PROLONGED INTER-SPECIFIC ASSOCIATION BETWEEN *ATELES FUSCICEPS FUSCICEPS* AND *ALOUATTA PALLIATA AEQUATORIALIS* (ATELIDAE) IN A FOREST FRAGMENT IN NORTH WESTERN ECUADOR

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Abstract

Changes in the behavior of primates caused by habitat disturbance are important indicators of their survival ability in fragmented landscapes. In Ecuador, few studies have examined the effect of habitat fragmentation on primate behavior. We present data of a prolonged interspecific association between a brown-headed spider monkey (*Ateles fusciceps fusciceps*) living within a troop of Ecuadorian mantled howler monkeys (*Alouatta palliata aequatorialis*) in a protected forest fragment in northwestern Ecuador. We collected 274 hours of observations, at 10-minute intervals, on the *A. f. fusciceps* individual in both the wet and dry seasons. Data included the amount of time that the *A. f. fusciceps* individual spent associating with, and apart from, the *A. p. aequatorialis* troop. Our observations suggest a close relationship between the individuals of the two species, with similarities in their behavior and diets found during the study. Interspecific communication was observed frequently, with all *A. p. aequatorialis* individuals interacting directly with the *A. f. fusciceps* individual. The behavior of the *A. f. fusciceps* individual was similar to that found in studies of other *Ateles* spp. living in fragmented and disturbed habitats, but differed from that observed in other studies of the same species in continuous forest, suggesting adaptation to conditions in fragmented habitat and possibly to living in close proximity with the howler troop.

Keywords: Primate behavior, habitat disturbance, symbiosis, adaptation.

Resumen

Cambios en el comportamiento de primates causados por la intervención de hábitat son indicadores importantes de habilidad de supervivencia en ecosistemas fragmentados. En Ecuador existen pocos estudios que examinen los cambios en el comportamiento de especies causados por la fragmentación. Este estudio documenta la asociación interespecífica entre un mono araña de cabeza café (*Ateles fusciceps fusciceps*) conviviendo con una tropa de monos aulladores de la costa (*Alouatta palliata aequatorialis*) dentro de un remanente de bosque protegido en el noroccidente del Ecuador. Colectamos 274 horas de muestras instantáneas, registradas cada 10 minutos, de *A. f. fusciceps* durante las estaciones lluviosa y seca. El registro de datos incluyó tiempo en el que *A. f. fusciceps* estaba asociado y separado de la tropa de *A. p. aequatorialis*. Los resultados sugieren que la relación entre ambas especies es estrecha, con similitudes en los patrones de comportamiento y dieta encontrados a lo largo del estudio. Se observó con frecuencia una comunicación interespecífica, con todos los individuos de *A. p. aequatorialis* interactuando de cierta forma directamente con *A. f. fusciceps* individualmente. El comportamiento del individuo *A. f. fusciceps* fue similar a lo encontrado en otros estudios de *Ateles* spp. viviendo en hábitats fragmentados e intervenidos, pero diferente de lo observado en otros estudios de la misma especie en bosque continuo. Esto último sugiere una adaptación a las condiciones de fragmentación de hábitat y posiblemente a la estrecha proximidad de la tropa de aulladores.

Palabras clave: Comportamiento de primates; alteración de hábitat; simbiosis; adaptación.

Introduction

Habitat destruction has led to reductions and isolation of many primate populations and, as consequence, various adaptations in behavioral and ecological responses in primate communities have occurred (Marsh *et al.*, 2013). This has included changes in dietary selection, population densities and group sizes, reproductive fitness, stress levels and susceptibility to disease (Martínez-Mota *et al.*, 2007; Schwitzer *et al.*, 2011; Abondano and Link, 2012; Marsh *et al.*, 2013; Carretero-Pinzón *et al.*, 2016; Rondón *et al.*, 2017) and those better able to adapt are, probably, more likely to survive this habitat alteration, at least for the short term (Schwitzer *et al.*, 2011).

