

RESEARCH ARTICLE

Double Effort: Parental Behavior of Wild Azara's Owl Monkeys in the Face of Twins

MAREN HUCK^{1*}, MARI VAN LUNENBURG², VICTOR DÁVALOS³, MARCELO ROTUNDO³, ANTHONY DI FIORE⁴, AND EDUARDO FERNANDEZ-DUQUE^{5,6}

¹Department of Biological and Forensic Sciences, University of Derby, Derby, United Kingdom

²Department of Behavioural Neuroscience, Utrecht University, Utrecht, The Netherlands

³Proyecto Mirikiná / Fundación ECO, Formosa, Argentina

⁴Department of Anthropology, University of Texas at Austin, Austin, Texas

⁵Centro de Ecología Aplicada del Litoral (Conicet, Corrientes), Corrientes, Argentina

⁶University of Pennsylvania, Philadelphia, Pennsylvania

In species of mammals that habitually bear single offspring, like most anthropoid primates, the occurrence of twins is expected to impose considerable energetic costs on the caretakers. The question then arises of how caregivers cope with the potentially increased costs of raising twins. These increased costs should lead to differing developmental rates in twins when compared to singletons, and/or to changes in the caregivers' behavior. Likewise, time budgets of parents of singletons are expected to differ from those of adults without offspring. Additionally, if twinning was an adaptive response to favorable ecological conditions, it should be more likely in years with high food abundance. Following the birth in 2011 of two sets of twins in a wild population of pair-living Azara's owl monkeys (*Aotus azarae*) in Northern Argentina, we used long-term demographic, behavioral, and phenological data to compare (a) the proportion of time that singleton and twin infants were carried by either parent; (b) adult time budgets and ranging behavior in groups with zero, one, or two infants; and (c) the availability of food in 2011 with food availability in other years. Twins, like singletons, were carried nearly exclusively by the male, and they were carried slightly more than singletons, suggesting a relatively inflexible pattern of infant care in the species. Time budgets showed that twin parents foraged more and moved less than singleton parents or groups without infants, despite the fact that phenological data indicate that fruit availability in 2011 was not substantially higher than in some of the other years. Overall, twinning thus presumably increased costs to breeders, especially males, but its effect on animals' long-term reproductive success remains unclear. *Am. J. Primatol.* 76:629–639, 2014. © 2014 Wiley Periodicals, Inc.

Key words: infant care; infant development; twinning; male care; reproductive trade-offs

INTRODUCTION

Caring for infants is often very costly. The costs of parental behavior in mammals arise through gestation, lactation, carrying, and other forms of care and infant protection, and may be detected indirectly through changed time budgets [Gittleman & Thompson, 1988; Huck et al., 2004; Prentice & Prentice, 1988; Sánchez et al., 1999; Tardif, 1997; Taylor et al., 1980]. Among those species of primates that habitually produce more than one offspring at a time, there seem to exist cost-reducing adaptations, such as the “parking” of infants observed in many strepsirrhines [Kappeler, 1998; Ross, 2001] and the cooperative breeding characteristics of the callitrichines [Goldizen, 1987b; Heymann, 2000; Huck et al., 2004; Tardif, 1997].

For the majority of anthropoid primates, however, the costs of parental behavior are usually associated with providing care to only one offspring, the modal litter size. Twinning is infrequent among wild anthropoids,

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*Correspondence to: Maren Huck, Department of Biological and Forensic Sciences, University of Derby, Kedleston Road, Derby DE22 1GB, United Kingdom. E-mail: m.huck@derby.ac.uk

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even though it has been reported for brown titi monkeys [*Callicebus brunneus*, Lawrence, 2007], red titi monkeys [*Callicebus cupreus*, Knogge & Heymann, 1995], white-bellied spider monkeys [*Ateles belzebuth*, Link et al., 2006], mantled howler monkeys [*Alouatta palliata*, Chapman & Chapman, 1986], Spix's night monkeys [*Aotus vociferans*, Aquino et al., 1990], and various catarrhines [review in Geissmann, 1990].

When either the number of available caregivers or the number of infants requiring care diverges substantially from the species-specific pattern, it might be predicted that parents would first adjust through modifications of their time budgets and possibly shared parental duties. Indeed, in some species, like banded langurs (*Presbytis melalophos*), general care patterns change and allomothering becomes more common in the presence of twins [Bennett, 1988]. The development of the infants themselves might also be affected. For example, in Japanese macaques (*Macaca fuscata*), twins were the smallest infants [Nakamichi, 1983], and even among captive Alaotran gentle lemurs (*Hapalemur griseus alaotrensis*), a species where twinning occurs frequently, a pair of twins had slower growth rates and were weaned later than singletons [Taylor & Feistner, 1996]. In the callitrichines, twins raised by lone pairs without helpers are rare and have a reduced survival probability compared to groups with helpers [Garber et al., 1984; Goldizen, 1987a; Heymann, 2000; Snowdon, 1996]. Hence, for species that habitually bear singletons, the occurrence of twins is expected to pose considerable energetic costs to caretakers. One hypothesis to explain variation in the occurrence of twinning posits that twinning may occur more frequently in years with particularly high food abundance. For example, among wild mule deer (*Odocoileus hemionus*), an ungulate in which twinning occurs regularly, females with higher body fat were more likely to bear twins [Johnstone-Yellin et al., 2009].

