ASSOCIATIONS AMONG HABITAT DESTRUCTION, INFANT CARE, AND MALE ACTIVITY IN SAN MARTIN TITI MONKEYS (*Plecturocebus oenanthe*) OF PERU

A Dissertation

by

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ABSTRACT

The San Martin titi monkey (*Plecturocebus oenanthe*) is a Critically Endangered Neotropical primate endemic to Peru, where forested habitat has been dramatically altered due to anthropogenic activities. In the face of ongoing habitat destruction, research is urgently needed on the ability of *P. oenanthe* to persist in disturbed environments. Prior research has indicated that titi monkeys are able to adapt behaviorally to disturbed habitats, however such studies have addressed such flexibility regarding general activities (e.g. traveling) only. This study aimed to clarify whether level of habitat destruction is related to variation in: 1) infant care; 2) conflict between caregivers and infants; and 3) male activity budgets. I habituated two *P. oenanthe* groups and assigned relative levels of habitat destruction per site by comparing forest fragment and home range size (and loss per season), logging rate, canopy cover, tree density, tree basal area, tree height, and fruit availability. Along with two field assistants, I observed study subjects over two field seasons. We conducted focal follows of four infants using instantaneous sampling to track: 1) the percentage of care provided by age and sex class, which included male, maternal, adult (male and maternal care), alloparental (sibling), and total care (all care combined); 2) caregiver-infant conflict; and 3) the activity budgets of males while caring for infants. I predicted that level of habitat destruction would reduce infant care (except by siblings), increase caregiver-infant conflict, and lead males to adopt a time-minimizing strategy in response to habitat destruction. I analyzed infant care and male activity budgets using generalized linear mixed models. I assessed conflict data qualitatively by comparing average, minimum, and maximum values. In support of care predictions, greater habitat destruction was associated with reduced male care and increased alloparental care. Contradicting my prediction, maternal care increased with habitat destruction. Maternal and alloparental care compensated for reduced male care at the higher destruction site. As expected, conflict increased with greater habitat destruction and the male experiencing greater habitat destruction reduced energetically-costly activities. The stark variation in caregiving, conflict, and male activity across sites indicates a substantial degree of flexibility in *P. oenanthe* infant care.

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My field assistants, Daniel Morales Rodríguez and Raul Saucedo Quispe, collected portions of the behavioral data analyzed in chapters 2 and 4. Additional volunteer assistants helped to collect portions of the habitat destruction data in chapter 2. All other work conducted for this dissertation was completed by the student independently. Proyecto Mono Tocón provided research permits (Permit #s: N°0208-2012-AG-DGFFS-DGEFFS and N°329-2016-SERFOR-DGGSPFFS).

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NOMENCLATURE

M	Meters
Km	Kilometers
Ha	Hectares
DBH	Diameter at breast height
Kg	Kilogram
UTM	Universal Transverse Mercator
°C	Degrees Celsius
HD	Habitat destruction
POC	Parent-offspring conflict
GLMM	Generalized linear mixed model
VIF	Variance inflation factor
ΔAICc	Delta Akaike Information Criterion
REML	Reduced maximum likelihood
X^2	Chi-squared
POC	Parent-offspring conflict

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1. INTRODUCTION

1.1. Habitat destruction alters primate behavior

Studies on how anthropogenic habitat destruction affects non-human primates (hereafter primates) have increased in recent decades in response to the severe threat to and dramatic loss of primate populations worldwide (Carvalho *et al*. 2019; de Almeida-Rocha *et al*. 2017; Estrada *et al*. 2018; Li *et al*. 2018). Anthropogenic habitat destruction encompasses habitat loss, fragmentation, and degradation, which often results in negative socioecological outcomes for primates (Cowlishaw and Dunbar 2000; IUCN 2012; Marsh 2003). The magnitude of devastation that habitat destruction causes to primate populations has been clearly demonstrated by demographic research. Adverse outcomes include decline in population levels (Arroyo-Rodríguez *et al*. 2013; Chapman *et al*. 2006; Porter *et al*. 2013), overcrowding in small fragments (Arroyo-Rodríguez *et al*. 2013), reduced fecundity (Boyle and Smith 2010; Mbora *et al*. 2009), with increased infant mortality rates and longer interbirth intervals (Altmann and Alberts 2003; Knott 1999; Thompson *et al*. 2007; Umapathy *et al*. 2011). Habitat destruction also affects multiple aspects of primate behavior, including diet (Cristobal-Azkarate and Arroyo-Rodriguez 2007; Irwin 2008), activity budget (Boyle 2008; Boyle and Smith 2010; Mekonnen *et al*. 2017; Silva and Ferrari 2009; Wong and Sicotte 2007), spatial use of habitat (Hoffman and O'Riain 2012; Mekonnen *et al*. 2018), grouping patterns (Irwin 2007; Mbora *et al*. 2009), social behavior (Rangel-Negrín *et al*. 2016), and mating behavior (Milich 2012; Wrangham 2002).

Behavioral studies complement demographic research by providing insight into the proximate changes that underpin the aforementioned, large-scale population outcomes. Specific features of disturbed habitat (e.g. reduced quality, increased isolation, and presence of anthropogenic landscapes) interact with the behavioral, dietary, and physiological flexibility of the primates living in them so that some primates develop new strategies, while others are unable to adapt (Lootvoet *et al*. 2015; Marsh 2003; Schwitzer *et al.* 2011). Further, primates that are able to survive in anthropogenic habitats may still experience harmful effects. For instance, typically frugivorous Boutourlini's blue monkeys (*Cercopithecus mitis*) were able to survive in fragmented forest by following a primarily folivorous diet through crop foraging (Tesfaye *et al*. 2013). However, this strategy may put them at increased risk of human-induced disease (Tarara *et al*. 1985), injury, and mortality (Beamish 2009).

1.2. Food availability and parental care

While it is clear that habitat destruction affects general behaviors such as resting, traveling, and foraging, no research has directly assessed its effects on parental investment and infant care. We know that habitat destruction alters primate habitat in ways that potentially disrupt the ability of parents to care for offspring; for example, by reducing access to food resources (Chapman *et al*. 2006). Under life history theory, food availability is an extrinsic factor that may affect infant survival, which may further influence an individual's decision to invest in either current or future offspring (Stearns 1992). Extrinsic factors are expected to decrease parental investment in current offspring because parents cannot control them (e.g. predation pressure and risk of disease), In contrast, intrinsic factors (e.g. the timing of birth and length of care) may be moderated to some degree by parental decisions. Eventually, parental care will reach a saturation point beyond which additional care does not improve current infant development or survival, and parents should be likelier to terminate care as they approach this threshold (Pennington and Harpending 1998). The presence of unfavorable extrinsic conditions may lower this saturation point. In support of this prediction, Quinlan (2007) found that the severity of extrinsic factors (famine and warfare) was negatively related to maternal care efforts in humans (measured as maternal proximity, responsiveness to crying, and bodily contact). In the same study, paternal care (measured as paternal proximity and involvement with infants) was negatively related to pathogen stress.

In primates, research has suggested that mothers decrease infant care when they have markedly limited access to food resources (Dias *et al*. 2018; Fairbanks and Hinde 2013; Lee *et al.* 1991). For example, a meta-analysis by Lee *et al*. (1991) found that primate and other mammalian mothers weaned infants the earliest under markedly food-limited conditions, and these infants had low survival rates. In contrast, mothers with more moderate limitations in food availability weaned infants the latest, and these infants had high survival rates. The authors suggest that mothers under the poorest environmental conditions were unable to improve infant survival by providing extended care, and thus terminated lactation in current offspring earliest. Mothers under less challenging conditions were able to improve infant survival with continued care, but only by extending the length of lactation. Rates of maternal rejection in primates have also been related to habitat quality and reproductive tradeoffs (Hauser and Fairbanks 1988).

While a range of studies has examined how environmental variables affect primate maternal care, no research to date has done the same for paternal care. However, callitrichid studies indicate that infant carrying is energetically costly for males and can alter activity budgets. For example, captive cotton-top tamarins (*Saguinus oedipus*) spent less time in energetically costly activities (feeding, foraging, or moving) while carrying infants (Price 1992; Sánchez *et al*. 1999). Males carrying infants also lost 9–11% of body weight within 5 weeks of infant birth (Achenbach and Snowdon 2002). Additional research is needed to determine how these energetic costs translate to paternal care decisions.

1.3. Titi monkeys as a behavioral model

The titi monkey is a primate model well-suited to research on paternal care in the context of habitat destruction. Titi monkeys (genera *Callicebus*, *Cheracebus*, and *Plecturocebus*) (Byrne *et al*. 2016) are small (1.0 kg) Neotropical primates that live in small groups comprised of one female and one male. Groups may further include several offspring of various ages. Adult titi monkeys exhibit a long-lasting pair bond that is characterized by coordination of daily activities, biparental care, territorial duetting, and distress in response to physical separation (Hinde *et al*. 2016; Spence-Aizenberg *et al*. 2016). The father provides the majority of care outside of nursing, including carrying the infant, protecting the infant from predators, retrieving the distressed infant, and spending a substantial amount of time in contact and in proximity with the infant (Spence-Aizenberg *et al*. 2016). Infants are strongly attached to the adult male caregiver, which is also the putative father (Hoffman *et al*. 1995). The female nurses the infant, but is largely intolerant to infant clinging outside of this context (Fragaszy *et al*. 1982; Mendoza *et al*. 1997). Siblings are also intolerant to infant carrying, exhibiting distress and attempts to remove clinging infants. Titi monkeys inhabit a range of habitats, from continuous primary forest to secondary and anthropogenic forest fragments of various sizes and levels of destruction (Shanee *et al*. 2013). This habitat variation provides the basis for comparative behavioral research.

Titi monkeys are habitat generalists that are more resilient to habitat disturbance by humans than many other primates (DeLuycker 2007; Ferrari *et al*. 2000; García *et al*. 2010; Heiduck 2002; van Kuijk *et al*. 2015; van Roosmalen *et al.* 2002). However, the ability of titi monkeys to persist in disturbed habitat relies on significant behavioral alteration, which has unknown consequences for these populations. For instance, Souza-Alves (2013) found that fragment size was positively correlated with time spent traveling and feeding for Coimbra-Filho's titi monkeys (*Callicebus coimbrai*), suggesting that titi monkeys cope with loss of resources by reducing energetically costly activities (Schoener 1971). Titi monkeys in disturbed habitats may also engage in terrestrial behaviors more often to forage and travel (Souza-Alves *et al*. 2019). Atypical grouping patterns have been observed disturbed environments. For example, titi monkeys living in small forest fragments with high population density may form groups containing multiple same-sex adults (Bicca-Marques *et al*. 2002; Dingess 2013).

Destruction and alternation of habitat may further impact titi monkey infant care patterns. Souza-Alves (2013) found that the length of lactation in *C. coimbrai* was positively correlated with fragment size. Further, the only two cases of parental infanticide that have been reported for titi monkeys (one maternal and one paternal) were observed in disturbed habitats with high population densities (Cäsar *et al*. 2008; Dingess and Doubleday 2012). These studies demonstrate that while titi monkeys are able to cope in the face of anthropogenic disturbance, this may be at the cost of extreme behavioral changes with unknown long-term significance for populations. Understanding how titi monkeys and other primates respond to habitat changes has become critical as habitat destruction has become increasingly widespread (Estrada *et al*. 2018; Gouveia *et al*. 2016). Studies that track how habitat destruction affects reproductive behaviors and success (Behie *et al*. 2015; Dunham and Rodriguez-Saona 2018; Milich 2012; Milich *et al*. 2014) are especially important for the conservation management of threatened primates and those with declining population levels.

1.4. Study aims and goals

In this study on two groups of San Martin titi monkeys (*Plecturocebus oenanthe*), I aimed to make the first report on variation in primate paternal, maternal, and alloparental care of infants in relation to habitat destruction. I further aimed to examine the roles of paternal activity budget, seasonality, and individual study subject and study group differences as sources of variation in *P. oenanthe* infant care patterns. The goals of this Dissertation are: 1) to identify possible relationships between anthropogenic habitat destruction and ecological outcomes (forest size, habitat loss, and habitat degradation) for *P. oenanthe* habitat; 3) to identify the possible relationships between ecological indicators of habitat destruction and additional socioecological factors (seasonality, social dynamics, study subject and study group differences, and infant age) with *P. oenanthe* infant care, infant conflict, and paternal activity budgets; 3) to characterize *P. oenanthe* infant care patterns, including the range of variation; and 4) to determine whether *P. oenanthe* is capable of providing adequate infant care under the pressures of habitat destruction. I compare these results with prior studies on infant care, conflict with infants (by parents and siblings), and activity budgets in titi monkeys and other primate species to identify whether study group behavior was typical for titi monkeys, and to survey possible explanations for variation between study groups. I studied two *P. oenanthe* groups in secondary forest fragments in the San Martín region of Peru. I assessed the relative level of habitat destruction in each site and identified marked variation for numerous habitat measures, however it should be noted that both sites may be classified as highly disturbed. Thus observations regarding the biological significance of these habitat differences for titi monkey behavior are tentative. In this study, I examine the ability of *P. oenanthe* adults to provide infant care and of *P. oenanthe* adult males to cope with the energetic demands of infant care in disturbed environments.

1.5. References

Altmann J, Alberts SC (2003) Variability in reproductive success viewed from a life-history perspective in baboons. Am J Hum Biol 15:401–410

Achenbach GG, Snowdon CT (2002) Costs of caregiving: weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. Int J Primatol 23:179–189

Arroyo-Rodríguez V, González-Perez IM, Garmendia A, Solà M, Estrada A (2013) The relative impact of forest patch and landscape attributes on black howler monkey populations in the fragmented Lacandona rainforest, Mexico. Landsc Ecol 28:1717–1727

Beamish EK (2009) Causes and Consequences of Mortality and Mutilation in the Cape Peninsula Baboon Population, South Africa. Master's thesis, University of Cape Town, Cape Town

Behie AM, Pavelka MSM (2015) Fruit as a key factor in howler monkey population density: conservation implications. In: Kowalewski MM, Garber PA, Cortés-Ortiz L, Urbani B, Youlatos D (eds) Howler monkeys: behavior, ecology, and conservation. Springer, New York, NY, pp 357–382

Bicca-Marques JC, Garber PA, Azevedo-Lopes MAO (2002) Evidence of three resident adult male group members in a species of monogamous primate, the red titi monkey (*Callicebus cupreus*). Mammalia 66:138-42

Boyle SA (2008) The effects of forest fragmentation on primates in the Brazilian Amazon. Doctoral thesis, Arizona State University, Tempe, AZ

Boyle SA, Smith AT (2010) Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. Primates 51:43–51

Byrne H, Rylands AB, Carneiro JC*, et al.* (2016) Phylogenetic relationships of the New World titi monkeys (*Callicebus*): first appraisal of taxonomy based on molecular evidence. Front Zool 13:10

Carvalho JS, Graham B, Rebelo H, Bocksberger G, Meyer CFJ, Wich S, Kuhl HS (2019) A global risk assessment of primates under climate and land use/cover scenarios. Glob Chang Biol 25:3163–3178

Cäsar C, Franco ES, de Castro Nogueira Soares G, Young RJ (2008) Observed case of maternal infanticide in a wild group of black-fronted titi monkeys (*Callicebus nigrifrons*). Primates 49:143–145

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anth 131:525–534

Cowlishaw G, Dunbar RIM (2000) Primate conservation biology. University of Chicago Press, Chicago, IL

de Almeida-Rocha JM, Peres CA, Oliveira LC (2017) Primate responses to anthropogenic habitat disturbance: pantropical meta-analysis. Biol Conserv 215:30–38

DeLuycker AM (2007) The ecology and behaviour of the Río Mayo titi monkey (*Callicebus oenanthe*) in the Alto Mayo, northern Peru. Doctoral thesis, Washington University, Saint Louis, MO

Dias PAD, Cano-Huertes B, Coyohua-Fuentes A, Chavira-Ramirez DR, Canales-Espinosa D, Rangel-Negrín A (2018) Maternal condition and maternal investment during lactation in mantled howler monkeys. Am J Phys Anthropol 167:178–184

Dingess K (2013) Social flexibility in the classically monogamous titi monkey: a response to increased population pressure. Am J Phys Anth 150 (S56):113

Dingess K, Doubleday A (2012) Paternal infanticide in the socially monogamous Bolivian gray titi monkey. Am J Phys Anth 147 (S54):132

Dunham NT, Rodriguez-Saona LE (2018) Nutrient intake and balancing among female *Colobus angolensis palliatus* inhabiting structurally distinct forest areas: effects of group, season, and reproductive state. Am J Primatol 80:e22878

Estrada A, Garber PA, Mittermeier RA, *et al.* (2018) Primates in peril: the significance of Brazil, Madagascar, Indonesia and the Democratic Republic of the Congo for global primate conservation. PeerJ 6:e4869

Fairbanks LA, Hinde K (2013) Behavioral response of mothers and infants to variation in maternal condition: adaptation, compensation, and resilience. In: Clancy KBM, Hinde K, Rutherford JN (eds) Building babies: primate development in proximate and ultimate perspective. Springer, New York, NY, pp 281–302

Ferrari SF, Iwanaga S, Messias MR, Ramos EM, Ramos PCS, da Cruz Neto EH, Coutinho PEG (2000) Titi monkeys (*Callicebus spp.*, Atelidae: Platyrrhini) in the Brazilian state of Rondônia. Primates 41:229–234

Fragaszy DM, Schwarz S, Shimosaka D (1982) Longitudinal observations of care and development of infant titi monkeys (*Callicebus moloch*). Am J Primatol 2:191–200

García J, Defler TR, Bueno ML (2010) The conservation status of *Callicebus caquetensis* (Pitheciidae): a new species in Southern Caquetá Department, Colombia. Neotrop Primates 17:37–46

Gouveia SF, Souza-Alves JP, Rattis L, Dobrovolski R, Jerusalinsky L, Beltrao-Mendes R, Ferrari SF (2016) Climate and land use changes will degrade the configuration of the landscape for titi monkeys in eastern Brazil. Glob Chang Biol 22:2003–2012

Hauser MD, Fairbanks LA (1988) Mother-offspring conflict in vervet monkeys: variation in response to ecological conditions. Anim Behav 36:802–813

Heiduck S (2002) The use of disturbed and undisturbed forest by masked titi monkeys *Callicebus personatus melanochir* is proportional to food availability. Oryx 36:133–139

Hinde K, Muth C, Maninger N, *et al.* (2016) Challenges to the pair bond: neural and hormonal effects of separation and reunion in a monogamous primate. Front Behav Neurosci 10:221

Hoffman KA, Mendoza SP, Hennessy MB, Mason WA (1995) Responses of infant titi monkeys *Callicebus moloch*, to removal of one or both parents: evidence for paternal attachment. Develop Psychobiol 28:399–407

Hoffman TS, O'Riain MJ (2012) Landscape requirements of a primate population in a human-dominated environment. Front Zool 9:1

Irwin MT (2007) Living in forest fragments reduces group cohesion in diademed sifakas (*Propithecus diadema*) in eastern Madagascar by reducing food patch size. Am J Primatol 69:434–447

Irwin MT (2008) Feeding ecology of *Propithecus diadema* in forest fragments and continuous forest. Int J Primatol 29:95–115

IUCN (2012) The IUCN Red List Categories and Criteria v. 3.1. 2nd Edition. URL: <http://www.iucnredlist.org> Accessed 28 March 2020

Knott CD (1999) Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability. Doctoral thesis, Harvard University, Cambridge, MA

Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning, and maternal investment from a comparative perspective. J Zool (London) 225:99–114

Li B, Li M, Li J, *et al*. (2018) The primate extinction crisis in China: immediate challenges and a way forward. Biodivers Conserv 27:3301–3327

Lootvoet AC, Philippon J, Bessa-Gomes C (2015) Behavioural correlates of primates conservation status: intrinsic vulnerability to anthropogenic threats. PLoS ONE 10:1–11

Marsh LK (2003) Primates in fragments: ecology and conservation, 1st ed. Springer, Boston, MA

Mbora DN, Wieczkowski J, Munene E (2009) Links between habitat degradation, and social group size, ranging, fecundity, and parasite prevalence in the Tana River mangabey (*Cercocebus galeritus*). Am J Phys Anth 140: 562–571

Mekonnen A, Fashing PJ, Bekele A, Hernandez-Aguilar RA, Rueness EK, Nguyen N, Stenseth NC (2017) Impacts of habitat loss and fragmentation on the activity budget, ranging ecology and habitat use of Bale monkeys (*Chlorocebus djamdjamensis*) in the southern Ethiopian Highlands. Am J Primatol 79:e22644

Mekonnen A, Fashing PJ, Sargis EJ, Venkataraman VV, Bekele A, Hernandez-Aguilar RA, Rueness EK, Stenseth NC (2018) Flexibility in positional behavior, strata use, and substrate utilization among Bale monkeys (*Chlorocebus djamdjamensis*) in response to habitat fragmentation and degradation. Am J Primatol 80: e22760

Mendoza SP, Mason WA (1997) Attachment relationships in New World primates. Ann NY Acad Sci 807:203–209

Milich KM (2012) The impact of habitat quality on female red colobus monkey (*Procolobus rufomitratus*) reproduction. Doctoral thesis, University of Illinois, IL

Milich KM, Stumpf RM, Chambers JM, Chapman CA (2014) Female red colobus monkeys maintain their densities through flexible feeding strategies in logged forests in Kibale National Park, Uganda. Am J Phys Anth 154:52–60

Pennington R, Harpending H (1988) Fitness and fertility among the Kalahari !Kung. Am J Phys Anthropol 77:303–319

Porter L, Chism J, Defler TR, *et al.* (2013) Pitheciid conservation in Ecuador, Colombia, Peru, Bolivia and Parguay. In: Veiga LM, Barnett AA, Ferrari SF, Norconk MA (eds) Evolutionary biology and conservation of titis, sakis and uacaris. Cambridge University Press, New York, NY, pp 320–333

Price EC (1992) The costs of infant carrying in captive cotton-top tamarins. Am J Primatol 26:23–33

Quinlan RJ (2007) Human parental effort and environmental risk. Proc R Soc Lond B 274:121–125

Rangel-Negrín A, Coyohua-Fuentes A, Canales-Espinosa D, Dias PAD (2016) The loss of behavioural diversity as a consequence of anthropogenic habitat disturbance: the social interactions of black howler monkeys. Primates 57:9–15

Sánchez S, Peláez F, Gil-Bürmann C, Kaumanns W (1999) Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). Am J Primatol 48:99–111

Schoener TW (1971) Theory of feeding strategies. Annu Rev Ecol Evol Syst 2:369–404

Schwitzer C, Glatt L, Nekaris KAI, Ganzhorn JU (2011) Responses of animals to habitat alteration: an overview focussing on primates. Endanger Species Res 14:31–38

Shanee S, Tello-Alvarado JC, Vermeer J, Bóveda-Penalba AJ (2013) GIS Risk Assessment and GAP analysis for the Andean titi monkey (*Callicebus oenanthe*). Primate Conserv 26:17–23

Silva SSB, Ferrari SF (2009) Behavior patterns of southern bearded sakis (*Chiropotes satanas*) in the fragmented landscape of Eastern Brazilian Amazonia. Am J Primatol 71:1–7

Souza-Alves JP (2013) Ecology and life-history of Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) in the Brazilian Atlantic Forest. Doctoral thesis, Universidade Federal da Paraíba

