



Variations in care for cottontop tamarin, *Saguinus oedipus*, infants as a function of parental experience and group size

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We examined the effects of parental experience and group size on infant care and development. Ten cottontop tamarin families were followed across three consecutive births of offspring to examine differences in survival, quality of care, developmental maturation and physical development for infants in two experimental conditions: (1) in large groups with previous parenting experience and (2) in small groups with little or no parenting experience. Although we found no differences in infant mortality, parents treated infants differently between conditions. However, when we examined the cumulative care provided by parents and sibling helpers together across experimental conditions, there were no differences in the rates of retrieval or rejection of infants. Overall levels of infant transport and food transfers were similar between conditions, with fathers and sibling helpers contributing the bulk of care. Fathers in small groups carried infants and transferred food with infants much more than helpers but, as group size increased, helpers augmented this role. Infant development varied with the experience of the family both between conditions and within a family. The results indicate that infants receive similar levels of care regardless of group size and parenting experience, although the individual contributions of family members change with both factors. Parental experience with previous infants had effects on early infant development, but only for the first sets of infants.

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The effects of prior experience with infants on parental care have been found in a number of species. For example, in ewes, multiparous mothers are less likely to experience disturbances in maternal behaviour following birth, whereas primiparous ewes have a 61% likelihood of disturbance (Poindron & Le Neindre 1980). Previous maternal experience also decreases aggression towards new lambs (Poindron & Le Neindre 1980). Parity also influences maternal behaviour (Carlier & Noirot 1966) and quality of care in rats (Moltz & Wiener 1966). Experienced female ring doves, *Streptopelia risoria*, show a greater frequency of regurgitation feeding when presented with foster chicks than do inexperienced females (Wang & Buntin 1999). Kittiwake, *Rissa tridactyla*, chicks have higher growth rates when both parents have had previous parenting experience (Coulson & Porter 1985). Inexperienced pairs of eastern kingbirds, *Tyrannus tyrannus*, lose more young to starvation and predation than experienced pairs. Having even one experienced breeder substantially improves the pair's reproductive success (Woodard & Murphy 1999).

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Experience with infant care as siblings in natal groups is important for later reproductive success in a number of callitrichid species (cottontop tamarins: Tardif et al. 1984; Snowdon et al. 1985; Johnson et al. 1991; golden lion tamarins, *Leontopithecus rosalia*: Baker & Woods 1992; saddle-back tamarins, *Saguinus fuscicollis*: Epple 1978). However, reproductive success can be further influenced by experience as a parent. As parents become more experienced, they may increase the chance of infant survival as well as the quality of care for their infants. For example, in cottontop tamarins, parental experience can have a significant impact on mortality, with primiparous parents having lower infant survival compared with multiparous parents (Snowdon 1996). First-time parents also show hormonal differences from experienced parents. During their mate's pregnancy, fathers experience a rise in prolactin, a hormone considered instrumental in quality caretaking by males. The timing of this hormonal rise is dependent on previous parenting experience (Ziegler & Snowdon 2000). Ziegler & Snowdon (2000) also found that male prolactin levels correlated positively with the number of previous births, indicating that experience may play an important role physiologically, as well as behaviourally.

The quality of care infants receive may also affect their development. In humans, negligent parenting styles can result in psychological and even physical retardation (Silver & Finkelstein 1967). Dramatic effects have also been documented in many nonhuman primate species including less play behaviour, less mobility and lower body weights in neglected common marmoset, *Callithrix jacchus*, infants (Chalmers & Locke-Hayden 1986) and difficulty dealing with novel stimuli in rhesus monkeys, *Macaca mulatta*, who experience brief separations from mothers early in life (Hinde 1977).

Studies of rhesus monkeys (Suomi 1987), baboons, *Papio cynocephalus* (Altmann 1980) and vervet monkeys, *Cercopithecus aethiops* (Fairbanks 1996) have shown that even when not negligent or abusive, maternal behaviour can affect the survival and development of infants. Infants with protective mothers develop more slowly, but are also more secure in potentially stressful situations. Laissez-faire mothers produce infants who are more independent and adventurous earlier, but respond poorly to stress (Fairbanks 1996). The style of parenting that mothers adopt can dictate the outcome of their infants' social development.