The four species of primates that inhabit the coastal region of Ecuador are threatened by hunting, habitat loss and fragmentation (Rowe and Myers, 2016). The most threatened species, the brown-headed spider monkey (*Ateles fusciceps fusciceps*), is restricted to remaining areas of forest on Ecuador's Pacific coast. This species is listed as Critically Endangered (Tirira *et al.*, 2017; IUCN, 2018a) and is considered one of the 25 most threatened primate species (Schwitzer *et al.*, 2017) due to a nearly 80 % reduction in its habitat (Tirira *et al.*, 2017). Hunting is also a major problem for remnant populations of this species (IUCN, 2018a). Similarly, the Ecuadorian mantled howler monkey (*Alouatta palliata aequatorialis*) is threatened due to population reduction from habitat loss and hunting (IUCN, 2018b) and is considered Vulnerable by the IUCN (2018b) and Endangered in the *Red Book of the Mammals of Ecuador* (Tirira, 2011). Despite these species' sympatry, no information on a close long-term relationship between them has been published to date.

Inter-specific associations have been documented in various Neotropical primates (e.g. van Roosmalen, 1985; Pontes, 1997; de la Torre, 2000; Heymann and Buchanan-Smith, 2000; Defler, 2004; Lehman *et al.*, 2006; Shanee *et al.*, 2007; Haugaasen and Peres, 2009; Silva and Ferrari, 2009; Oliveira and Dietz, 2011; Shaffer *et al.*, 2016). These associations provide advantages such as increased access to resources and predator avoidance (Norconk, 1990; Terborgh, 1990; de la Torre, 2000; Oliveira and Dietz, 2011). Some studies report low levels of interspecific interactions for *Ateles* spp. (van Roosmalen and Klein, 1988; Haugaasen and Peres, 2009), however, there are several published observations of inter-specific associations between spider monkeys and other sympatric primates (van Roosmalen, 1985; Defler, 2004; Shanee *et al.*, 2007; Blake *et al.*, 2010; Link *et al.*, 2011). Interspecific associations have also been reported between *Alouatta* spp. and other primates (Pontes, 1997; Lehman *et al.*, 2006; Haugaasen and Peres, 2009; Silva and Ferrari, 2009), including with spider monkeys (Cristóbal-Azkarate *et al.*, 2015).

We conducted a short study on the activity budgets, diet and inter-specific interactions of a solitary *A. f. fusciceps* living with a group of *A. p. aequatorialis* in a forest fragment in Ecuador. The aim of this study was to describe the possible behavioral and ecological responses of both species to the intense anthropogenic disturbance in the area and their close interspecific association.

Methods

Study site

The study was carried out in the Ashiringa Ecological Reserve, a private reserve in Pichincha province, Northwestern Ecuador (00°04'24.9"S, 78°58'04.4"W). The reserve consists of approximately 107 hectares of remnant forest (~50 hectares of primary forest and ~57 hectares of secondary forest), and altitudes ranging from 500 to 700 meters. The reserve is surrounded by a matrix of orchards, pasture and artisanal fish farms. An unpaved road runs through the reserve (Fig. 1).

Forests in the area are pre-montane evergreen Western Andes Cordillera forest (Sierra, 1999) with multiple vegetation strata, with both lowland and premontane forests (Guevara and Morales, 2013). Canopy height is 15 to 19 m with occasional emergent trees of up to 30 m with an average diameter at breast height of 405 cm (Moscoso, 2010). Weather is very humid sub-tropical with daytime temperatures between 17 and 26 °C and annual rainfall of 3,000 mm, and 500 mm in the wettest month (Hijmans *et al.*, 2005). Topography in the area is characterized by steep hills which have contributed to the conservation of remnant forest areas. The principle threats to habitat in the area come from mining and human population growth with its associated expansion of the agricultural frontier leading to deforestation and isolation of remaining forest fragments (Centro de Investigaciones Sociales del Milenio, 2006; Vandegrift *et al.*, 2018).

