

4. Hurricanes and coastlines: The role of natural disasters in the speciation of howler monkeys

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In his highly influential book *Primate Taxonomy*, Colin Groves discusses the importance of having an accurate account of primate taxa in order to understand evolutionary relationships that exist between species. This includes understanding genetic and morphological similarities between species as well as the processes of speciation. As the most widely ranging Neotropical monkey, the evolutionary relationships of the genus *Alouatta* have been examined from behavioural, morphological and most recently genetic data. According to Groves (2001) there are nine or 10 species of *Alouatta* and up to 19 subspecies (Table 4.1). Of these species, three are found in Mesoamerica: *A. palliata*, *A. pigra* and *A. coibensis*, with the rest located in South America. However, a more recent study of the molecular genetics of these species revealed *A. coibensis* to be indistinct from *A. palliata*, leaving *A. pigra* and *A. palliata* as the two remaining species in the Mesoamerican clade of howlers (Cortes-Ortiz et al., 2003). In 2012, while at a conference in Mexico, the lead author asked Colin what his thoughts were on the potential role of severe weather in speciation events, and more specifically on the biogeographical distribution on these two closely related species. He admitted he had never given it much thought, but was intrigued by the idea. This chapter further investigates this idea, by pulling together an array of evidence for both *A. pigra* and *A. palliata* in an attempt to add another piece to the puzzle of what factors are important in defining species.

Until 1970 *A. pigra* was considered a subspecies of *A. palliata*, when they were separated into two distinct species by Smith. This distinction was based on differences in their cranial size and morphology, characteristics of the upper molar dentition as well as the colour and texture of the pelage. Horwich and Johnson (1986) later noted that testes descend much earlier in *A. pigra*, and that *A. pigra* lives in consistently smaller social groups. The taxonomic separation of *A. pigra* and *A. palliata* was genetically confirmed by Cores-Ortiz and others (2007) who showed them to have a 5.7% difference in mitochondrial DNA.

Table 4.1: Howler species (genus *Alouatta*) as recognised by Colin Groves in *Primate Taxonomy* (2001).

<i>Alouatta palliata</i> group	
	<i>Alouatta palliata</i>
	<i>Alouatta pigra</i>
	<i>Alouatta coibensis</i>
<i>Alouatta seniculus</i> group	
	<i>Alouatta seniculus</i>
	<i>Alouatta seniculus arctoidea</i>
	<i>Alouatta seniculus juara</i>
	<i>Alouatta macconnelli</i>
	<i>Alouatta sara</i>
	<i>Alouatta belzebul</i>
	<i>Alouatta nigerrima</i>
	<i>Alouatta guariba</i>
	<i>Alouatta guariba guariba</i>
	<i>Alouatta guariba clamitans</i>
<i>Alouatta caraya</i> group	
	<i>Alouatta caraya</i>

Note: This chapter considers only the first group, which is the Central American group.

Source: After Groves (2001).

The dominant view of the colonisation of Mesoamerica by South American primate species revolves around the barrier created by the Andes, which limited the ability of taxa to move out of South America (Ford, 2006). When a land bridge formed between the two regions 3.5 million years ago, the only genera that were able to migrate were those already across this boundary in the northwest of South America. This included the genera *Alouatta*, *Ateles*, *Aotus*, *Cebus* and *Saguinus*. The divergence of the Mesoamerican *Alouatta* species into *A. pigra* and *A. palliata* could have occurred in one of two ways: colonisation by a single species that later split or speciation pre-colonisation and a first wave of *A. pigra* followed later by *A. palliata* (Smith, 1970). Cores-Ortiz and others' (2007) genetic data suggest a split of three million years ago for the two species, which coincides with the formation of the Panamanian land bridge. This is consistent with either the pre or post colonisation split. Ford (2006) supports a pre-colonisation speciation followed by four to five waves after the formation of the land bridge, however, cautions that due to the poorly resolved phylogenies of Mesoamerican primate species, the data do not support firm conclusions about this.