Offspring of cooperatively breeding species such as the cottontop tamarin are cared for not only by mothers, but other group members as well. In such breeding systems, additional caretakers may thus influence infant development. Furthermore, the presence of multiple caretakers might affect the behaviours of other caretakers as well as infant development. Some studies (cottontop tamarins: Cleveland & Snowdon 1984; Ziegler et al. 1990; common marmosets: Ingram 1977; Rothe et al. 1993) found that the role of callitrichid mothers diminished with the presence of social group members who helped care for infants. However, other studies have shown that fathers benefit more from the presence of these helpers (cottontop tamarins: McGrew 1988; Tardif et al. 1990; Price 1992; lion tamarins and marmosets: Santos et al. 1997). Sanchez et al. (1999) noted that both fathers and helpers experience a weight loss during periods of infant carrying, while mothers do not. Achenbach & Snowdon (2002) have observed a negative correlation between weight loss during infant care in cottontop tamarin males and number of helpers.

We examined the effects of parenting experience and the division of infant care within families. We chose pairs with similar experience in sibling care but varying in direct parenting experience to isolate the importance of parenting experience for infants. By comparing families of diverse experience as well as comparing within families as parents gained experience, we could determine the importance of experience in influencing infant development and examine the changing roles of caretaking as siblings increasingly shared care responsibility.

We predicted that infants born to parents with greater parenting experience would benefit in terms of survival, quality of care and physical development. We expected experienced families to be more protective and to allow longer periods of infant dependence through carrying and longer duration of provisioning both because of learned tolerance as well as having more helpers with

which to divide responsibilities. Price (1992) indicated that infants in large groups receive more provisioning and are carried more than those in small groups. In contrast, infants from families with less parenting experience might receive lower-quality care for a shorter period, thus forcing them to independent behaviour earlier.

As families grow we hypothesized that the contribution of care by parents would decrease. Increased numbers of helpers would do more caretaking and parents would benefit. These shifts in the division of labour would result in changing responsibilities for parents, but could result in the same level of overall care infants received previously. Other studies (cottontop tamarins: McGrew 1988; Tardif et al. 1990; Price 1992; Achenbach & Snowdon 2002; lion tamarins: Santos et al. 1997; marmosets: Santos et al. 1997) indicate that the shift in the father's level of involvement may be greater than the mother's, whose role in care is already minimal compared with other family members.

If parenting experience plays a significant role in influencing the quality of caretaking and infant development, we would expect to see this most clearly in early litters, compared with later ones within the same family. We would also expect to see the lowest quality of care, as well as accelerated development, for first-generation infants.

METHODS

Subjects

All infants were born between July 1997 and September 2000 at the University of Wisconsin Psychology Department. Ten families were categorized as either Experienced ($N=5$) or Less Experienced ($N=5$) based on the number of offspring the parents had raised previously. Experienced families were those where the parents had produced at least three sets of surviving offspring prior to the start of this study, whereas in Less Experienced families, three of the parents had no prior surviving infants and only two families had one previously surviving infant, indicating very little experience. Each family consisted of the parents and additional offspring born prior to this study (the range in family size prior to birth of first subject for Less Experienced=2–3 individuals; Experienced=4–7 individuals). All parents had experienced at least one sibling birth while in their natal family, thus having sibling experience. There was no difference between subject groups in the number of sibling births experienced prior to the start of this study ($\bar{X} \pm \text{SE}$: Experienced pairs: 3.40 ± 1.51 ; Less Experienced pairs: 2.60 ± 0.70 ; unpaired t tests, assuming unequal variances: $t_{13}=1.524$, NS) or between sexes (females: 3.30 ± 1.42 ; males: 2.73 ± 0.95 ; $t_{16}=1.112$, NS).

A total of 58 infants (31 females; 25 males) were born in 28 litters with 31 infants surviving (53.4% survival). These 31 infants (17 females; 14 males) were the offspring of three consecutive births from nine of the 10 families (female Cai gave birth to only one infant before the father died of natural causes several months later). We expected that with successive births, the Less Experienced parents would begin to behave similarly to the Experienced

Table 1. Infant subject details from Experienced versus Less Experienced families

