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1Double effort: Parental behavior of wild Azara's owl monkeys in the face of twins

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20**Short title:** Twinning in Owl Monkeys

21

22Abstract

23 In species of mammals that habitually bear single offspring, like most anthropoid
24primates, the occurrence of twins is expected to impose considerable energetic costs on the
25caretakers. The question then arises of how caregivers cope with the potentially increased
26costs of raising twins. These increased costs should lead to differing developmental rates in
27twins when compared to singletons, and/or to changes in the caregivers' behavior.
28Likewise, time budgets of parents of singletons are expected to differ from those of adults
29without offspring. Additionally, if twinning was an adaptive response to favorable
30ecological conditions, it should be more likely in years with high food abundance.
31Following the birth in 2011 of two sets of twins in a wild population of pair-living Azara's
32owl monkeys (*Aotus azarae*) in Northern Argentina, we used long-term demographic,
33behavioral, and phenological data to compare a) the proportion of time that singleton and
34twin infants were carried by either parent, b) adult time-budgets and ranging behavior in
35groups with zero, one, or two infants, and c) the availability of food in 2011 with food
36availability in other years. Twins, like singletons, were carried nearly exclusively by the
37male, and they were carried slightly more than singletons, suggesting a relatively inflexible
38pattern of infant care in the species. Time budgets showed that twin parents foraged more
39and moved less than singleton parents or groups without infants, despite the fact that
40phenological data indicate that fruit availability in 2011 was not substantially higher than in
41some of the other years. Overall, twinning thus presumably increased costs to breeders,
42especially males, but its effect on animals' long-term reproductive success remains unclear.

43

44**Key Words:** infant care; infant development; twinning; male care; reproductive trade-offs

45Introduction

46 Caring for infants is often very costly. The costs of parental behavior in mammals
47arise through gestation, lactation, carrying, and other forms of care and infant protection,
48and may be detected indirectly through changed time-budgets [Gittleman and Thompson
491988; Huck et al. 2004; Prentice and Prentice 1988; Sánchez et al. 1999; Tardif 1997;
50Taylor et al. 1980]. Among those species of primates that habitually produce more than one
51offspring at a time, there seem to exist cost-reducing adaptations, such as the "parking" of
52infants observed in many strepsirrhines [Kappeler 1998; Ross 2001] and the cooperative
53breeding characteristics of the callitrichines [Goldizen 1987b; Heymann 2000; Huck et al.
542004; Tardif 1997].

55 For the majority of anthropoid primates, however, the costs of parental behavior are
56usually associated with providing care to only one offspring, the modal litter size. Twinning
57is infrequent among wild anthropoids, even though it has been reported for brown titi
58monkeys [*Callicebus brunneus*, Lawrence 2007], red titi monkeys [*C. cupreus*, Knogge and
59Heymann 1995], white-bellied spider monkeys [*Ateles belzebuth*, Link et al. 2006], mantled
60howler monkeys [*Alouatta palliata*, Chapman and Chapman 1986], Spix's night monkeys
61[*Aotus vociferans*, Aquino et al. 1990], and various catarrhines [review in Geissmann
621990].

63 When either the number of available caregivers or the number of infants requiring
64care diverges substantially from the species-specific pattern, it might be predicted that
65parents would first adjust through modifications of their time budgets and possibly shared
66parental duties. Indeed, in some species, like banded langurs (*Presbytis melalophos*),
67general care patterns change and allomothering becomes more common in the presence of

