

CHAPTER FIVE

Population Structure of Black Howlers (*Alouatta pigra*) in Southern Belize and Responses to Hurricane Iris

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INTRODUCTION

A fundamental issue in ecology is determining factors regulating the density of animal populations. A variety of potential factors have been proposed including external factors, such as food resources, weather, predation, and disease, and internal conditions, such as territoriality and aggressive behaviors and life history traits (Andrewartha and Birch, 1954; Boutin, 1990; Krebs, 1978; Nicholson, 1933). The importance of understanding determinants of animal abundance

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New Perspectives in the Study of Mesoamerican Primates: Distribution, Ecology, Behavior, and Conservation, edited by Alejandro Estrada, Paul A. Garber, Mary S. M. Pavelka, and LeAndra Luecke. Springer, New York, 2005.

has increased with the need to develop informed management plans for endangered or threatened species. With respect to primates, these theoretical issues are critical because tropical forests occupied by primates are undergoing rapid anthropogenic transformation and modification (National Research Council, 1992). Cumulatively, countries with primate populations are losing approximately 125,000 km² of forest annually; based on global estimates of primate densities, this results in the loss of 32 million primates per year (Chapman and Peres, 2001). Other populations are being affected primarily by a subcategory of anthropogenic disturbance in the form of forest degradation due to logging, fire, and hunting. However, understanding and predicting factors that determine the abundance of particular primate species have proven extremely difficult, and examining the importance of internal conditions has proven to be the most difficult factor to quantify.

Natural disturbances to ecosystems, such as hurricanes, provide a unique opportunity to tease apart the importance of different factors that may determine the density of animal populations. However, few opportunities exist to document the effect of major natural habitat disturbance on primate populations, due to the unpredictable nature of natural disasters, such as hurricanes, and the absence of predisturbance data. From 1871 to 1964, an average of 4.6 hurricanes hit the Caribbean each year (Walker *et al.*, 1991), frequently causing severe damage to forests and animal populations. When Hurricane Iris struck the Belizean coastline on October 8, 2001, a Central American black howler (*Alouatta pigra*) study site was directly in its path. The population of monkeys inhabiting a 52-ha study area had been closely monitored for 3 years preceding the hurricane, and their exact population structure was known (Pavelka, 2003). Hurricane Iris was a small (winds extended for 40 km from the center), but powerful storm (category four on a scale of five) with sustained winds of 233 km/h and gusts of 282 km/h that caused massive structural damage to the forest and complete defoliation of the trees. For a description of the initial impact of the storm and its impact on the diet, activity, and food supply of the howler population, see Pavelka *et al.* (2003), Behie and Pavelka (2005), and Pavelka and Behie (2005). Continued monitoring over the subsequent 29 months has allowed us to document the affect of the hurricane on the population and to begin to consider which factors appear to be most important in determining population recovery and density. In this paper, we document changes to the population during this time period. Based on these documented changes and

observations over this period, we speculate on which of several factors, proposed in the literature to determine animal density, has played a primary role in this black howler population. We also outline what is currently being done to quantitatively determine the relative importance of the different factors.

A. pigra, previously one of the least well known of the currently recognized six howler species, is rapidly becoming well studied in Mexico and Belize (van Belle and Estrada, this volume; Brockett and Clark, 2000; Brockett *et al.*, 1999; 2000a,b; Clark and Brockett, 1999; Estrada *et al.*, 2002a,b,c, this volume; Gonzalez-Kirchner, 1998; Horwich *et al.*, 2001a,b; Ostro *et al.*, 1999, 2000, 2001; Silver *et al.*, 1998; Silver and Marsh, 2003; Treves *et al.*, 2001). Significantly smaller group sizes are reported for *A. pigra* (2–10 individuals per group) when compared to those of its geographic neighbor and close relative, *A. palliata* (2–45 individuals per group, mean = 12.3: Crocket and Eisenberg, 1987; see also Chapman and Balcomb, 1998). Small group size was one of the main factors leading to *A. pigra* being assigned species status in the early 1970s (Smith, 1970; Horwich, 1983; Horwich and Johnson, 1986).

