constant voltage (60-75 Volts). We examined ten enzyme systems, *i.e.* CA2, DIA, EST, GPI, LDH, MDH, PGD, PGM, SOD, and TPI. For each red cell enzyme we used the buffers and staining procedures recommended by Harris and Hopkinson (1978). We recorded the genotype of each individual.

Genetic analyses were conducted using the program POPGENE 1.32 (Yeh *et al.* 1999). We determined the levels of genetic diversity for each species using common indicators such as observed number of alleles, effective number of alleles, percentage polymorphic loci, observed heterozygosity, and expected heterozygosity.

Association between risk of extinction and ecological, life history, and genetic traits: The four primate species included in this study differ in their conservation status. *S. oerstedii* is considered to be endangered. This species has a very narrow geographic distribution, natural habitats have been destroyed through deforestation, and in some areas population sizes are small. All other species have wide geographic distributions within the country and the region, yet the conservation status of *A. geoffroyi* is considered to be vulnerable.

In order to determine which factors may explain the higher risk of extinction of *A. geoffroyi* compared to *A. palliata* and *C. capucinus*, we conducted a Pearson correlation analysis and examined the association between risk of extinction and ecological traits (mean size of protected areas in which the species is present, size of home range, proportion of fruits in diet, proportion of leaves, proportion of insects), life history (size of males, size of females, age at first birth, interval between births, birth rate,

intrinsic rate of population growth), and genetic diversity (observed number of alleles, effective number of alleles, percentage polymorphic loci, observed heterozygosity, and expected heterozygosity). The risk of extinction was assigned a categorical value based on the conservation status determined by Rylands *et al.* (1995) and Rylands (1997). *C. capucinus* and *A. palliata* have the lowest risk of extinction and were assigned a value of 1, *A. geoffroyi* has a higher risk was assigned a value of 2.

RESULTS

Isozyme analyses

A total of 13 putative loci were examined. Seven loci were monomorphic (CA2, LDH-1, LDH-2, MDH, PGM-1, PGM-2, and TPI); *i.e.* they showed only one electrophoretic variant. Six loci showed two or more variants (DIA, EST-1, EST-2, GPI, PGD, and SOD). Table 1 shows the frequency of the most common allele for all loci. *S. oerstedii* showed the greatest number of variable loci; 5 of the 13 loci studied had more than one variant (DIA, EST-1, EST-2, GPI, and PGD). *A. geoffroyi* had three loci showing more than one electrophoretic variant (DIA, EST-1, and EST-2). *C. capucinus* showed only one loci with more than one electrophoretic variant (SOD), but the sample size was very small (only five individuals). *A. palliata*, despite their much larger sample size, showed no variation and this was true for all the enzymes analyzed; all the individuals examined showed the same electrophoretic pattern at all loci.

The four species studied have different patterns of genetic variation according to the values of the indicators of genetic diversity shown in Table 1, *i.e.* observed number of alleles, effective number of alleles, percentage polymorphic loci, observed heterozygosity, and expected heterozygosity. For all indicators of genetic diversity, *S. oerstedii* show the greatest values, *A. geoffroyi* rank second, *C.*

capucinus rank third, and *A. palliata* rank last, since they show no genetic variation for any of the loci examined (Table 2).

Association between risk of extinction and ecological, life history, and genetic traits: Among widely distributed species, we found a negative association between risk of extinction and mean size of protected areas in which the species are found (Table 3); where species present in areas of larger mean size are at greater risk of extinction and species found in areas of smaller sizes are at lower risk. For all other ecological variables we did not find a statistically significant association with risk of extinction (Table 3). For the correlation analyses between risk of extinction and proportion of fruits in diet, proportion of leaves, proportion of insects, and home range, we used the mid-value of the ranges described in the Appendix. We did not find a statistically significant association between risk of extinction and size of males, size of females, age at first birth, and interval between births (Table 3). But we found that risk of extinction is negatively associated with birth rate and rate of

TABLE 3

Pearson correlation between risk of extinction and ecology, life history and genetic traits for widely distributed nonhuman primates from Costa Rica. Numbers in parentheses indicate P

Variable	r^2 (*P*)
Mean size of protected areas	**0.997 (0.053)**
Home range	- 0.339 (0.780)
Proportion of fruits in diet	0.614 (0.579)
Proportion of leaves in diet	- 0.435 (0.714)
Proportion of insects in diet	- 0.449 (0.703)
Size of males	0.780 (0.431)
Size of females	0.918 (0.260)
Age at first birth	0.981 (0.125)
Interbirth intervals	0.967 (0.164)
Birth Rate	**- 0.989 (0.095)**
Population growth rate	**- 0.997 (0.053)**
Observed number of alleles	0.971 (0.154)
Expected number of alleles	0.956 (0.189)
% Polymorphic loci	0.945 (0.212)
Observed heterozygosity	**1.000 (0.000)**
Expected heterozygosity	0.943 (0.216)

population growth (table 3); where species with greater birth and population growth rates are at lower risk of extinction and species with smaller birth and population growth rates are at greater risk. For most indicators of genetic diversity we found no statistically significant association between risk of extinction and genetic diversity, but species with greater observed heterozygosity were at greater risk than less diverse species.