Souza-Alves JP, Mourthe I, Hilário R, et al. (2019) Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus*): potential correlates, patterns, and differences between genera. Int J Primatol 40:553–572

Spence-Aizenberg A, Di Fiore A, Fernandez-Duque E (2016) Social monogamy, male-female relationships, and biparental care in wild titi monkeys (*Callicebus discolor*). Primates 57:103–112

Stearns S (1992) The evolution of life histories. Oxford University Press, Oxford, UK

Tarara R, Suleman MA, Sapolsky R, Wabomba MJ, Else JG (1985) Tuberculosis in wild olive baboons, *Papio cynocephalus anubis* (Lesson), in Kenya. J Widl Dis 21:137–140

Tesfaye D, Fashing PJ, Bekele A, Mekonnen A, Atickem A (2013) Ecological flexibility in Boutourlini's blue monkeys (*Cercopithecus mitis boutourlinii*) in Jibat Forest, Ethiopia: a comparison of habitat use, ranging behavior, and diet in intact and fragmented forest. Int J Primatol 34:615–640

Thompson ME, Kahlenberg SM, Gilby IC, Wrangham RW (2007) Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. Anim Behav 73:501–512

Umapathy G, Hussain S, Shivaji S (2011) Impact of habitat fragmentation on the eemography of lion-tailed macaque (*Macaca silenus*) populations in the rainforests of Anamalai Hills, Western Ghats, India. Int J Primatol 32:889–900

van Kuijk S, Garcia-Suikkanen C, Tello-Alvarado JC, Vermeer J, Hill CM (2015) Estimating population density of the San Martin titi monkey (*Callicebus oenanthe*) in Peru using vocalisations. Folia Primatol 86:525–533

van Roosmalen MGM, van Roosmalen T, Mittermeier RA (2002) A taxonomic review of the titi monkeys, genus *Callicebus* Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. Neotrop Primates 10(Suppl)

Wong SN, Sicotte P (2007) Activity budget and ranging patterns of *Colobus vellerosus* in forest fragments in central Ghana. Folia Primatol 78:245–254

Wrangham R (2002) The cost of sexual attraction: is there a trade-off in female *Pan* between sex appeal and received coercion? In: Boesch C, Hohmann G, Marchant IF (eds) Behavioural diversity in chimpanzees and bonobos. Cambridge University Press, Cambridge, MA, pp 204–215

2. ASSOCIATION BETWEEN HABITAT DESTRUCTION AND INFANT CARE IN SAN MARTIN TITI MONKEYS (*Plecturocebus oenanthe*)

2.1. Introduction

Due to human-caused habitat destruction (Cowlishaw and Dunbar 2000) and other anthropogenic activities, such as hunting and the illegal pet trade (Shanee 2012), 60% of primate species are threatened with extinction and 75% of populations are declining (Estrada *et al.* 2017). The activities that produce the most harmful outcomes for primate populations are loss of habitat due to agriculture, logging and wood harvesting, and livestock farming (de Almeida-Rocha *et al.* 2017; Estrada *et al*. 2017), which convert continuous forest habitat into small, poorly connected forested fragments with discontinuous canopy cover and reduced resource availability (Cowlishaw and Dunbar 2000). For example, long-term research in Kibale National Park, Uganda showed that heavy logging creates large gaps in the canopy (Chapman and Chapman 1997) and forest clearing for agriculture resulted in an average decrease of 29.5% in basal area of food trees for red colobus (*Piliocolobus tephrosceles*) in forest fragments (Chapman *et al.* 2006). These outcomes have been shown to lower primate survival and persistence, making them suitable proxies of habitat destruction for primate research (Andrén 1994; Anzures-Dadda and Manson 2007; Pyritz *et al*. 2010; Rangel-Negrín *et al*. 2016).

Habitat destruction affects multiple aspects of primate behavior, including diet, activity budget, grouping patterns, and spatial use of habitat (Schwitzer *et al*. 2011). Some primates have been able to adapt to anthropogenic landscapes depending on the behavioral, dietary, and physiological flexibility of the species (Lootvoet *et al.* 2015; Onderdonk and Chapman 2000;

Schwitzer *et al.* 2011). However, primates in such environments may still experience increased risk of human-induced disease, injury, and mortality (Beamish 2009; Tarara *et al.* 1985).

Despite the extensive literature on how habitat destruction alters general behavior in primates, only a few studies have discussed its impacts on reproductive behavior (e.g. Bicca-Marques *et al.* 2002; Dingess 2013; Milich 2012). Rangel-Negrín *et al.* (2016) recorded displays of 45 types of social interactions, including six reproductive behaviors related to mating, and found that the diversity of behavior was significantly negatively correlated with habitat loss (but not with group size) in black howler monkeys (*Alouatta pigra*). Strikingly, the behavioral repertoires of groups living in larger habitats were up to twice the size of those observed in groups occupying smaller areas. The authors hypothesized that because social interactions are energy-demanding activities, the loss of some behaviors may have been part of an energy-minimizing strategy.

Parental investment and infant care patterns might also change in response to habitat destruction. For instance, while titi monkeys living in captivity (Fragaszy *et al.* 1982) or in undisturbed habitat (Fernandez-Duque *et al.* 2013; Wright 1990) provide extensive parental care, some preliminary findings indicate that parental investment might change in response to habitat destruction. A study by Souza-Alves (2013) found that for Coimbra-Filho's titi monkeys (*Callicebus coimbrai*), living in a highly disturbed forest fragment was associated with earlier weaning and a longer interbirth interval compared with inhabiting a less disturbed fragment.

Additionally, anecdotal data from an extensive study on a group of San Martin titi monkeys (*Plecturocebus oenanthe*) inhabiting a 3-hectare (ha) fragment of anthropogenic forest in a Peruvian city noted that the female juvenile engaged in lengthy bouts of infant carrying (DeLuycker 2007). This was unusual since alloparental care by titi monkey siblings is typically brief in duration (bouts <1 minute) (DeLuycker 2007) and infrequent (2% of carrying: Fragaszy *et al.* 1982; 6% of infant contact: Wright 1984). Moreover, while titi monkeys do not typically produce twins, studies of rare cases in which twins are born did not document additional care by siblings to compensate for the inability of parents to raise multiple offspring simultaneously (de Santana *et al.* 2014; Knogge and Heymann 1995; Lawrence 2007; Valeggia *et al.* 1999).

Systematic, long-term research on how habitat destruction impacts primate reproductive behaviors is necessary to improve conservation planning. Such studies can help identify environmental thresholds at which behavior changes and adaptive limits are met (Fairbanks *et al.* 2010; Lee *et al.*1991; Strier 2009). Survival to maturity is an important factor for population growth (Blomquist *et al.* 2009). Additionally, habitat destruction and degradation may also influence energetic reserves and reproductive rates (Altmann and Alberts 2003). For these reasons, assessing changes in infant care behavior specifically will be important for designing conservation measures that aim to ensure long-term population survival.

To address this, I conducted comparative research to determine whether and how habitat destruction impacts primate parental investment and infant care patterns in the Critically Endangered San Martin titi monkey. I hypothesized that level of habitat destruction alters infant care in *P. oenanthe.* I predicted that the a higher level of HD would be associated with lower percentages of 1) male care, 2) maternal care, 3) adult care, and 4) total care. To determine whether adults exhibited compensatory care, I examined whether percentages of male care and percentages of maternal care were correlated. I expected 5) a negative correlation between male and maternal care under a higher level of HD and a positive correlation under a lower level of HD. As discussed previously, extensive care by siblings is unusual in titi monkeys, however their contributions may increase in disturbed environments (DeLuycker 2007). Therefore, I predicted that the percentages of alloparental care by siblings would increase 6) at the site with greater habitat destruction and 7) negatively correlated with adult care. Despite alloparenting efforts, I did not expect siblings to fully compensate for any losses in adult care.

2.2. Methods

2.2.1. Study sites

This study took place in the San Martín region of northeastern Peru (Figure 2-1) during two field seasons, from July to December 2015 and from August 2016 to January 2017. The dry season occurs roughly from May to September and the wet season extends from October to April (DeLuycker 2007). DeLuycker (2006) has previously described the geography and climate of the Alto Mayo Valley where sites were located. Vegetation is premontane tropical forest (DeLuycker 2007; Holdridge 1967). I selected two small secondary forest fragments located 8.67 km apart as study sites (Figure 2-1). I designated these by the names of towns that were in close proximity, Calzada (UTM coordinates: 9331207.84 northing, 267581.92 easting, 18M) and Yantaló (UTM coordinates: 9337614.99 northing, 273723.07 easting, 18M).

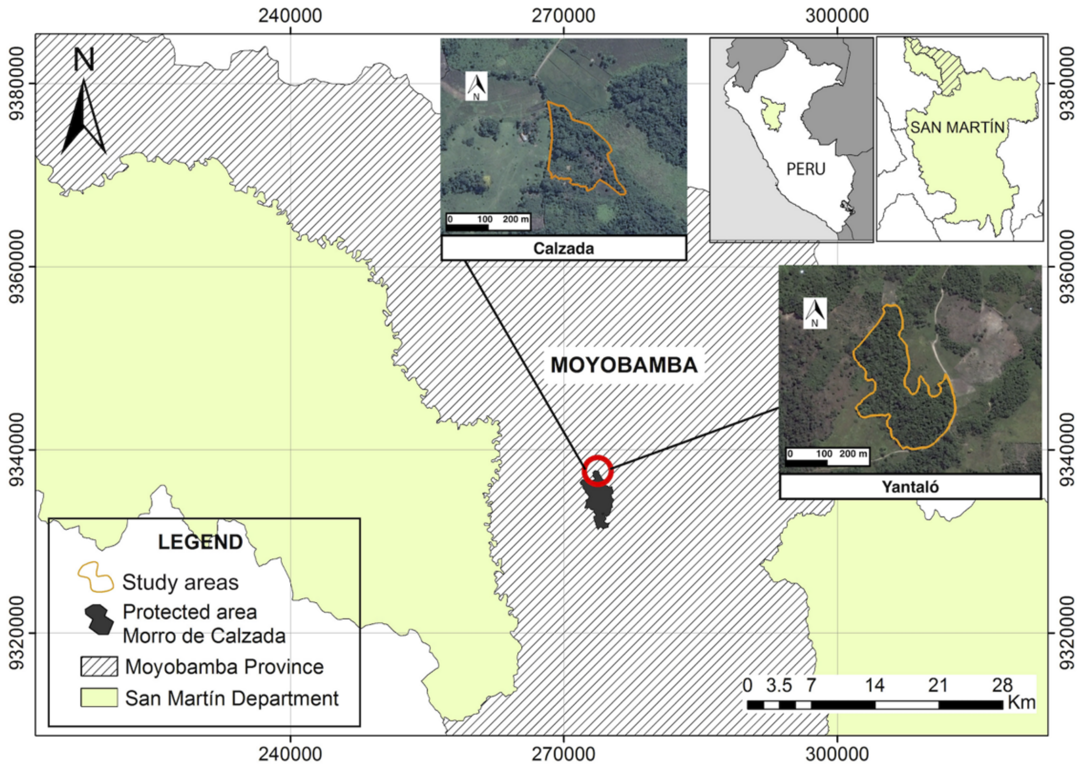

Figure 2-1 Field sites (*top center*: Calzada; *middle right*: Yantaló) were located in the Moyobamba Province of the San Martín region in Peru. This image was reproduced from the Figure 1 map in Hodges (2020b) with copyright permission from Japan Monkey Centre and Springer Japan KK.

Study site vegetation was characterized as secondary forest with *Cecropia*-dominated stands, Melastomataceae spp., shrubs, and viney thickets. Sites had undergone habitat destruction in the form of forest-clearing and selective logging. Each study location was surrounded by cultivated fields (crops were mainly rice, coffee, and plantains), cow pastures, and dirt roads. Study fragments were connected to several small neighboring fragments by areas of patchy connectivity with gaps of 5 meters (m) or more in forest canopy. The minimum distance between study fragments and neighboring fragments was 80 m at Calzada and 10 m at Yantaló. Several permanently and seasonally occupied residences were within 100 m of each site, and each study area was accessible by narrow dirt roads, which were used daily by foot traffic, motorcycles, and "mototaxis" (motorized rickshaws).

2.2.2. Habitat destruction data collection and analysis

I assigned relative level of habitat destruction at each site by conducting a broad, quantitative assessment of habitat. Historically, titi monkeys have inhabited undisturbed, continuous, primary forest. Therefore, in the first field season I made an approximate assessment of the relative level of habitat destruction (lower or higher) that had already occurred by estimating fragment size and home range size. I calculated fragment and home range sizes as area in m^2 using ArcGIS version 10.2.2 (ESRI 2014). I took the same measurements in the second field season, and compared the loss of fragment and home range size between field seasons to compare ongoing destruction.

In the second field season, I further characterized habitat and ongoing habitat destruction at each site by measuring canopy cover, logging frequency, tree density, tree basal area, tree height, and fruit availability. I collected these data in randomly-placed 2 x 50-m phenological transects (area = 100 m^2 per transect, 400 m^2 per site). I collected transect data from September (end of the dry season) through January (wet season). Within transects, I calculated canopy cover using a spherical densiometer in each transect by taking measurements every 5 m, from 0–50 m. At each sample point, four measurements of canopy gap were recorded, averaged, and multiplied by 1.04 to obtain sample percentages of overhead gap. These values were then subtracted from 1.0 to estimate canopy coverage. I assessed canopy cover once in the second field season.

I flagged and measured the diameter at breast height (DBH) of each living tree with a DBH of ≥10 cm within transects and took remaining indices of habitat destruction once per month for the five months during which behavioral data collection took place. I estimated logging frequency as the monthly proportion of trees logged within transects, divided by total number of trees present in the prior month. I estimated tree density as the number of trees per transect, and basal area (*BA*) as the total area (m^2) of trees using the following formula:

$$BA = \frac{(\pi)}{4*10000} * DBH^2$$

Prior to data collection, I practiced estimating tree height (m) by eye until I was able to obtain accurate and consistent measures. I recruited and trained field assistants in visual height estimation until estimates agreed reliably. Since fruit comprises approximately 35% of dietary composition for *P. oenanthe* (DeLuycker 2007), I used fruit availability as a rough calculation of food availability. Per transect, I calculated the mean basal area (m^2) of all fruit-bearing trees to obtain total fruit availability estimates. I divided these measurements by the respective number of individuals (adults and immature offspring, excluding infants) in each group.

I analyzed habitat data in R version 3.5.1 (R Core Team 2017). I reported raw data for indices with small sample sizes (fragment size, home range size, and habitat loss). For the remaining measures, I assessed normality with Shapiro-Wilk tests and compared data using *t*-tests for normally-distributed data and Mann-Whitney *U*-tests for non-normal data (alpha = 0.05 for all tests). I used Bartlett's test to assess equal variances for normal data. Prior research has shown that one of the most significant outcomes of habitat destruction for primates is loss of food, since food availability impacts population persistence, activity budgets, reproductive behavior, and maternal care (Cowlishaw and Dunbar 2000; Fairbanks *et al*. 2010; Fairbanks and McGuire 1995; Hauser and Fairbanks 1988; Milich 2012; Souza-Alves 2013). Therefore, of the measures taken I assigned the most importance to those that best reflected access to food resources. These were fragment size, home range size, tree density, basal area of trees, and fruit availability (Chapman *et al.* 1992; Chapman *et al*. 2006).

2.2.3. Study species and groups

Like other species of titi monkey, *P. oenanthe* gives birth to singletons and typically forms groups composed of a single pair of breeding adults and several offspring of various ages (Bicca-Marques and Heymann 2013; DeLuycker 2014; Spence-Aizenberg *et al.* 2016). The adult male (and putative father) is the primary attachment figure and carrier for infants. Paternal care is significant in *P. oenanthe* and mainly takes the form of infant transport and retrieval, which begins as early as 24 hours following birth (DeLuycker 2014). The bulk of maternal care consists of nursing. Siblings typically do not provide care other than briefly tolerating infants clinging to them (Fragaszy *et al.* 1982).

I conducted research on two groups – one at Calzada and one at Yantaló (shown in Figure 2-1). Over the two field seasons, I collected data on four infants total (one per season at each of the two sites). For each group, I identified the age and sex class of individuals based on pelage coloration, facial markings, body build, and genitalia (DeLuycker 2007). Using identifying marks, I was able to verify that the same adults were present in both field seasons. I classified study subjects into four categories: adult, subadult (mature but undispersed), juvenile (immature with a smaller body size, but weaned and traveling independently all of the time), and infant (dependent on the care of others for food and travel) (DeLuycker 2006). The Calzada group (Figure 2-2) was composed of an adult pair, a subadult female (absent the next field season), a subadult male, a juvenile female (classed as a subadult in next field season), and infants born in both field seasons who survived through the duration of the study. The Yantaló group (Figure 2-3) was composed of an adult pair, a subadult female, and infants born in each field season. The infant born in first field season disappeared sometime after data collection ended and was presumed to have died or been captured for the illegal pet trade. Since I was unable to genetically test the paternity of infants, I use the term "male care" instead of "paternal care."

Figure 2-2 The Calzada group. *Top left*: Adult male carrying the 2016 infant (2.1 months), adult female, subadult male. *Bottom left*: Subadult female (absent in 2016), subadult female (juvenile in 2015), and the 2015 infant pictured first as a juvenile (18 months) and again as an infant (4.3 months, born July 2015).

Figure 2-3 The Yantaló group. *Top left*: Adult male carrying the 2016 infant (3.5 months old, born August 2016) and adult female. *Bottom left*: Subadult female and the 2016 infant (3.1 months in this image).

2.2.4. Infant care data collection

I trained two field assistants to help with behavioral data collection, Daniel Morales Rodríguez and Raul Saucedo Quispe, and verified that we achieved consistent agreement on the individual identity and activity category designations prior to formal data collection. I used the index of concordance (Martin and Bateson 2007) to test for interobserver reliability between my observations and each of theirs in 30-minute parallel observation training sessions (Daniel: 93.33%, $N = 10$; Raul: 96%, $N = 10$). We collected infant care data on four infants total, focusing on behaviors that directly benefited infants while costing caregivers time and energy that could have been dedicated to personal survival or future reproduction (Clutton-Brock 1991). Infant care behaviors are defined in Table 2-1. Food-sharing was not observed in this study, and was thus not defined. In addition, play behavior was not included since is not clear that this is always an infant-directed behavior, or one that is costly to the caregiver.

Table 2-1 Ethogram of infant care behaviors in the San Martin titi monkey.

Activity	Definition
Nurse	Infant’s face is placed against the chest of the mother, sometimes accompanied by visible suckling
Carry	Infant clings to a caregiver in the absence of nursing
Crouch over	Caregiver positions their trunk ventrally over and in contact with the infant
Clean	Caregiver licks infant body parts
Inspect	Caregiver holds and scans infant’s body parts
Groom	Caregiver picks through infant's fur using hands
Retrieve	Caregiver places body in contact with infant and allows infant to cling to caregiver

Observers used instantaneous focal sampling every two minutes to record data during daily follows (Altmann 1974). Infants were the subjects of focal follows, and thus only the behavior of infants and individuals providing care was systematically recorded. Data collection on infants and caregivers stopped when infants were out of sight. When infants received care, we noted the individual that provided it and the study group, date, time of day, and the weather (no rain, light rain, or heavy rain). I later matched this data with infant age (in months), tropical season (wet or dry), and temperature in degrees Celsius (°C) based on climate data retrieved from the National Meteorology and Hydrology Service of Peru (SENAMHI 2017). I controlled for the effects of time of day on behavior by categorizing diurnal periods as morning (prior to 11:00), midday (11:00–13:00), or afternoon (after 13:00). We attempted to randomly rotate infant observations between groups, but this was often not possible due to staggered birthdates. On average, we conducted follows three days per week in 2015 and once per week in 2016.

Prior to analysis, I modified the dataset to improve its reliability. Since study subjects always rested during heavy rain, I removed observations recorded during this weather to control for its impact on behavior. Data characteristics are reported in Table 2-2. Infant IDs refer to the study site and field season. In total, we recorded 11,438 instantaneous sample points (roughly 390 hours) across 106 focal follow days. I observed Calzada infants for 62 days, and Yantaló infants for 44 days. I recorded approximately 1.5 times as much data in Calzada (239 hours) as in Yantaló (151 hours). Infant ranged from 0–6 months of age during data collection. Though observation began in month 0 for each infant, data collection began later (between weeks 1–3 of age) for both Yantaló infants than for Calzada infants (between weeks 0–2 of age).

Table 2-2 Data characteristics by San Martin titi monkey infant study subjects.

Infant ID	Birthdate	Days observed	Hours observed	Ages observed		Season
				Months	Weeks	
Calzada 1	14 July 2015	42	152.5	0–4 months	2–17 weeks	Dry–Wet
Calzada 2	24 Sept. 2016	20	86.6	0–4 months	0–18 weeks	Wet
Yantaló 1	2 Oct. 2015	21	66.9	0–2 months	3–8 weeks	Wet
Yantaló 2	10 Aug. 2016	23	83.8	0–6 months	1–24 weeks	Dry–Wet

Dry season occurs from May to September and wet season occurs from October to April.

I transformed raw data into percentages of infant care according to study site, infant age, field season, time of day, and sample observation day. This was done for each age and sex class to track the following five different percentages of infant care: male (and possibly paternal), maternal, adult (male and maternal care combined), alloparental (by siblings), or total care (adult plus alloparental care). I then removed instantaneous data points for those samples with fewer than 20 minutes of focal follow data. I calculated sample percentages ($N = 211$ per care category) by dividing the sum of instantaneous data points per activity by the total number of points recorded and multiplying these by 100 (package dplyr). I used R Studio (R Development Core Team 2017) to transform and analyze all data.

Qualitative analysis of data prior to modeling indicated that tropical season was highly conflated with infant age and group. For instance, infants in Calzada were born during the dry season, while one in Yantaló was born in the dry season and the other in the wet season. For this reason, I was unable to analyze the influence of season on infant care. The same was true of temperature, which I did not examine. Similarly, infant identity and study site were conflated, as there were only two infants per study site. Further, Bolker *et al.* (2009) recommend >5–6 levels per random effect. Therefore, I also excluded infant identity from models.

2.2.5. Infant care data analysis

I used generalized linear mixed models (GLMMs) in R (R Development Core Team, 2017) with package lme4 to examine the effect of level of habitat destruction (hereafter HD) on percentages of male, maternal, adult, alloparental, and total infant care (Bolker *et al.* 2009). Fixed effects included study site identity (later equated with a higher or lower level of HD), and infant age (in months). I further included field season (comprising variation in temperature, season, and infant identity) as a fixed effect instead of a random effect since there were only two levels. I coded time of day as a random effect and included sample number (1–204) as an observation level random effect to minimize overdispersion (Xavier 2014). I fit models with a binomial error distribution and logit link and used maximum likelihood to estimate parameters. Instantaneous observation counts provided weights for percentage samples. I assessed multicollinearity among fixed effects with variance inflation factors (VIFs) (package car) (Zuur *et al*. 2010).