The diet of black howlers is described as being as frugivorous as possible and as folivorous as necessary (Silver *et al.*, 1998; Pavelka and Knopff, 2004); however, they are believed to be capable of surviving for long periods on leaves (Silver *et al.*, 2000). Dietary flexibility should make black howlers good candidates for surviving disturbance (Johns and Skopura, 1987). While rare, studies of hurricane-affected invertebrates (Schowalter, 1994; Willig and Camillo, 1991), birds (Askins and Ewert, 1991; Will, 1991), bats (Gannon and Willig, 1994), frogs (Marsh and Pearman, 1997), and primates (Gould *et al.*, 1999; Menon and Poirer, 1996; Ratsimbazafy *et al.*, 2002) suggest that species with more flexible diets will be better able to survive in an environment with limited and/or dramatically altered food production. Black and white ruffed lemurs (*Varecia variegata*) living in a forest damaged by Cyclone Gretelle adjusted to their habitat by eating exotic plant species that were not consumed before the storm (Ratsimbazafy *et al.*, 2002). Lion-tailed macaques (*Macaca fascicularis*) were able to survive in a drought and fire disturbed environment by consuming less of the normally preferred fruit and more of the available insects and leaves (Berenstain, 1986). In addition to threatening individual survival, initially limited production of food in disturbed habitats can prevent females from producing viable offspring because they are unable to obtain adequate nutrients (Gould *et al.*, 1999; Ratsimbazafy *et al.*, 2002).

METHODS

The 52-ha study site is located in southern Belize on the north side of Monkey River, near the coast ($16^{\circ}21'N$, $88^{\circ}29'W$). This closely monitored area is part of a larger (approx 100 km^2) forested area along the Monkey River watershed, between the southern highway of Belize and the river mouth. Due to savannah and anthropogenic landscapes to the north and south, and the highway and agricultural development to the west, the monkey population in the watershed forest east of the highway is believed to be discontinuous with monkey populations that may occur further west along the Bladen and Swasey rivers, and into the Maya Mountains (Figure 1). The area receives on average 250 cm of rain annually, which primarily falls from June through December. The most common trees in this seasonally flooded semi-evergreen riparian forest are cohune palms

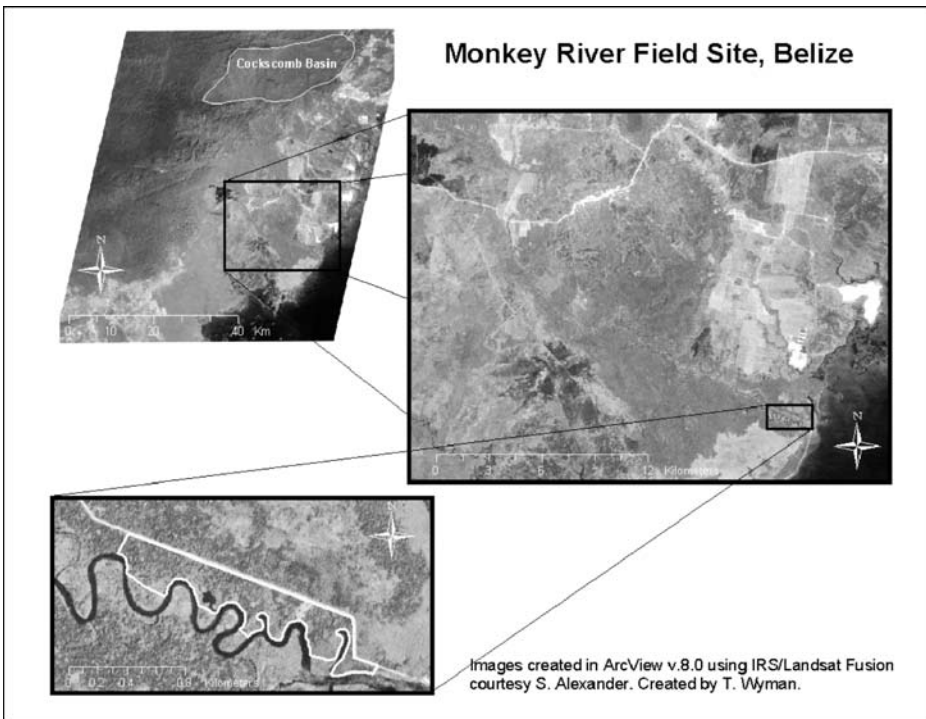


Figure 1. The location of the Monkey River Field Site, Belize. In the most small-scale map, the location of the 52-ha study site where eight groups of black howlers (*A. pigra*) existed prior to Hurricane Iris is indicated by a white line. The body of water in the SE corner is the Caribbean Sea.

(*Attalea* and *Orbigyna*), provision trees (*Pachira*), figs, (*Ficus* spp.), and swamp kaways (*Pterocarpus*) (Pavelka *et al.*, 2003).

Pre-hurricane data on the demography of groups in the 52-ha area were collected between May and August 1999, January and May 2000, January and May 2001, and October 6th and 7th, 2001. On October 6th and 7th we were able to confirm that group compositions were the same as they had been in May. By May 2001, group size, composition, and home range were known for eight groups and detailed behavioral data had been collected on five of them. Groups were recognized by consistent group membership and home range site fidelity.