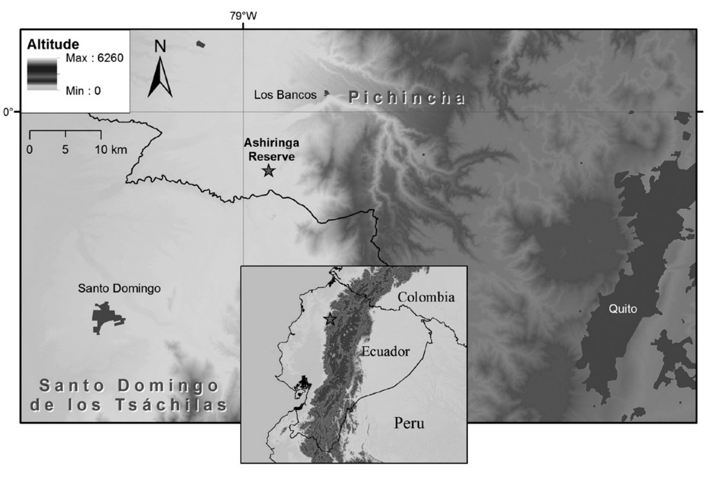

Figure 1. Map showing the location of the study area, Ashiringa Ecological Reserve, Pichincha Province, northwestern Ecuador.

Field surveys

Field work was carried out for four months in two periods: during the wet season (September to October 2008) and the dry season (June to July 2009). Focal animals were followed daily between 06:00 and 18:00 (Brockelman and Ali, 1987). At the start of the study period the *A. p. aequatorialis* troop consisted of four individuals: one adult male; one adult female with a dependent infant; and one juvenile female. A juvenile male joined the group during the last week of the study (July 2009). During the study period, we did not find any con-specifics of *A. f. fusciceps* in the surrounding area. Other groups of howler monkeys are found in adjacent fragments, however no interactions were observed with the *A. f. fusciceps* individual during the study period.

We used a combination of focal animal sampling for observations of the *A. f. fusciceps* individual, and group scan sampling for observations of the *A. p. aequatorialis* group (Altmann, 1974), recording activity of each visible individual in turn. We recorded activities every ten minutes using five previously defined, mutually exclusive behavioral categories based on Martin and Batenson (2007): resting, feeding, social activities, travelling, and vocalization (Appendix 1). We considered associations to be any time when the *A. f. fusciceps* individual was with the howler group. Details of all inter-specific interactions between individuals of both species were recorded in five categories: body contact, avoidance, aggression, play, and other. We identified food types consumed as: young leaves, mature leaves, unripe fruit, ripe fruit, flowers and other (including buds, bark, nectar, bromeliads, ferns, and insects). Plant resources consumed by both species were collected and identified. We also recorded forest strata used by all individuals at 10 minute intervals.

Data analysis

We calculated activity budgets using the frequency of occurrence of each behavioral category. We selected a 10 minutes interval between scans, and all data were averaged to reduce pseudoreplication (Martin and Bateson, 2007). Similarly, only non-parametric statistics were used as sample sizes were small and data may not have been normally distributed. To estimate dietary preference, we calculated frequencies for consumption of each food type as well as frequencies of plant families and species consumed by *A. f. fusciceps*. We tested for differences in activity budgets and dietary preferences using chi-square tests. To examine the relationship between the *A. f. fusciceps* individual and the *A. p. aequatorialis* troop we calculated frequencies for each type of interaction between each pair of individuals, also examining possible correlations in interactions between seasons. We also compared activity budgets from our study with those reported in the literature for *Ateles* spp. and *Alouatta* spp.

Results

Activity budgets and association times

We collected 274 hours of behavioral data over 41 days (23 full day follows and 18 partial follows). These were split between 147.3 hours (21 days) and 126.6 hours (20 days) during the wet and dry seasons, respectively. There were no differences in seasonal activity budgets for each species (all x^2, $p > 0.05$). Significant differences in activity budgets were found between species in the wet season ($x^2 = 25.259$, $df = 4$, $p < 0.001$), dry season ($x^2 = 9.634$, $df = 4$, $p = 0.047$) (Fig. 2). Post-hoc tests (Bonferroni), with Alpha significance set to 0.05 (adjusted significance for 10 comparisons = 0.005), showed that these differences were in the frequencies of resting and locomoting.