To assess model fit, I calculated the difference between small-sample corrected Akaike Information Criterion (ΔAICc) values with package aods3 (Burnham and Anderson 200). Next I compared nested models using likelihood X^2 ratio tests (alpha = 0.05) to determine whether simpler or more complex models were preferred (Anderson *et al*. 2000; Bolker *et al*. 2009). In the interest of full reporting, I refit both the interaction and main effects models using restricted maximum likelihood estimation (REML) and carried out Wald X^2 tests of fixed effects with package glmmTMB (alpha = 0.05) (Bolker *et al*. 2009).

I reported effect sizes as odds ratio estimates, which indicated the magnitude of each fixed effect on infant care (Fleiss and Berlin 2009). Odds ratios equal or close to 1 indicate that a predictor had a similar effect across all levels. Those <1 indicate a lower magnitude of influence, while those >1 signify a greater magnitude of influence. The odds ratios for level of HD specified the odds of infant care at Yantaló (lower HD site) with Calzada (higher HD site). The odds ratios for infant age (in months) indicate the change in odds of infant care per month. The interaction term (level of HD x age) odds ratio describes whether infant age had a greater or smaller effect on care in Yantaló compared with the Calzada. The odds ratios for field season indicate the odds of infant care in the second field season compared with the first.

I carried out *post-hoc* examinations of infant care by level of HD across infant ages using Mann-Whitney *U*-tests. The maximum age of infants during data collection was four months in Calzada and six months in Yantaló. Therefore, I conducted statistical comparisons of care percentages only for months 0–4 months of age ($N = 202$ daily focal follow percentages). Since three siblings were present each field season in Calzada while only one was present in Yantaló, I further calculated alloparental care percentages per individual by dividing values by the number of siblings in each group. To determine whether one adult provided compensatory care for the other, or if siblings provided additional alloparenting due to a lack of adult care, I assessed the relationship between male and maternal care, and between alloparental and adult care at each site. For Calzada, I tested this relationship for all alloparental care as well as alloparental care percentages per individual. These associations were evaluated using Spearman's rank correlation (data were determined to be non-normal). I generated box plots of percentage data used in GLMMs (package ggplot2).

2.3. Results

2.3.1. Level of habitat destruction

Table 2-3 shows values for the habitat destruction indices. Forest fragment size and tree density measures in Calzada were half the size of those in Yantaló, and fruit availability was lower by 16.09% (0.28 m^2) per transect in Calzada. The percentage of fragment size loss between the first and second field seasons similar between Yantaló (3.12%) and Calzada (2.16%). The loss of home range area (Table 2-3) for the Calzada group (7.10%) was much larger than that of the Yantaló group (4.17%). To compensate, for the loss of home range area due to forest clearing, the Calzada group expanded their home range into that of a neighboring titi monkey group, adding 436 m^2 (6.6%) of new home range area.

Table 2-3 Comparisons of indices of habitat destruction across field sites in Peru.

	Site comparison of habitat destruction measurements			
Index	Calzada (higher HD)	Yantaló (lower HD)	Statistic	*P*-value
Fragment 2015*	21,700 m^2	42,365 m^2	————	————
Fragment 2016*	21,232 m^2	40,600 m^2	————	————
Fragment loss*	2.16%	3.12%	————	————
Home range 2015*	6,595 m^2	22,503 m^2	————	————
Home range 2016*	6,563 m^2	21,800 m^2	————	————
Home range loss*	7.10%	4.17%	————	————
Canopy cover	94.60 ± 0.01%	94.70 ± 0.01%	t = -0.05	0.9580
Logging rate	0.008 ± 0.01%	0.002 ± 0.00%	U = 8.50	1.000
Tree density	**15.50 ± 1.59 trees**	**32.9 ± 1.32 trees**	**t = -8.43**	**<0.001**
Tree basal area	7.28 ± 1.24 m^2	5.21 ± 0.48 m^2	U = 225	0.5059
Forest height	8.00 ± 0.37 m	8.27 ± 0.18 m	U = 140	0.1062
Fruit availability	**1.46 ± 0.00 m^2**	**1.74 ± 0.01 m^2**	**U = 0**	**0.0114**

Logging rate was calculated as the mean value for all transects over five months. Remaining measures were estimated as mean values (± SEM) per 100 m^2 transect across five months. I used *T*-tests for normal data and Mann-Whitney *U*-tests for non-normal data. Significant results are bolded (P<0.05). *Raw measures reported.

Sites were not significantly different for the remaining indices (Table 2-3). Logging was relatively infrequent (<0.01% of trees per month) at both sites. Within transects, two trees were logged in Calzada and one in Yantaló in the second field season. Mean canopy cover and tree height were highly similar across sites. Interestingly, basal area was 40% larger in Calzada than in Yantaló, which is the only measure that indicated a lower level of HD in Calzada. However, this difference was not significant according to a Mann-Whitney *U*-test (P = 0.5059). Of the measures that best reflected access to food resources (fragment size, home range size, tree density, tree basal area, and fruit availability), Calzada exhibited reduced access compared with Yantaló for all but one metric (tree basal area). Based on these results, Calzada was considered to exhibit a higher degree of HD and Yantaló a lower degree of HD. These designations refer to categorical levels of HD within infant care models.

2.3.2. Final models of infant care

Table 2-4 shows the results of model comparisons based on ΔAICc and likelihood X^2 ratio testing. The interaction and full main effects models of male care performed similarly well with ΔAICc values ranging from 0–3.92. Likelihood test results indicated that more complex models were preferred over simpler ones ($P<0.05$). However, the interaction model exhibited a maximum VIF >2, indicating potential multicollinearity issues. Maternal care models exhibited the same patterns, though differences between ΔAICc values for interaction and full main effects model (16.25 vs. 3.92) were larger. The X^2 statistic comparing the interaction and full main effects model was larger as well (maternal: 18.39, male: 6.06).

Table 2-4 Comparisons of interaction and main effects models of infant care using ΔAICc, VIF values, and Likelihood X^2 ratio tests.

				Likelihood ratio tests		
	Models	ΔAICc	Max VIF	X^2	*df*	*P*-value
Male						
Interaction model	**HD x A + F**	**0.00**	**5.01**	**6.06**	**1**	**0.0138**
Main effects models	**HD + A + F**	**3.92**	**1.20**	**18.02**	**1**	**<0.001**
	A + F	**19.83**	**1.19**	**99.31**	**1**	**<0.001**
	F	117.04	——	0.87	1	0.3498
	Intercept	115.83	——	——	–	———
Maternal						
Interaction model	**HD x A + F**	**0.00**	**4.90**	**18.39**	**1**	**<0.001**
Main effects models	**HD + A + F**	**16.25**	**1.09**	**5.53**	**1**	**0.0187**
	A + F	**19.66**	**1.08**	**22.28**	**1**	**<0.001**
	F	**39.85**	——	**17.44**	**1**	**<0.001**
	Intercept	55.20	——	——	–	———
Adult						
Interaction model	HD x A + F	2.00	5.26	0.14	1	0.7133
Main effects models	**HD + A + F**	**0.00**	**1.24**	**10.71**	**1**	**0.0011**
	A + F	**8.60**	**1.22**	**181.33**	**1**	**<0.001**
	F	187.83	——	2.93	1	0.0867
	Intercept	188.68	——	——	–	———
Alloparental						
Interaction model	HD x A + F	2.11	3.02	0.03	1	0.8601
Main effects models	**HD + A + F**	**0.00**	**1.06**	**35.10**	**1**	**<0.001**
	A + F	32.98	1.00	0.50	1	0.4781
	F	**31.38**	——	**40.59**	**1**	**<0.001**
	Intercept	69.90	——	——	–	———
Total						
Interaction model	**HD x A + F**	**0.00**	**5.94**	**10.70**	**1**	**0.0011**
Main effects models	HD + A + F	7.40	1.26	0.95	1	0.3295
	A + F	**8.56**	**1.23**	**231.36**	**1**	**<0.001**
	F	**236.66**	——	**11.19**	**1**	**0.0008**
	Intercept	245.76	——	——	–	———

Infant care models fit by relative level of habitat destruction (HD), infant age (A), and field season (F). Likelihood ratio test results indicate whether a simpler model is preferred (null hypothesis) compared to the next most complex model. The likelihood-ratio *P*-value assesses the comparison of the model in the respective row (more complex) with the one below (simpler). Significant *P*-values ($P<0.05$) are bolded and indicate that more complex models (also bolded) are preferred.

The full main effects and two-term model (age and field season) fit adult care the best, while the other models were not preferred according to likelihood ratio testing ($P>0.05$). The interaction model of adult care also fit the data well (ΔAICc = 2.00), though likelihood ratio testing indicated that the interaction term did not improve data prediction ($P = 0.7133$). Alloparental care was best predicted by the full main effects model (ΔAICc = 0.00), while the two-term model (age and field season) and interaction model did not significantly improve data fit ($P = 0.8601$and $P = 0.4781$, respectively). The interaction and two-term models (age and field season) of total care were preferred over the other models ($P = 0.0011$ and $P<0.001$, respectively). Overall, interaction models had the lowest ΔAICc for male, maternal, and total infant care, but these also had maximum VIFs >2. The full main effects models had the lowest ΔAICc for adult and alloparental care.

2.3.3. Fixed effects tests of best performing infant care models

Table 2-5 summarizes the results of the Wald X^2 fixed effects tests for predictors in the most complex models (interaction and main effects), and reports the odds ratio of each predictor. For level of HD, the odds ratio compares the odds of care at the lower HD site (Yantaló) with the higher HD site (Calzada). The odds for field season are expressed as odds of care in the second field season compared with the first field season. For infant age, positive correlations are indicated by odds ratios >1 and negative correlations by odds ratios <1.

Table 2-5 Wald X^2 fixed effects tests and effect sizes for interaction and full main effects models of infant care.

		Effect size	Wald tests		
Models	Fixed effects	Odds ratio	X^2	*df*	*P*-value
Male					
Interaction model	**HD x Age**	0.64	4.21	**1**	**0.0426**
	HD	7.12	16.38	**1**	**<0.001**
	Age	0.38	104.33	**1**	**<0.001**
	F	2.22	0.31	1	0.5807
Main effects model	**HD**	3.05	16.40	**1**	**<0.001**
	Age	0.31	106.09	**1**	**<0.001**
	F	1.91	4.71	**1**	**0.0300**
Maternal					
Interaction model	**HD x Age**	2.71	14.98	**1**	**0.0001**
	HD	0.11	4.61	**1**	**0.0317**
	Age	0.34	20.28	**1**	**<0.001**
	F	0.41	6.79	**1**	**0.0092**
Main effects model	**HD**	0.52	4.29	**1**	**0.0384**
	Age	0.54	19.85	**1**	**<0.001**
	F	0.59	2.51	1	0.1130
Adult					
Interaction model	HD x Age	1.12	0.26	1	0.6072
	HD	1.83	9.80	**1**	**0.0017**
	Age	0.19	199.66	**1**	**<0.001**
	F	2.26	7.47	**1**	**0.0063**
Main effects model	**HD**	2.27	9.83	**1**	**0.0017**
	Age	0.20	199.65	**1**	**<0.001**
	F	2.33	8.67	**1**	**0.0032**
Alloparental					
Interaction model	HD x Age	1.00	0.0	1	0.9943
	HD	0.14	25.41	**1**	**<0.001**
	Age	0.79	2.08	1	0.1496
	F	0.17	18.46	**1**	**<0.001**

Table 2-5 Continued

Models	Fixed effects	Effect size Odds ratio	Wald tests X^2	*df*	*P*-value
Alloparental					
Main effects model	**HD**	0.14	25.65	**1**	**<0.001**
	Age	0.79	2.10	1	0.1474
	F	0.17	20.11	**1**	**<0.001**
Total					
Interaction model	**HD x Age**	1.97	10.00	**1**	**0.0016**
	HD	0.31	1.17	1	0.2800
	Age	0.10	246.83	**1**	**<0.001**
	F	1.66	3.08	1	0.0794
Main effects model	HD	1.29	0.96	1	0.3281
	Age	0.15	236.87	**1**	**<0.001**
	F	2.02	5.73	**1**	**0.0166**

Wald X^2 tests of fixed effects were carried out for interaction and main effects models. Terms with significant *P*-values (*P*<0.05) are bolded.

For male care, all predictors were significantly related to infant care in at least one of the models. The odds of male care were between 3.05–7.12 times greater at the lower HD site (Yantaló) than at the higher HD site (Calzada). Male care was significantly negatively related to infant age (*P*<0.001), so that with each increase in month of infant age the odds of male care were between 0.31–0.38 those of the previous month. The interaction between level of HD and infant age was also significant (*P* = 0.0426) for male care. The odds ratio of the interaction term (0.64) indicated that the effect of infant age on male care was smaller for the lower HD site than for the higher HD site. This signifies that with each month, the gap in care between sites grew larger. The odds ratios for field season (1.91–2.22) specified that the odds of male care were greater in the second season compared with the first season, however this predictor was only significant in the main effects model (*P* = 0.0300).

For maternal care, all terms were significant in the interaction model (including the interaction term) and only field season was non-significant in the full model. The odds of maternal care at the lower HD site were between 0.11–0.52 times those at the higher HD site. Taking the inverse of these values, this can be restated to show that the odds of maternal care were 1.92–9.09 times the odds at the lower HD site. Maternal care was significantly negatively related to infant age, and the odds of maternal care were 0.34–0.54 those of the previous month. The interaction odds ratio (2.71) showed that infant age had a greater effect on odds of maternal care the lower HD site than at the higher HD site, indicating a widening gap over time for this form of care.

All main effects, but not the interaction term, were significant in models of adult care. The odds of care at the lower HD site were between 1.83–2.27 times those at the higher HD site. Adult care was significantly negatively related to infant age. With each month of infant age, the odds of adult care were 0.19–0.20 those of the previous month. The odds of care in the second field season were 2.26–2.33 those of the first season. Though not significant, the odds ratio for the interaction term (1.12) showed that infant age had a slightly greater effect on adult care at the lower HD site. Given the higher rate of adult care at the lower HD site, this indicated a reduction in differences between adult care across sites with each month of infant age.

In both the interaction and full main effects alloparental models, only level of HD and field season were significant. Alloparental care differed significantly by level of HD (*P*<0.001). The odds of care at the lower HD site were 0.14 times those at the higher HD site. Taking the inverse, this means that the odds of alloparenting were 7.14 greater at the higher HD site. The odds ratio for field season (0.17) indicated much lower odds of alloparental care during the second field season compared with the first field season. Of the non-significant terms infant age showed an odds ratio of 0.79, indicating a large decrease in odds of alloparental care over time. The interaction odds ratio was 1.00, showing that infant age influenced alloparenting nearly equally across sites.

Models of total care were less straightforward. The interaction model indicated that the interaction term and infant age were significant, while level of HD was not. This may indicate a crossover effect or multicollinearity issues. The interaction between level of HD and infant age are further explored in *post-hoc* test results. Looking at the odds ratios, the interaction value (1.97) indicated that the effect of infant age were greater on the odds of total care at the lower HD site than at the higher HD site. This means that the difference between total care between sites closed over time. Total care was significantly negatively correlated with infant age in both models. Per month of infant age, odds of total care were 0.10–0.15 those of the previous month. In the main effects model, field season was significantly correlated with total care. The odds ratio (2.02) indicated that odds of total care were greater in the second field season compared with the first.

Finally, the odds ratios for level of HD exhibited large discrepancies between total care models. The odds ratio was 0.31 (decreased odds of care at the lower HD site) in the interaction model and 1.29 (increased odds of care at the lower HD site) in the main effects model. The large maximum VIF value (Table 2-4: 5.94) for the total care interaction model indicates that multicollinearity may have been an issue. Additionally, this may indicate a cross-over effect between level of HD and infant age. This could mean that infant age differentially affected total care at each site, while level of HD did not significantly affect total care.

2.3.4. *Post-hoc* inspections of infant care

Figure 2-4 displays mean daily care percentages by level of HD and infant age in box plots (N = 211). Mann-Whitney U-test results were conducted to compare percentages of care by month of infant age across sites. Significant differences are noted in Figure 2-2 with an asterisk. Male care was significantly lower at the higher HD site compared with the lower HD site in months 0 (U = 25, P = 0.0033), 2 (U = 122, P = 0.0104), 3 (U = 42, P = 0.0105), and 4 (U = 10, P = 0.0023). Differences in male care were close to significant in month 1 (U = 512, P = 0.0680). Maternal care was significantly greater at the higher HD site in month 0 (U = 114, P = 0.0434), with differences in month 1 also being close to significance (U = 838, P = 0.0822) and month 4 (U = 31, P = 0.1008).

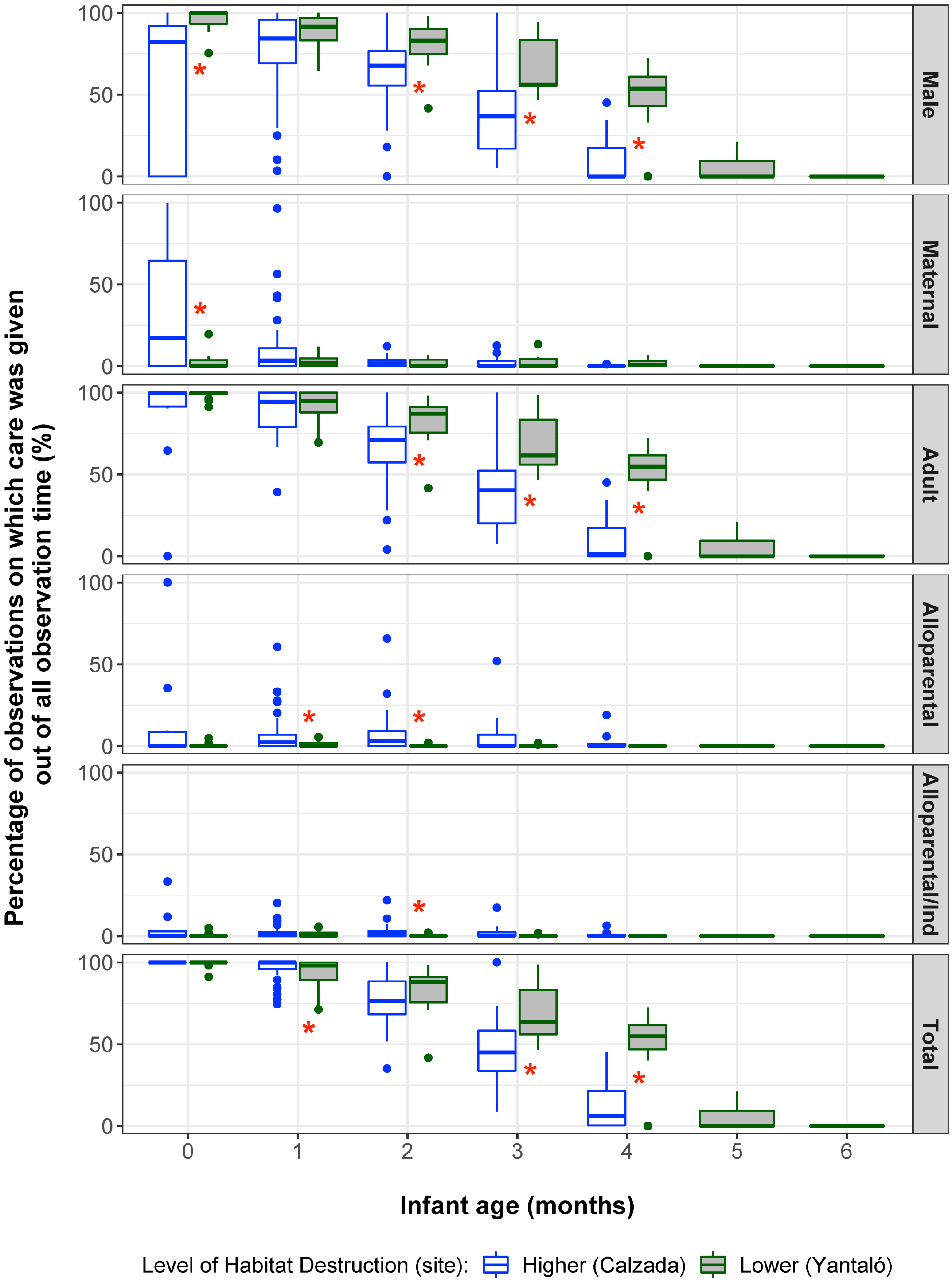

Figure 2-4 Values of mean daily percentages of infant care (derived from focal follow instantaneous data) shown by level of habitat destruction (HD) and infant age (months). I compared percentages of care between the two study groups using Mann-Whitney *U*-tests.

Adult care was significantly lower at the higher HD site during months 2 (*U* = 131, *P* = 0.0184), 3 (*U* = 41, *P* = 0.0093), and 4 (*U* = 9, *P* = 0.0020). Alloparental care was significantly greater at the higher HD site for months 1 (*U* = 872, *P* = 0.0264) and 2 (*U* = 395, *P* = 0.0004), with values close to significance in months 3 (*U* = 140, *P* = 0.0898) and 4 (*U* = 65, *P* = 0.0779). Interestingly, total infant care was significantly greater at the higher HD site in month 1 (*U* = 841, *P* = 0.0480), which coincided with greater maternal and alloparental caregiving. In contrast, total infant care was significantly lower at the higher HD site in months 3 (*U* = 44, *P* = 0.0134) and 4 (*U* = 10, *P* = 0.0024). The effects of level of HD were not uniform on care by age.

Table 2-6 Mean monthly infant care percentages derived from daily focal follow percentages.

	Level of HD (site) and infant age (months)											
	Higher HD (Calzada)					Lower HD (Yantaló)						
Care type	0	1	2	3	4	0	1	2	3	4	5	6
Male	**54.10**	77.36	**65.48**	**40.50**	**10.53**	**95.48**	88.80	**80.16**	**66.93**	**48.47**	5.59	0.00
Maternal	**33.68**	11.40	2.51	2.10	0.28	**3.07**	3.03	2.05	3.10	1.86	0.00	0.00
Adult	87.78	88.76	**67.99**	**42.51**	**10.81**	98.55	91.83	**82.21**	**70.03**	**50.33**	5.59	0.00
Alloparental	12.22	**7.33**	**7.86**	5.66	2.70	0.56	**1.37**	**0.17**	0.32	0.00	0.00	0.00
Alloparental/Ind	4.07	2.44	**2.62**	1.89	0.90	0.56	1.37	**0.17**	0.32	0.00	0.00	0.00
Total	100.00	**96.09**	75.85	**48.17**	**13.51**	99.11	**93.20**	82.38	**70.35**	**50.33**	5.59	0.00

Total care values include all adult and all alloparental care. Alloparental care per individual sibling was calculated by dividing alloparental care values by the number of siblings present in each site (Calzada = 3, Yantaló = 1). Bolded values indicate statistically significant differences in sample percentages of infant care between sites, according to Mann-Whitney *U*-tests ($P<0.05$). Sample percentages for each month were derived from the daily focal follow percentages of care. Sample sizes were as follows per month: 0 (*N* = 25), 1 (*N* = 74), 2 (*N* = 52), 3 (*N* = 32), 4 (*N* = 20), 5 (*N* = 6), and 6 (*N* = 2). Data collection ended before infants at Calzada reached >4 months of age, therefore only values from months 0–4 were compared between sites.

Table 2-7 Mean monthly infant care percentages per tropical season and level of HD.