The hurricane made landfall at 7 pm on October 8, 2001. Since October 16, 2001, the site has been under constant monitoring wherein all monkey groups are generally located every 2–3 days. Thus, it is likely that a change in group composition would have been noted within a day or two of its occurrence. Despite the fact that at least two researchers walk the extensive trail system (18.5 km) almost daily, we have not found a monkey carcass since immediately after the storm. However, with the deadfall and extensive new growth on the forest floor, movement off the trail system was very limited and it is possible that carcasses in the 52-ha area were undiscovered.

RESULTS

General Demographic Changes

Prior to Hurricane Iris, 53 individuals in eight groups lived within the 52-ha study area, and the population density was 102 individuals/km². Group size averaged 6.4 individuals, but varied from 2 to 10 individuals (Pavelka, 2003). The initial impact of the hurricane reduced the population by 42%. The surviving animals experienced a period of social disorganization involving transient individuals, high numbers of solitary monkeys, and small fragmentary social groups. Over the course of the first 12 weeks following the hurricane, groups began to reform and we found a decrease in the number of solitary individuals, and an increase in the average group size. By February of 2002, we were able to reestablish the trail system and confirm that 31 monkeys in 5 social groups now inhabited the 52-ha area (Pavelka *et al.*, 2003).

Continuous monitoring of this population for the next 29 months has shown a slow steady decline in total population size, density, number of groups, and

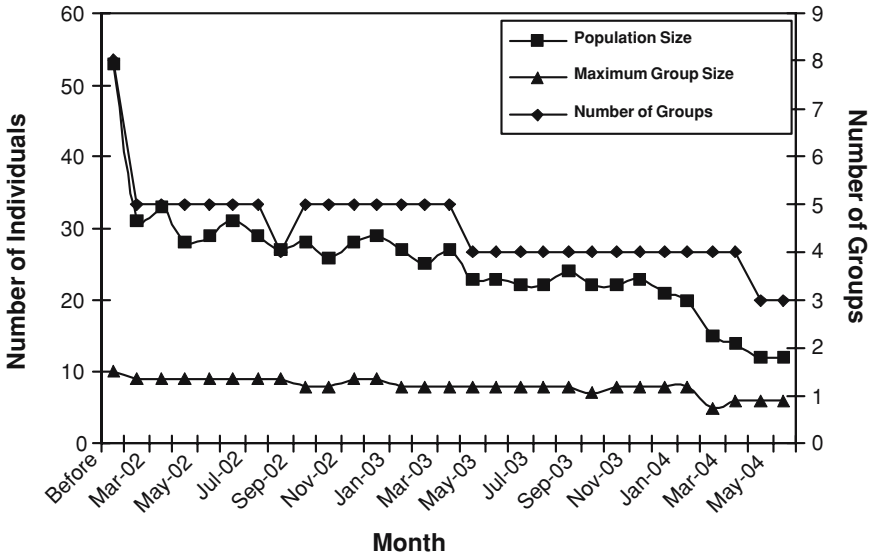


Figure 2. The total population size, number of groups, and maximum group size of the black howler (*A. pigra*) study population prior to Hurricane Iris and for the subsequent 29 months. Group size ($r = -0.657$; $p < 0.001$), number of groups ($r = -0.820$, $p < 0.001$), maximum group size ($r = -0.833$, $p < 0.001$), population size ($r = -0.848$, $p < 0.001$) are related to month and population size and maximum group size are also negatively related ($r = -0.843$, $p < 0.001$, $n = 29$ in all cases).

maximum group size (Figure 2). The population reduction is the result of both smaller and fewer groups. Prior to the hurricane, the maximum group size at Monkey River was 10 animals, with the majority of established groups containing 8 individuals (Pavelka, 2003). Since the storm, maximum group size has steadily declined from nine group members in February 2002 to six by May 2004 (Figure 2). Likewise, the number of groups has also declined from eight before the storm to five shortly after (February 2002) to only three groups as of May 2004. These three groups contain three, two, and six members; thus, the population total within the study area is 12. This constitutes a drop in population density from 102 individuals/km² before the storm to 23 individuals/km², 29 months after—a loss of 78% of the population in the study area, which is assumed to be reflective of changes in the larger watershed forest area.

