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The Effect of Infant Body Mass on Carrier Travel Speed in Cotton-top Tamarins (*Saguinus oedipus*)

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Abstract Infant carrying is common in primates and may be the second most costly activity related to reproduction, after lactation. In cooperative breeding groups of callitrichids, all group members carry and care for twin infants. Previous studies have described the costs of infant carrying in terms of body mass loss and reduced locomotor capability. However, infant carrying may also influence travel speed, an important potential cost because slower speed may handicap foraging, energetic budgets, and predator avoidance. We evaluated the impact of infant carrying on the travel speed of 27 adult and 9 subadult cotton-top tamarins (*Saguinus oedipus*) of both sexes in large outdoor enclosures. We compared carrier speed to speed when not carrying during the 10 weeks after nine births. Subadult tamarins, which have a lower body mass than adults do, moved faster than adults when not carrying. We found no difference between the mean speeds of subadults and adults while carrying. However, the speed of carriers decreased as infant mass increased, and the slope of this negative relationship was more pronounced in subadult carriers. For every 80 g of extra mass load (the body mass of newborn twins), adults reduced their speed by 6% and subadults by 19% relative to noncarrying speed. We also observed a reduction in speed while carrying two infants in adult tamarins as carrying time increased. Our results contribute to an understanding of the costs of infant carrying, and serve to emphasize the importance of cooperative breeding systems in coping with these costs.

Keywords Callitrichids · Cooperative breeding system · Infant-carrying cost · *Saguinus oedipus* · Travel speed

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Introduction

Infant carrying has evolved several times in the Primates. Once evolved, it has been conserved, suggesting that it has some benefits, the most likely being reduced mortality risk for carried infants (Kappeler 1998; Ross 2001). However, infant carrying incurs costs for the carrier, usually the mother, owing to the additional body mass of the carried infant (Altmann and Samuels 1992; Gittleman and Thompson 1988; Link *et al.* 2006; Williams *et al.* 2002a). Infant carrying is the second most costly aspect of reproduction after lactation (Altmann and Samuels 1992; Nicolson 1987; Wall-Scheffler *et al.* 2007). Carrying costs can take the form of greater energetic expenditure; the metabolic cost of terrestrial locomotion increases proportionally to the mass carried (Taylor *et al.* 1980). Infant carrying also reduces the efficiency of essential parental activities (Altmann 1980; Altmann and Samuels 1992). For example, maternal foraging efficiency declines during infant contact in a wide range of primates, including yellow baboons (*Papio cynocephalus*: Altmann 1980; Barrett *et al.* 1995) and rhesus (*Macaca mulatta*: Johnson 1986) and squirrel monkeys (*Saimiri sciureus*: Andrews *et al.* 1993). Infant carrying may also increase maternal vulnerability to predators by reducing their probability of escape (Altmann and Samuels 1992; Wall-Scheffler *et al.* 2007). Finally, infant carrying might impose other restrictions on locomotion, as seen in the reduced travel speeds of chimpanzees (*Pan troglodytes*: Williams *et al.* 2002a; Wrangham 2000) and spider monkeys (*Ateles belzebuth belzebuth*: Shimooka 2005) with infants.

Callitrichids are small primates with a cooperative breeding system in which parents and helpers carry the offspring, usually twins, delivered by the sole reproductive female in a group (Snowdon 1996; Tardif 1997). Understanding the costs and benefits of infant carrying in callitrichids is important to our comprehension of the evolution of their cooperative breeding system (Achenbach and Snowdon 2002; Snowdon 1996; Snowdon and Ziegler 2007; Tardif 1997). Infant carrying in these species is highly costly due to twinning, the large newborn body mass, and the rapid growth of the offspring (Garber and Leigh 1997). For example, infant cotton-top tamarins (*Saguinus oedipus*) weigh 45–50 g at birth, representing *ca.* 15% of maternal body mass in the case of twins (Leutenegger 1979; McGrew and Webster 1995). Further, infants double in body mass by weeks 5–6 (Ginther *et al.* 2002; Tardif *et al.* 1993). Cotton-top tamarins carry infants full-time until the fourth week after birth, and >50% of the time until weeks 8–10 (Cleveland and Snowdon 1984; Savage *et al.* 1996). By contributing to infant care helpers obtain potential direct or indirect benefits that may include increased inclusive fitness by caring for relatives, parental skill learning and interpersonal tolerance leading to group permanence (Snowdon and Ziegler 2007; Tardif 1997). Contribution to infant carrying is related to body mass loss in carriers in cotton-top tamarins (Sánchez *et al.* 1999), and carrying two 30-d-old infants increases the caloric cost per minute of travel by an estimated 21% (Tardif 1997). An experimental study of common marmosets (*Callithrix jacchus*) showed that carrying two newborn infants reduced carriers' leaping ability by 17% (Schradin and Anzenberger 2001). Carrying also imposes constraints on tamarin activities and tamarins spend more time resting and less time moving, foraging, or feeding when carrying (in the wild: Goldizen 1987; Huck *et al.* 2004; in captivity: Caperos *et al.* 2008; Price 1992).