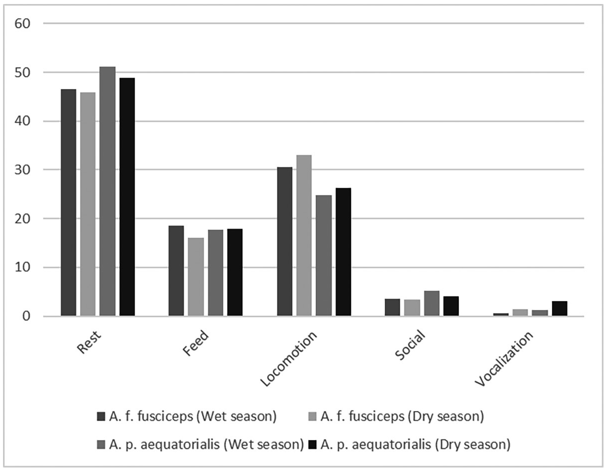

Figure 2. Comparative activity budgets between the wet and dry seasons for *Ateles fusciceps fusciceps* and *Alouatta palliata aequatorialis* at Ashiringa Ecological Reserve, Pichincha Province, northwestern Ecuador.

Comparisons of the activity budget for *A. f. fusciceps* from this study showed large differences with those found for *Ateles* spp. in other studies (Table 1).

Table 1. Comparison of activity budgets of *Ateles* spp. and *Alouatta* spp. from this and other studies.

Species	Rest	Social	Feed	Travel	Vocalization	Other	Source
Ateles f. fusciceps	46	4	17	33	1	<1	This study
At. f. fusciceps	10	23*	37	30	-	-	Gavilánez-Endara (2006)
At. f. fusciceps	8	-	17	58	17	-	Moscoso (2010)
At. f. fusciceps	20	10	20	34	14	-	Moscoso (2010)
At. f. fusciceps	-	10	-	80	-	10	Moscoso (2010)
At. f. fusciceps	25	4	36	30	-	4*	Fuentes *et al.* 2018
Ateles belzebuth	61	-	22	10	-	7***	Klein and Klein (1977)•
At. belzebuth	45	-	18	36	-	1***	Nunes (1995)•
At. belzebuth	58	-	17	25	-	17***	Suarez (2006)•
Ateles. chamek	45	-	29	26	-	12***	Symington (1988)•
At. chamek	46	-	19	30	-	6***	Wallace (2001)•
Ateles geoffroyi (Continuous forest average)**	34	-	40	15	-	11	Chavez *et al.* (2011)
At. geoffroyi (Fragmented forest average)**	34	-	48	9	-	10	Chavez *et al.* (2011)
At. geoffroyi	24	-	34	33	-	10***	Chapman *et al.* (1989)•
Alouatta p. aequatorialis	50	5	18	25	2	<1	This study
Al. p. aequatorialis	14	39*	23	19	*	-	Gavilánez-Endara (2006)
Alouatta belzebul	59	-	20	18	-	3***	Pinto (2002)•
Al. belzebul	56	-	8	19	-	17***	Bonvicino (1989)•
Alouatta caraya.	62	-	16	18	-	5***	Bicca-Marques (1993)•
Alouatta guariba	72	-	17	11	-	0***	Mendes (1989)•
Al. guariba	58	-	19	19	-	5***	De Marques (1995)•
Al. guariba	64	-	19	13	-	4***	Chiarello (1993)•
Alouatta palliata	66	-	16	10	-	8***	Milton (1980)•
Al. palliata	80	-	17	2	-	1***	Estrada et al (1999)•
Al. palliata	73	-	18	8	-	2***	Teaford and Glander (1996)•
Al. palliata	56	-	25	14	-	6***	Stoner (1996)•
Al. palliata	57	-	14	27	-	2***	Williams-Guillen (2003)•
Al. p. aequatorialis	66	8*	16	10	-	-	Milton (1980)
Alouatta pigra	62	-	24	10	-	4***	Silver et al (1998)•
Al. pigra	83	-	10	4	-	3	Pozo-Montuy *et al.* (2013)
Alouatta seniculus	79	-	13	6	-	3***	Gaulin and Gaulin (1982)•
Al. seniculus	67	-	22	11	-	-	Neves and Rylands
(1991)							
Al. seniculus	63	-	22	10	-	-	Palma *et al.* (2011)

=* Including vocalizations, ** Author calculation, *** includes social, • In Di Fiore et al. (2011).

Inter-specific interactions

Inter-specific associations between the species accounted for 218.2 observation hours (80%). Time spent in association between seasons was very similar, 83% and 79% during the wet and dry seasons, respectively. Over half of associations, 56%, lasted the full follow, with the remaining days' associations being partial (34%) or absent (10%).