All age–sex classes have declined more or less steadily, with the exception of the number of infants which, after an initial decline, has risen (Figure 3). Before the storm, there were slightly more males than females in the population (17 females and 21 males, including two solitary males). The number of males

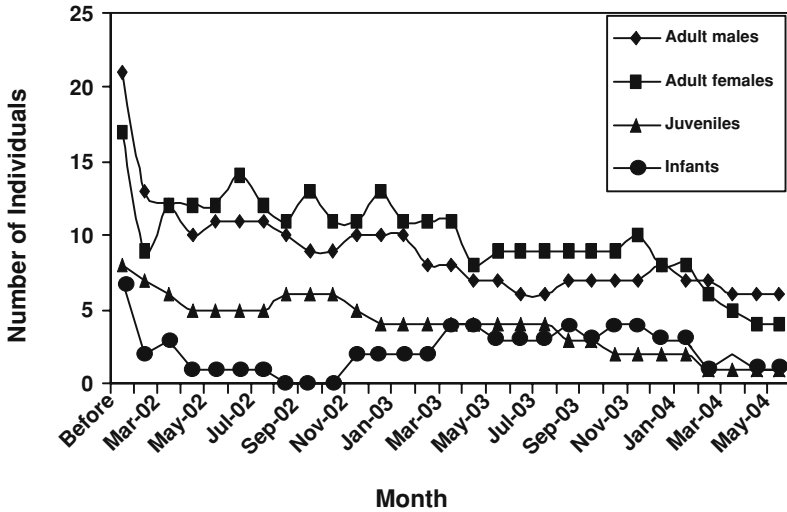


Figure 3. Number of black howlers (*A. pigra*) in each age–sex category for each month following Hurricane Iris.

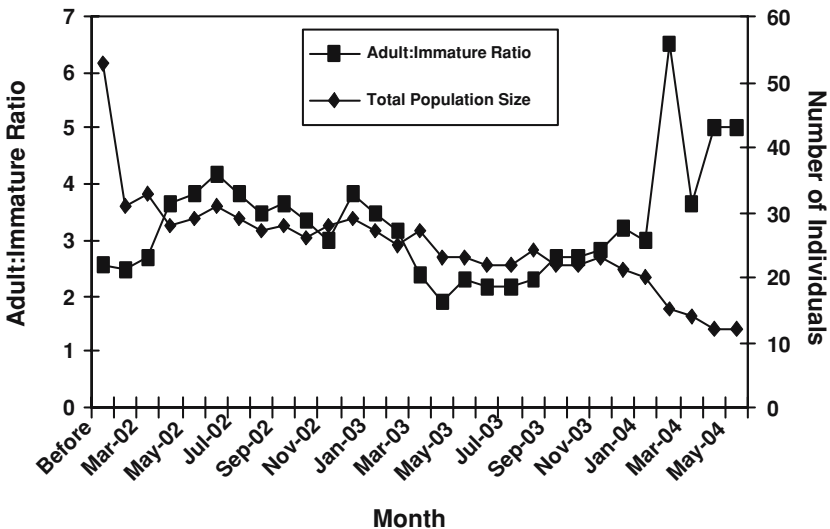
dropped below that of females after the storm and while both fell steadily, the number of males continued to be lower than the number of females until February 2004 (Figure 3).

Ten infants were born between November 2002 and March 2004 (Table 1). The first infants were born more than a full year after the hurricane. With a gestation length of 6 months (Brockett *et al.*, 2000a), these conceptions must have occurred in June or July 2002, 9 months after the storm. The fact that no infants were born for an entire year after Hurricane Iris suggests that either pregnant females did not carry their pregnancies to term or did not survive the storm.

The temporal distribution of the 10 births suggest 2 birth peaks, in the dry season months of March and April, and in the late wet season months of October and November; however, a larger sample is needed to confirm this suggestion. Six of the 10 infants born were male, 3 were female, and for 1 the sex was unknown, due to its disappearance shortly after birth (Table 1). Survivorship of infants after the storm has been very low (Table 1). As of June 2004, only 1 of the 10 infants was still alive. Four of the 10 infants disappeared with whole or partial groups, and thus may be alive elsewhere; however, we believe this is unlikely, as we have just completed a survey of the larger forested area of the watershed to determine if the data coming from the study area are

Table 1. Infants born into the black howler (*A. pigra*) study site population after Hurricane Iris made landfall in October 2001.

Date of birth	Sex	Fate
November 2002	F	Disappeared with entire N group, April 2003
November 2002	M	Disappeared alone, assumed dead, April 2003; B group
March 2003	?	Disappeared with entire N group, April 2003
March 2003	F	Disappeared with half of Q group, February 2004
April 2004	M	Killed by resident adult male, D group, May 2004
April 2003	F	Disappeared alone, assumed dead, January 2004; A group
August 2003	M	Disappeared after being injured by adult female in A group, November 2003
October 2003	M	Disappeared with half of Q group, February 2004
January 2004	M	Disappeared with mother in April, 2004, after D group breakup in March 2004
March 2004	M	Alive in June 2004

**Figure 4.** The ratio of adult black howlers (*A. pigra*) to immatures and total population size at Monkey River Field Site following Hurricane Iris.

representative of the larger area. This survey suggests that the low population densities and small social groups (no larger than five or six individuals) found at our study site characterize the whole area, which was equally affected by the hurricane (unpublished data).