The birth, in the same season, of two sets of twins in a wild population of Azara's owl monkey (*Aotus azarae*) offered a unique opportunity to evaluate the hypothesis described above. Owl monkeys (*Aotus* sp.) usually bear singletons, and twinning occurs only rarely in captive owl monkeys [Málaga et al., 1991]. Owl monkeys live in socially monogamous groups that only include one reproducing pair, with a clear division of labor with regard to infant care [Fernandez-Duque, 2011]. While females obviously bear the burden of gestation and lactation, transport of an infant after the first week of life is nearly exclusively performed by the resident male, who also plays and grooms with the infant more than the mother [Dixon & Fleming, 1981; Huck & Fernandez-Duque, 2012b; Wright, 1984]. A resident male pair-mate is usually the genetic father of infants born in a group [Huck et al., in prep.], but if a replacement of

the male occurs after conception, the new adult male also will care for the infant [Fernandez-Duque & Huck, 2013; Fernandez-Duque et al., 2008]. In sharp contrast to the callitrichines, other non-reproducing group members do not normally carry infants or directly assist in offspring care [Huck & Fernandez-Duque, 2012b].

In our study, we examined how caregivers cope with the potentially increased costs of raising twins. We studied a possible association between twinning and energetic costs by exploring three questions: (1) Did the unusual high costs of caregiving for the parents affect the infants' development? If so, we predicted that compared to the two sets of twins singletons would reach locomotor independence at an earlier age. (2) Did the behavior of animals in groups with twins differ from the behavior of animals in singleton groups? Firstly, we expected that increased costs might lead to changed time budgets, with increased resting, decreased locomotion and potentially increased feeding. Secondly, if group members can effectively respond to increased costs, we might expect the pattern of division of labor in caregiving behavior to be less pronounced, with the female (or juveniles) starting to contribute to infant carrying. (3) Did the birth of twins occur in a year of particularly high food availability? If owl monkeys are able to adaptively respond to favorable conditions by increasing litter size, we would expect food availability to be exceptionally high in the months preceding twin conceptions.

METHODS

Study Site and Study Population

The owl monkey subspecies *Aotus a. azarae* lives in the gallery forests of the Río Paraguay and its tributaries in the Argentinean provinces of Formosa and Chaco [Brown & Zunino, 1994]. The study area is located in the Guaycolec Ranch, 25 km from the city of Formosa in the Argentinean Gran Chaco of South America (58°11' W, 25°58' S). The owl monkey population in the area has been regularly studied since 1997 [e.g., Fernandez-Duque & Rotundo, 2003; Fernandez-Duque et al., 2001; Rotundo et al., 2005].

On October 28, 2011 (see below for details on demographic data collection), the reproductive female in group E500 gave birth to twins of noticeably different size. At the time of birth, group E500 consisted of an adult male, an adult female, and a 3-year-old subadult (born in 2008). The adults were individually identified and distinguishable prior to the 2011 birth season. The twins were the first litter born to the resident female in group E500 after she entered the group in March to April 2010. On the other hand, during the tenure of the resident adult male of E500 (Fabián), five singletons had already been born [two of these were confirmed to be sired by

him, and for the others no genetic data were available: Huck et al., in prep.]

The female of group D1200 was found carrying twins on November 26, 2011 (infants detected within their first week of life). This group included two adults and a 1-year-old juvenile (born in 2010). The adults were not fitted with collars but could be distinguished during the data collection period based on the enlarged teats of the female and a slightly hairless tip of the tail of the male. It was not possible to distinguish between the twins in this group. For group D1200, it was not known whether previous singleton litters were born to the parents of the twins because the adults in that group had not been identified previously.

The structure of the semi-deciduous, seasonally dry forest has been described in detail elsewhere [Fernandez-Duque & van der Heide, 2013; van der Heide et al., 2012]. The density of individual trees of all species known to provide food for owl monkeys was known for an area of 16.25 ha, encompassing the home ranges of four owl monkey groups [van der Heide et al., 2012]. This area included the home ranges used by one of the groups with twins (E500), but not the other. Owl monkeys in the study area show dietary flexibility, and three species are considered to be of particular importance either as apparently preferred or filler fallback foods [*sensu* Marshall et al., 2009]: *Chrysophyllum gonocarpum*, *Guazuma ulmifolia*, *Ficus* sp., and *Syagrus romanzoffianum* [Fernandez-Duque & van der Heide, 2013].