68twins [Bennett 1988]. The development of the infants themselves might also be affected.
69For example, in Japanese macaques (*Macaca fuscata*), twins were the smallest infants
70[Nakamichi 1983], and even among captive Alaotran gentle lemurs (*Hapalemur griseus*
71*alaotrensis*), a species where twinning occurs frequently, a pair of twins had slower growth
72rates and were weaned later than singletons [Taylor and Feistner 1996]. In the
73callitrichines, twins raised by lone pairs without helpers are rare and have a reduced
74survival probability compared to groups with helpers [Garber et al. 1984; Goldizen 1987a;
75Heymann 2000; Snowdon 1996]. Hence, for species that habitually bear singletons, the
76occurrence of twins is expected to pose considerable energetic costs to caretakers. One
77hypothesis to explain variation in the occurrence of twinning posits that twinning may
78occur more frequently in years with particularly high food abundance. For example, among
79wild mule deer (*Odocoileus hemionus*), an ungulate in which twinning occurs regularly,
80females with higher body fat were more likely to bear twins [Johnstone-Yellin et al. 2009].

81 The birth, in the same season, of two sets of twins in a wild population of Azara's owl
82monkey (*Aotus azarae*) offered a unique opportunity to evaluate the hypothesis described
83above. Owl monkeys (*Aotus* sp.) usually bear singletons, and twinning occurs only rarely in
84captive owl monkeys [Málaga et al. 1991]. Owl monkeys live in socially monogamous
85groups that only include one reproducing pair, with a clear division of labor with regard to
86infant care [Fernandez-Duque 2011]. While females obviously bear the burden of gestation
87and lactation, transport of an infant after the first week of life is nearly exclusively
88performed by the resident male, who also plays and grooms with the infant more than the
89mother [Dixson and Fleming 1981; Huck and Fernandez-Duque 2012b; Wright 1984]. A
90resident male pair-mate is usually the genetic father of infants born in a group [Huck et al.

91in prep.], but if a replacement of the male occurs after conception, the new adult male also
92will care for the infant [Fernandez-Duque and Huck 2013; Fernandez-Duque et al. 2008].
93In sharp contrast to the callitrichines, other non-reproducing group members do not
94normally carry infants or directly assist in offspring care [Juárez, 2008].

95 In our study we examined how caregivers cope with the potentially increased costs of
96raising twins. We studied a possible association between twinning and energetic costs by
97exploring three questions: 1) Did the unusual high costs of caregiving for the parents affect
98the infants' development? If so, we predicted that compared to the two sets of twins
99singletons would reach locomotor independence at an earlier age. 2) Did the behavior of
100animals in groups with twins differ from the behavior of animals in singleton groups?
101Firstly, we expected that increased costs might lead to changed time budgets, with
102increased resting, decreased locomotion and potentially increased feeding. Secondly, if
103group members can effectively respond to increased costs, we might expect the pattern of
104division of labor in caregiving behavior to be less pronounced, with the female (or
105juveniles) starting to contribute to infant carrying. 3) Did the birth of twins occur in a year
106of particularly high food availability? If owl monkeys are able to adaptively respond to
107favorable conditions by increasing litter size, we would expect food availability to be
108exceptionally high in the months preceding twin conceptions.

109

110**Methods**

111*Study site and study population*

112 The owl monkey subspecies *Aotus a. azarae* lives in the gallery forests of the Río
113Paraguay and its tributaries in the Argentinean provinces of Formosa and Chaco [Brown

114and Zunino 1994]. The study area is located in the Guaycolec Ranch, 25 km from the city
115of Formosa in the Argentinean Gran Chaco of South America (58°11 W, 25°58 S). The owl
116monkey population in the area has been regularly studied since 1997 [e.g., Fernandez-
117Duque and Rotundo 2003; Fernandez-Duque et al. 2001; Rotundo et al. 2005].

118 On the 28th of Oct. 2011 (see below for details on demographic data collection), the
119reproductive female in group E500 gave birth to twins of noticeably different size. At the
120time of birth, group E500 consisted of an adult male, an adult female, and a 3-year old
121subadult (born in 2008). The adults were individually identified and distinguishable prior to
122the 2011 birth season. The twins were the first litter born to the resident female in group
123E500 after she entered the group in Mar.-Apr. 2010. On the other hand, during the tenure of
124the resident adult male of E500 (Fabián), five singletons had already been born [two of
125these were confirmed to be sired by him, and for the others no genetic data were available:
126Huck et al. in prep].