Before the hurricane, the adult to immature ratio was 2.5:1 (38 adults and 15 immatures; Figure 4). Over the subsequent 29 months, the number of adults

to immatures has varied, climbing to a maximum of 6.5:1 in February 2004, when there were 13 adults and 2 infants, falling back to 5.0:1 by May of 2004 with the loss of 3 of those adults from the study area.

Description of Specific Losses

The immediate cause or sequence of events of the falling population appears to be dispersal events sometimes preceded by intragroup aggression as well as poor infant survival. The population is declining as whole groups or parts of groups suddenly disappear from the study area (Figures 5 and 6). The first major loss to the population after the initial period of decline came with the complete disappearance of N group (six members) in April 2003. The birth of two infants in A and D groups during the same month meant a net loss of four animals, reducing the population from 27 to 23. N group lived at the east end of the study area, closest to the coast, and was one of the groups that appeared to have remained intact following the hurricane. N group inhabited a patch of forest that is fairly discrete, bordered on the east by a road and anthropogenically cleared areas on the coast, the river to the south, a road to

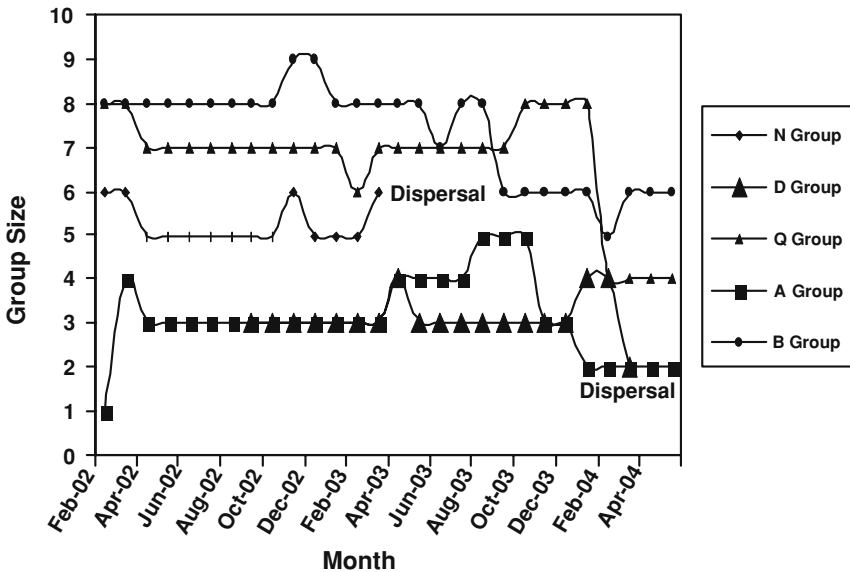


Figure 5. The size of individual groups of black howlers at Monkey River Field Site following Hurricane Iris. Groups N and D dispersed out of the study area and this is indicated by having the size data stop at the time of dispersal.

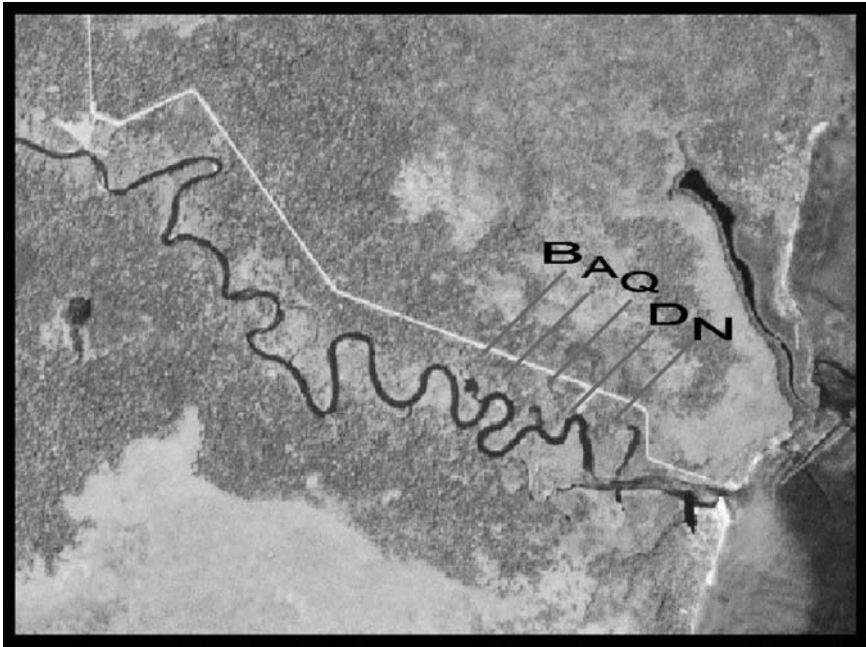


Figure 6. The study site showing the range location of the five study groups after the hurricane. Map prepared by Aaron Osicki.