It has been suggested that *A. palliata* may not have been able to colonise areas where *A. pigra* are found due to the ability of *A. pigra* to live in a wider range of habitat types including swamps, mangroves and dry deciduous forests (Reid,

1997). Further, *A. pigra* is mainly found in lowland coastal regions of less than 500 m (Horwich and Johnson, 1986; Baumgarten, 2006). Coastal forests of low elevation have an increased vulnerability to storms and severe stochastic weather patterns (Ford, 2006). As part of the Northern Atlantic Cyclone Basin, the Caribbean along with Central and South America are frequently hit by hurricanes, averaging six hurricanes and two tropical storms per year (www.noaa.com). Most of these, however, pass through the northern part of the hurricane basin in the Yucatan region. This type of regular exposure to severe weather events should have profound effects on the animals living in the area and, depending on frequency of exposure, could have influenced their behaviour and demographic profile (Ford, 2006). This is certainly the case in Madagascar, where the history of regular cyclones has resulted in changes to lemur behaviour and morphology including, small group size, high degrees of energy conserving behaviours (including torpor), and a limited number of species that are dedicated frugivores (Wright, 1999).

In this chapter we explore the possible role of severe weather events in determining the biogeographical distribution of *A. pigra* and *A. palliata* through a study of the forest characteristics that predict the occurrence of *A. pigra* in Belize. We also conduct an examination of group size and evidence of energy conservation in *A. pigra* and *A. palliata* to determine if *A. pigra* show any of the behavioural features associated with living in a stochastic environment. Finally we look for evidence of different levels of environmental stochasticity faced by *A. pigra* as compared to *A. palliata* by comparing the frequency of hurricanes and other tropical storms making landfall in the regions populated by each species. While we acknowledge that Colin Groves considers *A. coibensis* a separate species (Table 4.1), in this paper we focus on *A. palliata* and *A. pigra* due to limited data available on *A. coibensis* as well as the fact that its distribution is limited to the island of Coiba, which is located outside of a hurricane belt (Rylands et al., 2006).

Materials and methods

Forest characteristics associated with *A. pigra*

We used satellite imagery, local informants, guides, and published literature to identify areas that might contain *A. pigra* populations or be suitable habitat for *A. pigra* in Belize. To determine *A. pigra* presence or absence, and relative abundance, areas that were accessible were surveyed on foot using existing trails, logging roads, new trails or by boat along rivers. When a group of *A. pigra* was spotted, location data were collected using a hand held Global Positioning System device (Garmin GPSmap 60CSx). When possible this included the exact location of the

group, but when it was not possible we recorded our location and a compass bearing towards the group and a visual estimate of the distance to the group in metres. We also recorded the group size and composition, height in the canopy and group activity. When a group was heard vocalising we estimated the distance in metres and direction of the group. In previous studies (Pavelka et al., 2007), we found this overestimated the distance by 0.5 to 1.0 km, therefore we took this into account in our analysis here. All spatial data (visual and vocal contacts, confirmations of presence from local informants, and track information) were entered into ArcMap software (v.10.1). Relative abundance was calculated by dividing the number of monkeys sighted by the total distance (km) walked, in that patch.

To assess forest characteristics associated with *A. pigra*, we measured its presence or absence and relative abundance in relation to anthropogenic disturbance (road density, number of settlements, human population density, amount of edge, and presence of agriculture), natural disturbance (hurricanes), and patch characteristics (patch size, patch type, river density, and elevation). We used ArcMap GIS (v.10.1) software to measure road density, the number of settlements within a patch, human population density of the patch, amount of edge to area ratio of a patch, how many hurricanes of category 1–4 have occurred within a patch, patch size, patch type, river density, and mean area-weighted patch elevation. The data to measure the above variables were acquired from BERDS (Biodiversity and Environmental Resource Data System) for all variables except the number of hurricanes, which was acquired from the National Oceanic and Atmospheric Administration (NOAA, 2006).

Behavioural comparisons between *A. pigra* and *A. palliata*

We surveyed the available literature on *A. pigra* and *A. palliata* to determine the average and mean group size of each species as well as to determine the influence of fruit consumption on activity budgets to look for indications of energy minimising behaviour. For the behavioural studies, we only included studies that were done over greater than six months to allow for seasonal variation in fruit availability and consumption to be considered. This resulted in the inclusion of three studies for *A. pigra* and 13 for *A. palliata* (Table 4.2). Due to this limited sample size, no statistical analyses could be performed on the behavioural changes associated with seasonal fruit scarcity, however, these data were compared qualitatively.