	Season, level of HD (site), and infant age (months)											
	Dry season					Dry season						
	Higher HD (Calzada)					Lower HD (Yantaló)						
Care type	0	1	2	3	4	0	1	2	3	4	5	6
Male	49.26	73.59	—	—	—	100.0	—	—	—	—	—	—
Maternal	47.11	15.35	—	—	—	0.00	—	—	—	—	—	—
Adult	96.37	88.94	—	—	—	100.0	—	—	—	—	—	—
Alloparental	3.63	10.27	—	—	—	0.00	—	—	—	—	—	—
Alloparental/Ind	1.21	3.42	—	—	—	0.00	—	—	—	—	—	—
Total	100.0	99.21	—	—	—	100.0	—	—	—	—	—	—
	Wet season					Wet season						
Care type	0	1	2	3	4	0	1	2	3	4	5	6
Male	57.12	83.03	65.48	40.50	10.53	93.97	88.80	80.16	66.93	48.47	5.59	0.00
Maternal	25.29	5.47	2.51	2.10	0.28	4.09	3.03	2.05	3.10	1.86	0.00	0.00
Adult	82.41	88.50	67.99	42.51	10.81	98.06	91.83	82.21	70.03	50.33	5.59	0.00
Alloparental	17.59	2.92	7.86	5.66	2.70	0.75	1.37	0.17	0.32	0.00	0.00	0.00
Alloparental/Ind	5.86	0.97	2.62	1.89	0.90	0.75	1.37	0.17	0.32	0.00	0.00	0.00
Total	100.0	91.42	75.85	48.17	13.51	98.81	93.20	82.38	70.35	50.33	5.59	0.00

Total care values include all adult and all alloparental care. Alloparental care per individual sibling was calculated by dividing alloparental care values by the number of siblings present in each site (Calzada = 3, Yantaló = 1). Sample sizes were as follows per month during the dry season: 0 (*N* = 8) and 1 (*N* = 24). Sample sizes were as follows per month during the wet season: 0 (*N* = 17), 1 (*N* = 50), 2 (*N* = 52), 3 (*N* = 32), 4 (*N* = 20), 5 (*N* = 6), and 6 (*N* = 2).

Table 2-6 provides the overall mean values of care by level of HD and infant age. Table 2-7 shows the percentages of infant care for each level of HD by infant age and tropical season. In the higher HD site, male care was lower in the dry season than in the wet season. Maternal care displayed the opposite pattern. Alloparental care did not exhibit consistent trends by tropical season, but appeared to be negatively related to adult care. For both sites, total infant care was relatively similar across both seasons.

Lastly, the Spearman's rank correlation tests (*N* = 126 for higher HD, *N* = 85 for lower HD) showed that maternal care was not significantly correlated with male care at the higher HD site (r_s = -0.14, *S* = 379390, *P* = 0.1233) or the lower HD site (r_s = -0.04, *S* = 106070, *P* = 0.7406). In contrast, alloparental and parental care were significantly negatively correlated at the higher HD site considering all alloparental care (r_s = -0.40, *S* = 466290, $P<0.0001$) and alloparental care per individual (r_s = -0.40, *S* = 466290, $P<0.0001$), but uncorrelated at the lower HD site (r_s = -0.01, *S* = 101370, *P* = 0.9311).

2.4. Discussion

2.4.1. Level of habitat destruction

Over two field seasons, I evaluated the relative level of HD in two study groups of *P. oenanthe* that occupied two distinct secondary forest fragment sites in the San Martín region of Peru. Compared with Yantaló, Calzada had smaller fragment and home range sizes and exhibited significantly lower tree density and fruit availability per individual. Based on the significant differences in fragment size, home range size, tree density, and fruit availability, I considered Calzada to have a higher level of HD.

Both sites exhibited a low forest height and similar percentages of canopy cover, and sites experienced comparable levels of forest fragment and home range area loss between field seasons. The reduction in forest fragment size by ~2–3% across field seasons demonstrates that habitat destruction is ongoing at these sites. Additionally, I witnessed sections of forest being cleared by fire in fragments adjacent to study sites. Overall, both sites exhibited small home range sizes (<22,500 m^2) compared with *Plecturocebus* spp. living in primary forest (50,000–300,000 m^2) (Rowe and Myers 2017; Wright 1985). However, the results were similar to

Plecturocebus spp. inhabiting secondary and anthropogenic forests, which had home ranges of 20,000–30,200 m^2 (DeLuycker 2007; Lawrence 2007).

Unexpectedly, phenological transect measures of habitat destruction (taken only in the second field season) were consistent across all months of sampling within each site, and logging rates were low (<0.01% of monitored trees) for both sites (Appendix Table 5-1). This may reflect that fact that forests had already been decimated to a high degree to develop anthropogenic landscapes, and further intensive logging and pasture-clearing was not required to maintain existing agricultural practices. The high degree of loss and degradation observed at the study sites characterizes most of the remaining habitat for *P. oenanthe*, which is endemic to the San Martín region where some of the highest rates of habitat destruction in Peru have occurred (INEI 2014; Potapov *et al*. 2014). Since most populations of San Martin titi monkeys are living in areas that are significantly smaller and more degraded than their historical habitat of continuous forests (Shanee *et al*. 2013), it is important to determine the threshold at which fragment size and habitat characteristics affect aspects of San Martin titi monkey behavior (Pardini *et al*. 2010; Swift and Hannon 2010).

Given that both sites exhibited a high degree of anthropogenic disturbance, it is unclear whether variation between sites translated to biological effects. For example, I could not definitively conclude that titi monkeys in Calzada had more difficulty acquiring food, despite having lower fruit availability per individual. This is because titi monkeys have diverse diets and can supplement with insects, leaves, and flowers when fruit is less available (DeLuycker 2007). Since I did not systematically track diet, I was unable to investigate this possibility. Similarly, seasonality and temperature were conflated with infant age and I was not able to assess these factors statistically with GLMMs. However, I included field season (2015 vs. 2016–2017) as a fixed effect, which captured a portion of seasonal and climatic variation that was unaccounted for by level of HD and infant age. This is because a higher ratio of data was collected in the dry season than the wet in the first field season compared with the second. I further noted trends in seasonal patterns of infant care, which were reported in Table 2-7. I make tentative interpretations of these results below. Additionally, during the study I made observations of notable differences in adult male body condition and the interactions each group had with humans and wildlife. Therefore, in addition to explaining results in terms of habitat destruction, I further relate them to differences in study subjects and group experiences that may have impacted infant care.

2.4.2. Habitat destruction and infant care

I evaluated the relationship between level of HD and percentages of infant care in the two *P. oenanthe* study groups using GLMMs (controlling for infant age, time of day, and field season) and with *post-hoc* comparisons of care per month of infant age at each site. Results from GLMMS supported predictions 1 and 3, showing that habitat destruction was associated with reduced male and adult care. In contradiction to prediction 2, maternal care increased, rather than decreased, at the higher HD site. Prediction 4 was also unsupported since total care percentages did not differ by level of HD in GLMMs. However, *post-hoc* tests partially supported prediction 4 by showing that total care percentages were lower for months 3–4 of infant age at the higher HD site. Similarly, *post-hoc* tests showed significant differences between sites for all forms of infant care for at least one of the months of infant age. Male, adult, and total care were the most variable between sites (significant differences found in three to four of the five overlapping months of infant age), which is likely due to the fact that the latter two measures are highly correlated with male care (92.36% of adult care and 86.60% of total care). Contrary to prediction 5, male and maternal care were uncorrelated at both sites. In support of predictions 6 and 7, alloparental care was positively correlated with level of HD and negatively correlated with adult care.

Infant carrying terminated in month 4 in Calzada, and in month 5 Yantaló. Weaning took place from months 3–4 in Calzada, and may have continued thereafter though no data was collected beyond these ages at this field site. In Yantaló, weaning took places from months 4–5. Compared with prior research this indicates earlier locomotor independence for the infant in Calzada, and earlier weaning in both groups than was found for other wild titi monkeys. For instance, infant carrying ended when infants were 5 months old in wild *P. oenanthe* (DeLuycker 2007), captive coppery titi monkeys (*Plecturocebus cupreus*, previously *Callicebus moloch*) (Fragaszy *et al.* 1982), and wild Toppin's titi monkeys (*Plecturocebus toppini*, previously *Callicebus moloch*) (Wright 1984; 1990). The same studies reported different results regarding weaning. In wild titi monkeys (DeLuycker 2007; Wright 1984; 1990), weaning occurred at 7–8 months, while those in captivity weaned infants around 4–5 months (Fragaszy *et al*. 1982).

The marked variation in male care results by level of HD may suggest that reduced access to resources at Calzada (as indicated by the smaller fragment size, lower tree density, and reduced fruit availability) decreased male care. However, the costs of infant care are not fully known for titi monkeys (Tardif 1994) and the current study did not obtain a complete picture of resource availability. Therefore further data must be collected to evaluate this possibility. Prior research on the activity budges of males at the same study sites (Hodges 2020a) revealed that the Calzada male engaged in more time-minimizing behaviors that reduced energy expenditure relative to the Yantaló male. Specifically, he rested more and traveled less, which may indicate greater energetic stress.

The results concur with several primate studies on maternal investment, which shows that ecological conditions can lead to intraspecific variation in the process of reducing parental care (Fairbanks and McGuire 1995; Fite *et al*. 2005; Lycett *et al*. 1998). For instance, female vervet monkeys that lost 10% of body weight due to caloric restriction rejected infants significantly more often than those that remained on a more energy-dense diet. In humans, Quinlan (2007) found that maternal care was negatively correlated with famine and warfare. The author noted that linearity of this relationship indicated that additional care was not able to moderate the negative effects of these environmental stressors. This reduction under unfavorable conditions may represent adaptive maternal divestment in infants (Schino and Troisi 2005).

In contrast, other studies have found a negative correlation between greater habitat quality and infant care. For instance, a study on grivet monkeys (*Chlorocebus aethiops*) and green monkeys (*Chlorocebus sabaeus*) found that mothers in the wild were less rejecting of infants when food quality was worse compared with those that had access to better quality foods (Hauser and Fairbanks 1988). The authors indicated that the results might have reflected variation in the ability to shorten the interbirth interval while continuing to provide infant care. That is, mothers in the worst habitat were limited to reproducing at a slower rate, whether or not they were currently caring for an infant. Therefore continued care would not prolong the interbirth interval. In the higher-quality habitat, mothers were able to reproduce more quickly only by restricting care of current infants, which explained the higher rates of maternal rejection and mother-infant conflict. With respect to these findings, the reduction in male care at Calzada was most similar to results found for monkeys under the higher-quality habitat condition. Thus, the findings in the present study cannot straightforwardly be interpreted in relation to prior research. Additionally, caution should be used when comparing findings on male and female care, as we should not necessarily expect equivalent explanations. Primate research on male divestment of infant care under a wider range of habitats is required to make more solid conclusions.

2.4.3. Field season, seasonality, and infant care

Field season was included in GLMMs to capture additional variation in results that were not accounted for by level of HD and infant age. For instance, data collected during the first field season covered more of the dry season (two months) than did those in the second field season (a few weeks), thus differences in the field season predictor may partly reflect seasonal variation. A greater energetic burden (less fruit and increased thermoregulatory stress) was expected to occur during the dry versus wet season. The majority of interaction and full main effects models indicated that field season was significantly related with infant care for all types of care. Odds ratios from GLMMs showed that larger percentages of male, adult, and total care occurred in the second field season, when observations were made during proportionally more of the wet season months than dry season months. This suggests that male care was reduced during the dry season compared with the wet season. Odds ratios indicated that maternal and alloparental care were greater in the first field season than in the second. Thus maternal and alloparental care were inversely related to male care percentages by field season.

To further examine the effects of tropical season on infant care, I compared mean percentages of infant care by level of HD and infant age for the dry and wet seasons. In Calzada, I compared dry and wet season data for months 0–1, which were the only infant ages that coincided by tropical season. These comparisons showed that the Calzada male provided less care in the dry season (months: 0 = 49.26% and 1 = 73.59%) than in the wet season (months: 0 = 57.12% and 1 = 83.03%), which supports the expectation that energetic stress during the dry season reduces male care. In contrast, the female in Calzada provided more care in the dry season (months: 0 = 47.11% and 1 = 83.03%) than in the wet season (months: 0 = 25.28% and 1 = 5.47%). Variation in percentages of maternal care across dry and wet seasons may reflect differential compensation for loss of male care. As a result of the additional maternal care, adult care (male plus maternal care) was greater in the dry season (months: 0 = 96.37% and 1 = 88.94%) than in the wet season (months: 0 = 82.41% and 1 = 88.50%). Alloparental care by siblings in Calzada did not follow a distinct seasonal pattern across both months. For instance, in the dry season alloparental means were 3.63% in month 0 and 10.27% in month 1. While in the wet seasons mean care was 17.59% in month 0 and 2.92% in month 1. When looking at means of care within the same tropical season, alloparental percentages are negatively correlated with adult care. Therefore, siblings may have supplemented with more or less care based on how much care adults were providing.

Data on fruit availability indicated similar amounts of fruit in both the dry and wet seasons. However, data collection was highly limited in the dry season, having only taken place in September for the dry season rather than across the entire dry season (May to September). Further, September may be considered a transitional month between the dry and wet seasons, so differences in fruit during these months are expected to be less apparent than they would have been with more data taken earlier in the dry season. Additionally, DeLuycker (2007) recorded reduced fruit availability during the dry season (May through September) at a nearby *P.*

oenanthe field site in Moyobamba (12 km from Calzada and 6.9 km from Yantaló). Therefore data on fruit availability may not have accurately reflected seasonal differences.

2.4.4. Prior experiences and individual differences

During the course of this study, I made note of observations and personal communications regarding the prior experiences and individual differences of study subjects. The Yantaló infant in the first season disappeared sometime prior to the start of the second season. At the same site, a farmer that worked at the edge of the group's home range stated that he had kidnapped and sold an infant titi monkey a couple of years prior to the start of this study. These experiences may have influenced the Yantaló adults to increase care and protection due to the previous loss of infants.

In Calzada, the male appeared somewhat older and in worse physical condition than the Yantaló male, having whitish-grey streaks of fur, more visible scarring, and a thinner body. In light of this, the relative ages and physical condition of males may have contributed to the variation in male care. For example, the Calzada male may have been in worse physical condition due to older age and prior agonistic interactions, which might be expected to reduce the quality or amount of male care. Differences in caregiving style may have also played a role in results. For instance, research on the caregiving patterns of primate parents found stable individual differences in parental style, with some parents being more protective or rejecting (Fairbanks 1996).

2.4.5. Interaction among infant care types

Infant care in Calzada diverged from typical patterns in ways that indicate an important role for social dynamics between study subjects. As in prior titi monkey research, the Calzada male was the primary caregiver (male care = 86.60% of total care). However, that care was significantly reduced compared with male care in Yantaló and male care results from other titi monkey studies (DeLuycker 2007; Fragaszy *et al*. 1982; Wright 1984; 1990). Alongside this, maternal care in Calzada was significantly greater in months 0 (mean 33.6%) and 1 (mean 11.4%) compared with percentages in Yantaló (3.07% and 3.03%, respectively) and compared with percentages found by Wright (1984) (≤6% every month). As a result, adult care (combining male and maternal care) did not vary significantly between groups at 0 months. The increased care by the Calzada mother in month 0 partially compensated for the decline in care by her partner. It is possible that the high degree of infant dependence coupled with the lower male care in Calzada elicited increased maternal care, which has been observed in cooperatively breeding primates (Yamamoto *et al.* 1987) and non-primate species with biparental care (Lesells 2012).

Unusually high rates of alloparental care by the three Calzada siblings were found for month 0 (12.2%), month 1 (7.33%), and month 2 (7.86%) compared with alloparental care by one sibling in Yantaló (0.56%, 1.37%, and 0.17%, respectively). Prior studies have recorded alloparental care rates of no more than 6% by titi monkey siblings (Fragaszy *et al*. 1982; Wright 1984). However, Mann-Whitney *U*-tests indicated that alloparental care percentages were not significantly different between groups in month 0. This is because while the differences in the means were largest in absolute values for this month (11.64%), the rank-based method of the Mann-Whitney *U*-test does not consider the magnitudes of difference for sample values. Despite this statistical non-significance in month 0, this unusual behavior was strongly negatively correlated with male care in Calzada (see Spearman results) and continued for two more months.

When alloparental care was calculated as percentage of care per individual sibling (Calzada values were divided by three and Yantaló values by one), *post-hoc* results were still significantly larger in Calzada (2.62%) than in Yantaló (0.17%) in month 2. Measures of alloparental care per individual sibling in Calzada were also still highly correlated with male care. As a result of the additional alloparental care in Calzada, total care percentages were either equivalent or significantly greater than those in Yantaló from months 1–2. This indicates that in titi monkeys, siblings are capable of compensating to some degree for the loss of parental care. Further analysis of data, not reported here, showed that the lone male sibling (a subadult) consistently provided more care than the two female siblings (juvenile and subadult) at Calzada. The discrepancies in sibling care by individual may reflect the sex-specific roles for parenting.

The combined increases in maternal and alloparental care in months 0–2 in Calzada offset the lower rate of male care during that time. Percentages of adult and total care at Calzada were not significantly lower than those at Yantaló until month 2 (weeks 8–11), when infant titi monkeys are known to begin moving (but not traveling more than a few meters) independently for a majority of the time and to begin incorporating solids into their diet (DeLuycker 2014; Fragaszy *et al*. 1982). Despite this evidence of compensation for loss of male care in months 0–2, studies on twinning in titi monkeys indicate that infants are still highly dependent on caregivers during the entire period prior to weaning (de Santana *et al*. 2014; Knogge and Heymann 1995; Valeggia *et al*. 1999), which is approximately 6–7 months in *P. oenanthe* (DeLuycker 2014). Therefore, maternal and alloparental care did not mitigate declines in male care during the entire period of infant dependency.

While compensation by the adult female in Calzada may be explained by the immediate reproductive fitness gains, an understanding of the unusually high rates of alloparental care by siblings in Calzada is less straightforward. A prior study on a *P. oenanthe* group that experienced habitat loss and isolation noted anecdotal observations of prolonged infant-carrying by the female juvenile (DeLuycker 2007) and suggested that titi monkeys may choose to delay dispersal and provide care due to the increased risks associated with dispersal, few mating opportunities, or benefits of reduced predation risk for younger siblings that stay in natal groups. In addition, Goldizen and Terborgh (1989) have proposed that delayed breeding in callitrichids may be a response to oversaturation of suitable territories. However, titi monkeys do not disperse until they are subadults, so these hypotheses fails to explain sibling care by juveniles.

One juvenile and two subadults were present each field season in Calzada. The minimum age of subadult siblings remaining in Calzada during each field season was approximately 3–4 years old. These coincide with the age of dispersal (3–5 years) in titi monkeys (Bossuyt 2002; Souza-Alves 2013; Van Belle *et al*. 2016). Therefore it is plausible that the high degree of habitat destruction (including low connectivity with neighboring fragments) and anecdotal observations of numerous predators in Calzada (domesticated dogs, snakes, raptors, and humans) led subadults to at delay dispersal. It is further possible that subadults provided infant care to secure parental tolerance and remain in the natal group (i.e. pay-to-stay strategy: Emlen 1982). I believe this was the likeliest explanation for the infant care that was provided by the subadult male in Calzada, with whom the adult male was likeliest to be observed in conflict (anecdotally). In contrast, the female subadult present in 2015 was absent in the following season, possibly having dispersed.

2.4.6. Infant care results and potential infant outcomes

Lower percentages of male, adult, and total infant care were observed for several months in Calzada compared with Yantaló, while the opposite patterns were found for maternal and alloparental care. Infants also achieved earlier independence in Calzada than in Yantaló (earlier weaning and termination of carrying). The patterns observed in Yantaló more closely match typical the infant care patterns of wild titi monkeys (DeLuycker 2007; Wright 1984; 1990). The potential effects of the divergent infant caregiving pattern observed in Calzada may include increased predation risk and increased parent-offspring and sibling-offspring conflict.

In addition to reductions in male care at Calzada, this male also engaged in a pattern of risk-taking while transporting infants by entering human-occupied areas and traveling terrestrially both inside and outside the forest on several occasions during both field seasons (see study #57 in Table S1 in Souza-Alves *et al*. 2019). For example, I observed four occasions on which the Calzada male carried an infant (4–11 weeks old) while exploring a small hut or the ground nearby at the forest edge. On one of these excursions (infant age was 11 weeks), I was able to confirm that the male fed on plantains that were being stored on the ground at this location. At the same site, I observed the adult male carrying an infant (6 weeks old) descend to a height of 1 m to feed on *Miconia* fruits. The male then climbed to the ground and traveled 1 m to feed another shrub with *Miconia* fruits. Additionally, on a daily basis the Calzada male and other group members traveled on the ground for short distances (1–10 m) to traverse forested areas with canopy gaps. In contrast, observers never witnessed the Yantaló male engage in such risky behaviors while carrying infants.

I observed several potential predators at both sites, including domesticated dogs, snakes, raptors, and humans. Dogs and humans entered the Calzada site on a daily basis. In Yantaló, I only ever once observed a young dog (<6 months old) enter the forest and I observed other people inside the forest less regularly at this site. Titi monkeys are known to be preyed on by predators that I observed at study sites (Cäsar 2012; de Luna *et al*. 2010; Shanee 2012). By traveling terrestrially and entering human-occupied areas, the Calzada male likely increased the risk of predation.

At the same study sites, conflict between infants and all classes of caregivers occurred at higher rates than was observed in Yantaló (Hodges 2020b). These took place only when the infant was clinging to a caregiver, and involved carriers biting or pulling at the infant. While these behaviors appear to be typical of titi monkeys as parents reduce caregiving, they began at least a month earlier in Calzada (3 months) than in Yantaló (4 months). The ultimate outcomes of the reduction in care for population parameters are uncertain, but anthropogenic activities are known to alter behavior in ways that have long-term effects on primate demography (Sterck 1999).

2.4.7. Conclusions

In sum, the results of this study have emphasized the vulnerability and flexibility of primate infant care. While male care was significantly lower in Calzada, maternal and alloparental care partially supplemented this. The unusually high levels of alloparenting may be related to environmental factors, such as poor habitat connectivity and oversaturation of the landscape by conspecifics, which may have obliged siblings to remain in their natal groups. As a caveat, due to the small sample size I was unable to control for additional ecological and study subject variables that may have led to differences in infant care between sites. For this reason, interpretations regarding the relationship between infant care and habitat destruction are tentative. To better understand how habitat destruction in particular affects infant care, comparison with groups living in continuous, undisturbed forest is needed. Therefore, the findings of this study are conditional to these study groups and sites and cannot be generalized to the larger population. However, they provide a framework for future research into the impact of habitat destruction on primate parental investment and the ability of primates to cope in disturbed environments.