The 82 direct interspecific interactions observed were divided into five categories: body contact (42%), avoiding (22%), aggression (7%), play (17%) and other (12%). Individual inter-specific interactions between the *A. f. fusciceps* and *A. p. aequatorialis* group members showed differences between individuals. The juvenile female had the most inter-specific interactions (41%), followed by the adult male (21 %), juvenile male (14 %), adult female (13 %) and infant (10 %). Table 2 presents qualitative details of the interaction types observed. We also observed multi-member interactions, and vocal communication between the howler group and the *A. f. fusciceps* individual (group members responding to calls when ripe fruits were encountered). On occasion the *A. p. aequatorialis* group members would become agitated and vocally active when the *A. f. fusciceps* individual would approach the juvenile female, especially at the end of the dry season.

Table 2. Qualitative details of inter-specific interactions between the *A. f. fusciceps* individual and *A. p. aequatorialis* group members.

***A. palliata* group member**	**Frequency of interaction (%)**	**Description**
Juvenile female	41	Body contact, involving hugging, attempted mounting, pulling of tails and other body parts (by the *A. fusciceps*), often received with evasion or as play.
Adult male	21	Evasion, as moving away when the *A. fusciceps* came close, aggression and exploration of new areas away from the group.
Juvenile male	14	Aggression, evasion and body contact
Adult female	13	Body contact on few occasions received with evasion
Infant	10	Play

Diet

We observed 48 different plant species from 19 families consumed by the *A. f. fusciceps* individual during the study period (Appendix 2). Species from three families made up over 50 % of plant resources consumed: Moraceae (24 %), Fabaceae (17 %) and Cecropiaceae (12 %). Ripe fruit was the most commonly consumed food type by the *A. f. fusciceps* individual during the wet season (43 %), followed by immature leaves (41 %). During the dry season this changed to a higher consumption of immature leaves (62 %) and lower consumption of immature fruits (15 %); these differences were found to be significant ($x2$ 47.21, $df = 5$, $p < 0.001$). For *A. p. aequatorialis* immature leaves were the most commonly consumed food type during the wet season (52 %), followed by ripe fruit (34 %). During the dry season, there was a higher consumption of immature leaves (73 %) and lower of fruits (ripe fruit 9 % and immature fruit 8 %) these differences were also significant ($x2$ 29.62, $df = 5$, $p < 0.001$) (Fig. 3).

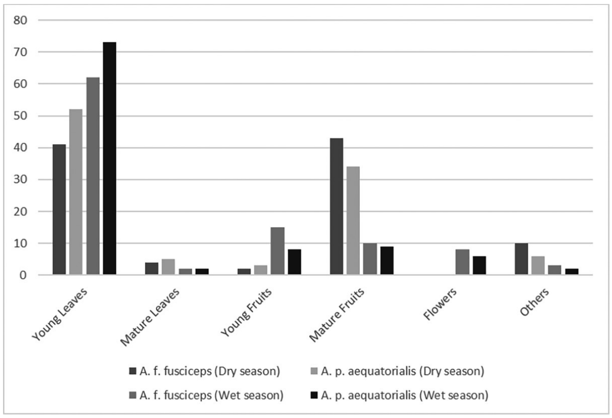

Figure 3. Percentage of dietary components between season for *Ateles fusciceps fusciceps* and *Alouatta palliata aequatorialis*.

Discussion

In this study both species had similar activity budgets, which may be surprising due to the intrinsic differences in the species' biology and ecology (Di Fiore *et al.*, 2011). Primates of the genus *Ateles* are physiologically adapted to travel large distances in a short time which has a large impact on their dietary requirements (Strier, 1992). On the other hand, *Alouatta* spp. are known for their sedentary behaviors and lower energetic requirements (Strier, 1992). However, studies on *Ateles* spp. in fragmented and disturbed habitats (i.e., under sub-optimal conditions), have shown that they can adapt their behavior and diet to better cope with available resources (Abondano and Link, 2012; Schaffner *et al.*, 2012).

