



Modelling spider monkeys *Ateles* spp. Gray, 1825: ecological responses and conservation implications to increased elevation

Sam Shanee

Neotropical Primate Conservation, 65 Whaddon Road, Cheltenham, Gloucestershire GL52 5NE, UK
Email: samshanee@gmail.com

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Author Details: SAM SHANEE has worked in primate conservation and reintroduction for the past eight years in South America and Asia. He studied primate conservation at Oxford Brookes University and in 2007 co-founded the UK based NGO Neotropical Primate Conservation. He currently works in Peru researching the Yellow-tailed Woolly Monkey.

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Abstract: Spider monkeys (*Ateles* spp.) are among the most widely-distributed and endangered neotropical primate genera. Throughout their distribution expanding human populations and associated demands for land are causing widespread deforestation, especially in low-lying areas where many populations of spider monkeys are being pushed to high elevation sites with sub-optimal conditions. In this paper ecological data from a wide range of sources has been collected and examined to try to better understand and predict spider monkey ecological responses to high elevation areas with lower environmental carrying capacities. Results show a significant reduction in group and foraging party sizes with increased elevation. A general reduction in density is also noted with increasing elevation, while home range sizes remain static. It is recommended that these observations be taken into account when planning conservation actions and new protected areas, and further implications are also discussed.

Keywords: Altitude, *Ateles*, carrying capacity, conservation, ecology, elevation, neotropics.

INTRODUCTION

The genus *Ateles* Gray, 1825, spider monkeys, is one of the most widely distributed of neotropical primate groups (Collins 2008). They are found from southern Mexico south to Bolivia and east through Venezuela and the Guianas to the Atlantic coast of Brazil (Groves 2001). This genus is also one of the most threatened, with two species: the Black-headed Spider Monkey (*A. fusciceps*) and the Brown Spider Monkey (*A. hybridus*) having featured on the IUCN's list of the top 25 most endangered primate species (Primate Specialist Group 2009). The IUCN Primate Specialist Group currently recognizes seven distinct species of *Ateles*; the monotypic *A. belzebuth*; *A. chamek*; *A. fusciceps*; *A. geoffroyi*; *A. marginatus*; *A. paniscus*; and *A. hybridus* (IUCN 2009). Both *A. fusciceps* and *A. hybridus* are listed as Critically Endangered (IUCN 2009). Although more recent studies dispute this taxonomy (Collins & Dubach 2000; Collins 2008), for the purposes of this paper I prefer to follow the taxonomy currently accepted by the IUCN.

The main threats to this genus are from anthropogenic hunting pressure and habitat loss (Ramos-Fernandez & Ayala-Orozoco 2003; DiFiore 2004; Wallace 2008). Spider monkeys are the largest-bodied of the neotropical primate groups (Di Fiore & Campbell 2007) and thus they are commonly hunted for food (Peres 2000; Thoisey et al. 2005; Ramos-Fernandez & Ayala-Orozoco 2003; Wallace 2008), which has led to their extirpation in large areas of their former distribution. Low reproductive rates, long interbirth intervals, high infant mortality, low population densities and a low intrinsic rate of natural increase (DiFiore & Campbell 2007) means that they are particularly vulnerable to anthropogenic hunting pressure. Spider monkeys are highly frugivorous primary forest specialists (DiFiore et al. 2008) that do not adapt well to degraded and secondary forest areas (Defler 2004), making them the most susceptible of new world primates to anthropogenic pressures (DiFiore & Campbell 2007). The preferred habitat of spider monkeys is <800m (Collins 2008), although many studies document their presence at higher elevations.

The fission-fusion social structure of spider monkey groups, similar to that of chimpanzees (Symington 1988, 1990), enables large groups to successfully forage for scattered resources by separating into smaller foraging parties of dynamic structure (Symington 1988; Wallace 2007). Even so, such large groups also require large home ranges; Pozo (2001) reports a home range size of 469ha for a single group of *A. belzebuth* in Ecuador. This may be a factor in their reduced ability to survive in small forest patches and areas of secondary and degraded forest.