Subject	Sex	Family	Prior offspring*	Litter size	Surviving litter size	Family size†
Experienced						
Da	M	Cai	5	1	1	7
Be	M	Gab	12	3	2	6
Ce	F	Gab	12	3	2	6
Ho	M	Gab	14	3	2	7
In	M	Gab	14	3	2	7
Ro	F	Gab	16	3	1	7
Ne	F	Hon	9	2	2	5
Or	F	Hon	9	2	2	5
Wi	F	Hon	11	2	2	6
Xy	M	Hon	11	2	2	6
Ec	F	Kok	6	2	2	8
Fu	F	Kok	6	2	2	8
Pu	F	Kok	8	2	2	7
Qu	M	Kok	8	2	2	7
Yo	F	Kok	10	2	2	8
Za	F	Kok	10	2	2	8
Mo	M	Van	4	3	1	4
Less Experienced						
Ga	F	Oct	1	1	1	3
Se	M	Oct	2	3	1	4
Ch	F	Oct	3	1	1	4
Ax	M	Phl	0	2	1	2
Kr	F	Phl	1	2	1	3
Ut	M	Qui	1	2	2	2
Vo	F	Qui	1	2	2	2
Zy	M	Val	0	2	2	2
An	F	Val	0	2	2	2
Ja	F	Val	2	2	2	4
Ka	M	Val	2	2	2	4
Lo	F	Zep	0	2	1	2
Tr	M	Zep	1	2	1	3
Dr	M	Zep	2	2	1	3

*The number of infants born previous to the subject's birth (does not include the subject or the subject's littermates).

†The number of animals present at the time of the subject's birth (does not include infants).

parents. See Table 1 for specific details on each subject. All families had at least one and no more than six living infants represented in this study. Most infants ($N=20$) were surviving twins and thus were observed together.

Husbandry

Small families and pairs were housed in cages measuring $1.6 \times 2.4 \times 1.9$ m to $1.6 \times 2.4 \times 0.9$ m, and larger families were housed in cages measuring $2.9 \times 2.3 \times 1.9$ m. When there was more than one cage per room, we hung opaque fabric sheets between cages to prevent the animals from having visual and tactile contact with other cages. Auditory and olfactory communication were limited, but not eliminated entirely. All cages were equipped with a complex system of branches, ropes and planks to simulate an arboreal habitat. Cage floors were covered with a layer of pine shavings. Each cage was equipped with a nestbox and one or two food platforms and water bottles. Cage environments were changed completely every 3 months both for sanitation and to provide a stimulating and changing environment.

Tamarins received a morning feeding of yogurt and applesauce between 0830 and 1000 hours. A main feed of Zupreem, Purina monkey chow, various fruits and vegetables, and bread was fed between 1200 and 1315 hours. An afternoon snack of high-protein food items was fed between 1430 and 1730 hours. Water was available ad libitum. Light cycles were maintained on a 12:12 h light:dark cycle, onset at 0800 hours (GE Chroma 75 full spectrum fluorescent lighting) and temperature was kept between 25.6 and 27.8 °C. Humidity could not be controlled and varied with the season.

Data Collection

Infant carry scans

Scan samples for each family were recorded daily at 0800 (when animals were awakened), 1000, 1200, 1400, and between 1430 and 1730 hours. The identification of any infants and the group member transporting the infant was recorded. Samples were recorded from day of birth through 100 days of age, when infants were either independent, or off a carrier most of the time. In a

Table 2. Caretaking behaviours

Behaviour	Definition of behaviour
Carrying	Location of infant on substrate/carrier. Recorded as scan sample.
Successful retrieval	Carrier invites and/or gathers infant.
Attempted retrieval	An unsuccessful attempt at retrieving infant from carrier/substrate.
Rejection	Carrier scratches, bites, or rubs at infant in attempt to dislodge the infant.
Rejection resulting in transfer	A Rejection (see above) that results in the infant being successfully retrieved or climbing off the carrier.
Nurse	Infant is in standard nurse position and is heard/observed suckling. Recorded as duration.

previous study scan sampling was found to be as reliable as focal animal sampling in determining distribution of carrying across families (Ziegler et al. 1990).

Several researchers recorded the scans and were thoroughly trained in identification of all individuals in the study and in methods of scan sampling. When there were twins, one infant was marked with Redken Deco Color Lapis (number 92) and/or Topaz (number 91) hair dye within a day of birth to be sure all observers could identify each infant in a family. Wilcoxon matched-pairs signed-ranks test indicated that there were no statistically significant differences in behaviour between infants (or the behaviour of caregivers) that were marked and those that were not.