127 The female of group D1200 was found carrying twins on the 26th of Nov. 2011
128(infants detected within their first week of life). This group included two adults and a one-
129year old juvenile (born in 2010). The adults were not fitted with collars but could be
130distinguished during the data collection period based on the enlarged teats of the female and
131a slightly hairless tip of the tail of the male. It was not possible to distinguish between the
132twins in this group. For group D1200, it was not known whether previous singleton litters
133were born to the parents of the twins because the adults in that group had not been
134identified previously.

135

136 The structure of the semi-deciduous, seasonally dry forest has been described in detail
137elsewhere [Fernandez-Duque and van der Heide 2013; van der Heide et al. 2012]. The
138density of individual trees of all species known to provide food for owl monkeys was
139known for an area of 16.25 ha, encompassing the home ranges of four owl monkey groups
140[van der Heide et al. 2012]. This area included the home ranges used by one of the groups
141with twins (E500), but not the other. Owl monkeys in the study area show dietary
142flexibility, and three species are considered to be of particular importance either as
143apparently preferred or filler fallback foods [*sensu* Marshall et al. 2009]: *Chrysophyllum*
144*gonocarpum*, *Guazuma ulmifolia*, *Ficus* sp, and *Syagrus romanzoffianum* [Fernandez-
145Duque and van der Heide 2013].

146

147*Demographic and behavioral data collection*

148 As part of the long-term monitoring of the population, we collected demographic data
149from ca. 30 groups, at least once per week for the main study groups and approximately
150once per month for secondary groups [Fernandez-Duque and Huck 2013]. At each contact
151with a group we record group size and age structure. Due to this intense monitoring, we are
152usually able to establish the dates of important demographic events (e.g., immigrations,
153disappearances) within a range of a few weeks; birth date estimates are further improved
154through more intense monitoring during the birth season (at least weekly for all groups) and
155using information on infant development [Rotundo et al. 2005]. On average, birth dates are
156estimated to within 9 days.

157 Since August 2002, we have collected behavioral data from 13 groups during 20-
158minute focal samples on individual monkeys. These 13 groups are a subset of those from

159which we collect demographic data. All 13 groups range in the central portion of the study
160area and are well habituated to observers. Most of the individuals in these groups had been
161captured and fitted with either radiocollars or bead collars or can be distinguished by size,
162thereby facilitating individual identification. We observe and collect behavioral data on
163individual monkeys during daylight using focal animal sampling, with most observation
164hours taking place at dusk and dawn when the animals are most active [Fernandez-Duque et
165al. 2010; Fernandez-Duque and Erkert 2006]. The two groups with twins were observed at
166least three times per week in the months following the births. Generally, during focal data
167collection, we note every two minutes the basic behavioral state (resting, foraging, moving,
168social, other, or out of view) of the focal animal, and between these instantaneous sampling
169points we record continuously all occurrences of a set of additional behaviors of interest
170(e.g., infant carrying). Field assistants are intensively trained and the first (ca. 30) focal
171samples of each new observer are not included for analyses until inter-observer reliability is
172>85%.

173 Capture, collaring, and behavioral observation procedures were approved by the
174National Wildlife Directorate in Argentina and by the ethics committees (IACUC) of the
175Zoological Society of San Diego (2000-2005) and of the University of Pennsylvania (2006-
1762012). This research adhered to the American Society of Primatologists' principles for the
177ethical treatment of primates.

178

179*Carrying behavior*

180 We characterized carrying behavior from the perspective of the adults as the
181proportion of that individual's activity budget spent carrying the infant(s) ('proportion of

182carrying'), and from the infant's perspective as the proportion of the time it was carried by
183*either* parent, at a given age. Other infant care behaviors like nursing or grooming were
184observed too infrequently to allow meaningful analyses.