Five of the seven species are found at least partially within 'Biodiversity Hotspots' (Myers et al. 2000) with *A. fusciceps* and *A. geoffroyi* endemic to the Choco/Darien/



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western Ecuador and Mesoamerica hotspots, respectively. Among other things these hotspots are characterized by the high level of threats they face. Tirrira (2004) estimates that 80% of *A. fusciceps*' habitat has already been lost. Similarly, only 20% of the Mesoamerican hotspot remains (Meyers et al. 2000). As demand for land increases along with increasing human populations (Estrada 2006), large scale clearance of forest cover has occurred in all neotropical ecosystems. Land clearance usually occurs first in more easily accessible lowland areas (Estrada & Coates-Estrada 1996) that are the preferred habitat of spider monkeys (Collins 2008). In some areas, notably in western Ecuador (Sam Shanee pers. obs.) and Veracruz in southern Mexico (Estrada & Coates-Estrada 1996), this large scale clearance of forest in low lying areas effectively forces the migration of species to areas of higher elevations with suboptimal conditions.

Many studies have documented changes in forest community structure and primary production levels with increasing elevation (Lawes 1992; Smith & Killeen 1998; Costa 2006; Bendix et al. 2008; Shanee & Peck 2008). These changes occur due to a number of interrelated factors including: temperature reduction, changes in soil pH and precipitation levels and increased exposure to solar radiation (Marshall et al. 2005). Generally, as elevation increases primary production levels decrease, reducing resource availability to consumers (Durham 1975; Caldecott 1980; Marshall et al. 2005). The spider monkeys *A. belzebuth*, *A. Chamek*, *A. fusciceps*, *A. geoffroyi*, *A. hybridus* and *A. paniscus* all have distributions which include high elevation sites.

Several studies have recorded changes in primate ecology at high elevations. Gesie et al. (2004) found that the frequency of primate species in the Itatiaia Nation Park, Brazil peaked at 1000m. The only representative of the sub-family Atelinae, *Brachyteles arachnoides* or southern Muriqui, was not present above ~1300m. Marshall et al. (2005) reported lower abundance of red colobus monkeys (*Procolobus gordonorum*) at higher elevations in Uganda, and Caldecott (1980) reported similar trends for gibbons (*Hylobatidae*) in Malaysia. Most interestingly in relation to this study, Durham (1975) reported progressively smaller groups of *A. chamek* (although referred to as *A. paniscus* by Durham) at increasing elevations, and Peck (2008) reported lower abundance of *A. fusciceps* with increasing elevation in Ecuador. In all cases these localized changes in the species' population ecology were attributed to changes in habitat and climatic conditions at the higher elevation sites.

In this study I have made a meta analysis of changes in spider monkey population ecology in relation to increasing elevation. Data from a wide range of sources has been used to obtain a fuller picture of changes in group sizes, foraging party size, home-range sizes and population densities. I have also tried to examine how these variables are related to each other and identify the major causes. It is felt that greater understanding of the effects of elevation will aid future conservation planning.

MATERIALS AND METHODS

Data used in this study include all areas of spider monkeys distribution throughout most of tropical South and Central America. Habitat types include: moist tropical, deciduous lowland rainforest and premontane and montane cloud forest

(DiFiore & Campbell 2007) as well as a number of climatic zones.

Mountain ranges within the distribution of the various species include: the eastern slopes of the Andes in Bolivia, Colombia Ecuador and Peru where *A. Belzebuth* and *A. Chamek* are present at 1950m (Sam Shanee pers. obs.) and 1432m (McFarland-Symington 1986) respectively; the western slopes of the Andes where *A. fusciceps* is present at >1800m (Gavilanez-Endara 2006); the Sierra Madre de Oaxaca in Mexico where *A. geoffroyi* is present up to 1398m (Briones-Salas et al. 2006); the Venezuelan coastal range where *A. hybridus* is cited to be present at 1100m (Cordero-Rodriguez & Biord 2001) and the Pakaraima and Roraima mountains of the Guianan shield where *A. paniscus* is cited to be present at > 600m (van Roosmalen 1985). Elevations given here only included sites where previous studies have taken place, all mountain ranges include areas of higher elevations where it is likely that spider monkeys are also present. No previous studies have documented the presence of *A. marginatus* at high elevations, thus this species is not included in this analysis. Only data for species where studies have included the relevant results at high elevation sites were used for the respective analyses which lead to the exclusion of *A. belzebuth* from the analyses, although this species has been observed at 1750m (Sam Shanee pers. obs.).