Table 4.2: Studies included in behavioural comparisons of *Alouatta pigra* and *A. palliata*.

Behavioural response to fruit shortage	Species	Study site	Group size (# individuals)	Reference
Decrease time spent travelling/ranging	<i>Alouatta palliata</i>	Los Tuxlas, Mexico	14	Estrada, 1984
		Arroyo Liza, Mexico	6	Asensio et al., 2007
	<i>Alouatta pigra</i>	Monkey River	6.6	Pavelka and Knopff, 2004
		Cockscomb Basin Wildlife Sanctuary, Belize	6.5	Silver and Marsh, 2003
Group fission	<i>Alouatta palliata</i>	Agaltepec Island, Mexico	59	Asensio et al., 2007
Increase time spent feeding	<i>Alouatta palliata</i>	Los Tuxlas, Mexico	4	Sheddon-Gonzalez and Rodriguez-Luna, 2010
		La Pacifica, Costa Rica	13	Glander 1978
Increased time spent travelling/ranging	<i>Alouatta palliata</i>	La Pacifica, Costa Rica	25	Williams-Guillen, 2003
		La Pacifica, Costa Rica	15	Williams-Guillen, 2003
		La Pacifica, Costa Rica	20	Williams-Guillen, 2003
		La Pacifica, Costa Rica	13	Glander, 1978
		Agaltepec Island, Mexico	10	Rodriguez Luna et al., 2003
		Agaltepec Island, Mexico	27	Rodriguez Luna et al., 2003
		Barro Colorado Island, Panama		Milton, 1980, 1981
No change in behaviour	<i>Alouatta palliata</i>	Los Tuxlas, Mexico	7	Estrada and Coates-Estrada, 1999
		La Selva, Mexico	20	Stoner, 1996
		La Selva, Mexico	11	Stoner, 1996
		Santa Rosa, Costa Rica	40	Chapman, 1987, 1988
		Playo Escondida, Mexico	7	Asensio et al., 2007
	<i>Alouatta pigra</i>	Community Baboon Sanctuary, Belize	5.9	Silver et al., 1998
Increase in time spent inactive	<i>Alouatta pigra</i>	Cockscomb Basin Wildlife Sanctuary, Belize	6.5	Silver and Marsh, 2003

Source: Data compiled from behavioural and diet studies of at least nine months in duration to account for seasonality. This resulted in three studies for *A. pigra* and 13 for *A. palliata*. See reference list for full references of studies included.

Hurricane-to-coastline ratios

In order to calculate the number of hurricanes in relation to length of coastline (a hurricane to coastline ratio) for *A. pigra* and *A. palliata*, species distribution maps based on Rylands and others (2006) and hurricane tracks obtained from the National Oceanic and Atmospheric Administration (NOAA) in digital format, were plotted in ArcGIS 10.1 (ESRI, 2012). Political boundary data of all Central American countries consisted of datasets from the Digital Chart of the World (Defence Mapping Agency, 1992). These datasets have a standard 1:1,000,000 scale and were used as the base for coastline measures. For the purpose of this study we chose to use a method that would be easily repeatable yet still provide a valid measure of coastline length with respect to the potential distance that tropical storms could cross. Coastline lengths for *A. pigra* and *A. palliata* ranges were calculated using the ‘detailed hull’ function in the extension XTools Pro 9.2 (Data East, 2012) in ArcGIS. The detailed hull function creates a ‘contour’ around outer points similar to that of a standard convex hull, except that it does include some concave angles when consecutive line segments fall below a certain length – the result of this detailed hull function is a ‘finer scaled convex hull’. If the actual length of coastline was used, it would overestimate length due to undulations caused by major inlets and bays along the actual coastline. These are especially apparent along the coast of Belize.