the north, and the field containing the research camp on the west (Figure 6). Monkeys were infrequently observed crossing the field to the west and the road to the north, but these movements were temporary and rare, and for the most part the group's home range was limited by these boundaries. This patch of forest has had monkeys living in it for as long as local people can recall, and since April 2003 it is vacant.

D group first appeared in the study area in September 2002, almost a year after the hurricane, as an adult male with two adult females (Figure 5). There was an infant born to this group in April 2003; however, it was killed by the resident adult male less than 10 days later (Knopff *et al.*, 2004). In January 2004, they produced another infant; however, in March, 2 months later, the adult male and the adult female without an infant disappeared, leaving the lactating mother and infant on their own. This mother–infant pair stayed in their range for almost a month, and was last seen heading west out of the study area on April 15, 2004. They moved through the ranges of Q, A, and B groups without joining any of these groups.

The adult female and infant remnant of D group did not join the remnant of neighboring Q group, despite the fact that the two groups were familiar with one another, having shared adjacent and sometimes overlapping ranges for 15 months. Q group was one of the largest and most stable groups until late January 2004, when they dropped from eight to four members (Figure 5). One adult female along with a large juvenile female and both infants disappeared, leaving behind two adult males, a subadult male, and one adult female and resulting in an unusual group composition, with an adult male to female sex ratio of 3:1. The actual circumstances of the 50% reduction in Q group are not known, but again in the absence of any evidence of predation or carcasses being found, we assume the adult female, juvenile, and infants left the study area, moving west through the forest along the river. The ultimate fate of these four members of Q group is unknown, however, given that conditions throughout the continuous watershed forest available to them appear to be the same as those in the study area, and that the population throughout the watershed is falling, we suspect that few are surviving. While a merger of the remaining D group adult female and infant pair with the neighboring Q group, three males and one female would have produced a group with a more typical composition, the D group female moved through Q's range without joining them. Perhaps, infanticide risk deterred the female from approaching a group containing three adult males (see Knopff *et al.*, 2004). Also, increasing group size due to merging of small groups is rare in primates and not known to occur in *A. pigra*.

The next group to the west, A group, formed after the hurricane when two adult females and one infant entered the study area and joined a solitary male to form a group of four (Figure 5). The adult females and the infant had been observed on the north side of the road outside of the study area, and the solitary male on the south side of the road within the study area, for several weeks. They formed another small group that showed promise of growing into a larger established group. The infant disappeared within a couple of weeks, and the group remained at three individuals until April of 2003 when an infant was born, then in August a second infant was born. This group of five remained together until November, when one female attacked the other female and infant, injuring the infant, who subsequently disappeared and is presumed to have died. The female continued directing agonistic behavior toward the other female until she left the group and area. Her fate is unknown. The infant

of the “aggressive” female disappeared a month later. This group now consists of a male–female pair.

DISCUSSION

The density-dependent factors that are most commonly suggested to influence population size and distribution are predation, food resource availability and quality, disease and parasitism, and social factors (Andrewartha and Birch, 1954; Boutin, 1990; Krebs, 1978; Nicholson, 1933). Although jaguars and tayras are found in the area, we have no evidence to suggest that predators are playing a significant role in determining the density of black howlers at Monkey River. Of course, this absence of evidence is not evidence of the absence of predation. It is possible that damage to the structure of the canopy has interfered with predation avoidance strategies. Like other howlers, *A. pigra* is known to prefer large trees, which are much less common at the site since the storm. Hunting by local farmers, in an effort to protect their livestock from the perceived threat of jaguar predation, does occur, and likely keeps the density low. At this point, it is not possible for us to say what role predation is playing in the continued population decline, only that we have no direct evidence of predation on the monkeys before or after the storm.