Elevation data presented a problem, as many of the studies did not include this in their published reports. Where elevation data were missing I searched the literature for studies made at the same sites, preferably by the same authors, to ensure accuracy. Failing this, elevation data on specific study sites and locations were requested from third parties currently active at these locations.

In addition to elevation, data collected included actual or mean spider monkey group size, foraging party size, individual and group density, home range size and daily path length.

Certain assumptions were made regarding the data used in the analysis (Dunbar 2002). Assumptions made for this analysis were necessary as data specific to differences in population ecology of spider monkeys (particularly concerning elevation) are scarce and distributed widely between species, geographically and on a temporal scale. For these reason the following assumptions were necessary:

- Spider monkey responses to high elevations are similar between species, sub-species and populations.
- Data gathered from the literature represents the true, natural, state of spider monkey populations at a given site.
- Anthropogenic factors have remained constant for the time period between studies.

RESULTS

Data were collected from a total of 38 published studies and one unpublished, covering all species of *Ateles*. This included studies at 33 sites in 11 countries throughout the genera's distribution (Table 1). Elevations ranged from sea level (+/- 0 m) to 1800m, a mean group size of 16.2 (min 3.3, max 45), mean foraging party size of 4.7 (min 2.5, max 6.85), mean density of 0.21 individuals per ha (min 0.01, max 0.66), mean home range of 227ha (min 108, max 316) and mean daily path length of 2236m (min 1977, max 2400) were found.

Data were entered into SPSS V16.0 for Windows for statistical analysis. All data sets showed normal (Shapiro-Wilk,

Table 1. Spider monkey group structure and elevations, studies used in this analysis

Species	Groves (2000)	Country	Elevation (m.a.s.l.)	Group Size	Foraging Party	Density (Ind/ha)	Home Range (ha)	Daily Path (m)	Source	Year
<i>A. belzebuth</i>	<i>A. chamek</i>	Peru	350	35.8	4.67	0.28	205	-	Symington	1988
<i>A. chamek</i>	<i>A. chamek</i>	Peru	91	7.3	-	0.51	-	-	Aquino & Bodmer	2006
<i>A. chamek</i>	<i>A. chamek</i>	Peru	134	13.0	-	0.48	-	-	Aquino et al.	2005
<i>A. chamek</i>	<i>A. chamek</i>	Brazil	200	3.3	-	-	-	-	Iwanaga & Ferrari	2002
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	50	18.5	-	-	316	-	Vick & Taub	1995
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Panama	84	27.5	-	-	-	-	Campbell	2006
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Guatemala	193	-	-	0.26	-	-	Cant	1978
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Costa Rica	59	45	6.0	0.09	-	-	Chapman	1990
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Guatemala	193	-	-	0.45	-	-	Coelho et al.	1976
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Panama	130	15	-	-	108	-	Dare	1974
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	860	5	-	0.022	-	-	Estrada & Coates-Estrada	1996
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Guatemala	175	17.1	6.2	-	-	-	Estrada et al.	2004
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	175	-	5.6	0.17	-	-	Estrada et al.	2004
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	250	-	5.67	0.17	-	-	Estrada et al.	2002
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	193	-	-	0.304	-	-	Flores & Gerez	1988
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	23	-	-	0.027	-	-	Gonzalez Kirchner	1999
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	23	-	-	0.014	-	-	Gonzalez Kirchner	1999
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Honduras	640	-	6.85	-	-	-	Hines	2004
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	50	28.5	-	0.063	-	-	Ramos-Fernandez & Ayala-Orozoco	2003
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	800	-	-	0.66	-	-	Silva Lopez & Jimenez Huerta	2000
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Costa Rica	150	-	-	0.565	-	-	Sorenson & Fedigan	2000
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Costa Rica	50	13	-	-	-	-	Tinney	2005
<i>A. hybridus</i>	<i>A. hybridus</i>	Venezuela	140	14	-	-	-	-	Congdon	1996
<i>A. hybridus</i>	<i>A. hybridus</i>	Venezuela	1100	20	-	-	-	-	Cordero-Rodriguez & Biord	2001
<i>A. hybridus</i>	<i>A. hybridus</i>	Venezuela	600	-	3.5	0.056	-	-	Eisenberg et al.	1979
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	275	18.5	-	-	-	-	Durham	1975
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	576	11	-	-	-	-	Durham	1975
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	889	7	-	-	-	-	Durham	1975
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	1424	4.5	-	-	-	-	Durham	1975
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	350	-	-	0.224	-	-	Freese et al.	1982
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	1432	-	-	-	275	1977	McFarland-Symington	1986
<i>A. paniscus</i>	<i>A. paniscus</i>	Surinam	600	12	-	-	-	-	Norconk & Kinzey	1994
<i>A. paniscus</i>	<i>A. paniscus</i>	Brazil	20	-	4.5	0.029	-	-	Parry	2004
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	202	-	-	0.25	-	-	Puertas & Bodmer	1993
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	95	-	-	0.04	-	-	Salovaara et al	2003
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	95	-	-	0.015	-	-	Salovaara et al	2003
<i>A. geoffroyi</i>	<i>A. geoffroyi</i>	Mexico	0	-	-	0.01	-	-	Silva-Lopez & Jimenez-Huerta	2000
<i>A. paniscus</i>	<i>A. paniscus</i>	Surinam	627	18	-	0.082	225	-	vanRoosmalen	1985
<i>A. paniscus</i>	<i>A. chamek</i>	Bolivia	300	-	-	-	234	2332	Wallace	2006
<i>A. paniscus</i>	<i>A. chamek</i>	Bolivia	300	6.2	5.3	0.321	-	-	Wallace et al.	1998
<i>A. paniscus</i>	<i>A. chamek</i>	Peru	1432	-	3.15	0.31	-	2400	White	1986
<i>A. fusciceps</i>	<i>A. fusciceps</i>	Ecuador	1799	-	2.5	0.012	-	-	Gavilanez-Endara	2006
<i>A. fusciceps</i>	<i>A. fusciceps</i>	Ecuador	1350	-	3	-	-	-	Shanee	Un-published