The complete dataset of hurricane tracks included hurricanes from Category 1 to 5, tropical storms, and tropical depressions of all known and recorded storms from the years 1851 to 2007. Because hurricane strength often changes once hitting land, it was not possible to calculate a reasonable comparative measure of number of hurricanes by species range area. Thus we calculated a ratio of the number of hurricanes crossing the coastline for each of the species’ range. Coastline measurements were clipped to create a measure for the two species ranges’ separately. Hurricane track data were filtered so that two measures could be performed: (1) all tropical depressions, tropical storms, and hurricanes Category 1 to 5; (2) hurricanes only (all categories).

Results

Forest patch characteristics of *A. pigra* in Belize

We recorded a total of 83 visual and 110 vocal contacts of *A. pigra* within Belize and collected another 284 confirmations of presence from other reliable sources. All patches were sampled in lowland habitat and a chi square test for independence ($p = 0.05$) found that *A. pigra* were more likely to be present in

a patch classified as lowland broad-leaf moist and wet forest, and more likely to be absent from patches classified as agriculture, lowland savannah, shrubland, or wetland. The area-weighted mean elevation of all patches ranged between sea level and 222 m ASL with the highest confirmation of an *A. pigra* group at 700 m and the highest reported sighting of a group at 289 m ASL. When considering factors influencing the relative abundance of *A. pigra*, only the amount of edge was positively associated ($r = 0.545$; $p = 0.006$) accounting for 30% of the variation in relative abundance ($r^2 = 0.297$).

We found a significant positive relationship between the number of settlements in a patch and the presence of *A. pigra*, with more settlements in present patches (1.19) than absent patches (0.14). There was also a significant relationship between *A. pigra* presence and patch size. Patches ranged in size from 0.13 km² to over 1256 km² with the largest patch occurring in the Rio Bravo and Gallon Jug region and the smallest patches (<1.0 km²) adjacent to the Belize River. We found present patches to be, on average, larger (117.24 km²) than absent patches (27.29 km²).

Behavioural comparisons of *A. pigra* and *A. palliata*

Our literature review found *A. pigra* to live in significantly smaller groups than *A. palliata* with *A. pigra* living in groups ranging from 5.9 to 9 individuals ($\bar{x} = 6.83$, $CV = 19.55$) and *A. palliata* living in groups ranging from 4 to 59 individuals ($\bar{x} = 15.37$, $CV = 79.78$). Group size in *A. palliata* was more variable, which may be due to the increased sample size for the comparatively well studied mantled howler or reflect group size constraints that may be present in *A. pigra* due to the stochastic nature of their environment.

When examining the relationship between fruit consumption and activity patterns we found no consistent differences within or between species in how populations adjust behaviour during periods of fruit shortage. Populations of *A. pigra* either decreased time spent travelling (from 9.52% to 5.45%), increased time spent inactive (from 69% to 77%) or did not adjust activity patterns in response to seasonal reductions in fruit intake (Behie and Pavelka, 2005; Silver et al., 1998; Pavelka and Knopff, 2004). While some groups of *A. palliata* also did not show changes in activity that correspond to fruit production, the most common response reported in the literature is an increase in either travel time (from 18.6% to 35.8% in *A. palliata* in Nicaragua, Williams-Guillen, 2003) or ranging distance (from 114.05 m to 502.88 m for a population in Mexico, Estrada, 1984), which is a response that has never been reported for a population of *A. pigra*.

Severe weather events in the ranges of *A. pigra* and *A. palliata*

The method described above resulted in a coastline length of 893 km for *A. pigra* and 1372 km for *A. palliata*. Since 1851, 118 Atlantic hurricanes, depressions or tropical storms have crossed into coastal regions populated by *A. pigra*, where only 40 have crossed into the range of *A. palliata*. There is a significantly higher storm to coastline ratio of 0.132 for *A. pigra* than the 0.0292 for *A. palliata* ($X^2 = 37.52$, $df = 1$, $p < 0.0001$) (Figure 4.1a). When considering hurricanes only, the difference is still evident. Many more hurricanes crossed the coastal regions of *A. pigra* (N = 49) compared to *A. palliata* (N = 19) (Figure 4.1b). The hurricane to coastline ratios (0.551 for *A. pigra* and 0.0138 for *A. palliata*) were significantly different ($X^2 = 12.36$, $df = 1$, $p = 0.0004$).