The only significant differences observed between the species' activity budgets, was, as expected, greater instances of travelling and lower instances of resting by the *A. f. fusciceps* individual. Spider monkeys tend to spend a large portion of their time travelling, much higher than howler monkeys (see Table 2). On the other hand, similar changes in activity budgets have been observed in some species of *Ateles* living in fragmented habitat. Schaffner *et al.* (2012) found that a group of *A. geoffroyi yucatanensis* substantially altered their activities in the aftermath of two hurricanes, reducing time spent travelling, whilst increasing time spent feeding on leaves, compared to prior to the hurricanes. Other studies have shown similar patterns in the behavior of *A. geoffroyi* and *A. hybridus* in fragmented habitats (Abondano and Link, 2012; Chaves *et al.*, 2011). For example, Chavez *et al.* (2011) reported that *A. geoffroyi* living in fragmented forests spent less time traveling and more time feeding than groups in continuous forest (Table 1).

Another interesting observation was the high percentage of resting seen in the *A. f. fusciceps* individual (Fig. 2), which again could be an adaptive behavior to living in sub-optimal habitat (Abondano and Link, 2012; Schaffner *et al.*, 2012), although comparative resting times in *Ateles geoffroyi* groups living in fragmented and continuous forest did not show such marked patterns (Chaves et al., 2011 and table 1). Similarly, Abondano and Link (2012) found that *A. hybridus* living in heavily fragmented habitat in Colombia spent more time resting than either feeding or travelling (~40 % resting, and ~25 % in feeding and travelling, respectively).

A. f. fusciceps individual in our study and those from other studies of the same species (Gavilanez-Endara, 2006; Moscoso, 2010; Fuentes *et al.*, 2018) show large differences in activity budgets (Table 1), especially in resting times, which are generally much lower in *A. f. fusciceps* (Gavilanez-Endara, 2006; Moscoso, 2010; Fuentes *et al.*, 2018). This may have had a knock-on effect, including lower resource consumption, as energetic requirements are lower with lower activity levels (van Roosmalen, 1985; Symington, 1988; Nunes, 1998; Suárez, 2006), and, the lower levels of travel similarly related to less need to find food, or *vice-versa*.

The inter-specific relationship observed is almost permanent and should not be considered as a casual association. The reason for the association could be that, as social animals (Strier, 2015), the *A. f. fusciceps* individual associated with the group as he could find no conspecifics in the area. Several well documented interspecific associations in Neotropical primates exist; in the Ecuadorian Amazon, *Sapajus macrocephalus* and *Saimiri cassiquiarensis* have a symbiotic relationship, where *S. cassiquiarensis* takes advantage of the ability of *S. macrocephalus* to access otherwise unattainable resources whilst *S. macrocephalus* gains an early warning system against predation (de la Torre, 2000). There are also reports of multi-specific relationships, for example between Callitrichids in the Bolivian, Brazilian and Peruvian Amazon where species travel together all taking advantage of the increased defensive benefit and foraging opportunities (Heymann and Buchanan-Smith, 2000). The advantages of *Ateles* spp. ecological cognitive abilities (Di Fiore and Suarez, 2007), combined with faster reaction times, when compared to those of *Alouatta* spp. could be useful in group defense.

There have also been a handful of reports of inter-specific relationships with species of the genus *Ateles*. Van Roosmalen (1985) reported the formation of temporal subgroups with *Chiropotes satanas*. Most interestingly for this study, Defler (2004) mentions a female *A. belzebuth* living within a troop of *A. seniculus* in Colombia, and Shanee et al. (2007) reported a solitary *A. belzebuth* associating with a troop of *Lagothrix flavicauda* in Peru. That same individual was seen associating with the same *L. flavicauda* troop on several subsequent occasions (S. Shanee, pers. obs.), the nearest known population of *A. belzebuth* is found ~10 km to the Northwest. Possibly a dispersing animal got lost or failed to be accepted into a new group and now associates with the nearest acceptable alternative, although in this case it is not a permanent association (S. Shanee, pers. obs.). Even so, observations of interspecific associations, and particularly long-term associations, with *Ateles* spp. are scarce, especially in competitive situations (van Roosmalen and Klein, 1988). The types of interactions observed between the *A. f. fusciceps* individual and each member of the howler group was different. There was a high level of interaction with the juvenile female, the only reproductively available member of the group when she reached the reproductive age. Conversely, interactions observed with the group's males were more of a solely cooperative nature, commonly observed intra-specifically in groups of both *Alouatta* spp. and *Ateles* spp. (Di Fiore *et al.*, 2011).