2.5. References

Altmann J (1974) Observational study of behaviour: sampling methods. Behaviour 49:227–267

Altmann J, Alberts SC (2003) Variability in reproductive success viewed from a life-history perspective in baboons. Am J Hum Biol 15:401–410

Anderson DE, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. J Widl Manage 64:912–923

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

Anzures-Dadda A, Manson RH (2007) Patch-and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. Anim Conserv 10:69–76

Beamish EK (2009) Causes and Consequences of Mortality and Mutilation in the Cape Peninsula Baboon Population, South Africa. Master's thesis, University of Cape Town, Cape Town, South Africa

Bicca-Marques JC, Garber PA, Azevedo-Lopes MAO (2002) Evidence of three resident adult male group members in a species of monogamous primate, the red titi monkey (*Callicebus cupreus*). Mammalia 66:138–142

Bicca-Marques JC, Heymann, EW (2013) Ecology and behaviour of titi monkeys (genus *Callicebus*). In: Barnett AA, Veiga LM, Norconk MA, Ferrari SF (eds) Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge University Press, New York, pp 295–302

Blomquist GE, Kowalewski MM, Leigh SR (2009) Demographic and morphological perspectives on life history evolution and conservation of New World monkeys. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South

American primates: comparative perspectives in the study of behaviour, ecology, and conservation. Springer, New York, pp 117–138

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bossuyt F (2002) Natal dispersal of titi monkeys (*Callicebus moloch*) at Cocha Cashu, Manu National Park, Peru. Am J Phys Anth S34: 47

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference, 2nd ed. Springer, New York

Cäsar C (2012) Anti-predator behaviour of black-fronted titi monkeys (*Callicebus nigrifrons*). Doctoral thesis, University of St. Andrews, St. Andrews, Scotland

Chapman CA, Chapman LJ (1997) Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. Biotropica 29:396–412

Chapman CA, Chapman LJ, Wrangham R, Hunt K, Gebo D, Gardner L (1992) Estimators of fruit abundance of tropical trees. Biotropica 24:527–531

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Ziegler TE (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anth 131:525–534

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ

Cowlishaw G, Dunbar RIM (2000) Primate conservation biology. University of Chicago Press, Chicago, IL

de Almeida-Rocha JM, Peres CA, Oliveira LC (2017) Primate responses to anthropogenic habitat disturbance: pantropical meta-analysis. Biol Conserv 215:30–38

de Luna AG, Sanmiguel R, Di Fiore A, Fernandez-Duque E (2010) Predation and predation attempts on red titimonkeys (*Callicebus discolor*) and equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador. Folia Primatol 81:86–95

DeLuycker AM (2006) Preliminary report and conservation status of the Río Mayo titi monkey, *Callicebus oenanthe* Thomas, 1924, in the Alto Mayo Valley, northeastern Peru. Primate Conserv 21:33–39

DeLuycker AM (2007) The ecology and behaviour of the Río Mayo titi monkey (*Callicebus oenanthe*) in the Alto Mayo, northern Peru. Doctoral thesis, Washington University, Saint Louis, MO

DeLuycker AM (2014) Observations of a daytime birthing event in wild titi monkeys (*Callicebus oenanthe*): implications of the male parental role. Primates 55:59–67

de Santana MM, Souza-Alves JP, Ferrari SF (2014) Twinning in titis (*Callicebus coimbrai*): stretching the limits of biparental infant caregiving? Neotrop Primates 21:189–191

Dingess K (2013) Social flexibility in the classically monogamous titi monkey: a response to increased population pressure. Am J Phys Anth 150 (S56):113

Emlen ST (1982) The evolution of helping: an ecological constraints model. Am Nat 119:29–39

ESRI (2014) ArcGIS desktop: release 10.2.2. Environmental Systems Research Institute, Redlands

Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, et al. (2017) Impending extinction crisis of the world's primates: why primates matter. Sci Adv 3:e1600946

Fairbanks LA (1996) Individual differences in maternal style: causes and consequences for mothers and offspring. In: Rosenblatt JS, Snowdon CT (eds) Parental care: evolution, mechanisms, and adaptive significance. Academic Press, pp 579–611

Fairbanks LA, Blau K, Jorgensen MJ (2010) High-fiber diet promotes weight loss and affects maternal behaviour in vervet monkeys. Am J Primatol 72:234–241

Fairbanks LA, McGuire MT (1995) Maternal condition and the quality of maternal care in vervet monkeys. Behaviour 132:733–754

Fernandez-Duque E, Di Fiore A, de Luna AG (2013) Pair-mate relationships and parenting in equatorial saki monkeys (*Pithecia aequatorialis*) and red titi monkeys (*Callicebus discolor*) of Ecuador. In Barnett AA, Veiga LM, Norconk MA, Ferrari SF (eds) Evolutionary Biology and Conservation of Titis, Sakis and Uacaris. Cambridge University Press, New York, pp 295–302

Fite JE, Patera KJ, French JA, Rukstalis M, Hopkins EC, Ross CN (2005) Opportunistic mothers: female marmosets (*Callithrix kuhlii*) reduce their investment in offspring when they have to, and when they can. J Hum Evol 49:122–142

Fleiss JL, Berlin JA (2009) Effect sizes for dichotomous data. In: Cooper H, Hedges LV, Valentine JC (eds) The Handbook of Research Synthesis and Meta-Analysis. Russell Sage Foundation, New York, NY, pp 237–253

Fragaszy DM, Schwarz S, Shimosaka D (1982) Longitudinal observations of care and development of infant titi monkeys (*Callicebus moloch*). Am J Primatol 2:191–200

Goldizen AW, Terborgh J (1989) Demography and dispersal patterns of a tamarin population possible causes of delayed breeding. Am Nat 134:208–224

Hauser MD, Fairbanks LA (1988) Mother-offspring conflict in vervet monkeys: variation in response to ecological conditions. Anim Behav 36:802–813

Hodges S (2020a) Paternal activity budgets of the Peruvian San Martin titi monkey (*Plecturocebus oenanthe*) in response to habitat destruction, seasonality, thermal stress, and infant care. Primate Conserv (published online). URL: <http://www.primate-sg.org/storage/pdf/PC34_Hodges_P_oenanthe.pdf>

Hodges S (2020b) Observations of infant conflict and avoidance in San Martin titi monkeys (*Plecturocebus oenanthe*). Primates (published online). URL: <https://doi.org/10.1007/s10329-020-00815-4>

Holdridge LR (1967) Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica

INEI Perú (2014) Perú en Cifras. URL: <http://www.inei.gob.pe>. Accessed 16 December 2018

Knogge C, Heymann EW (1995). Field observation of twinning in the dusky titi monkey, *Callicebus cupreus*. Folia Primatol 65:118–120

Lawrence JM (2007) Understanding the pair bond in brown titi monkeys (*Callicebus brunneus*): male and female reproductive interests. Doctoral thesis, Columbia University, New York

Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning, and maternal investment from a comparative perspective. J Zool (London) 225:99–114

Lesells CM (2012) Sexual conflict. In: Royle NJ, Smiseth PT, Kölliker M (eds) The evolution of parental care. Oxford University Press, Oxford, pp 150–170

Lootvoet AC, Philippon J, Bessa-Gomes C (2015) Behavioural correlates of primates conservation status: intrinsic vulnerability to anthropogenic threats. PLoS ONE 10:1–11

Lycett JE, Henzi SP, Barrett L (1998) Maternal investment in mountain baboons and the hypothesis of reduced care. Behav Ecol Sociobiol 42:49–56

Martin PR, Bateson PPG (2007) Measuring behaviour: an introductory guide. Cambridge University Press, Cambridge, MA

Milich KM (2012) The impact of habitat quality on female red colobus monkey (*Procolobus rufomitratus*) reproduction. Doctoral thesis, University of Illinois, IL

Rangel-Negrín A, Coyohua-Fuentes A, Canales-Espinosa D, Dias PAD (2016) The loss of behavioural diversity as a consequence of anthropogenic habitat disturbance: the social interactions of black howler monkeys. Primates 57:9–15

Onderdonk DA, Chapman CA (2000) Coping with forest fragmentation: the primates of Kibale National Park, Uganda. Int J Primatol 21:587–611

Pardini R, Bueno AdA, Gardner TA, Prado PI, Metzger JP (2010) Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS ONE 5:e13666

Potapov PV, Dempewolf J, Talero Y, et al. (2014) National Satellite-based Humid Tropical Forest Change Assessment in Peru in Support of REDD+ Implementation. Environ Res Lett 9:124012

Pyritz LW, Buntge AB, Herzog SK, Kessler M (2010) Effects of habitat structure and fragmentation on diversity and abundance of primates in tropical deciduous forests in Bolivia. Int J Primatol 31:796–812

Quinlan RJ (2007) Human parental effort and environmental risk. Proc R Soc Lond B 274:121–125

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL: <https://www.r-project.org/> Accessed 16 December 2018

Rowe N, Myers M (2017) All the world's primates. Pogonias Press, Charlestown, RI, pp 176–207

Schino G, Troisi A (2005) Neonatal abandonment in Japanese macaques. Am J Phys Anth 126:447–452

Schwitzer C, Glatt L, Nekaris KAI, Ganzhorn JU (2011) Responses of animals to habitat alteration: an overview focussing on primates. Endanger Species Res 14:31–38

SENAMHI 2017 Historical climate data. URL: <http://www. senamhi.gob.pe> Accessed 5 November 2017

Shanee N (2012) Trends in local wildlife hunting, trade and control in the Tropical Andes Biodiversity Hotspot, northeastern Peru. Endanger Species Res 19:177–186

Shanee S, Tello-Alvarado JC, Vermeer J, Bóveda-Penalba AJ (2013) GIS Risk Assessment and GAP analysis for the Andean titi monkey (*Callicebus oenanthe*). Primate Conserv 26:17–23

Souza-Alves JP (2013) Ecology and life-history of Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) in the Brazilian Atlantic Forest. Doctoral thesis, Universidade Federal da Paraíba, Brazil

Souza-Alves JP, Mourthe I, Hilário R, et al. (2019) Terrestrial behavior in titi monkeys (*Callicebus*, *Cheracebus*, and *Plecturocebus*): potential correlates, patterns, and differences between genera. Int J Primatol 40:553–572

Spence-Aizenberg A, Di Fiore A, Fernandez-Duque E (2016) Social monogamy, male-female relationships, and biparental care in wild titi monkeys (*Callicebus discolor*). Primates 57:103–112

Strier KB (2009) Seeing the forest through the seeds: mechanisms of primate behavioural diversity from individuals to populations and beyond. Curr Anthropol 50:213–228

Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biol Rev Camb Philos Soc 85:35–53

Tarara R, Suleman MA, Sapolsky R, Wabomba MJ, Else JG (1985) Tuberculosis in wild olive baboons, *Papio cynocephalus anubis* (Lesson), in Kenya. J Widl Dis 21:137–140

Tardif SD (1994) Relative energetic cost of infant care in small-bodied Neotropical primates and its relation to infant-care patterns. Am J Primatol 34:133–143

Valeggia CR, Mendoza SP, Fernandez-Duque E, Mason WA, Lasley B (1999) Reproductive biology of female titi monkeys (*Callicebus moloch*) in captivity. Am J Primatol 47:183–195

Van Belle S, Fernandez-Duque E, Di Fiore A (2016) Demography and life history of wild red titi monkeys (*Callicebus discolor*) and equatorial sakis (*Pithecia aequatorialis*) in Amazonian Ecuador: a 12-year study. Am J Primatol 78:204–215

Wright PC (1984) Biparental care in *Aotus* and *Callicebus*. In: Small MF (ed) Female primates: studies by women primatologists. Alan R. Liss, New York, NY, pp 59–75

Wright PC (1985) The costs and benefits of nocturnality for *Aotus trivirgatus* (the night monkey) Doctoral thesis, The City University of New York, New York

Wright PC (1990) Patterns of paternal care in primates. Int J Primatol 11:89–102

Xavier AH (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616

Yamamoto ME, Arruda M, Bueno OF (1987) Compensation in abnormal conditions of infant care in the common marmoset (*Callithrix jacchus*). J Comp Psychol 1:97–109

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

3. OBSERVATIONS OF INFANT CONFLICT AND AVOIDANCE IN SAN MARTIN TITI MONKEYS (*Plecturocebus oenanthe*)[*]

3.1. Introduction

Parent–offspring conflict (hereafter POC) is expected to occur as parents reduce their investment in young, who often react by attempting to secure additional care (Clutton-Brock 1991; Trivers 1974). In non-human primates, disagreements between mothers and infants over maternal investment are characterized by behavioral conflict over the amount of care given. Mothers may reduce the frequency or duration of nursing and contact, reject suckling or contact attempts, or avoid infants (Gomendio 1991; Maestriperi 2002; Trivers 1974; Wright 1990). Infant avoidance is usually included as a subset of rejection, but can be more specifically defined as efforts to prevent body contact with infants by leaving an infant's location and maintaining physical distance (Simpson *et al.* 1986). Rejections range from mild (leaving, breaking contact, or threatening) to more physically intense responses (pushing, slapping, hitting, or biting). Infants frequently respond to these changes with distress and may vigorously persist in trying to re-establish previous care or contact patterns (Gomendio 1991; Maestriperi 2002; Pavé *et al*. 2015). In species with obligate biparental care, father–infant conflict appears similar. For instance, male titi monkeys dislodge infants more frequently as infants grow (Fragaszy *et al.* 1982; Wright 1990).

According to the primate literature, various factors can influence mother–infant conflict. These include maternal reproductive status (*Macaca fuscata*: Collinge 1987; *Macaca mulatta*:

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Gomendio 1991; *Trachypithecus leucocephalus*: Zhao *et al*. 2008), maternal reproductive condition (*Chlorocebus sabaeus*: Fairbanks and McGuire 1995), the presence of newborns (*Alouatta caraya*: Pavé *et al*. 2010), the quality of parent–offspring relationships (*M. mulatta*: DeVinney *et al*. 2003, *A. caraya*: Pavé *et al*. 2015; *M. fuscata*: Schino *et al*. 2001), rates of infant distress (Collinge 1987), food availability (*Chlorocebus* spp.: Hauser and Fairbanks 1988), and the thermoregulatory needs of infants (*M. fuscata*: Schino and Troisi 1998). In contrast, only a handful of primate studies have described father–infant conflict in titi monkeys (Fragaszy *et al*. 1982; Wright 1990). To date, none have examined the causes of variation in such father–infant interactions.

Research that examines POC patterns is useful for identifying factors that influence struggles between parents and offspring over care and can help improve our understanding of parental investment strategies. Relatively few studies have been conducted on POC in wild primates and father–offspring conflict remains even less explored, despite the prevalence of biparental care. To address this gap in knowledge, I carried out preliminary research on POC in a primate with obligate biparental care, the Critically Endangered San Martin titi monkey (*Plecturocebus oenanthe*) (Veiga *et al*. 2013). Titi monkey groups typically consist of a single pair of breeding adults and zero to three offspring of various ages (DeLuycker 2014; Spence-Aizenberg *et al*. 2016). Titi monkeys give birth to singletons and the resident adult male (the putative father) is the primary infant carrier and attachment figure during the period of dependency (DeLuycker 2007; Spence-Aizenberg *et al*. 2016). A series of POCs occur during the transition to infant independence, consisting of physical attempts by parents to limit clinging and suckling. During this transitional period, Wright (1990) documented that fathers push infants off their back and mothers avoid, push, bite, or hit infants. Infants respond with distress and vigorous attempts to maintain contact.

Here I make the first description of POC and sibling–infant conflict in *P. oenanthe*. To do this, I recorded physical conflict between infants and other group members, including undispersed offspring (putative siblings). I also recorded instances when males avoided infants (termed “avoidance”), as this may constitute a form of infant rejection. I did not track avoidance by other group members since, typically, infants did not exhibit distress when the mother or other offspring left the infant. Through exploratory data analysis of two groups, I examine the timing and nature of infant conflict. I then discuss potentially important socioecological factors affecting variation, including individual study subject differences, habitat, and social dynamics. Given the small sample size, I was unable to formally test hypotheses regarding the influences of these variables. However, this study provides detailed documentation of a critical aspect of parent–offspring relationships and the results generate important questions for future research.

3.2. Methods

3.2.1. Study sites and groups

This study took place from July to December 2015 and from August to December 2016 in the San Martín region of Peru (Figure 3-1). Study groups inhabited secondary premontane tropical forest fragments (Holdridge 1967). One group lived in a 2.15-hectare (ha) fragment near the village Calzada (UTM coordinates: 9,331,207.84 northing, 267,581.92 easting, 18 M), and the other inhabited a 4.15-ha fragment close to the village Yantaló (UTM coordinates: 9,337,614.99 northing, 273,723.07 easting, 18 M). Both sites had undergone severe habitat destruction in the form of forest clearing and selective logging and were surrounded by cultivated fields and pastures.

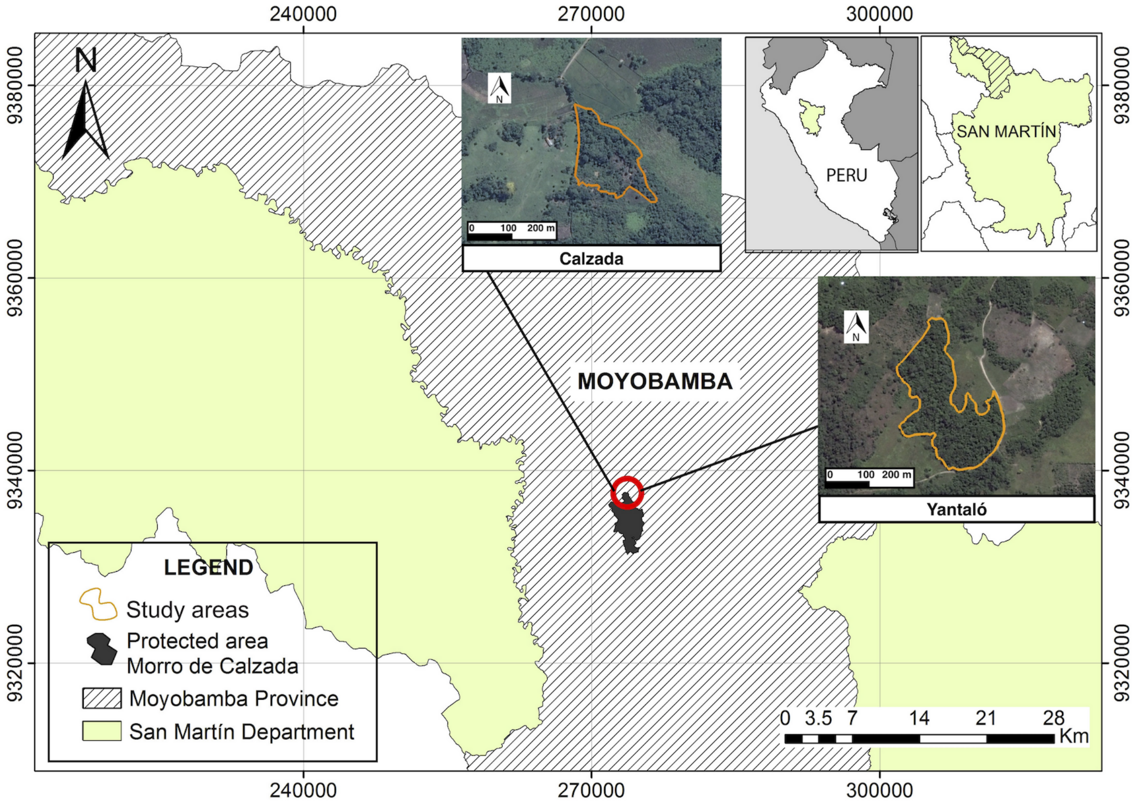

Figure 3-1 Field sites (*top center*: Calzada; *middle right*: Yantaló) were located in the Moyobamba Province of the San Martín region, Peru. This image was modified from the map in Huashuayo-Llamocca and Heymann (2017) under a Creative Commons Attribution 3.0 license.

For each group, I identified the age and sex class of individuals based on pelage coloration, facial markings, body build, and genitalia (DeLuycker 2007). The Calzada group consisted of an adult pair, a subadult Female primates: studies by women primatologists (absent in the second field season), a subadult male, a juvenile female (classed as a subadult in second field season), and one infant born each year. The Yantaló group consisted of an adult pair, a subadult female, and one infant born each year (the first infant later disappeared). I used the terms “male–infant” and “adult–infant” conflict (vs. “father–infant” or “POC”) as paternity was unconfirmed.

3.2.2. Data collection

Table 3-1 provides definitions of the behaviors recorded. I categorized the interactions of interest as “conflict” (involving physical aggression) and “avoidance” (leaving an infant and maintaining distance). I tracked avoidance only by males, as infants rarely exhibited distress or made attempts to follow when avoided by the mother or sibling. I collected data on conflict and avoidance during daily focal follows of infants (four total observed). This study was carried out as part of a larger investigation on infant care activities, for which I used instantaneous sampling every two minutes (Altmann 1974). Since conflict and avoidance tended to occur quickly, these behaviors are very likely to have been underestimated. I attempted to randomly rotate infant observations between groups, but discrepancies in sampling arose due to differing birthdates.

On average, I conducted follows 3 days per week in 2015 and once per week in 2016. In total, I collected 286.43 hours of observation on 83 focal follow days. I observed Calzada infants over 54 days and Yantaló infants over 29 days, and recorded twice as much data in Calzada (196.93 hours) as in Yantaló (89.50 hours). Data characteristics for each infant are given in Table 3-2. Infant age was conflated with season throughout the study and I was unable to analyze this factor.

Table 3-1 Ethogram of interactions between infants and other group members for the San Martin titi monkey.

Activity	Definition
Conflict	Aggression directed at the infant, including pulling, grabbing, hitting, or biting
Avoidance	Occurred when an adult male travelled away from an infant maintaining a distance that prevented the quick establishment of bodily contact (>3 m). The infant then made an attempt to follow the male, but did not reach him being either unable or unwilling to travel further. The infant then emitted distress cries, high-pitched whining vocalization accompanied by grimacing, until a caregiver retrieved it.

Table 3-2 Data characteristics by infant.

Infant ID	Birthdate	Days observed	Hours observed	Ages observed	Season
Calzada 1	14 July 2015	42	152.60	0–4 months	Dry-Wet
Calzada 2	24 Sept. 2016	12	44.33	0–2 months	Wet
Yantaló 1	02 Oct. 2015	12	39.90	0–1 months	Wet
Yantaló 2	10 Aug. 2016	17	49.60	0–4 months	Dry-Wet

To examine conflict and avoidance, I used R Studio (R Development Core Team 2017) to calculate the respective percentage of sample points devoted to conflict and avoidance per focal follow day. I investigated daily percentages by identifying the non-zero minimum and maximum values (weighted by points sampled per day). Next, I took the mean percentage of all daily estimates (including 0.00% values) to generate monthly means (weighted by days sampled per month). The overall mean was based on individual month means. This information is summarized in Tables 3-3, 3-4, and 3-5. Data are available as supplementary material or in the Open Science Framework repository https://osf.io/mpyz5.

To evaluate whether home-range size could be associated with infant conflict and avoidance behaviors, I calculated home-range size following the minimum convex polygon method (Hayne 1949). I recorded GPS locations of group members with ArcGIS version 10.2.2 (ESRI 2014).

3.3. Results

3.3.1. Conflict with the infant

Male–infant conflict took place on 13 of the 54 observation days at Calzada (24.07% of total days) while no instances of male–infant conflict were observed in Yantaló. Mother–infant conflict occurred on ten of 54 days at Calzada (18.52%) and on two of 29 days (6.9%) in Yantaló. I observed sibling–infant conflict on 31 of 54 days (57.41%) in Calzada and on 6 of 29 days in Yantaló (20.69%). Table 3-3 reports minimum, maximum, and weighted mean daily percentages of conflict considering only days on which at least one instance of conflict was recorded (i.e., non-zero values). Conflict estimates were greater at Calzada than in Yantaló for all age and sex classes. In Calzada, all conflict percentages were largest for siblings. The maximum value of conflict was larger for the male than the mother, but the minimum and mean were greater for the mother. In Yantaló, all conflict percentages were largest for the siblings and then for the mother.