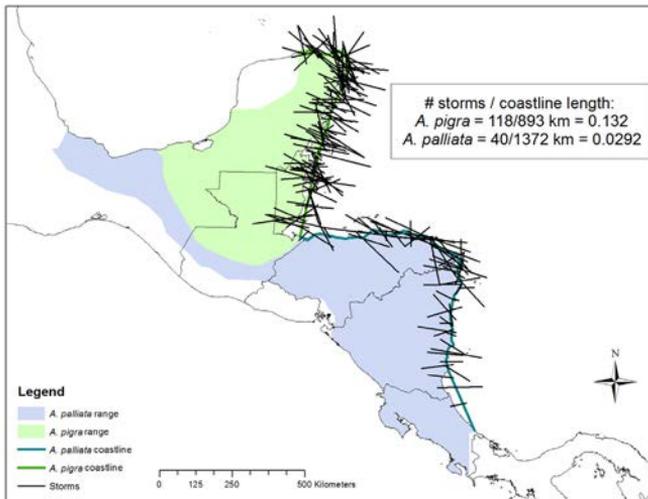


Figure 4.1a: Total number of storms that crossed through the ranges of *Alouatta pigra* and *Alouatta palliata* from 1851 to 2007.

Source: Data were obtained from the National Oceanic and Atmospheric Administration (NOAA) and plotted in ArcGIS 10.1 (ESRI, 2012). Political boundary data of all Central American countries consisted of datasets from the Digital Chart of the World (Defence Mapping Agency, 1992). These datasets have a standard 1:1,000,000 scale and were used as the base for coastline measures.

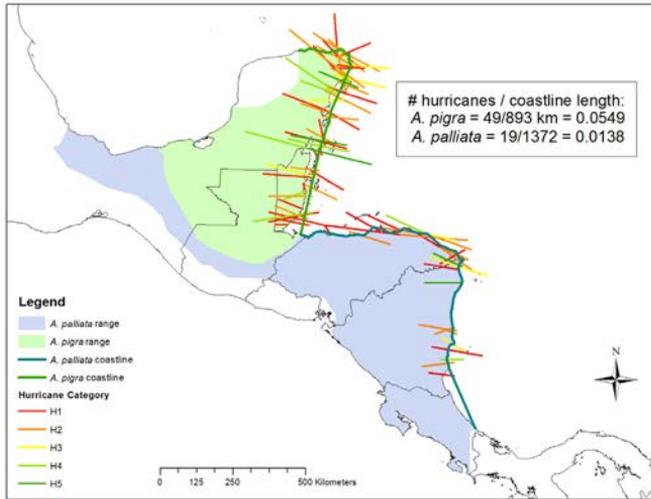


Figure 4.1b: Total number of hurricanes that crossed through the ranges of *Alouatta pigra* and *Alouatta palliata* from 1851 to 2007.

Source: Data were obtained from the National Oceanic and Atmospheric Administration (NOAA) and plotted in ArcGIS 10.1 (ESRI, 2012). Political boundary data of all Central American countries consisted of datasets from the Digital Chart of the World (Defence Mapping Agency, 1992). These datasets have a standard 1:1,000,000 scale and were used as the base for coastline measures.

Discussion

The evolutionary history of *A. pigra* and *A. palliata* in Mesoamerica is not entirely understood. Colonisation of Mesoamerica by South American species took place after the formation of a land bridge between the two regions approximately 3.5 million years ago (Ford, 2006), and genetic data suggest that the two *Alouatta* species diverged from one another close to 3.0 Mya (Cores-Ortiz et al., 2007). Whether they colonised Mesoamerica before or after this speciation event, *A. pigra* is currently limited to a small geographic range in the Yucatan Peninsula compared to a relatively wide distribution of *A. palliata*. The aim of this paper was to investigate the potential role of environmental stochasticity in the geographic distribution and possibly speciation of *A. pigra* and *A. palliata* through: an examination of the forest characteristics that predict the presence of *A. pigra*; a comparison of the behavioural traits of *A. pigra* and *A. palliata* that might suggest an evolutionary history shaped by living in a stochastic environment; and finally a comparison of the prevalence of severe weather events, such as hurricanes, in the ranges of the two species.