From the scan data, we tabulated the age (in days) when subjects were first observed to be independent of a carrier and on the substrate (including the branches, nestbox, cage mesh and other surfaces above the floor in the cage) both during a daytime scan, and when the animals were awakened in the morning. We also determined the age (in weeks) when infants were observed to be independent of carriers on at least 50% of the scans recorded. The 0800-hour scan sample was not used to calculate daily carrying patterns; groups huddling together at night may result in carrying roles that differ from daytime behaviour (Snowdon et al. 1993).

Focal observations

Focal animal samples (Martin & Bateson 1993) were collected on all infants from birth through to 11 weeks of age (77 days). Infants were sampled for 30 min, on three different days each week. Sessions alternated weekly so that morning and afternoon sessions were equally represented. All data were recorded on a Tandy Radio Shack TRS-80 model 100 or TRS-102 portable computer. Data were recorded using the KB+ Basic scoring program (Cook 1988) modified to score additional data. All observers had met predefined criteria of 85% (coefficient of concordance, Martin & Bateson 1993) in interobserver reliability tests prior to participating in data collection. Morning sessions were conducted at least 30 min following morning feed and prior to the noon feed, and afternoon sessions were conducted at least 30 min following the noon feed and prior to 1730 hours. Subjects did not receive any other supplementary food in the 30 min before an observation.

Computers were programed for 30-min sessions with scan samples at 30-s intervals, and a session was commenced following a 60-s habituation period. Caretaking behaviour (Table 2) and developmental markers of infant behaviour (Table 3) were scored. The actor and the recipient of each behaviour were recorded.

Food tests

Food provisioning is a cooperatively shared infant care responsibility that may influence infant growth and vary as a function of experience or the number of helpers present. Thus, food tests were conducted beginning at the age of 6 weeks, when young animals had begun to eat solid food, and we administered weekly food tests through 25 weeks of age. In cottontop tamarins, food transfers are more likely to occur with highly preferred foods (Feistner & Chamove 1986). Each week, in the afternoon, at least 30 min following the noon feed and no later than at 1730 hours, subjects were presented with a familiar food bowl (18 cm diameter and 6 cm deep) containing highly preferred Apple Newton cookies. These were cut into three pieces per animal, with pieces measuring approximately $2.2 \times 1.3 \times 0.4$ cm.

Prior to a food test, we removed regular food bowls and placed test bowls on food platforms. We recorded information on when the infant took food from the bowl independently, whom the infant approached to attempt a food transfer, and any attempts the infant made to get food from a caretaker, the bowl or other surface. A food transfer attempt was indicated by an infant approaching a family member with food and clawing at the food holder's hands, eating out of their hands, and/or vocalizing. Sessions lasted until all food was consumed. No food ever remained after 10 min. In families with twins, both subjects were tested simultaneously to avoid exposing them to the test more frequently than singleton subjects.

We used mean scores for each subject across all sessions to determine the number of food transfers infants attempted and the total number of food pieces they were successful in obtaining from group members or directly from the food bowl between conditions and among caregivers. Food obtained independently from the bowl or other surface was compared between conditions and among caregivers. We also scored the first instance of obtaining food independently.

Table 3. Infant developmental markers

Behaviour	Definition and measure of behaviour
Climb on/off	Infant successfully climbs from a carrier to the substrate or vice versa.
Climb from a carrier to substrate	Infant independently transfers from its carrier to the substrate for the first time.
Climb from one carrier to another	Infant independently transfers from its carrier to another for the first time.
Scratch	Infant scratches its own body. Examined for first occurrence and mean occurrences over 11 weeks.
Manipulate object	First occurrence of infant chewing/handling object in cage.
Cross cage division	Infant is independent of a carrier and crosses one cage section to another. This involves climbing over a small beam and locomoting around the cage. Scored for first occurrence and mean occurrences over 11 weeks.
Go to the floor	Infant goes to the floor for the first time.
Erection	Penis is in a nonflaccid state for the first time.
Baby squawk vocalization	Infant utters distress vocalization. Scored on a yes/no basis at 30-s scans.