185 For groups with singletons, we calculated for each focal sample the proportion of
186sampling points when the infant was carried, correcting for differing visibility of
187individuals. To determine carrying effort for males versus females, we calculated, for each
188infant, the mean proportion of time it was carried by different resident adults during the
189first week, during weeks 2 and 3, and then over successive three-week intervals from weeks
1904 to 18. Since some adults had infants in several years, some of the data points are not
191statistically independent. However, we present the data as averages per infant, rather than
192per adult, because the main purpose is to compare the behavior of twin groups with that of
193singleton groups.

194 Calculating the parental carrying effort for the two twin groups required some
195additional considerations because an adult could carry either one or two infants. We
196therefore calculated both the proportion of time an adult carried *any* infant (i.e., one or
197two), as well as the total effort (i.e., the sum of carrying infant 1 and infant 2).

198 Using a general linear mixed model, we compared, the arcsine-transformed
199proportion of time an infant spent on a parents' back during the different three-week periods
200until they were 18 weeks old, treating infant identity as a random factor. The fixed factor
201'litter size' had three levels: twins, singletons of the years 2004-2010 (N=18 infants), and
202singletons of 2011 (N=5 infants). We separated the singletons of 2011 to examine whether
203differences in twin-groups could be due to particular conditions in the months prior to
204conception rather than increased litter size. We validated the model graphically using

205 quantile-quantile plots against a normal distribution and standardized residual vs. fitted
206 value plots [Zuur et al. 2009]. Probability values for linear mixed models were estimated
207 using a Monte-Carlo Markov Chain procedure. Additionally to the statistical analyses, for
208 purely qualitative comparisons, we also present data on the two years (2004 and 2008) for
209 which we have data for group E500 with singletons. For group D1200, no behavioral data
210 were available from previous years. Thus, we cannot compare directly the parental behavior
211 of adults in this group in the year with versus years without twins.

212

213 *Adult time budgets*

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

223 We used general linear mixed models to investigate whether the variables 'proportion
224 of time spent foraging', 'proportion of time spent resting', 'proportion of time spent moving'
225 and the arcsine-transformed proportion of time spent eating fruits were associated with
226 litter size, and whether males and females differed in their time budgets. Besides the
227 categorical fixed effects of interest ('litter size' and 'sex'), we included 'year' as a

228categorical fixed effect to account for potential differences in general ecological conditions
229(e.g., food availability, rainfall, temperature) that might influence time budgets. We
230included ‘group identity’ and ‘individual identity’ as random factors. All models were
231validated graphically. As for carrying behavior, we additionally present the data for group
232E500 for 2004 and 2008.

233 For the two males in the twin groups we also tested (using G-tests) whether the
234frequencies of the behavioral categories 'Foraging', 'Moving', and 'Resting' differed
235depending on whether they were actually carrying one, two, or no infants while performing
236these behaviors.

237 All analyses were done using the statistical programming software R (version 2.15.0)
238and the packages 'lme4' and 'languageR' [Baayen 2011; Bates et al. 2011; R Development
239Core Team 2012]. We must stress that, given the singular nature of the twins' data,
240probability values associated with statistical comparisons between groups with twins and
241those with one or zero infants may be of limited value, although comparisons between
242singleton groups and groups without infants are statistically and biologically meaningful.
243

244*Phenological data collection*

245 To quantify food availability, we collect phenological data (leaf, flower, and flower
246bud phenophases and fruit loads) of 420 individual trees once per month. Here we only
247present data about fruits. In general, fruits account for 30 and 70% of owl monkey feeding
248time [Fernandez-Duque and van der Heide 2013]. We calculated number of fruits of
249immature, intermediate, mature, overmature fruits, and fruits of unknown maturity
250[Brugiere et al. 2002; Ganzhorn 2002; van der Heide et al. 2012] present monthly on this

251set of trees for the period from April to July of each year. We chose that period assuming
252that the months preceding the time of conception is the time when ecological conditions
253affecting a female's body condition are most likely to influence litter size or whether she
254conceives at all. Gestation length in this population has been estimated to last 120-140 days
255[Fernandez-Duque et al. 2011] and births occur between October-December [Fernandez-
256Duque et al. 2002].