In terms of patch characteristics, we found a higher relative abundance of *A. pigra* in Belize in lowland broad-leaf moist and wet forest, in line with previous reports that *A. pigra* inhabit primarily lowland riverine coastal forests (Horwich and Johnson, 1986; Reid, 1997). The highest published densities reported for *A. pigra* have been at the Community Baboon Sanctuary (CBS) near the Belize River (257 ind/km², Ostro et al., 1999) and at Monkey River (102 ind/km², Pavelka, 2003). Seasonally flooded forests create localised disturbance which may improve soil quality and thus the quality of the howler food supply (Peres, 1997). We also found a significant positive relationship between both human settlements and patch size and the occurrence of *A. pigra* and between the amount of edge and the relative abundance of *A. pigra*. This suggests that *A. pigra* is tolerant of disturbance and may even prefer disturbed forest patches. One reason for such a preference may be that disturbed areas are colonised by fast growing pioneer species that invest little in chemical defence, thus produce leaves high in protein and low in fibre and secondary compounds (Coley, 1983). Folivores are able to take advantage of this and maintain a high quality diet despite an overall reduction in stem density. We found this to be the case following hurricane Iris in Monkey River where *A. pigra* shifted their leaf consumption to include up to 75% *Cecropia peltata*, which had the highest protein to fibre ratio and the third highest concentration of sugar of all ingested species (Behie et al., 2014).

Living in disturbed forest patches may improve the food supply for folivores in the long term, but immediately following a severe natural disaster there would be substantial reductions in the available food supply. Many trees regenerate new leaves immediately following a hurricane (Klinger, 2006; Zimmerman and Covich, 2007; Waide, 1991), while other food sources such as fruit or flowers take longer to return (Waide, 1991; Behie and Pavelka, 2005; Ratsimbazafy et al., 2002). After Hurricane Iris hit Monkey River there was a 52 per cent loss of major fruit trees and an 18 month absence in all fruit production forcing resident *A. pigra* groups to rely on a completely folivorous diet (Behie and Pavelka, 2005; Behie and Pavelka, in press). Following natural disturbances ring-tailed lemurs (*Lemur catta*; LaFleur and Gould, 2009; Ratsimbazafy et al., 2002), ruffed lemurs (*Varecia v. editorium*; Ratsimbazafy, 2006) lion-tailed macaques (*Macaca silenus*; Menon and Poirer, 1996) and black howlers (*Alouatta pigra*; Behie and Pavelka, 2005) altered their diets to include plant parts and species not previously ingested, some of which were exotic to the region or were located outside of the regular forest habitat.

Such changes in food supply would be expected to result in demographic and behavioural changes to deal with an unpredictable and irregular food supply. One such mechanism to cope with this would be to reduce group size to deal with increased feeding competition. The average group size of black-and-

white lemurs decreased from seven individuals before Cyclone Gretelle to 2.5 individuals after (Ratsimbazafy et al., 2002) and after wildfires moved through Borneo, the number of gibbon groups of more than five members significantly decreased, while the number of pairs increased (O'Brien et al., 2004). Group size in *A. pigra* in Monkey River following Hurricane Iris fell from 6.32 individuals before the storm to less than five in the first year following the storm. This suggests that animals exposed to severe disturbance adapt in the short term by reducing group size.