Weights

As noted previously, physical development, as well as behavioural development, of infants might be greatly influenced by the care of family members. Thus, one indication of quality of care might be evident via infant weight gain during early development. We weighed infants using a Satorius LC 1600 S platform balance every other week from the time of birth through to their first year of life (Achenbach & Snowdon 2002). Weighing sessions occurred in the afternoon at least 30 min following feeding and before 1730 hours. A typical weighing session lasted several hours depending on subject co-operation (see below). One to five weights were collected per subject each session and were averaged.

When possible, weights were scored only when subjects jumped onto the scale surface independently. All adult animals were well habituated to the scale by the start of the study and young animals were generally comfortable sitting alone on the scale by the age of 20 weeks. However, tamarin infants were almost constantly carried by family members for their first 6 weeks and became fully independent only at 12–18 weeks of age. Thus, weights were also gathered when infants were riding on another family member. The weight of the carrier was then subtracted from the total weight to get the infant weight. We recorded these weights only when a family member was carrying the subject alone and only when both the weights of the carrier with the infant and without the infant were obtained in the same weighing session.

Data Analysis and Statistics

Data summary and analyses were conducted using Microsoft Excel 6.0. Twin infants were treated independently for all analysis. We used two-way parametric analyses of variance (ANOVAs) to examine patterns of infant carrying (infant carry scan samples) according to sex of carriers, and the experience level of the family.

Mann–Whitney *U* tests were used to evaluate differences based on size of the surviving litter. We used only the first 8 weeks for this analysis as most infants were carried consistently during this time. The 8 weeks were divided into two 4-week periods (Month 1 and Month 2). ANOVA and two-tailed *t* tests assuming unequal variances were used to evaluate the effect of experience.

We used regression analysis to assess the correlation between number of helpers, food test results, infant carry scan data, weights and development markers (behaviours that develop with maturity and could be observed for the first time, or were a mark of infant progress over the first 11 weeks of life). We compared scores from food tests between experience conditions and among caregivers using two-tailed *t* tests assuming unequal variances.

Family experience was compared with sex differences in caretaking as well as age of the infant (Month 1 versus Month 2). As with infant carrying patterns, we used only the first 8 weeks. Caretaking behaviours were compared using two-way ANOVA, and regression analysis was used to evaluate the effect of helpers. Subjects Yo and Za from family Kok were not included in focal behaviour analysis as data were not complete. Four other subjects represent the family Kok.

In addition to evaluating the effects of number of helpers with linear regression tests, we also tested for a possible threshold effect (0–1 helpers versus 2+ helpers) and then for categorical differences (category 1=0–1 helpers, category 2=2–3 helpers, category 3=4+ helpers). For the threshold comparison, we analysed groups 0–1 versus 2+ helpers using *t* tests for unequal variances and analysed the categorical comparison groups with ANOVA tests with post hoc analysis. Where results were significant for the categorical comparison, post hoc analysis indicated that there were significant differences between categories 2 and 3 as well as between 1 and 2.

Development markers were analysed using a Mann–Whitney *U* test (two-tailed) for the experience condition of the family (Siegel 1956). We also examined these

behaviours in relation to the number of helpers in the family.

We compared weights at week 12 to a number of factors that might affect them including experience of the family, number of helpers, sex of infants and number of surviving birth siblings. Experience, sex of infants and number of surviving birth siblings were analysed using the Mann–Whitney U test. A regression analysis was used to evaluate effects of the number of helpers on weight data.

Growth rates for subjects following birth (weight at week 12 – weight at week 2) were examined separately for effects of experience of a family and subject's sex. We also examined the number of surviving birth siblings in relation to growth rates using the Mann–Whitney U test.

Using the intraclass correlation (Sokal & Rohlf 1981), we compared differences between twin siblings to differences between litters, for caretaking behaviours by all family members and for infant behaviours.

Because the number of helpers in a family group was so closely associated with experience level of that family, we often found significant results for both family size and experience. In the results that follow, where number of helpers is not listed, only experience level resulted in a significant result.

RESULTS

Infant Survival

Infant survival for the three successive births in each family did not differ as a function of family experience (Experienced survival: 68%; Less Experienced survival: 50%; chi-square test: $\chi^2_1=1.10$, NS). We calculated the chi-square to consider expected outcomes. That is, triplet births very rarely result in 100% survival, thus expected survival was reduced to two infants for triplet births for this analysis. Although there was a tendency towards female births, we found no significant difference in birth sex ratio (0.806:1), nor any difference in survivor sex ratio (0.823:1) ($\chi^2_1<0.277$, NS). There was a distribution of 11% singleton, 71% twin and 18% triplet births among 28 litters. One family was responsible for three of the five triplet births. No family was able to sustain all three infants and in all cases at least one infant died.