257 Because the forest structure for the home range of one of the two groups with twins
258(D1200) had not been fully characterized, we estimated fruit availability as follows. We
259calculated the mean values for all individual trees in each month. From this we calculated
260the mean across all months of a given year to obtain a single value/year for each species.
261This value was then multiplied by the tree density of the species as reported elsewhere
262[supplementary table in van der Heide et al. 2012], providing for each fruit species an
263estimate of the number of fruits/ha.

264 Although fruits likely differ greatly in their specific energy or protein content,
265specific data on the nutritional content of fruits are not yet available. Therefore, absolute
266energy or protein availability cannot be calculated. Thus, in order to account, at least
267roughly, for size differences between the different species of fruits, we classified fruits in
268four relative size classes from small to very large. The number of fruits/ha was then
269multiplied by 0.5 (small fruits), or 2, 3, or 4 for medium sized, large, and very large fruits,
270respectively, to give a rough estimate of the relative amount of fruits/ha. Changing the
271correction factors did not qualitatively change the results (preliminary analyses, data not
272shown).

273

274Results

275Demographic context of twin births

276 The two twin births recorded in 2011 were the only ones of 223 total births recorded
277between 1997 and 2012. All twins survived the first 12 weeks of life. In group D1200, one
278infant disappeared at 2.9 months (12 weeks) of age, while the second one survived to at
279least 18.6 months (74 weeks). In group E500, the larger twin disappeared at 5.0 months (21
280weeks) of age, while the smaller one survived to at least 21.9 months of age (87.7 weeks).
281The adult male in group E500 died when he was 13.7 years old and the surviving twin was
2827.9 months old. A new male entered the group the following day. The difference in the rate
283of infancy survival (i.e., at least to an age of six months) between the four twins (2 died/2
284survived) and singletons [9/43, recalculated from Huck and Fernandez-Duque 2012a] was
285not statistically significant (Fisher exact test, $P = 0.15$).

286

287Infant care behavior

288 In the two groups with twins, the resident male was the main carrier of the infants, as
289is the norm in singleton groups. The male often carried both twins at the same time (group
290D1200: 92% of carrying time from age 1 - 8 weeks, 74.8% from age 8 - 12 weeks; E500:
29178.8% from age 5 - 8 weeks, 42.9% from age 8 - 16 weeks; Table 1). Mothers of twins did
292not carry their infants more than mothers of singleton offspring (Table 1). On two
293occasions, a single twin was carried by the subadult of group E500, who dispersed when
294the twins were 8 weeks old. In group D1200, the one-year-old juvenile was never seen
295carrying a twin.

296

PLACE TABLE 1 ABOUT HERE

297 From the infants' perspective, twins were not carried less often than singletons.
298 Rather, between five and nine weeks of age, the twins were carried slightly more often than
299 the three singletons born in the same year, but still within the range observed across years
300 (Figure 1, Table 1). When the twins were 7-9 weeks of age, they spent more time on their
301 parents' back than singletons from previous years (2004-2010), but not more than
302 singletons born in 2011 (LME: singletons 2004-2010: estimate = -20.07, $t = -2.54$, $P =$
303 0.02 ; singletons 2011: estimate = 2.69, $t = 0.31$, $P = 0.76$). Neither before nor after this time
304 did the amount of time twins were carried differ from that of singletons (all absolute t -
305 values < 1.33 , all $P > 0.20$).