Table 3-4 reports mean conflict percentages by group and infant age (including 0.00% values). Estimates were higher in Calzada than in Yantaló for all classes. In Calzada, siblings exhibited the most conflict in all months. Male–infant conflict was greater than mother–infant conflict overall and in months 2–4, but was lower in month 1. In Yantaló, conflict with siblings exceeded maternal estimates in months 1–3, but not in month 4.

Table 3-3 Minimum, maximum, and mean daily percentages (%) of conflict records.

	Male-infant conflict		Mother-infant conflict		Sibling-infant conflict	
	Calzada	Yantaló	Calzada	Yantaló	Calzada	Yantaló
Minimum	0.55	*NA	0.75	0.54	0.75	0.66
Maximum	9.33	*NA	5.34	0.66	20.31	3.16
Mean	1.84 (13)	*NA	2.16 (10)	0.60 (2)	4.73 (31)	1.15 (6)

The minimum non-zero value is reported to more fully show the range of conflict with infants when it occurred. Mean percentages (including days with no conflict) were weighted by the number sample days analyzed (*N*). *No observations of conflict were available for calculation.

Table 3-4 Mean monthly percentages (%) of conflict between infants and other group members.

	Male-infant conflict		Mother-infant conflict		Sibling-infant conflict	
Infant age	Calzada	Yantaló	Calzada	Yantaló	Calzada	Yantaló
Month 0	0.00 (7)	0.00 (8)	0.00 (7)	0.00 (8)	0.61 (7)	0.47 (8)
Month 1	0.08 (21)	0.00 (11)	0.26 (21)	0.00 (11)	0.86 (21)	0.14 (11)
Month 2	0.40 (17)	0.00 (4)	0.37 (17)	0.00 (4)	3.35 (17)	0.00 (4)
Month 3	2.11 (7)	0.00 (4)	1.05 (7)	0.17 (4)	7.86 (7)	0.36 (4)
Month 4	0.77 (2)	0.00 (2)	0.00 (2)	0.27 (2)	4.41 (2)	0.00 (2)
Overall mean	0.67	*NA	0.34	0.09	3.42	0.19

Means were estimated from daily percentages (total sample points on which conflict occurred divided by total sample points recorded for respective days) and weighted by the number sample days (*N*) recorded per month. The overall mean was derived from the means of months 0–4. *No observations of male-infant conflict at Yantaló were made for calculation.

3.3.2. Infant avoidance by males

The Calzada male was observed avoiding infants on 38 of 54 observation days (70.37% of total days). Considering only the days when avoidance was recorded, the minimum daily percentage of avoidance was 0.71%, the maximum was 73.17%, and the weighted mean was 11.24%. In Yantaló, avoidance took place on three of 29 days (10.34%). When avoidance was observed, the minimum daily value was 1.09%, the maximum 1.32%, and the weighted mean 1.16%. Table 3-5 reports weighted monthly means of infant avoidance (including 0.00% values). Avoidance means were higher in Calzada than in Yantaló each month and the overall mean was 62 times greater in Calzada.

Table 3-5 Mean monthly percentages (%) of avoidance by males.

Infant age	Calzada (*N*)	Yantaló (*N*)
Month 0	18.73 (7)	0.00 (8)
Month 1	2.80 (21)	0.08 (11)
Month 2	6.99 (17)	0.00 (4)
Month 3	16.58 (7)	0.33 (4)
Month 4	13.55 (2)	0.55 (2)
Overall mean	11.73 (months 0–4)	0.19 (months 0–4)

Means were estimated from daily percentages (total number of sample points on which avoidance occurred, divided by the total sample points recorded on respective days). Means were weighted by the number of sample days (*N*) recorded per month of infant age.

3.3.3. Home-range size

The Calzada group occupied a home range of 0.76 ha (Figure 3-2a) and the Yantaló group inhabited a home range of 2.18 ha (Figure 3-2b).

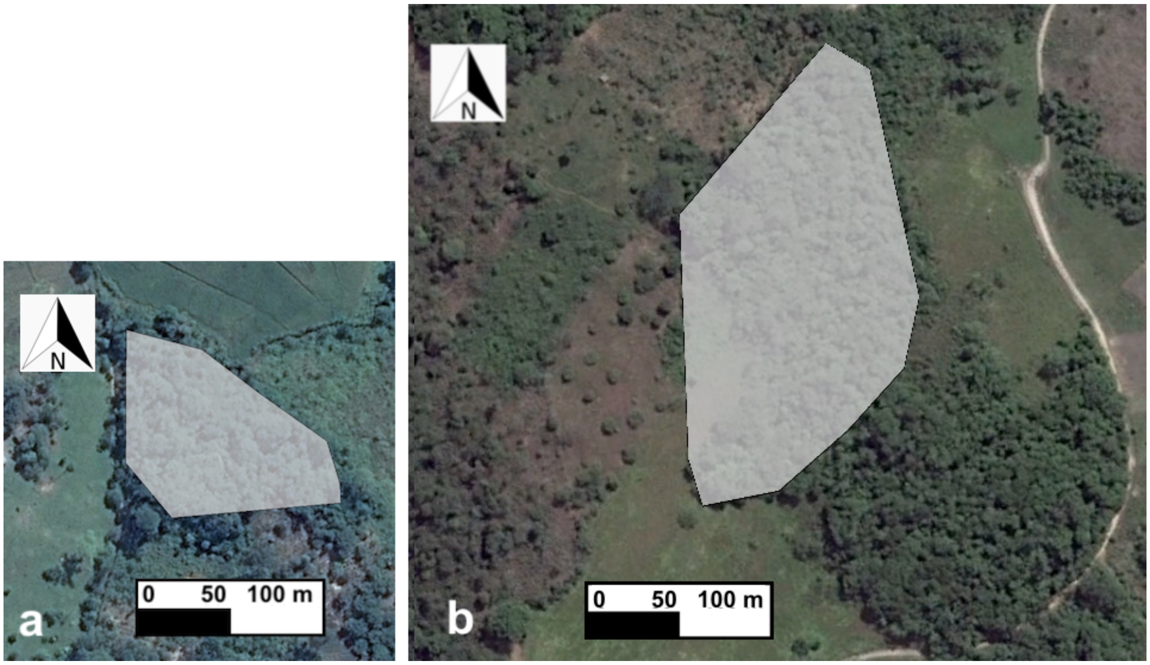

Figure 3-2 Home ranges as determined by the minimum convex polygon method. **a** Calzada, 0.76 ha; **b** Yantaló, 2.18 ha.

3.4. Discussion

According to my observations of San Martin titi monkeys, there was substantial variation in behavior between the two groups. In Calzada, POC and avoidance began at younger ages and was sampled at higher percentages than in Yantaló for all classes. Mother–infant and male–infant conflict peaked in month 3 in Calzada, while mother–infant conflict peaked in month 4 at Yantaló. Notably, I never observed male–infant conflict in Yantaló. Below I discuss my results in the context of prior studies and the socioecological factors that may have led to the striking behavioral differences. As I monitored only two groups, it was not possible to definitively conclude which variables may have affected activity patterns.

The onset and intensity of adult–infant conflict in both study groups appear outlying relative to the current literature on titi monkeys. According to prior research, adults began to reject infant clinging at months 4–5 in both captive (Fragaszy *et al*. 1982) and wild groups (Wright 1984; 1990). Compared to these previous studies, adult–infant conflict began earlier in Calzada (month 1), was observed later by the Yantaló mother (month 3), and was never observed by the Yantaló male. Infant carrying ended by month 5 in both wild *P. oenanthe* (DeLuycker 2007) and other captive and wild titi monkey species (Fragaszy *et al*. 1982; Wright 1984; 1990). Given the similar timing of infant independence, it is unclear why adult–infant conflicts began at younger ages in Calzada compared with findings from other titi monkey species, or why overt male–infant conflicts were unobserved in Yantaló.

There are multiple socioecological conditions that may have influenced titi monkey behavior, such as habitat quality and seasonality. In the current study, I compared site habitat using fragment and home-range size. The Calzada group was composed of six individuals (including the infant) inhabiting a 2.15-ha fragment with a home range of 0.76 ha. The Yantaló group consisted of four individuals (including the infant) living in 4.15-ha fragment with a home range of 2.18 ha. Similarly, DeLuycker (2007) documented a home range of 3 ha for a group of four *P. oenanthe* occupying an anthropogenic forest fragment in the nearby city of Moyobamba (12 km from Calzada and 6.9 km from Yantaló).

It is unknown what the typical home-range size is for this species in continuous forest, however study site fragments lacked connectivity to other forested areas, which may have limited home-range areas. The documented home ranges for *P. oenanthe* are much smaller than those observed for eight of the ten other *Plecturocebus* species for which home range has been recorded (5–30 ha) (Rowe and Myers 2017; Wright 1985). However, home-range size has been shown to be smaller for titi monkeys occupying secondary forest compared with those in primary forest. For example, *Plecturocebus toppini* (previously *Callicebus brunneus*) living in secondary forest occupied home ranges of 2–3.2 ha (Lawrence 2007), while those in primary forest inhabited 6–18 ha (Wright 1985). High rates of deforestation persist in the San Martín region, where the average forest fragment size is 6.43 ha (Shanee *et al*. 2013).

The differences between study groups in fragment and home-range sizes may reflect variation in food quality and access (Chapman *et al*. 2006). Further, in Chapter 2 I showed that food availability was indicated to be significantly lower at Calzada than in Yantaló. Food abundance has been shown to vary seasonally for this species, which may have influenced caregiver–infant interactions in this study (DeLuycker 2007). Since season was conflated with infant age, I was unable to investigate this factor. Further research is required to assess whether ecological conditions differed significantly between sites, as possibly suggested by measurements of habitat. If resources were more severely limited in Calzada compared with Yantaló (based on fragment and home range size), then adults may have been unable to reliably provide care while also meeting personal survival needs, triggering earlier, more frequent conflicts in this group. This has been observed in *Chlorocebus* spp. (Hauser and Fairbanks 1988). Additional data on habitat and season factors is needed to clarify the role of ecological conditions in POC.

Additionally, variation in tolerance of infants or caregiver style may have affected conflict and avoidance. This has been shown in research on *C. sabaeus*, which found stable individual differences in maternal style (protectiveness and rejection) across infant age and identity (Fairbanks 1996). Further, prior parental experiences may have affected the overall form of caregiving by adults (reviewed in Fairbanks 1996). For instance, in Yantaló, one infant disappeared before the start of the study and one infant disappeared between field seasons. This may have influenced parents to be more protective and less rejecting of infants.

Finally, the elevated percentages of sibling–infant conflict relative to those of adults in both groups is unsurprising as titi monkey siblings are known to exhibit distress and intolerance when infants cling to them (Fragaszy *et al*. 1982). Since males are the primary infant caregivers, conflict values for mothers and siblings in each group may have been related to instances of male–infant conflict. Specifically, increased levels of male–infant conflict and avoidance in Calzada may have redirected infant clinging attempts to other group members, thereby elevating conflict estimates for the mother and siblings. This behavioral sequence has been documented in captive titi monkeys (Fragaszy *et al*. 1982).

As a final caveat, it is possible that the higher rate of sampling at Calzada compared with Yantaló produced the discrepancy in outcomes. However, I consistently documented the divergent interaction patterns in two sets of infants over two field seasons with roughly equivalent rates of sampling in the second season. Therefore I do not expect that sampling bias played a significant role in the results. Despite the limitations of my data, the findings provide an in-depth representation of conflict with, and avoidance of, infants by titi monkey caregivers that can be used to shape future research on POC and parental investment.

3.5. References

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:227–267

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, Zielger TE (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anth 131:525–534

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ

Collinge NE (1987) Weaning variability in semi-free-ranging Japanese macaques (*Macaca fuscata*). Folia Primatol 48:137–150

DeLuycker AM (2007) The ecology and behavior of the Río Mayo titi monkey (*Callicebus oenanthe*) in the Alto Mayo, northern Peru. Ph.D. Doctoral thesis. Saint Louis, Washington University

DeLuycker AM (2014) Observations of a daytime birthing event in wild titi monkeys (*Callicebus oenanthe*): Implications of the male parental role. Primates 55:59–67

DeVinney BJ, Berman CM, Rasmussen KLR (2003) Individual differences in response to sibling birth among free-ranging yearling rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. Behaviour 140:899–924

ESRI (2014) ArcGIS desktop: release 10.2.2. Environmental Systems Research Institute, Redlands

Fairbanks LA (1996) Individual differences in maternal style: causes and consequences for mothers and offspring. In: Rosenblatt JS, Snowdon CT (eds) Parental care: evolution, mechanisms, and adaptive significance. Academic Press, pp 579–611

Fairbanks LA, McGuire MT (1995) Maternal condition and the quality of maternal care in vervet monkeys. Behaviour 132:733–754

Fragaszy DM, Schwarz S, Shimosaka D (1982) Longitudinal observations of care and development of infant titi monkeys (*Callicebus moloch*). Am J Primatol 2:191–200

Gomendio M (1991) Parent/offspring conflict and maternal investment in rhesus macaques. Anim Behav 42:993–1005

Hauser MD, Fairbanks LA (1988) Mother-offspring conflict in vervet monkeys: variation in response to ecological conditions. Anim Behav 36:802–813

Hayne WD (1949) Calculation of size of home range. J Mammal 30:1–7

Hodges S (2020) Observations of infant conflict and avoidance in San Martin titi monkeys (*Plecturocebus oenanthe*). Primates 61:365–371. URL: <https://doi.org/10.1007/s10329-020-00815-4>

Huashuayo-Llamocca R, Heymann EW (2017) Fur-rubbing with *Piper* leaves in the San Martín titi monkey, *Callicebus oenanthe*. Figure 1. Location of the study area. Primate Biol 4:127–130. Adapted under a Creative Commons Attribution 3.0 license. URL: <https://creativecommons.org/licenses/by/3.0/us/>

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose, Costa Rica

Lawrence JM (2007) Understanding the pair bond in brown titi monkeys (*Callicebus brunneus*): male and female reproductive interests. Ph.D. Doctoral thesis. New York, Columbia University.

Maestriperi D (2002) Parent–offspring conflict in primates. Int J Primatol 23:923–951

Pavé R, Kowalewski MM, Peker SM, Zunino GE (2010) Preliminary study of mother–offspring conflict in black and gold howler monkeys (*Alouatta caraya*). Primates 51:221–226

Pavé R, Kowalewski MM, Zunino GE, Giraudo AR (2015) How do demographic and social factors influence parent-offspring conflict? The case of wild black and gold howler monkeys (*Alouatta caraya*). Am J Primatol 77:911–923

R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing Vienna Austria. URL: <https://www.r-project.org/> Accessed 16 December 2018

Rowe N, Myers M (2017) All the world's primates. Pogonias Press, Charlestown, RI, pp 176–207

Schino G, Troisi A (1998) Mother-infant conflict over behavioral thermoregulation in Japanese macaques. Behav Ecol Sociobiol 43:81–86

Schino G, Speranza L, Troisi A (2001) Early maternal rejection and later social anxiety in juvenile and adult Japanese macaques. Dev Psychobiol 38:186–190

Shanee S, Tello-Alvarado JC, Vermeer J, Bóveda-Penalba AJ (2013) GIS Risk Assessment and GAP analysis for the Andean titi monkey (*Callicebus oenanthe*). Primate Conserv 26:17–23

Simpson MJA, Simpson AE, Howe S (1986) Changes in the rhesus mother-infant relationship through the first four months of life. Anim Behav 34:1528–1539

Spence-Aizenberg A, Di Fiore A, Fernandez-Duque E (2016) Social monogamy, male-female relationships, and biparental care in wild titi monkeys (*Callicebus discolor*). Primates 57:103–112

Trivers RL (1974) Parent-offspring conflict. Am Zool 14:249–264

Veiga L, Bóveda-Penalba A, Vermeer J, Tello-Alvarado JC, Cornejo F (2013) *Callicebus oenanthe*. The IUCN Red List of Threatened Species 2013: e.T3553A9939083. URL: <http://dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T3553A9939083.en> Accessed 30 July 2019

Wright PC (1984) Biparental care in *Aotus* and *Callicebus*. In: Small MF (ed) Female primates: studies by women primatologists. Alan R. Liss, New York, NY, pp 59–75

Wright PC (1985) The costs and benefits of nocturnality for *Aotus trivirgatus* (the night monkey). Doctoral thesis. New York, The City University of New York

Wright PC (1990) Patterns of paternal care in primates. Int J Primatol 11:89–102

Zhao Q, Tan CL, Pan W (2008) Weaning age, infant care, and behavioral development in *Trachypithecus leucocephalus*. Int J Primatol 29:583–591

4. PATERNAL ACTIVITY BUDGETS OF THE PERUVIAN SAN MARTIN TITI MONKEY (*Plecturocebus oenanthe*) IN RESPONSE TO HABITAT DESTRUCTION, SEASONALITY, THERMAL STRESS, AND INFANT CARE[*]

4.1. Introduction

A range of ecological factors can affect primate activity budgets, and the way that primates allocate time to daily activities can greatly affect their ability to survive and reproduce (Coelho 1986; Defler 1995). Under natural conditions, primates cope with the energetic costs arising from seasonal fluctuations in food availability (dispersion, abundance), ambient temperature, and the need for infant care. Habitat destruction can increase these existing demands by reducing access to resources and altering local climate patterns. Clarifying how primates cope with anthropogenic habitat disturbance in addition to naturally occurring ecological demands can lead to improvements in the development of conservation strategies.

The availability and quality of food resources are known to be the most important ecological factors affecting primate behavior since they entail a tradeoff between energy acquisition and expenditure (Chapman *et al*. 2015; Chaves *et al.* 2011; Knott 1999; Lambert and Rothman 2015). In addition, ambient temperature has been shown to significantly influence behavior as primates attempt to balance thermoregulation and energy intake in response to climatic conditions (Kamilar and Beaudrot 2018). The two main drivers of variation in food resources and thermal stress are habitat destruction (Arroyo-Rodríguez and Mandujano 2006;

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Arroyo-Rodríguez *et al*. 2017; Chapman *et al*. 2006) and seasonality (Bunker and Carson 2005; Murphy and Lugo 1995), which can lead to major fluctuations in ecological pressures (Chapman *et al*. 2015; Charpentier *et al.* 2018; Thompson *et al*. 2014).

Shifts in resource availability and quality represent critical challenges for primates, and some species cope by adopting energy maximizing or time minimizing approaches. Originally proposed by Schoener (1971), this model claims that energy maximizers attempt to obtain the maximum amount of energy during the available foraging time (Hixon 1982) by foraging and feeding for as long as possible. For instance, in periods of seasonal scarcity when preferred foods were less available, François' langurs (*Trachypithecus francoisi*) (Zhou *et al.* 2007) and Gursky's spectral tarsier (*Tarsius spectrum gurskyae*) (Gursky 2000) followed an energy maximizing strategy by increasing the proportion of time spent foraging, supplementing their diet with alternative foods, and reducing rates of resting and socializing.

In contrast, time minimizers prioritize energy conservation and forage and feed only until they meet their net metabolic requirements. For example, bearded saki monkeys (*Chiropotes satanas chiropotes*) living in 1-ha, 10-ha, and 100-ha forest fragments traveled less and rested more than those in continuous forest (Boyle and Smith 2010), indicating time minimization. Similar alterations to activity have been shown in diademed sifakas (*Propithecus diadema*) living in fragmented forest compared with those living in continuous forest (Irwin 2008). Primates may employ similar activity budgeting in response to lower food abundance and quality in the dry season by limiting costly behaviors, such as traveling and foraging, and increasing time spent inactive and socializing. This has been observed in San Martín titi monkeys (*Plecturocebus oenanthe*) (DeLuycker 2007), buffy-headed marmosets (*Callithrix flaviceps*) (Ferrari and Hilário 2014), and black-fronted titi monkeys (*Callicebus nigrifrons*) (Nagy-Reis and Setz 2017). Time minimizing has also been used by primates to thermoregulate when exposed to extreme temperatures. For example, as temperatures become warmer black howler monkeys (*Alouatta pigra*) rest more often (Aristizabal *et al*. 2018), Barbary macaques (*Macaca sylvanus*) (Majolo *et al.* 2013) feed less, while chimpanzees (*Pan troglodytes*) (Kosheleff and Anderson 2009) and southern muriquis (*Brachyteles arachnoides*) (Talebi and Lee 2010) increase resting and decrease time spent feeding.

Infant care also represents a significant energetic challenge for caregivers. For female primates, lactation is the most expensive activity in terms of caloric demands (Clutton-Brock 1991). Mothers cope with reproductive costs by altering diet, such as by increasing the quality or quantity of foods (McCabe and Fedigan 2007; Murray *et al*. 2009), or by adjusting time allocation decisions to either maximize or conserve energy (Dunham and Rodriguez-Saona 2018; Lappan 2009; Rose 1994). Females may intensify their use of such strategies as resources become scarcer due to habitat destruction or seasonal changes. For instance, a study on red colobus (*Procolobus rufomitratus*) living in logged and old-growth forest found that females in logged areas compensated for a loss of resources by following an energy maximizing approach (Milich *et al.* 2014). They did this by adopting a more varied diet with a higher proportion of readily available, but less-preferred and possibly lower-quality, food items. Compared with females in old-growth habitat, they also devoted more time to feeding and less time to all other activities. These behavioral changes allowed female *P. rufomitratus* living in logged areas to maintain similar densities to those in old-growth forest.

After lactation, infant transport is the next most costly form of infant care (Altmann and Samuels 1992) and is the typical way that male primates contribute to infant care (Kleiman 1985; Wright 1990). In species with substantial male care, adult males provide the bulk of infant transportation and dedicate proportionally more time to infant care than other group members (Fernandez-Duque *et al*. 2009; Kleiman 1985; Storey and Ziegler 2016). In several species with obligate paternal care, fathers invest significantly more time providing care at the earliest stages of infant development (Price 1992a; Rotundo *et al.* 2005; Wright 1984). For instance, wild adult male Toppin's titi monkeys (*Plecturocebus toppini*, previously *Callicebus moloch*) allocate >90% of their time to infant care during the first two months of life, which gradually declines (40–60%) by three to four months of age (Wright 1990). Paternal care costs are evident in loss of time and also disruption of daily activities such as foraging and traveling. For example, infant carrying diminished insect foraging success of fathers in *P. toppini* (see Wright 1984), and lowered feeding rates of *P. oenanthe* fathers (see DeLuycker 2007). In captive cotton-top tamarins (*Saguinus oedipus*), greater infant body mass and longer durations of carrying reduced travel speeds in adults (Caperos *et al.* 2012).

For species with considerable male care it is important to understand how adult males adapt behaviorally to socioecological stressors, since this may affect infant care and development as has been seen in studies on maternal care (Dunbar *et al.* 2002; Lee *et al.* 1991; Maestripieri *et al.* 2009; Milich *et al.* 2014). Since mothers experience the added demands of gestation and lactation it cannot be assumed that paternal and maternal responses will be equivalent. There has been a lack of research on paternal responses to seasonal and parental sources of stress, and no studies thus far have examined the impacts of habitat destruction on male activity in primates with obligate paternal care. *Plecturocebus oenanthe*, endemic to premontane tropical forests in the San Martín region of Peru, is an ideal species for a study of the co-occurring effects of habitat destruction, thermal stress, seasonality, and infant care on paternal activity budgets. It suffers from varying degrees of habitat degradation and fragmentation (Shanee *et al.* 2013) and climatic seasons are strongly demarcated by variation in food availability and temperature (DeLuycker 2007; 2012). The adult males are the principal infant carriers, and DeLuycker (2007; 2014) showed that infant carrying was associated with changes in their daily activity patterns.