The most apparent factor that could explain both the initial drop in population density and the subsequent decline over 29 months is the change in food availability that resulted from hurricane damage. Pavelka and Behie (2005) found that the hurricane caused the mortality of 35% of the major food trees with a circumference of more than 40 cm. If the abundance and quality of available food were lower than needed by the population, one might expect to see low infant survival and an increase in emigration. It is interesting to note that after a hiatus of 1 year, infants continued to be born in this population. Thus, while food stress is undoubtedly part of the explanation for the falling population, it did not translate directly into a failure of females to produce infants (see Glander, discussion of seasonal weight loss and survival/reproduction, this volume). On the other hand, the fact that larger groups at Monkey River did not have longer day ranges or spend less time inactive than smaller groups (after controlling for habitat quality differences; Knopff and Pavelka, submitted) suggests that food resources may not currently be limited for this population. In general, black howler group size may be below the threshold at which limited food would require a behavioral response (Chapman and Pavelka, 2005).

While it is clear that there is less food available, particularly fruits (Pavelka and Behie, 2005), it is also possible that the quality of the available foods have changed. It is well documented that in response to real or simulated herbivory, plants can increase concentrations of secondary compounds (Schultz, 1988) making their leaves less palatable. In contrast, Coley (1983) demonstrated that canopy gaps are typically colonized by climbers and fast-growing pioneer tree species whose leaves generally have more protein, less fiber, and a lower phenolic content than the leaves of persistent canopy tree species. Protein and fiber content of foods are known to be important to leaf-eating monkeys (Milton, 1979, 1998; Chapman and Chapman, 2002; Chapman *et al.*, 2002). Thus, the species of trees that are colonizing and regenerating in the areas opened by Hurricane Iris may be suitable food sources. These two observations present conflicting possibilities for how the quality of the foods available to the black howlers would have changed after the hurricane. We are currently investigating the potential role of food quality and availability by quantifying the secondary compounds in available foods (saponins, alkaloids, and cyanogenic glycosides) and examining the applicability of Milton's protein/fiber model to this black howler population. Milton (1979) proposed that the protein to fiber ratio was a good predictor of leaf choice in mantled howlers (see also McKey, 1978). By measuring overall mature leaf acceptability as the ratio of protein to fiber, several subsequent studies have found positive correlations between colobine biomass and this index of leaf quality at local (Chapman *et al.*, 2002; Ganzhorn, 2002) and regional scales (Oates *et al.*, 1990; Waterman *et al.*, 1988). After determining whether their population was at a level that could be predicted by this model before the hurricane, we can test the prediction that the population should stabilize at a level suggested by the current protein to fiber levels in their foods.

Finding single-factor explanations for complex biological phenomena, such as determinants of black howler abundance, is unlikely. Rather, recent long-term studies have highlighted the importance of multifactorial explanations. For example, based on a 68-month study of howler monkeys (*A. palliata*) and a parasitic botfly (*Alouattamyia baeri*), Milton (1996) concluded that the annual pattern of howler mortality results from a combination of effects including age, physical condition, and larval burden of the parasitized individual, which becomes critical when the population experiences dietary stress. Similarly, Gulland (1992) studied the interactions of Soay sheep (*Ovis aries*) and nematode parasites and demonstrated that at times of population crashes sheep

were emaciated, had high nematode burdens, and showed signs of protein-energy malnutrition. In the field, sheep treated with antihelminthics had lower mortality rates, while experimentally infected sheep with high parasite loads, but fed nutritious diets, showed no sign of malnutrition.

It is also likely that the hurricane has altered black howler/parasite relationships in such a way as to negatively impact the howlers. For example, for directly transmitted parasites the reduction in the physical structure of the forest and in the number of food trees may mean that the animals spend more time in one location and thus infection risk increases. Gillespie *et al.* (submitted) demonstrated that selective logging has resulted in higher densities of infective-stage parasites common to red colobus (*Ptilocolobus badius*), black-and-white colobus (*Colobus guereza*), and redtail guenons (*Cercopithecus ascanius*). The redtail guenons in logged areas had higher prevalence and richness of gastrointestinal parasites than individuals in unlogged areas.

It is also possible that the initial dietary stress caused by food tree reduction (Pavelka and Behie, 2005) may have adversely affected resistance to parasitic infection by reducing the effectiveness of the immune system (Holmes, 1995; Milton, 1996). This food shortage could have resulted in a higher parasite burden, which in turn could have increased nutritional demands on the howlers and accentuated the effects of food shortages. Thus, nutritional status and parasitism could have had synergistic effects on the host, i.e., the individual effects of each factor would be amplified when co-occurring. The interaction between nutritional stress and parasitism has been examined in a number of laboratories (Crompton *et al.*, 1985; Munger and Karasov, 1989) and in field studies (Gulland, 1992; Murray *et al.*, 1996, 1998; Toque, 1993). These have led to speculation that the interacting effects of food shortage and parasitism may influence vertebrate populations (Holmes, 1995; Keymer and Dobson, 1987). The interactive effects of parasitism and nutritional status have rarely been examined in primates (but see Milton, 1996). Social stress caused by the disruption of the groups' normal composition could also cause stress that could have interacted with both nutritional stress and parasite burden to negatively influence the howler population recovery. Currently we (Alison Behie, Pavelka, and Chapman) are investigating the possible role played by parasites, particularly helminths, by assessing parasite infections through fecal analysis. Since data are not available from before the hurricane, we are comparing the parasite community from Monkey River with those at the Community Baboon Sanctuary, a healthy control population that was not affected by Hurricane Iris.