306 **##### PLACE FIGURE 1 ABOUT HERE #####**

307

308 *Parental time budgets*

309 Time budgets between adult males and females did not differ markedly. Still, adults
310 of both sexes foraged more and moved less in the groups with twins than in those with
311 singletons (Table 2). These results also held when compared only to singleton parents of
312 the same year. Adults in E500 in years with singletons likewise foraged less, moved more
313 (in one year), and rested more than during the twin year (Figure 2). There were no
314 differences in time budgets of groups without infants and groups with singletons. Resident
315 males in the groups with twins moved significantly less ($G = 17.3$ and 9.9 , $df = 2$, $P < 0.001$
316 and $P = 0.007$ for E500 and D1200, respectively) when they were not carrying an infant
317 than when they carried one or both infants (Figure 3). Males also foraged more when they
318 had no infant to carry than if they were carrying twins (G -test, $G = 19.8$ and $G = 49.9$, $df =$
319 2 , $P < 0.001$ for E500 and D1200, respectively: Figure 3). The male in group E500 also

320rested more when carrying one infant than when carrying two or none ($G = 7.3$, $df = 2$, $P =$
3210.02).

322 **##### PLACE TABLE 2 ABOUT HERE #####**

323 **##### PLACE FIGURE 2 ABOUT HERE #####**

324 **##### PLACE FIGURE 3 ABOUT HERE #####**

325*Food availability during pre-conception period*

326 Prior to the conception of the twins in 2011, mature fruit availability (measured either
327as the total number of fruits or as the size-corrected index of availability) was the second
328highest among all of the recorded years (Table 3). During April-July 2011, fruits of
329*Chrysophyllum gonocarpum* and *Syagrus (Arecastrum) romanzoffianum*, two important
330food sources during the lean dry season [Fernandez-Duque and van der Heide 2013; van
331der Heide et al. 2012], were very abundant. Ripe fruit of *Guazuma ulmifolia* can be
332considered a filler fallback food [*sensu* Marshall et al. 2009]. In the "twin year", this fruit
333was at least as available as in other years, but our data do *not* indicate that fruit availability
334was exceptionally high compared to other years. In other words there are no strong
335indications that food availability had any effect on conception and twinning.

336 **##### PLACE TABLE 3 ABOUT HERE #####**

337

338**Discussion**

339 Our study set out to examine three questions concerning the rare occurrence of
340twinning in a wild population of Azara's owl monkeys, namely whether the development of
341twins is impaired compared to singletons, whether time budgets and general care behavior
342differ between animals in groups with twins versus those without, and whether the twinning

343 might have been triggered by exceptional ecological conditions in 2011. As expected, the
344 time budgets of reproductive adults did differ between groups with twins compared to
345 parents in singleton groups and groups with no offspring. In particular, twin parents foraged
346 more and moved less than groups with singletons or without infants. Twins, like singletons,
347 were carried nearly exclusively by the resident adult male. However, the phenological data
348 indicate that fruit availability in 2011 was not substantially greater than in some of the other
349 years.

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

364 Our data are not sufficiently conclusive to show whether the development of the
365 twins was slower than the development of singletons, as has been suggested for several

366other primates. For example, among white-bellied spider monkeys (*Ateles belzebuth*) twins
367were smaller and started independent excursions relatively later than singletons [Link et al.
3682006]. Similarly, banded langur twins (*Presbytis melalophos*) left their mother less often
369than singletons of comparable age [Bennett 1988]. Although our data show a slightly higher
370carrying rate for twins than singletons, singletons of the same year (2011) were carried
371similarly often. This result, pointing at some important differences between years, could
372reflect ecological differences between years such as other aspects of food availability we
373did not analyze in this study, or differences in predation risk, rather than behavioral
374differences between twins and singletons.

375 If the owl monkey twins were able to develop at a similar pace as singletons, it would
376suggest that owl monkey parents may not compromise the care provided per infant, but
377may instead almost double their usual costs. Males were not only carrying each twin longer
378than average, but were transporting both at the same time. Twinning, however, need not
379always double the cost for parents. In roe deer (*Capreolus capreolus*), a species that
380normally produces two fawns, the lactational cost of twins to mothers was estimated to be
381only 1.6 times that of singletons [Mauget et al. 1999].