We aimed to evaluate the impact of infant carrying on the speed of adult and subadult carriers of cotton-top tamarins in captivity. We predicted that speed of carriers would decrease as mass carried increases, and that these relationships would be stronger in subadults, which are still growing and are smaller in size than adults.

Methods

Subjects and Housing

We studied 27 adult (9 fathers, 10 male and 8 female helpers, mean age=63±SD 30 mo, range=26–119) and 9 subadult helper (6 males and 3 females, mean age in months=16±4, range=13–20) cotton-top tamarins belonging to nine family groups (Table I). We considered individuals as subadults from the onset to the end of puberty (13–24 mo), after which we classified them as adults (Ginther *et al.* 2002; Price 1991). We excluded mothers from our analyses because they frequently carried infants in a ventral position during lactation, which may affect their speed differently to other positions. We recorded data from October 1999 to February 2009, observing the birth of one litter in each group. In all cases twins were born, but one infant died during the first week in four litters (groups A, B, C, D).

The tamarins belonged to the Universidad Autónoma de Madrid (UAM; Spain). The facilities consisted of a large outdoor area (42.0 m²×3.3 m) adjacent to a small indoor enclosure (3.5 m²×2.2 m) with controlled humidity and temperature. The tamarins had free access to both enclosures, which had wooden perches, branches, and climbing structures and were equipped with *ad libitum* water dispensers. We controlled food schedules strictly and subjects were habituated to this routine (for more details of the colony husbandry, see Sánchez *et al.* 2005). This research complied with protocols approved by the appropriate institutional animal care committee (Research Ethic Committee: CEI-UAM 2–23; CEI-UAM 11–188; CEI-UAM 16–362).

Table I Composition of focal groups, which were composed of a reproductive pair (adults) and their offspring

Group	Litter size	Group size ^a	Adult		Subadult	
			♀	♂	♀	♂
A	1	2	1	1		
B		3	1	1		
C		8	3	2		2
D		10	4	4		
E	2	3	1	1		
F		6	1	1	1	2
G		7	1	2	1	1
H		6	2	3		1
I		8	3	4	1	

Fathers from groups A and E were first observed as helpers (subadult and adult) in groups H and D, respectively.^aTotal group size includes juveniles.

Sampling Procedure

We weighed all subjects at least three times a week (Sánchez *et al.* 2005, 2008). We trained tamarins to step onto a scale (± 1 g) (Sartorius Universal Type 46100) by placing highly preferred foods, such as mealworms, on it as the first food in the morning when they were particularly hungry. Once they were familiar with this routine, tamarins rested on the scale frequently. When we were unable to weigh an infant alone, we calculated its body mass by subtracting the body mass of the carrier from the mass of the carrier plus infant, measured on the same day.

We conducted observations in the outside enclosure 5 d/wk during the 10 wk after each birth. We conducted two 5-min focal follows on each tamarin each day. Observation sessions lasted 30–90 min depending on group size. We observed each animal for a total of 50 min/wk (a total of 8.3 h/individual). Individuals in our colony are active from 07:00–08:00 h to 17:00–18:00 h (Caperos *et al.* 2011); we randomized the start time of observation sessions and the order of subjects between 09:00 h and 14:00 h. Two observers recorded the time spent moving and the distance covered by the focal tamarin continuously, noting whether it was carrying zero, one, or two infants. We marked branches with yellow lines for 1 m and red for 0.5 m distances to facilitate distance estimation. When subjects jumped, we estimated the linear distance based on the nearest marks. Observers underwent a training period in which we estimated the distance covered by the tamarins and compared the estimates with an actual measure of length covered in the enclosure. We assessed interobserver reliability in 30 focal samples and found high reliability between observers (time moving: $r_s=0.95$, $P<0.001$; distance length: $r_s=0.97$, $P<0.001$). We recorded all data using The Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands) and a Psion Workabout hand-held computer.