If exposed to severe environmental change on a regular basis, it stands to reason that group size may be constrained, placing upper limits on how many animals could live in a group without suffering the ill effects of increased competition at times of food scarcity. This was suggested by Wright (1999) who noted that lemur populations affected by frequent cyclones lived in smaller groups than groups not impacted by severe weather. In our comparison with *A. palliata* we found that *A. pigra* have significantly smaller and less variable group sizes than do *A. palliata*. Mean group size in *A. palliata* is 15.37 (Glander, 1978; Estrada, 1982, 1984; Chapman, 1987; Larose, 1996; Stoner, 1996; Estrada et al., 1999; Serio-Silva et al., 1999; Solano et al., 1999; Rodriguez-Luna, 2003; Williams Guillen, 2003; Munoz et al., 2006; Asensio et al., 2007; Dunn et al., 2009; Dunn et al., 2010) and mean group size in *A. pigra* is 6.83 (Silver et al., 1998; Silver and Marsh, 2003; Pavelka and Knopff, 2004; Pozo-Montuy and Serio-Silva, 2006). Considering the hurricane activity that occurs in the range of *A. pigra*, low group size could very well represent an adaptation to living in a stochastic environment. James et al. (1997) studied groups of *A. pigra* living at Bermudian Landing, Belize that were subjected to population declines from hurricanes in 1931, 1954 and 1978 as well as from a yellow fever epidemic which occurred in 1971. Each of these severe weather events caused a drastic decline in population numbers, and although they have recovered, the average group size in this region is only 4.6 individuals, lower than most other species of howlers. In 1999 this number increased to between four to 10 individuals, which although larger, is still smaller than other howler species (Ostro et al., 1999). A similar decline in group size was recorded in Monkey River following Hurricane Iris where group size remains smaller than before the storm even after more than a decade has passed.

We also found differences in activity patterns between *A. pigra* and *A. palliata* during periods of fruit scarcity. The prolonged fruit shortage following Hurricane Iris resulted in differences in activity levels between periods when fruit was not available (2002–mid-2004; mean fruit intake 4.93%) and when it was available at close to pre-hurricane levels (mid-2004–2007; mean fruit intake 28.75%). When fruit consumption was absent or very low, animals spent more time inactive and less time feeding and locomoting, probably minimising energy

expenditure in response to low energy intake. An increase in time spent inactive and a reduction in time spent feeding has also been seen in howler monkeys following translocation to an unfamiliar environment (Silver and Marsh, 2003) and in lemurs in response to unpredictable resource availability and dramatic and prolonged shortages in fruit production in Madagascar (Wright, 1999). In lemurs this is also associated with a lower basal metabolic rate, which varies in response to changing fruit production, allowing them to maximise energy conservation (Pereira, 1993; Jolly, 1966). Increasing inactivity in the howlers at Monkey River in response to prolonged fruit shortage likely serves a similar function allowing howlers to conserve energy at times when higher quality resources (e.g. fruit) are not ingested. This however is not the response seen in *A. palliata* who have been reported to increase travel time (Williams-Guillen, 2003) or ranging distance (Estrada, 1984) when fruit is less available. This may be reflective of increased scramble competition in the larger groups of *A. palliata*, however, it may also be a result of *A. palliata* living in regions that show more predictability in fruit production with less need to conserve energy for long periods of food scarcity.

This successful dispersal of *A. palliata* may have resulted in their outcompeting *A. pigra* in most areas, pushing them up into their currently restricted range of southern Mexico, Belize and northern Guatemala (Ford, 2006). If this is true, and *A. palliata* were able to outcompete *A. pigra* and push them out of many regions, then the current range of *A. pigra* must represent areas that are not tolerated by *A. palliata*. There is no denying that exposure to hurricanes would create a selective pressure for animals living in hurricane belts, an idea that Colin himself agrees may have influenced speciation and/or current biogeographical distributions. Data presented here show that significantly more hurricanes pass into the range of *A. pigra* than the range of *A. palliata*. This may have been one reason why *A. palliata* did not extend their range into the hurricane belt of the Yucatan Peninsula, leaving *A. pigra* as the only *Alouatta* species to colonise the area. This is supported by the fact that *A. pigra* are commonly found in and may actually prefer disturbed forests and live in small groups who exhibit energy conservation strategies with regards to their activity budgets. Such adaptations to environmental stochasticity are also seen in lemurs regularly exposed to cyclones in Madagascar (Wright, 1999) suggesting they are necessary adaptive mechanisms to cope with high degrees of environmental perturbations. *A. palliata* may be less able to tolerate hurricane activity and unable to colonise the hurricane belt of the Yucatan Peninsula. While there may be other reasons contributing to the range separation of *A. pigra* and *A. palliata*, we argue that the role of hurricane activity cannot be ruled out as a possible explanation for the current biogeographical separation and potentially of speciation in these two species and potentially other species exposed to severe weather conditions.

This is an idea rarely considered in theories of primate speciation or when considering current biogeographical ranges, but as severe weather events become more frequent and intense is one that warrants further investigation.

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