Demographic and Behavioral Data Collection

As part of the long-term monitoring of the population, we collected demographic data from ca. 30 groups, at least once per week for the main study groups and approximately once per month for secondary groups [Fernandez-Duque & Huck, 2013]. At each contact with a group we record group size and age structure. Due to this intense monitoring, we are usually able to establish the dates of important demographic events (e.g., immigrations, disappearances) within a range of a few weeks; birth date estimates are further improved through more intense monitoring during the birth season (at least weekly for all groups) and using information on infant development [Rotundo et al., 2005]. On average, birth dates are estimated to within 9 days.

Since August 2002, we have collected behavioral data from 13 groups during 20-min focal samples on individual monkeys. These 13 groups are a subset of those from which we collect demographic data. All 13 groups range in the central portion of the study area and are well habituated to observers. Most of the individuals in these groups had been captured and fitted with either radiocollars or bead collars or can be distinguished by size, thereby facilitating individual identification. We observe and collect behavioral data

on individual monkeys during daylight using focal animal sampling, with most observation hours taking place at dusk and dawn when the animals are most active [Fernandez-Duque & Erkert, 2006; Fernandez-Duque et al., 2010]. The two groups with twins were observed at least three times per week in the months following the births. Generally, during focal data collection, we note every 2 min the basic behavioral state (resting, foraging, moving, social, other, or out of view) of the focal animal, and between these instantaneous sampling points we record continuously all occurrences of a set of additional behaviors of interest (e.g., infant carrying). Field assistants are intensively trained and the first (ca. 30) focal samples of each new observer are not included for analyses until inter-observer reliability is >85%.

Capture, collaring, and behavioral observation procedures were approved by the National Wildlife Directorate in Argentina and by the ethics committees (IACUC) of the Zoological Society of San Diego (2000–2005) and of the University of Pennsylvania (2006–2012). This research adhered to the American Society of Primatologists' principles for the ethical treatment of primates.

Carrying Behavior

We characterized carrying behavior from the perspective of the adults as the proportion of that individual's activity budget spent carrying the infant(s) ("proportion of carrying"), and from the infant's perspective as the proportion of the time it was carried by *either* parent, at a given age. Other infant care behaviors like nursing or grooming were observed too infrequently to allow meaningful analyses.

For groups with singletons, we calculated for each focal sample the proportion of sampling points when the infant was carried, correcting for differing visibility of individuals. To determine carrying effort for males versus females, we calculated, for each infant, the mean proportion of time it was carried by different resident adults during the first week, during weeks 2 and 3, and then over successive 3-week intervals from weeks 4 to 18. Since some adults had infants in several years, some of the data points are not statistically independent. However, we present the data as averages per infant, rather than per adult, because the main purpose is to compare the behavior of twin groups with that of singleton groups.

Calculating the parental carrying effort for the two twin groups required some additional considerations because an adult could carry either one or two infants. We therefore calculated both the proportion of time an adult carried *any* infant (i.e., one or two), as well as the total effort (i.e., the sum of carrying infant 1 and infant 2).

Using a general linear-mixed model, we compared, the arcsine-transformed proportion of time an infant spent on a parents' back during the different 3-week periods until they were 18 weeks old, treating infant identity as a random factor. The fixed factor "litter size" had three levels: twins, singletons of the years 2004–2010 ($N = 18$ infants), and singletons of 2011 ($N = 5$ infants). We separated the singletons of 2011 to examine whether differences in twin groups could be due to particular conditions in the months prior to conception rather than increased litter size. We validated the model graphically using quantile–quantile plots against a normal distribution and standardized residual versus fitted value plots [Zuur et al., 2009]. Probability values for linear-mixed models were estimated using a Monte–Carlo Markov Chain procedure. Additionally to the statistical analyses, for purely qualitative comparisons, we also present data on the 2 years (2004 and 2008) for which we have data for group E500 with singletons. For group D1200, no behavioral data were available from previous years. Thus, we cannot compare directly the parental behavior of adults in this group in the year with versus years without twins.

Adult Time Budgets

For adult males and females, we calculated the proportion of time the animal spent foraging (eating and searching for food), resting, and moving during focal samples while visible to the observer. We did this separately for groups without infants ($N = 9$ groups), with singletons ($N = 23$ groups), and with twins ($N = 2$ groups). We also calculated the proportion of time spent eating fruit relative to all (visible) feeding time. For groups with singletons, we analyzed the time budgets of adults for the time interval spanning from the birth of an infant to an infant age of 18 weeks. For groups without infants, we analyzed time budget data for the time period delimited by the earliest and latest date used for groups with infants during the same year.