Measures

First we calculated individual measures for each tamarin: body mass (mean body mass during the 10 wk), infant carrying (percentage of time carrying infants during the 10 wk), and mean travel speed when not carrying and when carrying one or two infants (meters traveled during the study in each carrying condition divided by time moving in the same condition). Second, because mass carried increases with both infant growth and the number of infants carried, we calculated mass carried for each week and carrying condition (weekly means of infant body mass for one-infant and two-infant conditions, respectively). Finally, for each weekly carrying condition, we also calculated the mean carrying speed as the mean speed of the subjects observed in each condition. Because we expected differences between adults and subadults, we calculated separate means for each age class. Variable numbers of subjects contributed to each weekly carrying mean, because we observed different numbers of individuals in carrying condition each week, so we considered only means calculated for at least two subjects (Table II).

Data Analysis

We assessed the distributions of the variables with Shapiro-Wilk tests and found no significant deviations from normality with the exception of carrying time, which we

Table II Sample size, mean and SD of mass carried and speed by week and carrying condition

Week	Infants carried	Adults					Subadults						
		N		Mass carried (g)		Speed (m/s)		N		Mass carried (g)		Speed (m/s)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
1	1	15	46	4	0.52	0.20	2	47	3	0.67	0.27		
	2	6	92	6	0.52	0.12							
2	1	14	50	5	0.57	0.14	3	50	5	0.68	0.17		
	2	7	98	7	0.57	0.10							
3	1	15	58	4	0.57	0.21	4	59	4	0.59	0.26		
	2	6	111	4	0.53	0.14							
4	1	23	65	5	0.56	0.22	7	66	4	0.65	0.15		
	2	7	126	3	0.53	0.12	1 ^a	131		0.50			
5	1	20	72	9	0.67	0.23	8	74	8	0.54	0.22		
	2	6	139	9	0.55	0.13	4	145	13	0.54	0.38		
6	1	21	83	11	0.55	0.17	7	85	11	0.56	0.21		
	2	5	155	9	0.46	0.04	3	158	9	0.42	0.04		
7	1	20	92	10	0.64	0.48	9	97	9	0.60	0.26		
	2	5	181	7	0.55	0.18	2	186	9	0.34	0.37		
8	1	21	101	12	0.59	0.20	5	101	12	0.57	0.09		
	2	5	193	13	0.53	0.10							
9	1	17	112	14	0.54	0.30	2	110	9	0.71	0.23		
	2	4	210	12	0.47	0.08							
10	1	12	125	16	0.52	0.16							
	2												

Sample sizes (*N*) vary because only subjects observed in each carrying condition in each week contributed to the mean for that week.

^a We excluded this mean because only one subject contributed to it.

log-transformed to fit a normal distribution. We used Student's *t*-tests for independent samples to compare body mass, carrying time, and speed between adult and subadult tamarins. We used Pearson product-moment correlations to assess the relationships between speed while carrying and body mass of the carrier and between speed and carrying time. Finally, we ran a linear regression model including mean carrying speed as the dependent variable, mass carried as a covariate, and age class (adult vs. subadult) as a fixed factor to evaluate the relationship between mass carried and speed. To ease interpretation, we expressed carrying speed as a percentage of non-carrying speed (carrying speed/noncarrying speed * 100). First, we assessed collinearity between the factor and the covariate and found no relationship between mass carried and age class of helper ($r=0.14$; $N=31$; $P=0.45$). We established statistical differences in the regression coefficients between adults and subadults through examination of the *t* value (the ratio between the coefficient and the standardized error) (Pardo and San Martín 2010). Because the same subjects can contribute to

different means of carrying speed, the samples used in the regression analysis were not completely independent. Thus we evaluated the dependence of the data with the Durbin-Watson statistic of residual correlation (Pardo and San Martín 2010); we found no evidence of dependence among the means (adults: $N=19$; $d=2.58$; subadults: $N=12$; $d=1.77$) (Draper and Smith 1998). We performed all analyses with the Statistical Package for Social Sciences (SPSS, 17.0), all tests were two-tailed, and we considered differences significant when $P<0.05$.