> 0.05) distributions except spider monkey densities (Shapiro-Wilk, <0.05), which were log (Base-10 Logarithm) transformed to give a normal distribution.

Preliminary analyses were made on *A. geoffroyi*, as this species presented the largest individual data set (18 studies). Linear regression scatter plots suggested relationships between changes in elevation and density, group size and foraging party size. Non-parametric correlation analyses, spearman's rho, showed a significant relationship between changes in elevation and density ($r = 0.724$, $df = 11$, $p < 0.01$). No significant relationship was found between elevation and group size ($r = 0.439$, $df = 7$, $p > 0.05$) or foraging party size ($r = 0.359$, $df = 4$, $p > 0.05$).

Linear regression scatter plot graphs with 95% mean prediction intervals were produced using combined data for the five species to be included in the final analyses; *A. chamek*, *A. fusciceps*, *A. geoffroyi*, *A. hybridus* and *A. paniscus*. Spider monkey densities, group sizes and foraging party sizes can all be seen to decrease with increasing elevation (Figs. 1, 2 & 3), whereas home range size was seen to be fairly constant with increasing elevation. Non-parametric statistical analyses, Spearman's rho,

showed significant correlations between changes in spider monkey group size ($r = 0.548$, $df = 16$, $p < 0.01$) and foraging party size ($r = 0.594$, $df = 7$, $p < 0.05$) with increasing elevation. Elevation did not have a significant effect on spider monkey home range size ($r = 0.479$, $df = 4$, $p > 0.05$) or density ($r = 0.068$, $df = 23$, $p > 0.05$). Tests showed no significant correlation between differences in group size and home range size ($r = 0.30$, $df = 2$, $p > 0.05$).

Regression curve estimation showed a decrease in average group size of approximately one individual for 100m increase in elevation, a decrease in density of 0.002 individuals per hectare was also shown for 100m increase in elevation. By adapting the results of the regression analysis we get the predictive equation for the density of spider monkey species found at high elevations:

$$D_p = D_k + (0.002 (ED_k - ED_p))$$

Where D_p is the predicted density at elevation x , D_k is the known density at elevation y , ED_k is elevation y and ED_p is elevation x , with elevation measured in meters. A similar