I examined whether *P. oenanthe* adult males employ either energy maximizing or time minimizing strategies to cope with the demands of infant care under various environmental stressors. Building on prior titi monkey research (DeLuycker 2007; Nagy-Reis and Setz 2017; Souza-Alves 2013), I examined whether adult male *P. oenanthe* adopt a time minimizing approach in response to elevated energetic burdens. Specifically, I investigated the effects of habitat destruction, tropical season, daily temperature range, and infant age (a proxy for infant care costs). I predicted that resting (including social rest) would increase in response to a higher level of habitat destruction, in the dry season, with greater daily temperature ranges, and with younger infant ages. I expected the opposite outcomes for traveling, feeding, and social interaction.

4.2. Methods

4.2.1. Study sites

This study took place in the San Martín region of northeastern Peru (Figure 4-1) over 11 months during two field seasons—from July to December 2015 and from August 2016 to January 2017. I collected data on adult males living in two different premontane tropical forest fragments (Holdridge 1967). Sites were previously assessed (Chapter 2) for relative level of habitat destruction (hereafter HD), and I designated these as either lower or higher HD sites. The lower HD site was near the town of Yantaló (5°59'21.64"S, 77°2'42.96"E) at an elevation of 868 m. The higher HD site was near the village of Calzada (6°2'47.18"S, 77°5'58.92"E) at 820 m. The lower HD site was 4.15 ha, nearly twice the size of the higher HD site (2.15 ha). Tree density (32.9 vs. 15.5 m^2/100 m^2) and fruit availability per individual (1.74 vs. 1.46 m^2/100 m^2) were significantly reduced at the higher compared with the lower HD site. Crop fields of mainly plantains, rice, and coffee surrounded both forest fragments. Domesticated dogs roamed the area and entered the forest at the higher HD site daily, but rarely did so at the lower HD site.

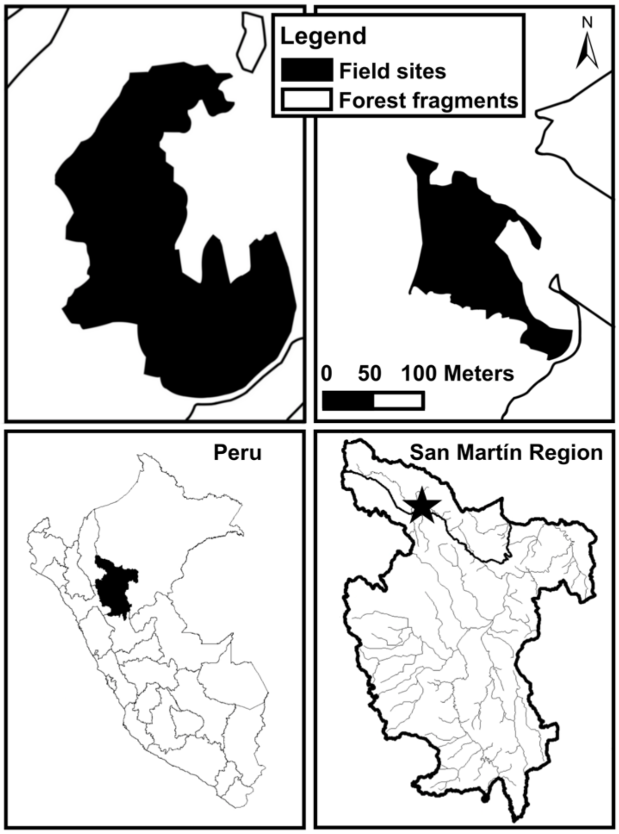

Figure 4-1 Field sites (*top left*: lower HD site; *top right*: higher HD site) and their location in the San Martín region (*bottom right*) of Peru (*bottom left*).

4.2.2. Study species and groups

The small *P. oenanthe* (~1.0 kg) inhabits premontane tropical forest at maximum elevations of approximately 1,129 m (Bóveda-Penalba *et al.* 2009). It eats mainly fruits and insects, supplementing its diet with new leaves, flowers, and seeds (DeLuycker 2007; 2012). Fathers carry infants within 24 hours of their birth and are the primary infant caregivers and attachment figures (DeLuycker 2007; 2014). I collected data on the activity budgets of the resident adult male of each study group ($N = 2$). I compared body size, fur length and color, facial mask development, and visually identified genitalia to determine the age and sex class of all study group individuals (DeLuycker 2007). Since I did not confirm genetic paternity of infants, I use the term “males” rather than “fathers.”

In both groups, males cared for one infant per field season (Figure 4-2). The adult male at the lower HD site (Yantaló) lived with an adult female and a juvenile female (classed as a subadult in the second season). The infant observed in the first field season was missing in the second season and may have either died or been captured for the illegal pet trade, which had occurred previously at this site according to a local farmer. The adult male at the higher HD site (Calzada) resided with an adult female, one subadult female that was absent in the second field season, a subadult male, and a juvenile female (classed as a subadult in the second season). The infant born in the first season was classed as a juvenile the following year.

Figure 4-2 *Left*: Adult male carrying an infant (3.5 months old) at Yantaló. *Right*: Adult male carrying an infant (1.0 months old) at Calzada.

4.2.3. Activity budget data collection

I trained two field assistants to help with behavioral data collection, Daniel Morales Rodríguez and Raul Saucedo Quispe, and verified that we achieved consistent agreement on the individual identity and activity category designations prior to formal data collection. Assistants worked in different field seasons, therefore I used the index of concordance (Martin and Bateson 2007) to test for interobserver reliability between my observations and each of theirs in 30-minute parallel observation training sessions (Daniel: 93.33%, $N = 10$; Raul: 96%, $N = 10$). We collected activity budget data and sorted behaviors into the categories of rest, travel, feed, social interaction, and other (Table 4-1). Behaviors classified as other occurred too infrequently (3% of budget) to be analyzed in this study. During daily focal follows, we tracked males while they cared for infants (for example, carrying, crouching over, retrieving, grooming, and cleaning) and used instantaneous focal sampling to collect data every two minutes (Altmann 1974). The size of the dataset was limited by the paternal care rate of study subjects since we did not consistently monitor males when they were not engaging in infant care.

Table 4-1 Activity ethogram for adult male San Martin titi monkeys (*Plecturocebus oenanthe*).

Activity	Definition
Rest	A period of inactivity, including sitting, standing, lying down, huddling, or self-grooming
Travel	To move from one location to another, including walking, running, climbing, or leaping
Feed	To search for, chew, or swallow food items
Social	Dyadic interactions, including playing, allogrooming, agonism, or sexual activity
Other	Refers to infrequent behaviors not included above, such as vocalizing or scent-marking

For each data point, we recorded the relative level of HD for each study site (lower or higher based on prior research). I classified tropical seasons as dry (May–September) or wet (October–April), and calculated daily temperature range in degrees Celsius (°C) based on climate data retrieved from the National Meteorology and Hydrology Service of Peru (SENAMHI 2017). Infant age in months functioned as a proxy of infant care costs since infant care is considered to be potentially incompatible with certain activities such as foraging and traveling (Caperos *et al.* 2012; DeLuycker 2007; Price 1992b) and is physically demanding for small Neotropical primates (Achenbach and Snowdon 2002; Sánchez *et al*. 1999; Tardif 1994). To control for the effects of time of day, I classified diurnal periods as morning (prior to 11:00), midday (11:00–13:00), or afternoon (after 13:00). We tracked weather conditions under the categories of no rain, light rain, or heavy rain. Study subjects always rested during heavy rain, so I removed observations recorded during this weather to control for its impact on behavior.

To improve dataset reliability, I removed instantaneous data points for those days during which fewer than 20 minutes of focal follow observation were recorded. Infant age ranged from 0–6 months during the field study. Prior to analysis, I also excluded observations months 5 and 6 due to insufficient data collected on activity budgets. I used R Studio (R Development Core Team 2017) to transform and analyze all data.

After data cleanup, instantaneous data totaled 7,069 sample points (243.5 hours) collected on 96 focal follow days. I transformed data prior to analysis by calculating activity percentages for each category-based level of HD, season, daily temperature range, infant age, time of day, and day of observation. I calculated sample percentages (*N* = 172 per behavior category) by dividing the sum of instantaneous data points per activity by the total number of points recorded and multiplying these by 100 (package dplyr).

4.2.4. Statistical analysis

I used generalized linear mixed models (GLMMs) with package lme4 to examine my predictions. I created separate models for each behavior category (rest, travel, feed, and social interaction) and used activity percentages as the response variable. Fixed effects included level of HD, season, daily temperature range, and infant age. I coded time of day as a random effect and included sample number (1–172) as an observation level random effect to minimize overdispersion (Xavier 2014). I fit models with a binomial error distribution and logit link, and estimated parameters using maximum likelihood for model comparison (Bolker *et al.* 2009). Instantaneous observation counts provided weights for percentage samples.

I built GLMMs ranging from intercept-only (null) to full interaction models, keeping the same random effects in each model. I used variance inflation factor (VIF) estimates to assess multicollinearity among fixed effects (package car) and discarded models with VIFs ≥4.0 (Zuur *et al*. 2010). Several of the interaction models failed to converge, likely due to small sample size, and I discarded these. For the remaining GLMMs, I explored the data to verify that they met model assumptions. I identified highly influential outliers using Cook's distance with package stats and used 2.0 as a cutoff value. Next, I refit models after removing the most severe outliers for each activity category, ensuring that categorical behavior models used the same dataset. I discarded all interaction models either due to convergence or multicollinearity issues.

To initially evaluate models, I calculated the difference between delta AICc (ΔAICc) values (package aods3) and considered models with ΔAICc ≥10.0 to be implausible (Burnham and Anderson 2002). I then compared nested models. I identified best-fitting models using likelihood X^2 ratio tests (alpha = 0.05) in package stats (Anderson *et al*. 2000; Bolker *et al*. 2009). In the interest of full reporting, I refit both the best and full models using restricted maximum likelihood estimation (REML) and carried out Wald X^2 tests of fixed effects with package glmmTMB (alpha = 0.05) (Bolker *et al.* 2009). I reported effect sizes as odds ratio estimates. Level of HD odds ratios specified the odds of each type of activity occurring at the higher HD site compared with odds at the lower HD site. Season odds ratios indicated the odds of activity during the wet season compared with the dry season. Odds ratios for temperature and infant age (in months) indicate the change in odds of each activity per one unit increase in °C and month, respectively.

I generated box plots of data used in GLMMs with package ggplot2. I carried out *post-hoc* examinations of feeding percentages across levels of HD and seasons to investigate foraging on crops or foods that people have stored (anthropogenic foraging). To do this, I sorted instantaneous feeding observations as either anthropogenic or natural, and then carried out X^2 tests of independence to evaluate differences in feeding bout type holding either level of HD or season (alpha = 0.05) constant.

4.3. Results

4.3.1. Activity models and tests of fixed effects

Table 4-2 shows the results of model comparisons based on ΔAICc and likelihood X^2 ratio testing. The model with level of HD, daily temperature range, and infant age fit the resting and traveling data best. The two-term model with temperature and infant age predicted feeding better than other models, though ΔAICc and X^2 testing indicated that the model including season also fit the data adequately (ΔAICc = 0.00, $P = 0.0994$). Level of HD was the only term included in the best-fitting model of social interaction. Models with fixed effects were typically much more plausible than intercept-only models based on the smaller ΔAICc values and according to likelihood X^2 ratio tests.

Table 4-2 Comparisons of adult male activity models with ΔAICc and likelihood X^2 ratio tests.

			Likelihood ratio tests		
	Activity models	**ΔAICc**	**X^2**	***df***	***P*-value**
Rest (*N* = 169)	HD + Season + Temperature + Age	0.19	1.99	1	0.1582
	HD + Temperature + Age	**0.00**	**12.52**	**1**	**0.0004***
	HD + Age	10.36	14.63	1	0.0001*
	Age	22.87	25.56	1	<0.0001*
	Intercept	46.33	–	–	–
Travel (*N* = 163)	HD + Season + Temperature + Age	2.10	0.08	1	0.7782
	HD + Temperature + Age	**0.00**	**4.45**	**1**	**0.0349***
	HD + Age	2.29	15.08	1	0.0001*
	Age	15.24	50.46	1	<0.0001*
	Intercept	63.61	–	–	–
Feed (*N* = 171)	HD + Season + Temperature + Age	0.58	1.60	1	0.2058
	Season + Temperature + Age	0.00	2.72	1	0.0994
	Temperature + Age	**0.57**	**5.51**	**1**	**0.0189***
	Temperature	3.95	14.10	1	0.0002*
	Intercept	15.95	–	–	–
Social (*N* = 172)	HD + Season + Temperature + Age	5.39	0.07	1	0.7860
	HD + Temperature + Age	3.28	0.10	1	0.7549
	HD + Age	1.24	0.88	1	0.3470
	HD	**0.00**	**5.45**	**1**	**0.0196***
	Intercept	3.35	–	–	–

Activity budget models fit by relative level of habitat destruction, season, daily temperature range, and infant age. Likelihood X^2 ratio test results indicate whether a simpler model is preferred (null hypothesis) compared to the next most complex model (i.e. compared in ascending order of complexity). Bolded terms indicate best-fitting models based on ΔAICc (<10.0) and likelihood ratio tests (P<0.05). Sample sizes for activity percentages are showed in parentheses.

Table 4-3 shows the odds ratio estimates and Wald X^2 tests of fixed effects results. All terms in the best-fitting models were significant ($P<0.05$). According to the best model, odds of rest increased with a higher level of HD and greater daily temperature ranges and decreased with each increase in month of infant age. Similarly, only level of HD, daily temperature range, and infant age had statistically significant impacts in the full model of rest. Resting was non-significantly more likely to occur in the wet than in the dry season, as shown by the odds ratio estimate. In the best-fitting traveling model, odds decreased with a higher level of HD and greater daily temperature ranges and increased with infant age. The full model indicated that odds of traveling were non-significantly higher during the wet compared with the dry season.

Table 4-3 Wald X^2 fixed effects tests of best-fitting and full models of adult male activity.

			Effect size	Wald tests of fixed effects		
	Models	Fixed effects	Odds ratio	X^2	*df*	*P*-value
Rest (*N* = 169)	Best model	**HD**	1.70	13.05	1	**0.0003**
		Temperature	1.12	11.80	1	**0.0006**
		Age	0.69	27.83	1	**<0.0001**
	Full model	**HD**	1.82	14.91	1	**0.0001**
		Season	1.36	1.83	1	0.1763
		Temperature	1.11	12.65	1	**0.0004**
		Age	0.67	29.35	1	**<0.0001**
Travel (*N* = 163)	Best model	**HD**	0.64	13.45	1	**0.0002**
		Temperature	0.95	4.26	1	**0.0391**
		Age	1.55	63.42	1	**<0.0001**
	Full model	**HD**	0.65	11.65	1	**0.0006**
		Season	1.05	0.07	1	0.7847
		Temperature	0.95	4.09	1	**0.0431**
		Age	1.54	53.78	1	**<0.0001**
Feed (*N* = 171)	Best model	**Temperature**	0.87	12.52	1	**0.0004**
		Age	1.21	4.99	1	**0.0255**
	Full model	HD	0.80	1.29	1	0.2563
		Season	0.59	3.46	1	0.0629
		Temperature	0.86	13.54	1	**0.0002**
		Age	1.29	7.75	1	**0.0054**
Social (*N* = 172)	Best model	**HD**	0.58	4.66	1	**0.0308**
	Full model	HD	0.61	3.47	1	0.0626
		Season	0.90	0.58	1	0.4454
		Temperature	1.11	0.07	1	0.7856
		Age	0.99	0.08	1	0.7840

Fixed effects tests of model terms using restricted maximum likelihood estimation (REML). Terms with significant *P*-values ($P<0.05$) are bolded. Sample sizes for activity percentages are showed in parentheses.

Similarly, for both best-fitting and full models of feeding, the odds were lower with more extreme temperature ranges and higher as infants grew older. Odds of feeding were non-significantly greater at the higher compared with the lower HD site, and greater in the dry than in the wet season. Finally, the best-fitting model indicated that the odds of social interaction were more likely at the lower than at the higher HD site. According to the full model, odds of socializing were non-significantly more likely during the wet season and decreased with larger temperature ranges and older infant ages. Figure 4-3 displays data used in GLMMs as box plots of mean proportion of time per day allocated to activities by level of HD, season, mean daily temperature range, and infant age.

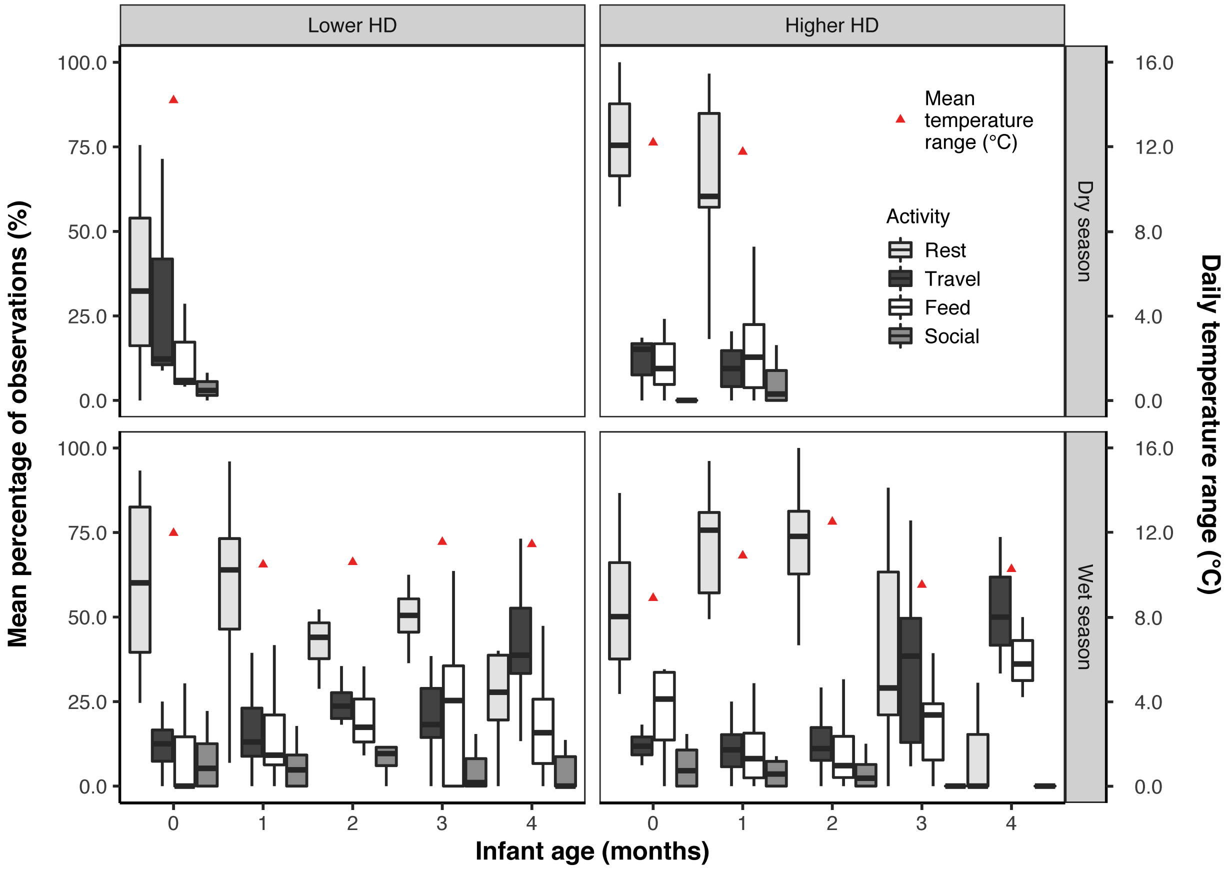

Figure 4-3 Mean percentage of time that adult males devoted to each activity by relative level of habitat destruction (HD), season, mean daily temperature range (°C), and infant age (months) (*N* = 172 percentage samples).

4.3.2. *Post-hoc* tests of foraging

According to X^2 tests of independence, bouts of anthropogenic foraging (Figure 4-4 and Figure 4-5) took place significantly more often at the higher HD site compared with the lower HD site ($X^2 = 5.46$, $df = 1$, $P = 0.0194$). At the higher HD site, this type of foraging accounted for 2.91% of instantaneous feeding observations versus 0.84% of feeding observations at the lower HD site. There were no statistically significant differences in anthropogenic foraging across seasons ($X^2 = 0.19$, $df = 1$, $P = 0.4716$).

Figure 4-4 Adult female (*left*) and subadult female (*right*) feeding on cultivated plantains located 9 m from the forest edge in Yantaló.

Figure 4-5 Adult male (*background*), carrying an infant (2.6 months old), and subadult male (*foreground*) exploring a shack where plantains are stored.

4.4. Discussion

The results provide strong support for the hypothesis that *P. oenanthe* males followed a time minimizing strategy to cope with elevated energetic demands that resulted from habitat destruction, thermal stress, and infant care, but not in response to seasonality. As expected, I found that a greater degree of habitat destruction was significantly associated with higher percentages of resting and lower percentages of traveling and socializing. These results concur with prior research showing that titi monkeys employ a time minimization to cope with lower food availability due to habitat destruction. For instance, research by Souza-Alves (2013) on Coimbra Filho's titi monkeys (*Callicebus coimbrai*) showed that individuals living in a smaller forest fragment (14 ha) spent significantly less time traveling and feeding than those living in a larger area (522 ha). The smaller fragment group also spent more time resting and socializing, though intergroup differences were not significant. Similar energy-conserving responses to habitat destruction have been found in primates with a range of dietary needs, including folivores (*Alouatta palliata*: Dunn *et al*. 2009; *Chlorocebus djamdjamensis*: Mekonnen *et al*. 2017; *Colobus vellerosus*: Wong and Sicotte 2007), frugivores (*Ateles geoffroyi*: Chaves *et al*. 2011), and seed predators (*C. satanas chiropotes*: Boyle *et al.* 2009; Silva and Ferrari 2009).

Contrary to my prediction, feeding did not differ between levels of HD, though feeding percentages were larger at the lower HD site. This indicates that males in the present study devoted equivalent amounts of time to food acquisition, despite the difference in fruit availability between sites. Since I did not systematically record which foods study subjects consumed, I was unable to investigate whether the higher HD male increased consumption of non-fruit resources to compensate for lower fruit availability. Prior research has indicated that fruit is a major component of the diet of *P. oenanthe* (44%) (DeLuycker 2007), however the results in the present study suggest that fruit is less important to *P. oenanthe* than previously thought.