Results

Adult tamarins weigh more (mean = $539 \pm \text{SD } 70$ g) than subadults (436 ± 57 g) ($t_{34} = 4.02$; $P < 0.001$). Adults (mean carrying time = $23.0 \pm 19.4\%$) carried infants three to four times more often than subadult helpers did ($6.7 \pm 4.9\%$) ($t_{33} = 2.80$, $P = 0.009$). Subadults rarely carried very young infants (during the first 3 wk of infant life) or large weights (data from two infants in the last weeks of the study; Table II). When noncarrying subadult tamarins moved faster (0.93 ± 0.15 m/s) than adults (0.70 ± 0.17 m/s) ($t_{34} = -3.61$, $P = 0.001$), but we found no difference in the mean speed when carrying between adults (0.54 ± 0.13 m/s) and subadults (0.59 ± 0.15 m/s) ($t_{34} = -0.99$, $P = 0.33$).

The linear model showed an adequate fit to the data ($F_{3,30} = 25.54$, $P < 0.001$, $\eta^2 = 0.74$). We found an interaction between mass carried and age class ($F_{1,30} = 8.67$, $P = 0.007$, $\eta^2 = 0.24$); the reduction in speed per unit of mass carried ($F_{1,30} = 33.62$, $P < 0.001$, $\eta^2 = 0.55$) was larger in subadults than in adults ($t = 2.94$, $P = 0.007$; Fig. 1).

Finally, we found no relationship between speed when carrying and carrier body mass (adults: $r = -0.03$, $N = 27$, $P = 0.88$; subadults: $r = 0.39$, $N = 9$, $P = 0.30$); neither did we find a relationship between speed and time when carrying one infant (adults: $r = 0.19$, $N = 26$, $P = 0.34$; subadults: $r = 0.15$, $N = 9$, $P = 0.71$). However, in the case of adults, tamarins that spent more time carrying moved more slowly while carrying two infants ($r = -0.77$, $N = 11$, $P = 0.005$). Too few subadults carried two infants ($N = 5$) to explore this effect in subadults.

Discussion

Our results indicate that cotton-top tamarins decreased their travel speed proportional to the mass carried when carrying infants. A lower speed may imply a reduced ability to travel (Pontzer and Wrangham 2006), leading them to choose between becoming isolated or increasing their locomotion effort to follow the group. In larger primates, body size affords a reduced susceptibility to predators (Chapman *et al.* 1995; Waser 1984), and mothers can travel alone or in small parties with their infants. For example, female chimpanzees usually travel alone with their offspring (Doran 1997; Williams *et al.* 2002b), and although juveniles appear to constrain maternal ranging, they do not constrain that of the entire group because mother and juveniles leave the groups as the day range increases (Pontzer and Wrangham 2006). Similarly, female spider monkeys travel alone or in smaller parties more often when with an infant (*Ateles geoffroyi*: Chapman 1990; Fedigan and Baxter 1984), and constrain

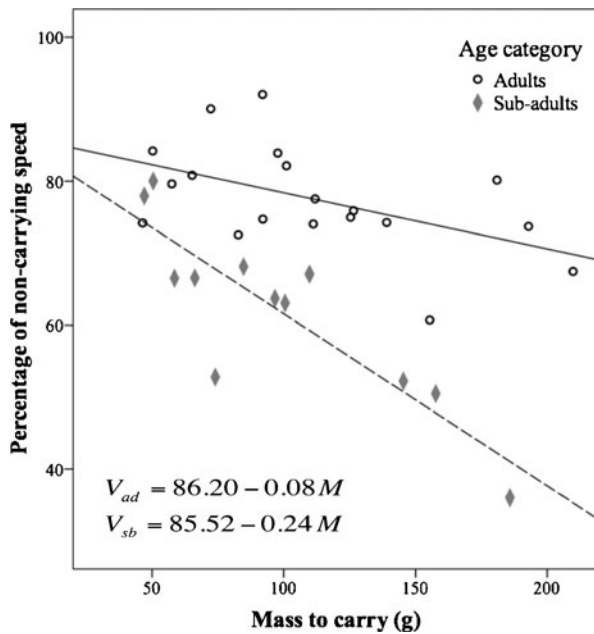


Fig. 1 Relationship between mass carried (g) and speed relative to noncarrying speed (%) for adults (circles; solid line) and subadults (diamonds; dashed line). The slopes of the regression equations are expressed per g of extra mass carried.