DISCUSSION

Our analysis of isozyme variation revealed that *S. o. citrinellus* and *A. geoffroyi* showed high levels of isozyme variation whereas *A. palliata* and *C. capucinus* showed very low levels of genetic variation. *A. palliata* did not show variation for any of the isozymes studied, even though we examined more samples of this species than for any other (Zaldivar *et al.* 2003).

The values of isozyme variation that we find for *S. o. citrinellus*, *A. geoffroyi*, and *C. capucinus* concur with the results reported for these same groups in South America. South American *Saimiri* showed genetic variation for EST, GPI, LDH, MDH, PGD, and PGM (Vandeberg *et al.* 1990, Silva *et al.* 1993). Heterozygosity estimates ranged between 0.086 and 0.025 (Vandeberg *et al.* 1990, Silva *et al.* 1993) and are comparable to the value reported by us. South American spider monkeys (*A. paniscus*) showed variation in one out of 20 loci (CA2) and *A. chamek* showed variation in three (ADA, ESD, and GLO) (Sampaio *et al.* 1993). Average heterozygosity was slightly lower than the value found by us (0.06) and it ranged between 0.021 and 0.031 (Sampaio *et al.* 1993). South American capuchins showed low levels of genetic variation. Sampaio *et al.* (1993) found that *C. apella paraguayanus* was polymorphic for two loci (GLO and GPI) and showed an average heterozygosity of 0.014.

The absence of genetic variation that we found for *A. palliata* (Zaldivar *et al.* 2003) is

comparable to the low values of genetic diversity previously reported for this and other Central American populations, and contrasts with the high values reported for South American *Alouatta*. Genetic studies of *A. palliata* in Central America indicate that this species has extremely low levels of isozyme variation. Malmgren and Brush (1978), using two-dimensional electrophoresis, found 2 of 15 polymorphic loci, including MDH, reported as monomorphic by us. Froelich and Thorington (1982) reported 3 of 25 polymorphic loci (ADA and two serum proteins). Ellsworth (2000) analyzed microsatellite variation in *A. palliata* from Panama, Costa Rica, and Mexico, and found that this species has extremely low genetic variability; the mean number of alleles was 6.3 and the mean observed heterozygosity was 0.35 in a sample of 117 individuals. Genetic studies of the other Central American howler, *A. pigra*, also found low levels of isozyme and DNA variation (James *et al.* 1997, Ellsworth 2000). *A. pigra* shows variation in 2 of 36 loci, including GPI, monomorphic in *A. palliata* (James *et al.* 1997). It also shows low levels of microsatellite variation (Ellsworth 2000); in a sample of 28 individuals, the mean number of alleles was 3.8 and the mean observed heterozygosity was 0.45. Genetic studies of South American *Alouatta* indicate that these species have very high levels of genetic variation. In *A. seniculus*, Pope (1992) found variation in 10 out of 29 loci and Lima *et al.* (1990) found variation in 9 out of 26 loci. *A. belzebul* showed comparably high levels of genetic variation (Sampaio 1996). Ellsworth (2000), using microsatellite analysis, found that the mean number of alleles per individual in *A. seniculus* (0.71) is much higher than in *A. palliata* (0.165). Mean observed heterozygosity values were also higher; 0.56 in a sample of six individuals (Ellsworth 2000).

Among the three species with a wider geographic distribution, we found no association between risk of extinction and most ecological variables such as degree of frugivory or home range size. Home range and diet were highly variable, both between species and within species, and they show both temporal and spatial variation (Schultz 1940, Baldwin and Baldwin 1972, Glander 1981, Freese 1983, Boinski 1987, Chapman 1987, Robinson and Janson 1987, Fedigan *et al.* 1988, Chapman and Fedigan 1990, Wong 1990a, 1990b, Chapman and Chapman 1991, Sanchez 1991, Strier 1992, Clarke and Zucker 1994, Stoner 1994, 1996, Boinski and Sirot 1997, Sorensen and Fedigan 2000). Variation within species would obscure any possible association due to variation between species. We do find an association between risk of extinction and mean size of protected areas in which the species is present; *A. geoffroyi* are present in areas of larger average mean size and are at greater risk of extinction. *A. geoffroyi* are seldom present in protected areas of smaller size and they seem to require larger areas of forest.