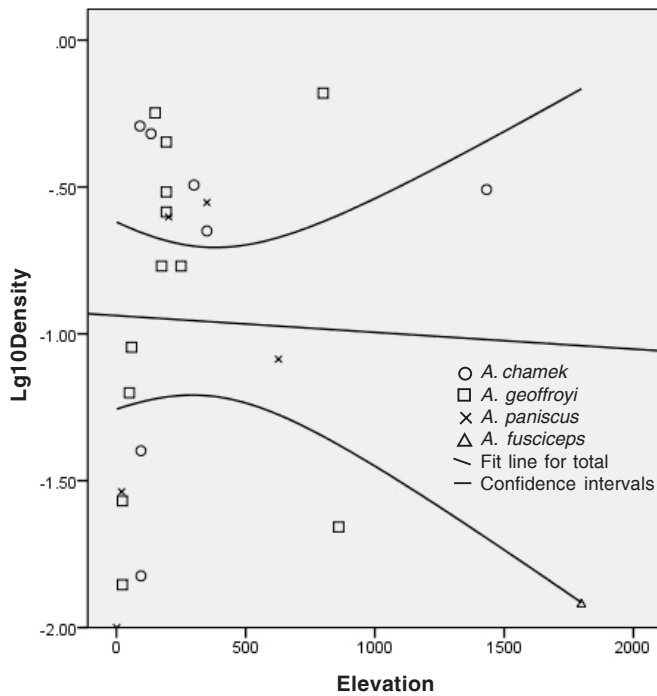


Figure 1. Regression of log spider monkey density against elevation

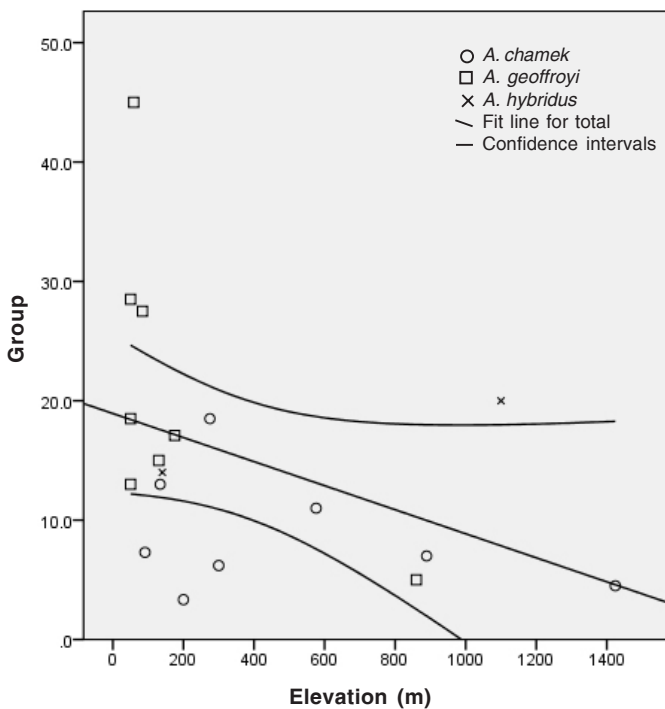


Figure 2. Regression of spider monkey group size against elevation.

predictive equation is produced for group sizes of spider monkey species found at high elevation sites:

$$G_p = G_k + (0.01 (EG_k - EG_p))$$

Where G_p is the predicted group size at elevation x , G_k is the known group size at elevation y , EG_k is elevation y and EG_p is elevation x , with elevation measured in meters.

DISCUSSION & CONCLUSIONS

With decreased food quantity and quality at higher elevations (Durham 1975; Caldecott 1980; Marshall et al. 2005), home range size would be expected to increase if group sizes and densities remained static, due to the extra area needed for successful foraging. No correlation was found between elevation and home range area suggesting the most efficient way of maximizing food intake per animal per unit area is through decreasing group size and density (McFarland-Symington 1986; Wrangham et al. 1993); which is supported by the significant correlation found between decreases in group size and increased elevation. This logically extends to foraging party size, as it is in these units that spider monkeys need to find sufficient food per day/per unit area, which is backed up by the significant correlation found between decreases in foraging party size with increases in elevation. This suggests that there is an optimum range size (Cowlshaw & Dunbar 2000) found with a balance between energy expenditure and intake (Wrangham et al. 1993) as well as competition for resources and predator avoidance. This should be especially important with the increased energetic costs of high elevation living (Marshall et al. 2005). Increases in range sizes with increasing group sizes would most likely be seen where populations are not primarily limited by environmental factors (Cowlshaw & Dunbar 2000; Gillespie & Chapman 2001).