Infant Carrying and Food Test Results

We used a total of 4391 scans to analyse infant carrying patterns. Although we found no significant difference in overall levels of infant carrying between Experienced and Less Experienced families (Experienced: 80.0%; Less Experienced: 72.3%; unpaired t test, assuming unequal variances: $t_6=0.84$, NS), helpers as a group played a significant role in the distribution of carrying within a family. While patterns of carrying by mothers did not change with their level of experience and in fact remained significantly low in number, patterns for fathers and sibling helpers changed between conditions (Fig. 1). Thus, families maintained similar rates of overall infant carrying across the first 8 weeks, but used different

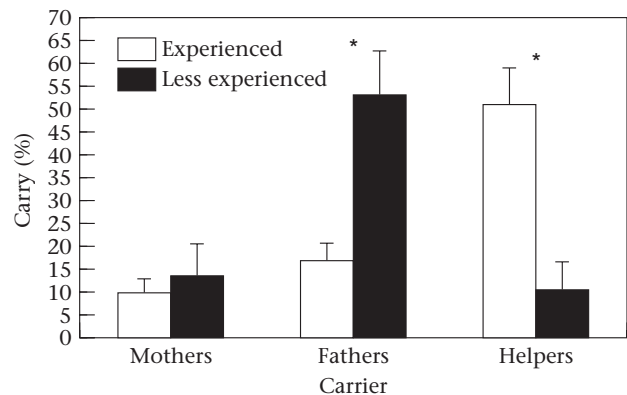


Figure 1. Percentage of infant carry responsibility among caregivers by experience condition. Mothers carried significantly less than fathers (unpaired t test: $t_{10}=-3.25$, $P<0.009$) and helpers ($t_{10}=-2.36$, $P<0.04$). There were no significant differences between fathers and helpers across conditions (ANOVA: $F_{1,9}=0.76$, NS). Fathers, and also helpers, varied significantly in carrying responsibility between the two conditions.

strategies to maintain these rates: carrying by fathers decreased when carrying by helpers increased. Less Experienced fathers carried infants significantly more than Experienced fathers (unpaired t test, assuming unequal variances: $t_5=-3.42$, $P=0.019$) and the Experienced helpers carried more than the Less Experienced helpers ($t_8=5.99$, $P=0.0003$). There were no differences in carrying based on the number of surviving infant siblings (singletons versus twins).

In addition, we found that nonreproductive helpers experiencing the presence of new infants for the first time differed in their carrying contributions. Even across births, helpers that were 12 months of age or younger carried significantly more in the Less Experienced condition than those in the Experienced condition (ANOVA: $F_{1,6}=8.59$, $P=0.026$). There were no significant differences for older helpers, however ($F_{1,6}=1.85$, NS).

Food transfers with infants were similarly distributed among family members (Fig. 2). There was no significant difference between the total number of food pieces infants obtained from Experienced or Less Experienced families (unpaired t test: $t_{25}=-0.28$, NS), however, the contributions within families varied for fathers and helpers depending on condition. Whereas Less Experienced fathers and mothers did not differ significantly in level of food transfers, Experienced fathers transferred food less than mothers did. There were also significant differences between parents and helpers. Mothers and fathers in the Experienced condition transferred food significantly less than their helpers, while mothers and fathers in the Less Experienced condition transferred more than helpers. Across both conditions, however, infants obtained food independently significantly more often than from caregivers across all weeks.