Also, among the three species with a wider geographic distribution, we found no association between risk of extinction and most life history traits. But we did observe that lower birth rates and lower population growth rates were associated with greater risks of extinction. These results allow us to explain the vulnerability of *A. geoffroyi*. Our interpretation agrees with those of other authors who find that lower rates of population growth, limit the potential of *A. geoffroyi* populations to recover rapidly after experiencing reductions in population size (Mc Farland 1989, Sorensen and Fedigan 2000).

Finally, we found no association between risk of extinction and genetic diversity. Contrary to the prediction that low levels of genetic diversity increase extinction risks, we found that less variable species, such as *C. capucinus* and *A. palliata*, had lower risks of extinction than more variable species, such as *S. oerstedii* and *A. geoffroyi*. Despite their low levels of genetic variation *C. capucinus* and *A. palliata* are very resilient and recover quickly from environmental disturbance (Pope 1995, Crockett 1998, Horwich 1998, Sorensen and Fedigan 2000). Lack of genetic variation has not limited the capacity of *A. palliata* and *C.*

capucinus to occupy a variety of habitats, including altered environments and small forest patches. Also, it has not limited their ability to recover from habitat destruction (Pope 1995, Fedigan *et al.* 1998, Sorensen and Fedigan 2000). *A. palliata* from the population at La Pacífica, Costa Rica, have experienced rapid recovery from habitat deforestation and their population size has remained stable (Clarke *et al.* 2002a, 2002b). *A. palliata* from the Santa Rosa National Park show a sevenfold increase in size in 28 years since the establishment of protection and regeneration of the dry forest (Fedigan *et al.* 1998, Fedigan and Jack 2001). *C. capucinus* doubled their population size in this same period (Sorensen and Fedigan 2000).

To conclude, geographic distribution and life history traits seem to be more important determinants of extinction risks than genetic variation, at least for nonhuman primates from Costa Rica. Conservation efforts should emphasize the relevance of these variables. Our data support the need to expand and enforce protection measures for squirrel monkeys. Squirrel monkeys are the most endangered primate species in Central America (Rylands *et al.* 1995, Rylands 1997). Their narrow geographic distribution and habitat range, coupled to extensive habitat destruction and fragmentation in the region, are responsible for the low numbers of populations and individuals remaining (Boinski and Sirot 1997). Spider monkeys are also very vulnerable to disturbances due to their low rate of population growth. The successful recovery of primate populations in the Santa Rosa National Park (Fedigan *et al.* 1998, Sorensen and Fedigan 2000, Fedigan and Jack 2001) should encourage further habitat protection and restoration efforts.

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RESUMEN

Se estudió la asociación entre la distribución geográfica, algunos rasgos ecológicos, las historias de vida, la diversidad genética y el riesgo de extinción, en primates no humanos de Costa Rica. Se incluyen todas las especies de primates no humanos del país: los monos araña (*Ateles geoffroyi*), congo (*Alouatta palliata*), cara blanca (*Cebus capucinus*), y tití (*Saimiri oerstedii*). La distribución geográfica se caracterizó utilizando principalmente bases de datos existentes. Se obtuvo información acerca de sus características ecológicas y de historias de vida mediante una revisión bibliográfica. Se estudió su diversidad genética utilizando electroforesis de isoenzimas. El riesgo de extinción se evaluó usando información bibliográfica. Se encontró que las cuatro especies presentaban variación en todos estos rasgos. Con estos datos, se realizó una correlación de Pearson entre el riesgo de extinción y las variables indicadoras de la distribución geográfica, los rasgos ecológicos, las historias de vida y la diversidad genética, para aquellas especies con una amplia distribución geográfica. Se encontró una asociación entre el riesgo de extinción y la natalidad y la tasa de crecimiento poblacional; las especies

con menor natalidad y menor tasa de crecimiento poblacional tenían mayor riesgo de extinción. Se encontró una asociación positiva entre la diversidad genética y el riesgo de extinción; las especies con mayor diversidad genética tenían mayor riesgo de extinción. Se discute la importancia de estos rasgos para la conservación de estas especies.