Dietary preferences observed in the *A. f. fusciceps* individual were similar to those reported for some other *Ateles* spp. (van Roosmalen and Klein, 1988; Suárez, 2006). Although the choice of items differed from previous studies on this species (Gavilánez-Endara, 2006; Estévez-Noboa, 2009; Tirira, 2011). The low consumption of ripe fruits by the *A. f. fusciceps* individual was initially surprising, as was the high consumption of young leaves in a predominantly frugivorous species. However, this kind of adaptation has been seen in both *A. hybridus* and *A. geoffroyi* in fragmented or heavily disturbed areas (Chaves *et al.*, 2011; Abondano and Link, 2012; Schaffner *et al.*, 2012; De Luna *et al.*, 2017), with both species consuming a much higher percentage of leaves then expected from previous studies of *Ateles* spp.

Although diets were similar between the two species there was separation in food resource consumption, especially during the wet season, which might have reduced interspecific competition and facilitated the acceptance of the *A. f. fusciceps* by the howler troop. Dietary separation was noted by Defler (2004) as a possible mechanism to avoid conflict between sympatric populations of *A. belzebuth* and *Lagothrix lagothricha* in the southern Colombian Amazon. The differences found in the diets of both species between seasons will probably be a result of differences in resource availability (van Shaik *et al.*, 1993), with both species consuming a wide variety of food types. The comparatively high consumption of fruits by the *A. p. aequatorialis* group could result from their availability (Milton, 1981; Janson and Chapman, 1999) and possibly, from the absence of other large bodied arboreal frugivorous in the Ashiringa Reserve (José Macas, pers. comm.). The high consumption of leaves by the *A. f. fusciceps* individual is probably an adaptive behavior to survive in this highly fragmented area (Abondano and Link, 2012; Schaffner *et al.*, 2012; De Luna *et al.*, 2017), where higher quality resources are scarce, especially during the dry season.

An alternative, or at least complementary hypothesis for the similarities we found between the species' behaviour and diets in this study, stems from the fact that similar species living under the same ecological conditions and environmental pressures can develop similar behavioural and ecological tendencies, even more so than two separate populations of the same species living under different conditions (Strier, 2015). The similarity in activity budgets between the species could be an adaptation of the *A. f. fusciceps'* activity rhythms to living with the *A. p. aequatorialis* group, as well as to fragmentation. The observed association could represent a symbiotic relationship, rather than more tolerance (or even difficulty on the part of the *A. p aequatorialis* group in 'escaping' the presence of the *A. f. fusciceps* individual), in that both benefit from the relationship (Strier, 2015). The *A. f. fusciceps* individual benefits from incorporation into a group, winning greater protection and social contact (Chance, 1955). Whereas, the *A. p. aequatorialis* group benefits through increased group size for vigilance and in locating resources. The association also appears to be stable, with the *A. f. fusciceps* individual relating socially with all the howler group members. It is likely that the philopatric dispersal system of *Alouatta* spp. (Di Fiore *et al.*, 2011) facilitated the acceptance/tolerance of the *A. f. fusciceps* individual and/or that the individual was adopted by the howler troop as an infant, which has previously been reported by Strier (2015). However, this interpretation would need much more investigation before being accepted.

This study shows that forest fragmentation and population reductions can lead to various adaptations in behavioral and ecological responses in primates (Schwitzer *et al.*, 2011). It is possible that observations such as ours will become more common in the future as habitats are reduced and groups/individuals become increasingly isolated from populations of conspecifics.

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Appendices

Appendix 1. Description of behavioral definitions for *Ateles fusciceps fusciceps* and *Alouatta palliata aequatorialis* at Ashiringa Ecological Reserve, Pichincha Province, northwestern Ecuador.