Alternatively, the male at the higher HD site may have been able to supplement natural foraging with anthropogenic foraging to maintain equivalent feeding levels. According to *post-hoc* X^2 tests, the male at the higher HD site engaged in anthropogenic foraging significantly more often than the male at the lower HD site. All study group members at both sites entered human-occupied areas to feed on plantains (a high value food) at least once during data collection. Titi monkeys risked confronting humans and dogs during these excursions, though I never witnessed any such encounters. It is unclear whether titi monkeys employed this foraging tactic due to reduced fruit availability, or if anthropogenic resources were preferred to natural ones despite the accompanying risks. Given the elevated percentage of anthropogenic foraging at the higher HD site, it is reasonable to suggest that this strategy was used more often to compensate for the overall lower abundance of fruit. I did not consider human resources in my prior evaluation of fruit availability; however, titi monkeys appeared to have equal access to these foods at both sites.

None of the predictions regarding the influence of season were supported by the results. First, there were no differences in respective percentages of activities in any category between seasons. Second, males fed more often in the dry season, contradicting my expectations of decreased feeding during this period. The influence of seasonality on feeding was non-significant according to fixed effects tests, however the results indicated that it might be somewhat influential on this behavior ($P = 0.0629$). Seasonality has been shown to affect feeding behavior in other studies on titi monkeys. For example, *P. oenanthe* and *C. nigrifrons* fed more often during the wet than in the dry season, in line with a time minimization (DeLuycker 2007; Nagy-Reis and Setz 2017).

In support of my predictions, I found that wider daily temperature ranges were associated with increased resting and a reduction in traveling and feeding. Social activity also occurred non-significantly less frequently as temperature ranges increased, which was in the expected direction. These outcomes provide evidence of behavioral thermoregulation by *P. oenanthe*, which agrees with DeLuycker's (2007) study of this species. My findings are also in line with research on thermal stress in other primates (*Cebus capucinus*: Campos and Fedigan 2009; *Hoolock leuconedys*: Fan *et al*. 2013). Changes in *P. oenanthe* traveling are expected since arboreal locomotion in this small (1.0 kg) species is characterized by movements (for example, hopping, jumping, clambering, leaping, and climbing) (DeLuycker 2007) that are evidently energetically expensive (Hanna and Schmitt 2011) and more so when carrying infants (see, for example, Schradin and Anzenberger 2001; Tardif 1994). Prey foraging in this species involves propelling the body with quick and powerful movements like grabbing and lunging (DeLuycker 2012), and is made more difficult when carrying and infants. Given these potential costs, titi monkeys likely traveled and fed less under increased thermal stress in order to conserve energy.

Activity percentages varied according to infant age as predicted. Males rested less often and increased traveling and feeding as infants grew older. I expected this result based on prior titi monkey research suggesting that infant care might conflict with important activities, including foraging (DeLuycker 2007; Wright 1984). Though infant transportation does not affect foraging success of fathers *per se*, foraging percentages are lower when males carry infants than when they do not (DeLuycker 2007). It has been suggested that *P. oenanthe* fathers feed less often while transporting infants because this behavior competes with predator vigilance (DeLuycker 2007).

Another factor that may explain why carrying impacts foraging is its impact on traveling speeds. For example, captive *S. oedipus* adults moved more slowly when carrying infants for longer durations and as infants grew heavier (Caperos *et al.* 2012; see also Schradin and Anzenberger 2001). If infant carrying hampers the ability of *P. oenanthe* carriers to move quickly, then a strategy of reducing detection by predators through crypticity rather than relying on evasion only could be more successful in the long term. I did not witness any instances of predation, but I observed titi monkeys adopt cryptic behavior when potential predators (including hawks, dogs, and humans) were near.

Though traveling was less common during younger infant ages, it is unclear whether significant costs accompany infant transport for *P. oenanthe* fathers. Sánchez *et al.* (1999) explored the physical costs of paternal carrying in a study on captive cotton-top tamarins. Infant carrying reduced both feeding and traveling time in fathers. Paternal caregivers also lost weight during weeks 0–5 of infant age when they carried infants most frequently and gained weight thereafter as infants traveled independently for a majority of the time. Similarly, another captive study showed that *S. oedipus* fathers lost weight (range 1.3–10.8%) following the birth of infants, and that fathers with no alloparental helpers lost the most weight (10.0–10.8%) (Achenbach and Snowdon 2002). Based on such findings, I would expect that *P. oenanthe* fathers also lose weight when infant carrying durations are longest and regain weight as carrying declines. However, prior research has indicated that carrying costs are lower for titi monkeys compared with smaller Neotropical primates (Tardif 1994). Additional data and conditions should be explored to better understand these changes.

As a final caveat, I acknowledge that data trends (or lack thereof) may be related to the small sample size, especially across seasons. In addition, data collection did not consistently cover all the study groups' waking hours and thus the estimates presented here do not represent a true time budget for *P. oenanthe* males. This is an important consideration when day lengths differ given that time-adjusted budgets reveal greater variation among groups (Ferrari and Hilário 2014). Nevertheless, the findings indicate that males altered their time allocation patterns to manage a variety of co-occurring energetic challenges.

Overall, the results indicate that habitat destruction, temperature, and infant age had roles in shaping the activity patterns of *P. oenanthe* males. Understanding how anthropogenic activities affect this Critically Endangered species (Veiga *et al*. 2013) is vital for conservation efforts (Shanee *et al.* 2013), yet few behavioral studies have been conducted on *P. oenanthe* (DeLuycker 2007; 2012; 2014). Primate research has demonstrated that human-caused habitat disturbance alters typical activity patterns and challenges the ability of primates to persist in impacted areas (de Almeida-Rocha *et al.* 2017). I observed such changes in the present study, including anthropogenic foraging by *P. oenanthe.* Based on the results, I suggest that conservation strategies should aim to protect larger areas of forest habitat where *P. oenanthe* behavior is less likely to be disrupted. I also recommend that population management should focus on preventing opportunities for *P. oenanthe* to engage in anthropogenic foraging as this can increase the risk of disease, injury, and death (Beamish 2009; Tarara *et al.* 1985).

4.5. References

Achenbach GG, Snowdon CT (2002) Costs of caregiving: weight loss in captive adult male cotton-top tamarins (*Saguinus oedipus*) following the birth of infants. Int J Primatol 23:179–189

Altmann J (1974) Observational study of behavior: sampling methods. Behaviour 49:27–267

Altmann J, Samuels A (1992) Costs of maternal care infant-carrying in baboons. Behav Ecol Sociobiol 29:391–398

Anderson DE, Burnham KP, Thompson WL (2000) Null hypothesis testing: problems, prevalence, and an alternative. J Wildl Manage 64:912–923

Aristizabal JF, Leveque L, Chapman CA, Serio-Silva JC (2018) Impacts of temperature on behaviour of the Mexican Endangered black howler monkey *Alouatta pigra* Lawrence, 1933 (Primates: Atelidae) in a fragmented landscape. Acta Zool Bulgar 70:377–382

Arroyo-Rodríguez V, Mandujano S (2006) Forest fragmentation modifies habitat quality for *Alouatta palliata.* Int J Primatol 27:1079–1096

Arroyo-Rodríguez V, Saldana-Vazquez RA, Fahrig L, Santos B (2017) Does forest fragmentation cause an increase in forest temperature? Ecol Res 32:81–88

Beamish EK (2009) Causes and consequences of mortality and mutilation in the Cape Peninsula Baboon Population, South Africa. Masters thesis, University of Cape Town, Cape Town

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MH, White JS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bóveda-Penalba AJ, Vermeer J, Rodrigo F, Guerra-Vásquez F (2009) Preliminary report on the distribution of *Callicebus oenanthe* on the eastern feet of the Andes. Int J Primatol 30:467–480

Boyle SA, Lourenço WC, da Silva LR, Smith AT (2009) Travel and spatial patterns change when *Chiropotes satanas chiropotes* inhabit forest fragments. Int J Primatol 30:515–531

Boyle SA, Smith AT (2010) Behavioral modifications in northern bearded saki monkeys (*Chiropotes satanas chiropotes*) in forest fragments of central Amazonia. Primates 51:43–51

Bunker DE, Carson WP (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. J Ecol 93:794–806

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd ed. Springer, New York

Campos FA, Fedigan LM (2009) Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Am J Phys Anthropol 138:101–111

Caperos JM, Morcillo A, Peláez F, Fidalgo A, Sánchez S (2012) The effect of infant body mass on carrier travel speed in cotton-top tamarins (*Saguinus oedipus*). Int J Primatol 33:447–459

Chapman CA, Schoof VA, Bonnell TR, Gogarten JF, Calme S (2015) Competing pressures on populations: long-term dynamics of food availability, food quality, disease, stress and animal abundance. Philos Trans R Soc B 370:20140112

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL, *et al.* (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? Am J Phys Anthropol 131:525–534

Charpentier MJE, Givalois L, Faurie C, Soghessa O, Simon F, Kappeler PM (2018) Seasonal glucocorticoid production correlates with a suite of small-magnitude environmental, demographic, and physiological effects in mandrills. Am J Phys Anthropol 165:20–33

Chaves OM, Stoner KE, Arroyo-Rodríguez V (2011) Seasonal differences in activity patterns of Geoffroy's spider monkeys (*Ateles geoffroyi*) living in continuous and fragmented forests in southern Mexico. Int J Primatol 32:960–973

Clutton-Brock TH (1991) The Evolution of Parental Care. Princeton University Press, Princeton, NJ

Coelho A (1986) Time and energy budgets. In: Mitchell G, Erwin J (eds) Comparative primate biology: behavior, conservation, and ecology. Alan R. Liss, New York, pp 141–166

de Almeida-Rocha JM, Peres CA, Oliveira LC (2017) Primate responses to anthropogenic habitat disturbance: a pantropical meta-analysis. Biol Conserv 215:30–38

Defler TR (1995) The time budget of a group of wild woolly monkeys (*Lagothrix lagotricha*). Int J Primatol 16:107–120

DeLuycker AM (2007) The ecology and behavior of the Río Mayo titi monkey (*Callicebus oenanthe*) in the Alto Mayo, northern Peru. Doctoral thesis, Washington University, Saint Louis, MO

DeLuycker AM (2012) Insect prey foraging strategies in *Callicebus oenanthe* in northern Peru. Am J Primatol 74:450–461

DeLuycker AM (2014) Observations of a daytime birthing event in wild titi monkeys (*Callicebus oenanthe*): implications of the male parental role. Primates 55:59–67

Dunbar RIM, Hannah-Stewart L, Dunbar P (2002) Forage quality and the costs of lactation for female gelada baboons. Anim Behav 64:801–805

Dunham NT, Rodríguez-Saona LE (2018) Nutrient intake and balancing among female *Colobus angolensis palliatus* inhabiting structurally distinct forest areas: effects of group, season, and reproductive state. Am J Primatol 80(10):e22878

Dunn JC, Cristobal-Azkarate J, Vea JJ (2009) Differences in diet and activity pattern between two groups of *Alouatta palliata* associated with the availability of big trees and fruit of top food taxa. Am J Primatol 71:654–662

Fan PF, Ai, HS, Fei HL, Zhang D, Yuan SD (2013) Seasonal variation of diet and time budget of eastern hoolock gibbons (*Hoolock leuconedys*) living in a northern montane forest. Primates 54:137–146

Fernandez-Duque E, Valeggia CR, Mendoza SP (2009) The biology of paternal care in human and nonhuman primates. Ann Rev Anthropol 38:115–130

Ferrari SF, Hilário RR (2014) Seasonal variation in the length of the daily activity period in buffy-headed marmosets (*Callithrix flaviceps*): an important consideration for the analysis of foraging strategies in observational field studies of primates. Am J Primatol 76:385–392

Gursky S (2000) Effect of seasonality on the behavior of an insectivorous primate, *Tarsius spectrum.* Int J Primatol 21:477–495

Hanna JB, Schmitt D (2011) Locomotor energetics in primates: gait mechanics and their relationship to the energetics of vertical and horizontal locomotion. Am J Phys Anthropol 145:43–54

Hixon MA (1982) Energy maximizers and time minimizers: theory and reality. Am Nat 119:596–599

Hodges S (2020) Paternal activity budgets of the Peruvian San Martin titi monkey (*Plecturocebus oenanthe*) in response to habitat destruction, seasonality, thermal stress, and infant care. Primate Conserv (published online). URL: <http://www.primate-sg.org/storage/pdf/PC34_Hodges_P_oenanthe.pdf>

Holdridge LR (1967) Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica

Irwin MT (2008) Diademed sifaka (*Propithecus diadema*) ranging and habitat use in continuous and fragmented forest: higher density but lower viability in fragments? Biotropica 40:231–240

Kamilar JM, Beaudrot L (2018) Effects of environmental stress on primate populations. Ann Rev Anthropol 47:417–434

Kleiman DG (1985) Paternal care in New World Primates. Am Zool 3:857–859

Knott CD (1999) Reproductive, physiological and behavioral responses of orangutans in Borneo to fluctuations in food availability. Doctoral thesis, Harvard University, Cambridge, MA

Kosheleff VP, Anderson CN (2009) Temperature's influence on the activity budget, terrestriality, and sun exposure of chimpanzees in the Budongo Forest, Uganda. Am J Phys Anthropol 139:172–181

Lambert JE, Rothman JM (2015) Fallback foods, optimal diets, and nutritional targets: primate responses to varying food availability and quality. Ann Rev Anthropol 44:493–512

Lappan S (2009) The effects of lactation and infant care on adult energy budgets in wild siamangs (*Symphalangus syndactylus*). Am J Phys Anthropol 140:290–301

Lee PC, Majluf P, Gordon IJ (1991) Growth, weaning, and maternal investment from a comparative perspective. J Zool, Lond 225:99–114

Maestripieri D, Hoffman CL, Anderson GM, Carter CS, Higley JD (2009) Mother-infant interactions in free-ranging rhesus macaques: relationships between physiological and behavioral variables. Physiol Behav 96:613–619

Majolo B, McFarland R, Young C, Qarro M (2013) The effect of climatic factors on the activity budgets of Barbary macaques (*Macaca sylvanus*). Int J Primatol 34:500–514

Martin P, Bateson P (2007) Measuring behaviour: an introductory guide. 3rd edition. Cambridge University Press, Cambridge, UK

McCabe GM, Fedigan LM (2007) Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female *Cebus capucinus* at Santa Rosa, Costa Rica. Int J Primatol 28:837–851

Mekonnen A, Fashing PJ, Bekele A, Hernandez-Aguilar RA, Rueness EK, Nguyen N, Stenseth NC (2017) Impacts of habitat loss and fragmentation on the activity budget, ranging ecology and habitat use of Bale monkeys (*Chlorocebus djamdjamensis*) in the southern Ethiopian Highlands. Am J Primatol 79:e22644

Milich KM, Stumpf RM, Chambers JM, Chapman CA (2014) Female red colobus monkeys maintain their densities through flexible feeding strategies in logged forests in Kibale National Park, Uganda. Am J Phys Anthropol 154:52–60

Murphy P, Lugo AE (1995) Dry forests of Central America and the Caribbean. In: Bullock SH, Mooney HM, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, UK, pp 146–194

Murray CM, Lonsdorf EV, Eberly LE, Pusey AE (2009) Reproductive energetics in free-living female chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol 20:1211–1216

Nagy-Reis MB, Setz EZ (2017) Foraging strategies of black-fronted titi monkeys (*Callicebus nigrifrons*) in relation to food availability in a seasonal tropical forest. Primates 58:149–158

Price EC (1992a) Contributions to infant care in captive cotton-top tamarins (*Saguinus oedipus*): the influence of age, sex, and reproductive status. Int J Primatol 13:125–141

Price EC (1992b) The costs of infant carrying in captive cotton-top tamarins. Am J Primatol 26:23–33

R Development Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.r-project.org/> Accessed 16 December 2018

Rose LM (1994) Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). Int J Primatol 15:95–114

Rotundo M, Fernandez-Duque E, Dixson AF (2005) Infant development and parental care in free-ranging *Aotus azarai azarai* in Argentina. Int J Primatol 26:1459–1473

Sánchez S, Peláez F, Gil-Bürmann C, Kaumanns W (1999) Costs of infant-carrying in the cotton-top tamarin (*Saguinus oedipus*). Am J Primatol 48:99–111

Schoener TW (1971) Theory of feeding strategies. Ann Rev Ecol Evol Syst 2:369–404

Schradin C, Anzenberger G (2001) Costs of infant carrying in common marmosets, *Callithrix jacchus*: an experimental analysis. Anim Behav 62:289–295

SENAMHI (2017) Historical climate data. URL: <http://www. senamhi.gob.pe> Accessed 5 November 2017

Shanee S, Tello-Alvarado JC, Vermeer J, Bóveda-Penalba AJ (2013) GIS Risk Assessment and GAP analysis for the Andean titi monkey (*Callicebus oenanthe*). Primate Conserv 26:17–23

Silva SSB, Ferrari SF (2009) Behavior patterns of southern bearded sakis (*Chiropotes satanas*) in the fragmented landscape of eastern Brazilian Amazonia. Am J Primatol 71:1–7

Souza-Alves JP (2013) Ecology and life-history of Coimbra-Filho's titi monkeys (*Callicebus coimbrai*) in the Brazilian Atlantic Forest. Doctoral thesis, Universidade Federal da Paraíba, João Pessoa

Storey AE, Ziegler TE (2016) Primate paternal care: interactions between biology and social experience. Horm Behav 77:260–271

Talebi MG, Lee PC (2010) Activity patterns of *Brachyteles arachnoides* in the largest remaining fragment of Brazilian Atlantic Forest. Int J Primatol 31:571–583

Tarara R, Suleman MA, Sapolsky R, Wabomba MJ, Else JG (1985) Tuberculosis in wild olive baboons, *Papio cynocephalus anubis* (Lesson), in Kenya. J Wild Dis 21:137–140

Tardif SD (1994) Relative energetic cost of infant care in small-bodied Neotropical primates and its relation to infant-care patterns. Am J Primatol 34:133–143

Thompson CL, Williams SH, Glander KE, Teaford MF, Vinyard CJ (2014) Body temperature and thermal environment in a generalized arboreal anthropoid, wild mantled howling monkeys (*Alouatta palliata*). Am J Phys Anthropol 154:1–10

Veiga L, Bóveda-Penalba A, Vermeer J, Tello-Alvarado JC, Cornejo F (2013) *Plecturocebus oenanthe*. The IUCN Red List of Threatened Species 2013:eT3553A9939083. URL: <http://www.iucnredlist.org> Accessed 30 July 2019

Wong SN, Sicotte P (2007) Activity budget and ranging patterns of *Colobus vellerosus* in forest fragments in central Ghana. Folia Primatol 78:245–254

Wright PC (1984) Biparental care in *Aotus* and *Callicebus*. In: Small MF (ed) Female primates: studies by women primatologists. Alan R. Liss, New York, pp 59–75

Wright PC (1990) Patterns of paternal care in primates. Int J Primatol 11:89–102

Xavier AH (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2:e616

Zhou Q, Wei F, Huang C, Li M, Ren B, Luo B (2007) Seasonal variation in the activity patterns and time budgets of *Trachypithecus francoisi* in the Nonggang Nature Reserve, China. Int J Primatol 28:657–671

Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14

5. CONCLUSIONS

5.1. Infant caregiving in *Plecturocebus oenanthe*

This study found considerable variation in the parental care patterns of San Martin titi monkeys, which has not been documented previously in this species. This level of flexibility in infant care mirrors the significant variation found in the general behaviors (e.g. traveling and feeding) of titi monkeys. This study concurs with prior findings that titi monkeys are adaptable to highly disturbed environments in the short-term. However, additional research is necessary to identify the long-term consequences of these behavioral changes for infant survival, reproductive fitness, and population persistence.

In chapter 2, I described the infant care patterns of *P. oenanthe.* I found that male care was significantly reduced at the higher habitat destruction (HD) site (Calzada) compared with the male care at lower HD site (Yantaló). The opposite patterns were found for maternal care and alloparental, which were more common at the higher HD site. Despite the significant differences observed in infant care patterns, groups provided roughly equivalent levels of care for the first three months of life.

Infants in the higher HD site began transitioning to independent locomotion earlier than was observed at the lower HD site (month 3 vs. month 4 of infant age). The results of chapter 3 showed that infant independence at the higher HD site was facilitated by increased amounts of infant conflict and avoidance by male in months 3 to 4, whereas the lower HD male was never observed in conflict with infants. Conflict was also more common for the female and siblings at the higher HD site. Sibling-infant conflict occurred the most often for both groups, which was expected since siblings are highly intolerant of infant clinging.

In chapters 2 and 3, I discussed how differences in study subjects study groups may have influenced infant care and conflict. In particular, the male at the higher HD site appeared to be older and in worse physical condition (thinner and with more scars) than the lower HD male. It is possible that the higher HD male had a diminished capacity to provide care, which may have led to earlier and more frequent disagreements with the infant over care. This conflict led infants to care from the mother and siblings, which facilitated further conflict with individuals that would not typically provide substantial amounts of care (excepting lactation). In addition, the adults at Calzada experienced infant loss prior to and during the study. This may have led the male to be more protective and less rejecting of infants. All of these are factors that may have confounded the importance of habitat destruction on behavior.

In chapter 4, I described variation in male activity budgets to investigate whether males attempt to reduce energetic costs while meeting the challenges of infant care, habitat destruction, seasonality, and thermal stress. The male at the higher HD site rested more, traveled less, and socialized less than the male at the lower HD site, indicating the adopting of a time-minimizing strategy to cope with reduced resources. Despite the differences in habitat, similar percentages of feeding were observed between males. The male at the higher HD site may have accomplished this by engaging in anthropogenic foraging to supplement dietary needs. Results on the effects of seasonality were inconclusive since this factor was highly correlated with infant age, and not enough data was collected during the dry season to make a thorough comparison. In line with expectations, males rested more and traveled and fed less under extreme daily temperatures.

In sum, this is the first study to date that has investigated the effects of habitat destruction on infant care, and only the second study to provide an in-depth examination of *P. oenanthe* behavioral ecology. Therefore the results of this study contribute novel findings on the interaction between habitat destruction and parental investment to the primate literature, which has thus far made limited connections between parenting and ecological correlates of habitat destruction (e.g. food quality and availability). Further, this is the first research to date that has examined the ecological factors influencing variation in paternal (or even male) care in primates. This is also the first study to report significant amounts of alloparental care by siblings in titi monkeys. These results provide a basis for comparison with future research on the reproductive ecology of titi monkeys and can be used to inform conservation planning for this Critically Endangered species.

APPENDIX

Appendix Table 5-1 Mean measures of phenological transect data.

	Sites									
	Calzada (higher HD)					Yantaló (lower HD)				
Measure	Sept	Oct	Nov	Dec	Jan	Sept	Oct	Nov	Dec	Jan
Logging %	–	0.0308	0	0	0	–	0	0.0075	0	0
Density (# trees)	16.25	15.75	15.50	15.00	15.00	33.25	33.25	33.00	32.50	32.50
Basal area (m^2)	7.3025	7.3025	7.2900	7.2550	7.2550	5.2350	5.2350	5.2325	5.1650	5.1650
Height (m)	7.9150	7.9450	8.0025	8.0600	8.0600	8.2600	8.2600	8.2925	8.2800	8.2800
Fruit (m^2)	1.4617	1.4605	1.4582	1.4508	1.4508	1.7454	1.7454	1.7448	1.7216	1.7216

Phenological data collection began in September 2017 and concluded in January 2017. Logging averages represent the percentage of trees logged in all transects per month at each site. All other measures were averaged across the four transects at respective sites.