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APPENDIX 1

Distribution of nonhuman primates from Costa Rica by protected areas and conservation areas
(Presence=1, Absence=0)

Conservation area	Protected area	Size (ha)	A. geoffroyi	A. palliata	C. capucinus	S. oerstedii
Arenal	Volcán Tenorio	12 872	1	1	1	0
Arenal	Volcán Arenal	12 124	1	1	1	0
Arenal	Monteverde	32 810	0	1	1	0
Arenal	Manuel A. Brenes	7 799	1	1	1	0
Caribe	Barbilla	11 944	1	1	1	0
Caribe	Cahuita	1 106	0	1	1	0
Caribe	Gandoca	3 833	1	1	1	0
Caribe	Hitoy Cerere	9 950	0	1	1	0
Caribe	La Amistad	174 881	1	1	1	0
Crd.Vlc.Central	La Selva	1 600	1	1	1	0
Crd.Vlc.Central	Braulio Carrillo	47 583	1	1	1	0
Guanacaste	Guanacaste	34 651	1	1	1	0
Guanacaste	Rincón de la Vieja	14 161	1	1	1	0
Guanacaste	Santa Rosa	38 674	1	1	1	0
Huetar Norte	Juan Castro Blnco	14 453	1	1	1	0
Huetar Norte	Caño Negro	9 969	1	1	1	0
LA Pacífico	La Amistad (LA)	50 849	1	1	1	0
LA Pacífico	Tapantí	58 323	1	1	1	0
Osa	Corcovado	42 469	1	1	1	1
Osa	Piedras Blancas	14 025	1	1	1	1
Osa	Golfito	1 309	1	1	1	1
Pacífico Central	Carara	5 242	0	1	1	1
Pacífico Central	Manuel Antonio	1 625	0	1	1	0
Tempisque	Baulas	379	0	1	0	0
Tempisque	Ostional	162	0	1	1	0
Tempisque	Lomas Barbudal	2 646	0	1	1	0
Tempisque	Palo Verde	18 418	1	1	1	0
Tempisque	Barra Honda	2 295	0	1	1	0
Tempisque	Cabo Blanco	1 270	1	1	1	0
Tempisque	Curú	84	0	1	1	0
Tortuguero	Barra Colorado	81 211	1	1	1	0
Tortuguero	Tortuguero	31 187	1	1	1	0

APPENDIX 2

Ecology and life history traits of nonhuman primates from Costa Rica

Species	*Ateles geoffroyi*	*Alouatta palliata*	*Cebus capucinus*	*Saimiri oerstedii*
Male size (gr)	8375 (*N*=2) [a]	6528 (*N*=14) [a]	3333 (*N*=3) [a]	890 (*N*=8) [b], 750 (*N*=3) [c]
Female size (gr)	6624 (*N*=12) [a]	4020 (*N*=18) [a]	2283 (*N*=3) [a]	740 (*N*=4) [b] <600 (*N*=3)[c]
Age at first birth (yr)	5.62 [d]	3.58 [d]	4.00 [d]	—
Interbirth interval (yr)	2.66 [d]	1.88 [d]	1.60 [d]	—
Birth rate	0.38 [d]	0.59 [d]	0.63 [d]	—
Population growth rate	0.113 [d]	0.178 [d]	0.172 [d]	—
Home range (ha)	25-98 [e,f]	27-91 [f,g]	50-100 [f,h]	35-110 [i,j]
% time foraging fruits	71-78 [k,l]	13-29 [k,m,n]	53-81 [k,o]	0-12 [b,p,q]
% time foraging leaves	13-11 [k,l]	49-64 [k,m,n]	1-15 [k,o]	0-28 [b,p,q]
% time foraging flowers	14-10 [k,l]	18-23 [k,m,n]	0-2[k,o]	0 [b,p,q]
% time foraging insects	1-2 [k,l]	0 [k,m,n]	17-45 [k,o]	78-82 [b,p,q]

Note: ([a]) Glander *et al.* 1991, ([b]) Baldwin & Baldwin 1972, ([c]) Boinski & Cropp 1999, ([d]) Ross & Jones 1999 (data on *Saimiri* provided for *S. sciureus*), ([e]) Fedigan *et al.* 1988, ([f]) Sorensen & Fedigan 2000, ([g]) Stoner 1994, ([h]) Freese 1983, ([i]) Boinski 1987, ([j]) Wong 1990a, b, ([k]) Chapman 1987, ([l]) Chapman & Chapman 1991, ([m]) Glander 1981, ([n]) Stoner 1996, ([o]) Chapman & Fedigan 1990, ([p]) Robinson & Janson 1987, ([q]) Schultz 1940, ([r]) Carrillo *et al.* 1999 ([s]) Glander 1983, ([t]) Boinski & Sirot 1997.