We used general linear-mixed models to investigate whether the variables "proportion of time spent foraging," "proportion of time spent resting," "proportion of time spent moving" and the arcsine-transformed proportion of time spent eating fruits were associated with litter size, and whether males and females differed in their time budgets. Besides the categorical fixed effects of interest ("litter size" and "sex"), we included "year" as a categorical fixed effect to account for potential differences in general ecological conditions (e.g., food availability, rainfall, temperature) that might influence time budgets. We included "group identity" and "individual identity" as random factors. All models were validated graphically. As for carrying behavior, we additionally present the data for group E500 for 2004 and 2008.

For the two males in the twin groups we also tested (using G -tests) whether the frequencies of the behavioral categories "Foraging", "Moving", and "Resting" differed depending on whether they were actually carrying one, two, or no infants while performing these behaviors.

All analyses were done using the statistical programming software R (version 2.15.0) and the packages "lme4" and "languageR" [Baayen, 2011; Bates et al., 2011; R Development Core Team 2012]. We must stress that, given the singular nature of the twins' data, probability values associated with statistical comparisons between groups with twins and those with one or zero infants may be of limited value, although comparisons between singleton groups and groups without infants are statistically and biologically meaningful.

Phenological Data Collection

To quantify food availability, we collect phenological data (leaf, flower, and flower bud phenophases and fruit loads) of 420 individual trees once per month. Here, we only present data about fruits. In general, fruits account for 30% and 70% of owl monkey feeding time [Fernandez-Duque & van der Heide, 2013]. We calculated number of fruits of immature, intermediate, mature, overmature fruits, and fruits of unknown maturity [Brugiere et al., 2002; Ganzhorn, 2002; van der Heide et al., 2012] present monthly on this set of trees for the period from April to July of each year. We chose that period assuming that the months preceding the time of conception is the time when ecological conditions affecting a female's body condition are most likely to influence litter size or whether she conceives at all. Gestation length in this population has been estimated to last 120–140 days [Fernandez-Duque et al., 2011] and births occur between October and December [Fernandez-Duque et al., 2002].

Because the forest structure for the home range of one of the two groups with twins (D1200) had not been fully characterized, we estimated fruit availability as follows. We calculated the mean values for all individual trees in each month. From this we calculated the mean across all months of a given year to obtain a single value/year for each species. This value was then multiplied by the tree density of the species as reported elsewhere [supplementary table in van der Heide et al., 2012], providing for each fruit species an estimate of the number of fruits/ha.

Although fruits likely differ greatly in their specific energy or protein content, specific data on the nutritional content of fruits are not yet available. Therefore, absolute energy or protein availability cannot be calculated. Thus, in order to account, at least roughly, for size differences between the different species of fruits, we classified fruits in four relative size classes from small to very large. The number of

fruits/ha was then multiplied by 0.5 (small fruits), or 2, 3, or 4 for medium sized, large, and very large fruits, respectively, to give a rough estimate of the relative amount of fruits/ha. Changing the correction factors did not qualitatively change the results (preliminary analyses, data not shown).

RESULTS

Demographic Context of Twin Births

The two twin births recorded in 2011 were the only 1 of 223 total births recorded between 1997 and 2012. All twins survived the first 12 weeks of life. In group D1200, one infant disappeared at 2.9 months (12 weeks) of age, while the second one survived to at least 18.6 months (74 weeks). In group E500, the larger twin disappeared at 5.0 months (21 weeks) of age, while the smaller one survived to at least 21.9 months of age (87.7 weeks). The adult male in group E500 died when he was 13.7 years old and the surviving twin was 7.9 months old. A new male entered the group the following day. The difference in the rate of infancy survival (i.e., at least to an age of 6 months) between the four twins (two died/two survived) and singletons [9/43, recalculated from Huck & Fernandez-Duque 2012a] was not statistically significant (Fisher’s exact test, $P = 0.15$).

Infant Care Behavior

In the two groups with twins, the resident male was the main carrier of the infants, as is the norm in singleton groups. The male often carried both twins at the same time (group D1200: 92% of carrying time from age 1 to 8 weeks, 74.8% from age 8 to 12 weeks; E500: 78.8% from age 5 to 8 weeks, 42.9% from age 8 to 16 weeks; Table I). Mothers of twins did not carry their infants more than mothers of singleton offspring (Table I). On two occasions, a single twin was carried by the subadult of group E500, who dispersed when the twins were 8 weeks old. In