Behavioral category	Behavioral sub-category	Definition
Resting		To be inactive in either a standing, sitting or lying position (either alone or in a group) including auto-grooming.
Feeding	Feeding	To handle, process or consume any food item.
	Foraging	To be actively and engaged in searching for food items as the predominant behavior.
Locomotion		To purposefully change location, either within or between trees, or further. This is exclusive of incidental movement whilst foraging or engaged in another behavior within the same tree.
Vocalization		To be primarily active in calling, exclusive of vocalizations during play, aggressive or sexual encounters.
Social activities	Play	To be actively engaged in repetitive, exaggerated and disjointed, solitary or social behavior with no observable goal (exclusive of all other active behaviors).
	Sexual	To be engaged in copulation or related behaviors.
	Allo-grooming	To be primarily engaged in non-aggressive physical contact with another individual (either grooming or being groomed by another individual or individuals, exclusive of sexual contact).
	Aggression/evasion	To attack, provoke or show fear towards a conspecific from within the same group or with another group (including vocalizations, branch shacking, mooning and physical contact).
Other		Watching observer. Out of sight.

Appendix 2. List of plants consumed by *A. f. fusciceps* at Ashiringa Ecological Reserve, Pichincha Province, northwestern Ecuador.

Family	Scientific name	*Item*
Apocynaceae	*Aspidosperma spruceanum*	Young leaves
Apocynaceae	*Forsteronia myriantha*	Young leaves
Bromeliaceae	*Bromelia* spp.	Young leaves
Boraginaceae	*Cordia hebeclada*	Flowers
Boraginaceae	*Cordia eriostigma*	Leaves/flowers/fruits
Cardiopteridaceae	*Dendrobangia boliviana*	Mature fruits
Cecropiaceae	*Cecropia garciae*	Hearts
Cecropiaceae	*Coussapoa herthae*	Leaves/flowers/fruits
Cecropiaceae	*Coussapoa contorta*	Mature leaves
Cecropiaceae	*Coussapoa* spp.	Fruits
Cecropiaceae	*Pourouma* spp.	Leaves
Ericaceae	*Macleania pentaptera*	Flowers
Euphorbiaceae	*Tetrorchidium macrophyllum*	Mature fruits
Fabaceae	*Dioclea* spp.	Young leaves
Fabaceae	*Pterocarpus officinalis*	Young leaves
Fabaceae	*Abarema barbouriana*	Leaves
Fabaceae	*Inga acuminata*	Fruits
Fabaceae	*Inga pezizifera*	Leaves
Fabaceae	*Inga lallensis*	Leaves/mature fruits
Fabaceae	*Inga nobilis*	Leaves
Fabaceae	*Inga silanchensis*	Fruits
Fabaceae	*Inga oerstediana*	Fruits/leaves
Fabaceae	*Dussia lehmannii*	Mature fruits
Meliaceae	*Carapa guianensis*	Bark
Meliaceae	*Guarea kunthiana*	Mature fruits
Moraceae	*Castilla* spp.	Fruits
Moraceae	*Sorocea jaramilloi*	Mature fruits
Moraceae	*Ficus trigona*	Leaves
Moraceae	*Ficus* spp.	Young leaves
Moraceae	*Ficus tonduzii*	Leaves
Moraceae	*Ficus maxima*	Young leaves
Moraceae	*Ficus rieberiana*	Leaves
Moraceae	*Ficus cuatrecasasiana*	Young leaves
Moraceae	*Naucleopsis naga*	Leaves
Moraceae	*Maquira guianensis*	Young leaves
Moraceae	*Ficus cuatrecasasiana*	Leaves
Moraceae	*Ficus carchiana*	Young leaves/hearts
Moraceae	*Brosimum utile*	Leaves/mature fruits
Myristicaceae	*Virola reidii*	Mature fruits
Myrtaceae	*Myrcia fallax*	Leaves/mature fruits
Myrtaceae	*Psidium* spp.	Mature fruits
Rubiaceae	*Guettarda ochreata*	Mature fruits
Rubiaceae	*Guettarda hirsuta*	Mature fruits
Sapindaceae	*Paullinia capreolata*	Leaves
Sapindaceae	*Billia rosea*	Mature fruits
Sapotaceae	*Pouteria capacifolia*	Young leaves/fruits
Solanaceae	*Solanum* spp.	Fruits
Violaceae	*Gloeospermum grandifolium*	Mature fruits/leaves