The hurricane resulted in social disorganization within the area (Pavelka *et al.*, 2003). The possible influence of this social stress on the black howler population dynamics is difficult to assess. However, we have witnessed an adult male killing an infant in his group (Knopff *et al.*, 2004) and a female being so aggressive to another that the recipient left the group. These, along with the dispersal/disappearance of whole and partial groups, suggest that the population is not stable and may be under stress. To evaluate this, we are monitoring stress in general through the quantification of fecal glucocorticoid levels. A considerable body of research on humans and other mammals demonstrates that large and prolonged elevated glucocorticoid levels (cortisol is one type of glucocorticoid) typically reduces survival and reproduction (Bercovitch and Ziegler, 2002; Creel, 2001; Sapolsky, 1986; Wasser *et al.*, 1997). Although data on fitness effects of elevated glucocorticoid levels in the wild are currently limited, the expectation from lab studies is that fitness will decrease as population level stressors become more severe or more prolonged. For specific individuals, we can examine factors coinciding with periods of elevated cortisol levels, be it social stress, food scarcity, or changes in parasite burden.

In conclusion, we have documented that following Hurricane Iris's passing through an area that contained a study population of black howlers, there was a dramatic decline in the population's size and composition. Major disruptions are still occurring some 29 months after the storm and the population is in progressive decline and may be headed for local extinction (see Ford, this volume, for a discussion of population fragmentation and local extinction). We are investigating the possibility that the decline is caused by the reduction of available food trees, and also possible synergistic interactions between this nutritional stress, social disruption, and parasite burden.

SUMMARY

A Central American black howler population in Monkey River, Belize, was monitored from May of 1999 to May of 2001 and was determined to have similar small group size with multi- and single-male groups. Fifty-three monkeys lived in 8 social groups in a 52-ha study area (population density 102 individuals/km²) that is part of the larger continuous forested area of the Monkey River watershed. On October 8, 2001, the study area was severely damaged by Hurricane Iris, a category four storm that resulted in complete defoliation of the forest along with severe structural damage to those trees not

snapped or uprooted. When the area could be accessed again in February 2002, it was determined that the population had dropped by 42%, with 31 monkeys in 5 social groups inhabiting the study area. While initially it was hoped that the population would stabilize at this level, subsequent monitoring through May of 2004 (29 months post hurricane) has revealed a slow but steady decline in the population through the apparent dispersal of whole or parts of social groups, and poor infant survival. We hypothesize that a combination of nutritional and social stress interacting with increased parasite loads (and possibly increased predation) is leading groups and individuals to leave the area, moving west along the river in search of better habitat that is not available. The watershed forest fragment (approximately 100 km²) was equally damaged by the storm from the southern highway of Belize to the coast, leading us to believe that survival of the animals leaving the study site is unlikely. We are currently investigating phytochemical, hormonal, and parasite contributions to the continued decline of the Monkey River howler monkey population following hurricane Iris.

ACKNOWLEDGMENTS

We would like to thank Tracy Wyman, Aaron Osicki, Laura McKenzie, Andrea Faulkner, Melanie Luinstra, Keriann McGoogan, Travis Steffens, Lisa Corewyn, Kyle Knopff, Aliah Knopff, Shelley Alexander, and the students in the Belize Primatology Field School for help with various aspects of this project. In particular, we wish to acknowledge the ongoing research of Alison Behie, a doctoral student at the University of Calgary, who has collected much of the demographic data described in this paper, as well as all of the fecal samples that will allow us to understand the role of parasite load and stress hormone levels in the population decline following a hurricane. This forms the basis of A. Behie's doctoral research. We are also grateful to Alejandro Estrada, Paul Garber, and Leandra Lueke for organizing the Mesoamerican Primate symposium and the ASP meetings in 2004 and this volume, and Paul Garber, Alejandro Estrada, Tracy Wyman, and an anonymous reviewer for helpful feedback on the manuscript. As always we thank the people of Monkey River, including the Village Council and the Monkey River Tour Guide Association for continued support for this project. Funding was provided by the National Sciences and Engineering Research Council, the National Geographic Society, Conservation

International Margo Marsh Biodiversity Fund, The University of Calgary, and the Calgary Institute for Humanities.

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