As with infant carrying, the division of labour fell mainly to fathers and helpers. Mothers in the two conditions did not differ significantly in food transfers, but Less Experienced fathers transferred food significantly more often than those from Experienced groups

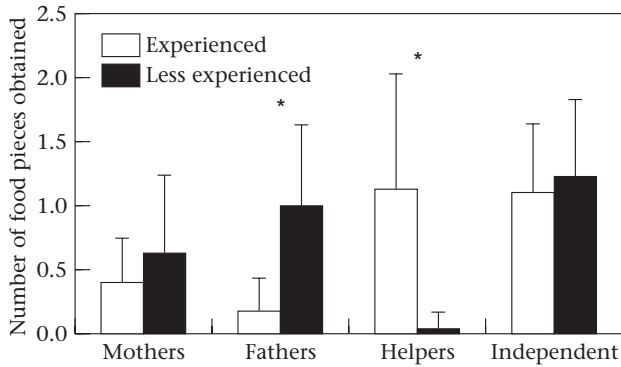


Figure 2. Infant food transfer sources by experience condition. Overall, infants obtained food independently more than from mothers (unpaired t test: $t_{59}=-4.90$, $P<0.0001$), fathers ($t_{59}=-4.09$, $P=0.0001$), or helpers ($t_{51}=-2.82$, $P<0.007$). Experienced helpers transferred more than Experienced fathers ($t_{19}=-4.19$, $P=0.0005$) and mothers ($t_{21}=-3.11$, $P=0.005$). Less Experienced fathers ($t_{14}=5.60$, $P<0.0001$) and mothers ($t_{14}=3.59$, $P<0.003$) also shared more than their helpers. Experienced mothers shared with infants significantly more than Experienced fathers ($t_{30}=2.18$, $P<0.04$), but there was no difference between Less Experienced parents ($t_{26}=-1.57$, NS). There were no differences in quantity of food obtained from mothers ($t_{20}=-1.27$, NS) or independently ($t_{26}=-0.59$, NS) between conditions.

(unpaired t test: $t_{17}=-4.60$, $P<0.0003$). Infants from the Experienced families more often went to helpers to attempt to transfer food ($t_{17}=4.92$, $P=0.0001$) than infants from the Less Experienced families.

Observational Results

Parental caretaking

The experience level of parents influenced the caretaking outcomes, with age of the infant playing a secondary role. Less Experienced parents successfully retrieved infants from other carriers or substrate more often than Experienced parents (Fig. 3a). Experienced parents displayed lower rates of infant rejection (Fig. 3b). Transfers as a result of rejection occurred less often in Experienced families, but for both groups, they occurred significantly more frequently in Month 2 than in Month 1 (Fig. 3c). Both Experienced and Less Experienced parents made attempts to retrieve their infants more frequently when infants were younger (Fig. 4). Nursing duration did not differ between Experienced and Less Experienced mothers, nor were there changes in duration between Month 1 and Month 2. Nursing bouts ranged between 108.3 and 492.3 s, but did not differ as a function of parental experience.

Family caretaking

As shown above, parents in the two conditions treated their infants differently. When we analysed the same caretaking behaviours combined over all members of the family, infants generally received similar levels of behaviour, regardless of how many animals were contributing to care. Thus, most significant differences we found as a result of experience were a consequence of the quality of