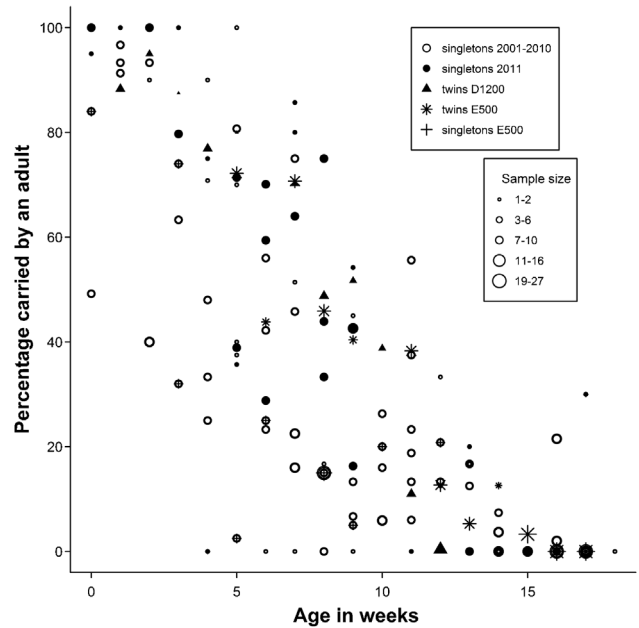


Fig. 1. Percentages of time infants are carried by either adult. Each dot (open circles: infants from 2001 to 2010; filled circles: singletons from 2011, crosses: singletons in E500 from 2004 and 2008) represents the average for a specific infant in a given week. For the twins in group D1200 (black triangles) and E500 (asterisks) average values over both infants are used.

group D1200, the 1-year-old juvenile was never seen carrying a twin.

From the infants’ perspective, twins were not carried less often than singletons. Rather, between 5 and 9 weeks of age, the twins were carried slightly more often than the three singletons born in the same year, but still within the range observed across years (Fig. 1; Table I). When the twins were 7–9 weeks of age, they spent more time on their parents’ back than singletons from previous years (2004–2010), but not more than singletons born in 2011 (LME: singletons 2004–2010: estimate = -20.07 , $t = -2.54$, $P = 0.02$;

TABLE I. Proportion of Carrying Behavior by the Father and the Mother in Groups With Singletons or Twins During the First 18 Weeks of Life of the Infants

Behavior	Groups	Week 1	Weeks 2–3	Weeks 4–6	Weeks 7–9	Weeks 10–12	Weeks 13–15	Weeks 16–18
Carrying by mother	All single	0.82	0.18	0.04	0.01	0.00	0.00	0.00
	Single 2011	0.83	0.17	0.08	0.01	0.02	0.00	NA
	Single E500	0.84	NA	0.06	0.01	0.00	0.00	0.00
	Twins (each)		0.02	0.00	0.01	0.00	0.00	0.00
	Twins (either)		0.05	0.00	0.01	0.00	0.00	0.00
Carrying by father	All single	0.05	0.75	0.62	0.36	0.23	0.09	0.05
	Single 2011	0.10	0.84	0.74	0.55	0.39	0.20	NA
	Single E500	0	NA	0.40	0.16	0.12	0.10	0.3
	Twins (each)		0.88	0.76	0.55	0.34	0.05	0.01
	Twins (either)		1.00	0.79	0.63	0.47	0.08	0.01

For twins both the values for an individual infant are given and for “one or two” of the twins simultaneous. Values for singleton years of group E500 are presented for qualitative comparisons, but it should be noted that they are based on small sample sizes.

singletons 2011: estimate = 2.69, $t = 0.31$, $P = 0.76$). Neither before nor after this time did the amount of time twins were carried differ from that of singletons (all absolute t -values < 1.33 , all $P > 0.20$).

Parental Time Budgets

Time budgets between adult males and females did not differ markedly. Still, adults of both sexes foraged more and moved less in the groups with twins than in those with singletons (Table II). These results also held when compared only to singleton parents of the same year. Adults in E500 in years with singletons likewise foraged less, moved more (in 1 year), and rested more than during the twin year (Fig. 2). There were no differences in time budgets of groups without infants and groups with singletons. Resident males in the groups with twins moved significantly less ($G = 17.3$ and 9.9 , $df = 2$, $P < 0.001$ and $P = 0.007$ for E500 and D1200, respectively) when they were not carrying an infant than when they carried one or both infants (Fig. 3). Males also foraged more when they had no infant to carry than if they were carrying twins (G -test, $G = 19.8$ and $G = 49.9$, $df = 2$, $P < 0.001$ for E500 and D1200, respectively; Fig. 3). The male in group E500 also rested more when carrying one infant than when carrying two or none ($G = 7.3$, $df = 2$, $P = 0.02$).