382 Parents of owl monkey twins may have compensated for the increased cost of
383carrying by increasing their foraging time and reducing the time they spend moving. The
384reduced movement of twin parents found here is in line with results from other studies. For
385example, a white-bellied spider monkey female with twins also moved less than singleton
386mothers [Link et al. 2006], and several studies of callitrichines have shown that when
387transporting infants carriers moved less and/or rested more than non-carriers [Digby and
388Barreto 1996; Huck et al. 2004; Price 1992; Sánchez et al. 1999; Tardif 1994]. Contrary to

389our findings, however, each of these studies found that caregivers for twins foraged less
390than other individuals, not more. In the case of the callitrichines, it could be that individuals
391shift their foraging activity to periods when they are not carrying the infants. This
392interpretation is supported by our observations that the males carrying twins foraged less
393while transporting the infants (10.9%) than when they were free of their burden (36.6%) or
394carried only one infant (34.8%). Thus, males might compensate for the costs of infant care
395in two ways: reduced movement and increased foraging during the period of dependent
396infants, or reduced foraging and increased resting while actually carrying infants.

397 While one twin in each group survived the period of infancy (0 to 6 months), the
398overall infant survival rate did not differ statistically from the survival rate seen for
399singleton offspring [Huck and Fernandez-Duque 2012a], and both groups lost one of the
400infants. It is possible that predation on infants might be facilitated if a male has to retrieve
401two, instead of one, infant under the threat of a predator, but any conclusions about the
402survival rates of twins versus singletons are unwarranted at this point.

403 Unfortunately, we are not able to conclusively assess the long-term effects of
404twinning on a pair's reproductive output. In group E500, the adult male died, so it was not
405possible to unequivocally record whether this pair skipped a breeding season or had other
406long-term reproductive costs following the birth of the twins. Such costs have been
407demonstrated in other primates, however. For example, in a semi-natural experiment in
408captive rhesus macaques (*Macaca mulatta*), four females adopted additional infants; not
409only did all of these "twins" have a slower development than singleton offspring, but three
410of these four females had an abortion or stillbirth the following breeding season, compared
411to only one of six singleton mothers suffering an early loss [Ellsworth and Andersen 1997].

412 In group D1200, both adults were unidentified, so we cannot be sure whether the group
413 occupying the area in 2012 is indeed the same. However, this group did have an infant in
414 2012. Because it is rare that newly formed pairs have infants in the same year [Fernandez-
415 Duque and Huck 2013], it is likely that the adults in group D1200 were indeed the same as
416 in 2011, and that they reproduced despite having raised twins in the previous year.

417 Finally, the year when the twins were born was a good, but not an extraordinarily
418 good year in terms of fruit abundance. Although the months leading to conception in 2011
419 were rich in fruit, it would be premature to suggest that owl monkeys are able to adaptively
420 respond to good conditions by increasing their litter size. Some of the other years of our
421 study were also characterized by similarly high overall fruit availability in the period before
422 conception, but twinning was not recorded. Also, in a previous study, we did not find a
423 strong relationship between fruit availability during the dry season and female reproduction
424 [Fernandez-Duque and van der Heide 2013]. In contrast, for mammalian species that give
425 birth to a variable number of offspring, there is good evidence that maternal body condition
426 can influence litter size. For example, after a masting year, wild boar (*Sus scrofa*) were
427 likely to produce more and larger litters than in lean years [Massei et al. 1996]. Likewise, in
428 years of European beech (*Fagus sylvatica*) mast, as well as with experimental food
429 provisioning, litter sizes and the proportion of reproducing females increased in edible
430 dormice [*Glis glis*, Kager and Fietz 2009].