their movements to the core of their range (*A. paniscus chamnek*: Symington 1988). In contrast, primates subject to greater predation risk must remain in groups to reduce such risks (Alexander 1974; Hill and Lee 1998; van Schaik 1983). For example, female chacma baboons (*Papio ursinus*) with dependent offspring remain in the center of the group near male protectors during group movements (Stueckle and Zinner 2008). Similarly, the birth of infants has no detectable influence on group movements in yellow baboons (Altmann 1980), and mothers expend substantial effort to stay with the group, even immediately after parturition (Altmann and Samuels 1992). Callitrichids are subject to high predation pressure, but maintain egalitarian societies (Caine 1993; Schaffner and Caine 2000) in which group members cooperate in both antipredator vigilance and infant care (Savage *et al.* 1996; Snowdon and Ziegler 2007). They move and forage as a cohesive social unit, usually separated by <15 m (Caine 1993; Peres 2000), and exhibit high levels of attraction among group members (Menzel and Beck 2000). The cohesive social relationships are reflected in their tendencies to follow one another or to wait if they are not followed (Menzel 1993). This behavior occurs also in callitrichids (Menzel and Beck 2000). Cooperative-breeding meerkats (*Suricata suricatta*), which also share infant care and antipredator behaviors, coordinate group speed among individuals by a vocal voting mechanism that allows cohesive travel (Bousquet *et al.* 2011). Thus, in cooperative breeders, the reduced speed of the carriers may also affect other group members. For example, in wild common marmosets, other group members foraged near carriers that remain in central areas of the home range (Digby and Barreto 1996).

As expected, we found that an increase in body mass of growing twins had an increasing impact on speed, and tamarins moved slower as infant mass increased.

Rapid postnatal growth and early attainment of large body size may enhance infant survival by reducing predation and starvation risks (Mitani and Watts 1997). Comparative analyses in primates also reveal that allocare correlates with relatively fast infant growth (Mitani and Watts 1997; Ross and MacLarnon 1995). Large home ranges, long daily ranging distances, and fast travel speeds in *Saguinus* sp. may promote longer periods of infant dependence (Tardif *et al.* 1993). For example, cotton-top tamarin infants reach locomotor independence on average 2 wk later in the field than in captivity, and allocare helps to cope with this infant dependence (Snowdon 1996). Allomothering may have favored rapid infant growth and long dependence periods in those species. It seems unlikely that, even with the help of a father, mothers could cope with an all-day reduction in their travel speeds, especially one that increases as infants grow.

We also found that the effect of mass carried on speed was larger in subadult than in adult carriers: adult cotton-top tamarins decreased their speed by 0.08% for each extra gram carried, but this reduction was increased threefold in the case of subadults to 0.24%. This means that a mass of 80 g, which represents the combined body mass of twin newborn cotton-top tamarin infants (Leutenegger 1979; McGrew and Webster 1995), entails a reduction in speed of 6% and 19% relative to noncarrying speed for adults and subadults, respectively. The larger reduction in relative speed in subadults may be explained by the fact that subadults moved faster than adults when not carrying. Motor slowing is a universal feature of aging (Zhang *et al.* 2000), and subadult tamarins spend a great proportion of their time in play activities (Achenbach and Snowdon 1998; de Oliveira *et al.* 2003), which involve large amounts of rapid locomotion (Chalmers and Locke-Haydon 1981; Cleveland and Snowdon 1984). However, subadults are immature, with reduced skeletal and muscular development (Bolter 2011; Bolter and Zihlman 2003), and infant carrying may pose a larger handicap for them than for adults. The reduced involvement of subadult helpers in carrying behavior is related to their lack of infant-care experience (Cleveland and Snowdon 1984; Price 1991). This may explain the lower frequency at which subadults carried infants during the first 3 wk, when infants are weak and fully dependent (Cleveland and Snowdon 1984). However, subadults also carried twins less frequently in wk 8–10, which might be better explained by the larger relative body mass of infants at this stage.