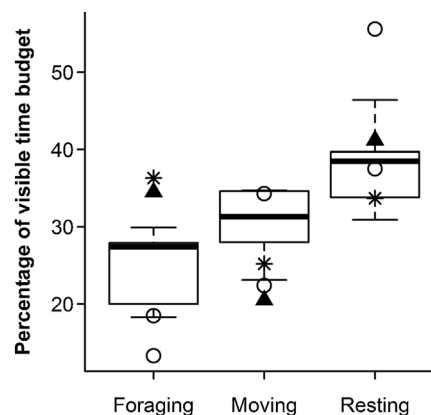


Fig. 2. Percentages of different activities for different groups with singletons in 2011 ($N = 5$), and the twin groups E500 (asterisks) and D1200 (filled triangles). Values for group E500 with singletons in 2004 and 2008 are represented by open circles.

Food Availability During Pre-Conception Period

Prior to the conception of the twins in 2011, mature fruit availability (measured either as the total number of fruits or as the size-corrected index of availability) was the second highest among all of the recorded years (Table III). During April–July 2011, fruits of *C. gonocarpum* and *S. (Arecastrum)*

TABLE II. Test Statistics of the Linear-Mixed Models Testing the Proportion of a Specific Behavioral Category Relative to the Visible Observation Time, Taking Sex of the Adult, Year of Observation and Litter Size and the Random Factors “Group” and “Individual ID” into Account

Variable	df	Estimate	F-value	t-value	MCMC P-value
Foraging					
Sex	1	-0.03	1.54	-1.19	0.24
Year	6	-0.17 to -0.03	3.05	-3.59 to -0.07	<0.001 -0.48
Litter size	2		3.25		
No offspring		0.01		0.21	0.84
Twins		0.15		2.5	0.01
Resting					
Sex	1	0.02	0.81	0.87	0.39
Year	6	-0.08 to 0.08	5.54	-1.83 to 1.72	0.07-0.84
Litter size	2		0.21		
No offspring		-0.01		-0.64	0.52
Twins		-0.004		-0.07	0.95
Moving					
Sex	1	0.003	0.06	0.24	0.81
Year	6	-0.02 to 0.10	2.36	-0.69 to 3.13	0.003 -0.81
Litter size	2		4.86		
No offspring		0.03		1.53	0.13
Twins		-0.11		-2.72	0.009
Fruit eating					
Sex	1	1	0.09	0.29	0.77
Year	6	-21.8 to 2.6	4.85	-2.64 to 0.31	0.01 -0.88
Litter size	2		0.29		
No offspring		1.79		0.41	0.68
Twins		-5.6		-0.64	0.52

P-values were estimated using a Monte-Carlo Markov chain simulation. The bold values in the last column are the significance values.

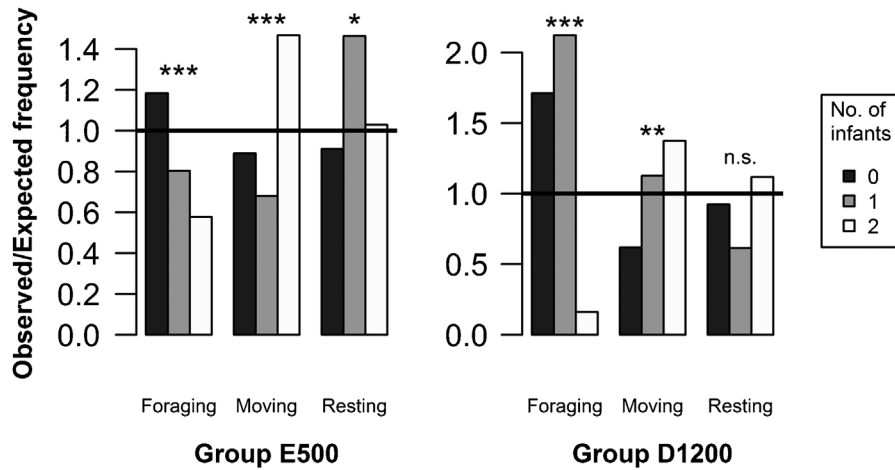


Fig. 3. Relative frequency of the behavioral categories Foraging, Moving, and Resting for the adult males in group E500 and D1200 while not carrying any infant (dark bars), carrying one of the twins (light bars), or carrying both twins simultaneously (white bars). For group D1200 no data are represented for the time the male carried one infant since the total frequency was only 16. Statistical significance using G-tests is indicated with * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, or $P > 0.05$ (n.s.). Values below 1.0 (the horizontal line) represent behavior shown less often than expected, values above 1.0 represent behavior shown more frequently than expected.

romanzoffianum, two important food sources during the lean dry season [Fernandez-Duque & van der Heide, 2013; van der Heide et al., 2012], were very abundant. Ripe fruit of *G. ulmifolia* can be considered a filler fallback food [sensu Marshall et al., 2009]. In the “twin year,” this fruit was at least as available as in other years, but our data do not indicate that fruit availability was exceptionally high compared to other years. In other words there are no strong indications that food availability had any effect on conception and twinning.