When planning protected area systems altitudinal effects on environmental carrying capacity need to be considered. Minimum viable population sizes have been estimated to be between 500-1000 (Franklin & Frankham 1998; Lynch & Lande 1998). Results here suggest that reserves designed to protect viable populations of *Ateles* would need to encompass larger areas depending on the elevation above sea level of the area. Recent studies (Peck 2008) have documented decreases in the occurrence of *A. fusciceps* with increased elevation in the Choco forests of Ecuador. In the same area the occurrence and fruit production of *Ficus* spp. trees, one of the most important food resource for spider monkeys (DiFiore et al. 2008), have been shown to significantly decrease with elevation (Shanee & Peck 2008), thus increasing the importance of preserving the preferred, lowland, habitat of spider monkeys (Collins 2008).

Results suggest that spider monkeys tend to live in smaller groups and at lower densities in higher elevation sites, whilst maintaining similar size home ranges. This could lead to greater risk of extinction in populations forced to live in isolated forest fragments at higher elevations, as well as in populations naturally found at high elevations. Although the decrease in density predicted here is relatively small, 0.02 individuals/100m increase in elevation, the decrease predicted in group size is much more pronounced, 1 individual/100m increase in elevation. This could cause pronounced differences in the viability of populations. For example, with an average spider

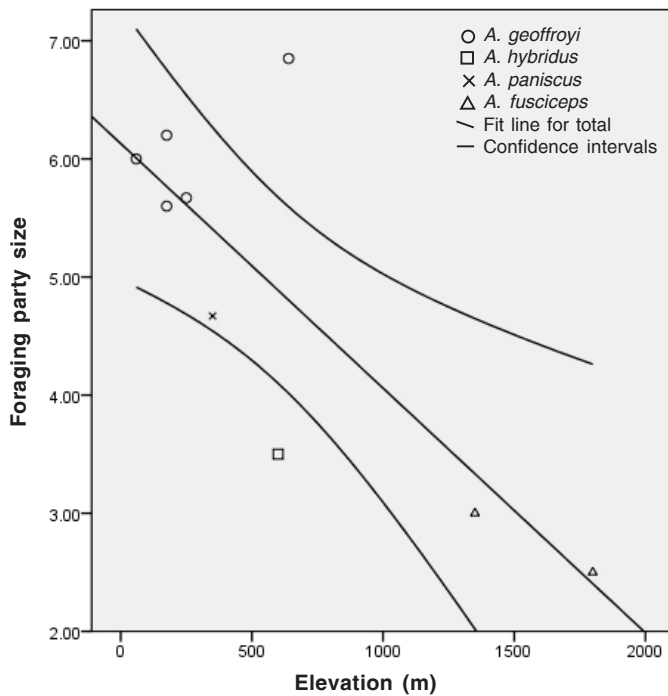


Figure 3. Regression of spider monkey foraging party size against elevation.

monkey group size below 100m of 20, such a decrease would lead to a 50% drop in group size at 1000m. This drop is caused by the differences in habitat and primary production levels creating suboptimal conditions in relation to spider monkey evolutionary and behavioural adaptations (Estrada & Coates-Estrada 1996). This is further complicated by interspecific competition for resources with species which are better adapted to the conditions prevalent in high elevation sites.

Relatively few investigations have focused on primate ecological responses to increased elevation. However, several studies do exist (for example: Henzi et al. 1990; Kumara & Singh 2004). Generally findings have shown a decrease in individual and group densities at higher elevation sites in comparison to lower elevations (Caldecott 1980; Marshall et al. 2005) similar to those predicted in this study. Many more studies exist on changes to animal ecology in relation to elevational gradients, including frugivorous neotropical bats (Giannini 1999) and Birds (Loiselle & Blake 1991), as well as on forest structure in general (Lieberman et al. 1996) which show similar changes due to increases and decreases in elevation. The analyses presented here were severely limited by a lack of data from high elevation sites. However, findings, combined with results from other studies, show the need for the effects of increased elevation on carrying capacity and group ecology to be taken into account when planning conservation measures such as new protected areas. I recommend more field studies be made to investigate the causes and effects of these changes in detail especially in light of current and predicted climate change which is causing marked shifts in species altitudinal distributions as well as vegetation types (Wilson et al. 2005; Lenoir et al. 2008) which pose interesting questions as to where species will find suitable habitat in the future.

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