431 However, it is unlikely whether an adaptive response to ecological conditions should
432 be expected in species that habitually produce singletons, like most anthropoid primates. If
433 even in good years usually only one offspring can be raised successfully, twinning might in
434 fact not represent an adaptive response to particularly good ecological conditions

435 (otherwise the rate of twinning incidents would be expected to be higher), but rather a
436 physiological "accident". In Hawaiian monk seals (*Monachus schauinslandi*), where
437 twinning occurs in only 0.1% of births, twins have significantly lower survival rates than
438 singletons, and thus twinning might be considered a maladaptive trait [Schultz et al. 2011].
439 The owl monkey pairs in our study seemed to cope comparatively well with their twins, and
440 it is also notable that we have recorded only two such cases in a single year, after 14 years
441 of only singleton births. Unfortunately, there are very few reliable data available on
442 twinning rates for primate species that habitually bear singletons [Geissmann 1990]. In
443 humans, who are aseasonal breeders, the main factors affecting twinning rates are thought
444 to be maternal age, parity, and genetic inheritance, but some minor effect of seasonal
445 changes in food supply also have been considered [reviewed in Hoekstra et al. 2008].

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

452

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470

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615 **Table 1:** Proportion of carrying behavior by the father and the mother in groups with
 616 singletons or twins during the first 18 weeks of life of the infants. For twins both the
 617 values for an individual infant are given and for 'one or two' of the twins simultaneous.
 618 Values for singleton years of group E500 are presented for qualitative comparisons, but
 619 it should be noted that they are based on small sample sizes.

Behavior	Groups	Week 1	Week 2-3	Week 4- 6	Week 7-9	Week 10-12	Week 13-15	Week 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	n.a.	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	n.a.	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

620

621**Table 2:** Test statistics of the linear mixed models testing the proportion of a specific
622behavioral category relative to the visible observation time, taking sex of the adult, year of
623observation 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 to 0.48
Littersize	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 to 0.84
Littersize	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 to 0.81
Littersize	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 to 0.88
Littersize	2		0.29		
no offspring		1.79		0.41	0.68
twins		-5.6		-0.64	0.52

624P-values were estimated using a Monte-Carlo Marcov chain simulation.

625

626**Table 3:** Average fruit availability [fruits/ha] per month during the pre-conception periods
627 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	2143	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 sp.</i>	5.5	middle	36	631	0	642	0
<i>Guazuma ulmifolia</i>	4.8	large	476	757	2618	1040	48
<i>Syagrus romanzoffianum</i>	7.1	large	83	0	0	346	0
Total			1215	4039	2720	3222	176
Size corrected total			3836	9320	8058	8187	539

628The "twin year" is shaded. Four species identified previously as important dry season food
629for owl monkeys are printed in bold, for the remaining species we present only average
630values and median density for each fruit size category.

631^a *Cecropia pachystachya*; *Banara arguta*, *Eugenia moraviana*, *Eugenia uniflora*,
632*Gymnanthes discolor*, *Phyllostylon rhamnoides*; ^b *Caesalpinia paraguariensis*, *Myrcianthes*
633*pungens*, *Phytolacca dioica*, *Psidium kennedyanum*, *Sideroxylon obtusifolia*, *Trichilia*
634*catigua*; ^c *Diplokeleba floribunda*, *Enterolobium contortisiliquum*, *Gleditsia amorphoides*,
635*Inga uruguensis*; ^d *Crataeva tapia*, *Genipa americana*

636 Figure legends

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

642

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

646

647 **Figure 3:** Relative frequency of the behavioral categories Foraging, Moving, and Resting
648 for the adult males in group E500 and D1200 while not carrying any infant (dark bars),
649 carrying one of the twins (light bars), or carrying both twins simultaneously (white bars).
650 For group D1200 no data are represented for the time the male carried one infant since the
651 total frequency was only 16. Statistical significance using G-tests is indicated with * ($P <$
652 0.05), ** ($P < 0.01$), *** ($P < 0.001$), or n.s. ($P > 0.05$). Values below 1.0 (the horizontal
653 line) represent behavior shown less often than expected, values above 1.0 represent
654 behavior shown more frequently than expected.

655