DISCUSSION

Our study set out to examine three questions concerning the rare occurrence of twinning in a wild population of Azara’s owl monkeys, namely whether

the development of twins is impaired compared to singletons, whether time budgets and general care behavior differ between animals in groups with twins versus those without, and whether the twinning might have been triggered by exceptional ecological conditions in 2011. As expected, the time budgets of reproductive adults did differ between groups with twins compared to parents in singleton groups and groups with no offspring. In particular, twin parents foraged more and moved less than groups with singletons or without infants. Twins, like singletons, were carried nearly exclusively by the resident adult male. However, the phenological data indicate that fruit availability in 2011 was not substantially greater than in some of the other years.

Our comparisons of wild owl monkey care behavior towards twins and singletons strongly

TABLE III. Average Fruit Availability (Fruits/ha) per Month During the Pre-Conception Periods Between 2008 and 2012

Species	Density	Rel. size	2008	2009	2010	2011	2012
Diverse small fruit ^a	4.1	Small	0	9	0	0	0
Diverse middle fruit ^b	6.5	Middle	125	2,143	89	222	0
Diverse large fruit ^c	6.8	Large	131	498	0	352	114
Diverse very large fruit ^d	4.6	Very large	358	0	0	3	14
<i>Chrysophyllum gonocarpum</i>	35.9	Middle	6	1	13	619	0
<i>Ficus</i> sp.	5.5	Middle	36	631	0	642	0
<i>Guazuma ulmifolia</i>	4.8	Large	476	757	2,618	1,040	48
<i>Syagrus romanzoffianum</i>	7.1	Large	83	0	0	346	0
Total			1,215	4,039	2,720	3,222	176
Size-corrected total			3,836	9,320	8,058	8,187	539

The “twin year” is shaded. Four species identified previously as important dry season food for owl monkeys are printed in bold, for the remaining species we present only average values and median density for each fruit size category.

^a*Cecropia pachystachya*, *Banara arguta*, *Eugenia moraviana*, *Eugenia uniflora*, *Gymnanthes discolor*, *Phyllostylon rhamnoides*.

^b*Caesalpinia paraguariensis*, *Myrcianthes pungens*, *Phytolacca dioica*, *Psidium kennedyanum*, *Sideroxylon obtusifolia*, *Trichilia catigua*.

^c*Diplokeleba floribunda*, *Enterolobium contortisiliquum*, *Gleditsia amorphoides*, *Inga uruguensis*.

^d*Crataeva tapia*, *Genipa americana*.

confirm the essential role of male care characteristic of this taxon. Even in the presence of twins, adult males were the nearly exclusive carriers of the infants from the second week of life onwards, and males usually carried both twins simultaneously. Anecdotal evidence both from captive and wild owl monkeys suggests that in the absence of a male partner, females cannot fully cope even with a single infant [Huck & Fernandez-Duque, 2012b; Jantschke et al., 1998]. In these two studies of females that had no partners, infants were carried less frequently than normal, whereas in the present study the twins were carried by the male slightly more than infants of similar age. Likewise, in one case of twinning observed in wild brown titi monkey (*C. brunneus*), the male was the nearly exclusive carrier of twins [Lawrence, 2007]. Together, these observations suggest that the behavioral response to twinning associated with infant transport in both taxa does not appear to be altered in spite of the likely increased costs associated with rearing an additional infant.

Our data are not sufficiently conclusive to show whether the development of the twins was slower than the development of singletons, as has been suggested for several other primates. For example, among white-bellied spider monkeys (*A. belzebuth*) twins were smaller and started independent excursions relatively later than singletons [Link et al., 2006]. Similarly, banded langur twins (*P. melalophos*) left their mother less often than singletons of comparable age [Bennett, 1988]. Although our data show a slightly higher carrying rate for twins than singletons, singletons of the same year [2011] were carried similarly often. This result, pointing at some important differences between years, could reflect ecological differences between years such as other aspects of food availability we did not analyze in this study, or differences in predation risk, rather than behavioral differences between twins and singletons.

If the owl monkey twins were able to develop at a similar pace as singletons, it would suggest that owl monkey parents may not compromise the care provided per infant, but may instead almost double their usual costs. Males were not only carrying each twin longer than average, but were transporting both at the same time. Twinning, however, need not always double the cost for parents. In roe deer (*Capreolus capreolus*), a species that normally produces two fawns, the lactational cost of twins to mothers was estimated to be only 1.6 times that of singletons [Mauget et al., 1999].