Adults carrying two infants moved slower as infant carrying time increased, which may be related to fatigue. The mass of two infants ranges from 80 to 100 g at birth to almost 250 g at wk 10. Caregivers reject and transfer twin infants more often than singletons, which may be related to the greater effort required to care for them (Price 1991; Snowdon 1996). Further, artificially increasing the mass carried by Goeldi's monkey mothers resulted in earlier rejection of infants and subsequent paternal carrying (*Callimico goeldii*: Anzenberger *et al.* 2007). Similarly, the occasional birth of twins involves greater than normal rates of allomothering in noncooperative breeding species, such as spider monkeys (*Ateles belzebuth*: Link *et al.* 2006), Japanese monkeys (*Macaca fuscata*: Nakamichi 1983), or banded langurs (*Presbytis melalophos*: Bennett 1988). In small groups of cotton-top tamarins, helpers carry infants more than in large groups (Washabaugh *et al.* 2002; Zahed *et al.* 2010), and they also assume greater costs (Achenbach and Snowdon 2002). If fatigue plays a role in tamarin speed, we would expect helpers from smaller groups to move more slowly, especially when

carrying two infants. Unfortunately, the majority of our groups were large, with more than three helpers (Zahed *et al.* 2010), and only one father was the sole helper in a twin birth, which prevented us from exploring this effect.

A reduction in group mobility may entail larger costs in the field by affecting access to feeding resources and reducing the ability of the group to defend large territories (Peres 2000). Tamarins have large home ranges (Digby *et al.* 2007), through which they move extensively daily to access scattered feeding resources, expending 10–30% of their activity time on locomotion (Dietz *et al.* 1997; Porter 2004; Raboy and Dietz 2004; Terborgh 1983). For example, mustached (*Saguinus mystax*) and saddle-back tamarins (*S. fuscicollis*) fed from a mean of 12.4 and 13.3 trees/d, respectively, and the mean nearest distance between trees was 100 m (Garber 1993a). They rarely revisited a feeding site in the same day, leading to daily journeys of nearly 2 km (Garber 1993a). However, seasonality of births at the beginning of the rainy season (Löttker *et al.* 2004; Rylands 1993; Savage *et al.* 1996), when mature fruits are more abundant (Garber 1993b; Terborgh 1983) and home ranges and daily ranges are smaller (Dawson 1979; de la Torre *et al.* 1995; Passamani and Rylands 2000), may buffer the potential costs of speed reduction. If moving more slowly through the forest implies longer periods of locomotion, this may also have an impact on energy budgets. Energy consumption per meter traveled is inversely related to speed (Taylor *et al.* 1982), but the energy expenditure of humans moving while loaded follows a U shape, increasing at both low and high speeds (Abe *et al.* 2004), and particularly at very low speeds (Bastien *et al.* 2005). Reduced agility also entails an increased risk of predation (Schradin and Anzenberger 2001), which is one of the most important ecological pressures in callitrichids (Caine 1993). Carriers usually behave in a cryptic manner, standing still and hiding, minimizing predation risk (Caine 1993; Huck *et al.* 2004). The reduction in locomotion and feeding behaviors found in several callitrichid species when carrying (Goldizen 1987; Huck *et al.* 2004) may be related to increased predation risk, in addition to increased energy expenditure or difficulty in accessing feeding resources. Even in captivity, where food is close and easy to access, tamarins feed less when carrying (Caperos *et al.* 2008; Price 1992; Sánchez *et al.* 1999), suggesting that this must be an important conserved trait for predator avoidance.

Other studies that measured the cost of infant carrying showed that callitrichids moved less often (Price 1992), decreased jumping ability (Schradin and Anzenberger 2001), and lost weight (Sánchez *et al.* 1999) when carrying infants. Our study provides empirical evidence that infant carrying in the cotton-top tamarin is associated with reduced travel speed, which ultimately may affect foraging efficiency, predator evasion, and energy budgets. We also showed that twinning and rapid infant growth, two of the most salient features of callitrichids, both impact the speed of carriers. From an evolutionary perspective, carriers must obtain fitness benefits to balance the high costs of infant carrying in cooperative systems.

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