Parents of owl monkey twins may have compensated for the increased cost of carrying by increasing their foraging time and reducing the time they spend moving. The reduced movement of twin parents found here is in line with results from other studies. For example, a white-bellied spider monkey female with twins also moved less than singleton mothers

[Link et al., 2006], and several studies of callitrichines have shown that when transporting infants carriers moved less and/or rested more than non-carriers [Digby & Barreto, 1996; Huck et al., 2004; Price, 1992; Sánchez et al., 1999; Tardif, 1994]. Contrary to our findings, however, each of these studies found that caregivers for twins foraged less than other individuals, not more. In the case of the callitrichines, it could be that individuals shift their foraging activity to periods when they are not carrying the infants. This interpretation is supported by our observations that the males carrying twins foraged less while transporting the infants (10.9%) than when they were free of their burden (36.6%) or carried only one infant (34.8%). Thus, males might compensate for the costs of infant care in two ways: reduced movement and increased foraging during the period of dependent infants, or reduced foraging and increased resting while actually carrying infants.

While one twin in each group survived the period of infancy (0–6 months), the overall infant survival rate did not differ statistically from the survival rate seen for singleton offspring [Huck & Fernandez-Duque, 2012a], and both groups lost one of the infants. It is possible that predation on infants might be facilitated if a male has to retrieve two, instead of one, infant under the threat of a predator, but any conclusions about the survival rates of twins versus singletons are unwarranted at this point.

Unfortunately, we are not able to conclusively assess the long-term effects of twinning on a pair's reproductive output. In group E500, the adult male died, so it was not possible to unequivocally record whether this pair skipped a breeding season or had other long-term reproductive costs following the birth of the twins. Such costs have been demonstrated in other primates, however. For example, in a semi-natural experiment in captive rhesus macaques (*Macaca mulatta*), four females adopted additional infants; not only did all of these "twins" have a slower development than singleton offspring, but three of these four females had an abortion or stillbirth the following breeding season, compared to only one of six singleton mothers suffering an early loss [Ellsworth & Andersen, 1997]. In group D1200, both adults were unidentified, so we cannot be sure whether the group occupying the area in 2012 is indeed the same. However, this group did have an infant in 2012. Because, it is rare that newly formed pairs have infants in the same year [Fernandez-Duque & Huck, 2013], it is likely that the adults in group D1200 were indeed the same as in 2011, and that they reproduced despite having raised twins in the previous year.

Finally, the year when the twins were born was a good, but not an extraordinarily good year in terms of fruit abundance. Although the months leading to conception in 2011 were rich in fruit, it would be premature to suggest that owl monkeys are able to

adaptively respond to good conditions by increasing their litter size. Some of the other years of our study were also characterized by similarly high overall fruit availability in the period before conception, but twinning was not recorded. Also, in a previous study, we did not find a strong relationship between fruit availability during the dry season and female reproduction [Fernandez-Duque & van der Heide, 2013]. In contrast, for mammalian species that give birth to a variable number of offspring, there is good evidence that maternal body condition can influence litter size. For example, after a masting year, wild boar (*Sus scrofa*) were likely to produce more and larger litters than in lean years [Massei et al., 1996]. Likewise, in years of European beech (*Fagus sylvatica*) mast, as well as with experimental food provisioning, litter sizes and the proportion of reproducing females increased in edible dormice [*Glis glis*, Kager & Fietz, 2009].

However, it is unlikely whether an adaptive response to ecological conditions should be expected in species that habitually produce singletons, like most anthropoid primates. If even in good years usually only one offspring can be raised successfully, twinning might in fact not represent an adaptive response to particularly good ecological conditions (otherwise the rate of twinning incidents would be expected to be higher), but rather a physiological “accident.” In Hawaiian monk seals (*Monachus schauinslandi*), where twinning occurs in only 0.1% of births, twins have significantly lower survival rates than singletons, and thus twinning might be considered a maladaptive trait [Schultz et al., 2011]. The owl monkey pairs in our study seemed to cope comparatively well with their twins, and it is also notable that we have recorded only two such cases in a single year, after 14 years of only singleton births. Unfortunately, there are very few reliable data available on twinning rates for primate species that habitually bear singletons [Geissmann, 1990]. In humans, who are aseasonal breeders, the main factors affecting twinning rates are thought to be maternal age, parity, and genetic inheritance, but some minor effect of seasonal changes in food supply also have been considered [reviewed in Hoekstra et al., 2008].

In conclusion, owl monkeys seem to depend on adult males as providers of infant care in a rather hard-wired way. While normal caretaking does not seem to have any strong effect on time budgets or ranging behavior of adults, twinning does. Hence, while the costs of raising a single offspring would normally be covered by a pair of owl monkeys through a sexual division of labor (female: nursing, male: carrying), this may not be possible if they have to care for twins.

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