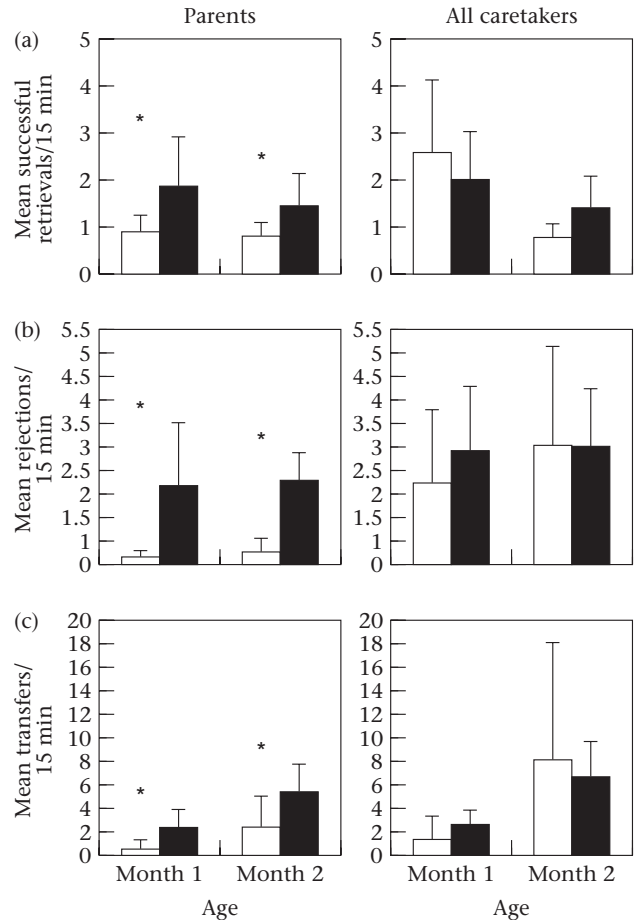


Figure 3. (a) Rate of successful retrievals per 15 min. There were significant differences between conditions for parents only (ANOVA: experience: $F_{1,16}=6.95$, $P=0.018$; age: $F_{1,16}=0.86$, NS), but there were no significant differences in successful retrievals between conditions for all caretakers ($F_{1,16}=0.0008$, NS). (b) Rate of rejection per 15 min. There were significant differences between conditions for parents only (experience: $F_{1,16}=14.56$, $P<0.002$; age: $F_{1,16}=0.77$, NS), but there were no significant differences in rejections between conditions for all caretakers ($F_{1,16}=0.21$, NS). (c) Rate of transfer as a result of rejection per 15 min. There were significant differences between conditions for parents only (experience: $F_{1,16}=7.18$, $P=0.017$; age: $F_{1,16}=7.38$, $P=0.015$). There were no significant differences in transfers as a result of rejection between conditions for all caretakers (experience: $F_{1,16}=0.002$, NS; age: $F_{1,16}=5.35$, $P=0.034$). Both parents and all caretakers transferred infants as a result of rejection more frequently in Month 2. □: Experienced; ■: Less Experienced.

parental care specifically, but were not related to overall levels of care for infants. That is, significant differences found between the conditions were largely a result of differences between parents rather than all family members.

Although successful retrievals by parents occurred significantly more often in Experienced families, we found no differences between Experienced and Less Experienced families when all caretakers were considered (Fig. 3a). There was a significant correlation between the number of helpers in a group and the frequency of successful retrievals, however (linear regression: $r^2=0.428$, $N=10$,

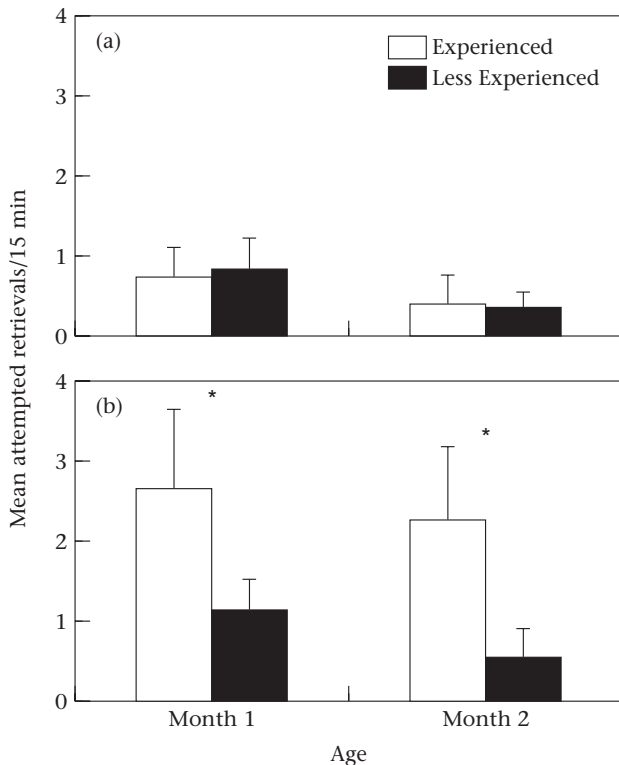


Figure 4. Rate of attempted retrievals per 15 min by (a) parents and (b) all caretakers. While there were significant differences between conditions for all caretakers (experience: $F_{1,16}=24.97$, $P=0.0001$; age: $F_{1,16}=2.43$, NS), parents' attempts to retrieve infants varied only as a function of infant age (experience: $F_{1,16}=0.04$, NS; age: $F_{1,16}=7.73$, $P=0.013$).

$P=0.04$). However, the number of helpers was not significant in either the threshold or categorical analysis. Rejection by family members did not differ significantly between experience levels (Fig. 3b) and, as with parents alone, transfers as a result of rejection occurred more frequently as infants matured (Fig. 3c). Rejections and transfers as a result of rejection were not significantly related to the number of helpers. Number of helpers was positively correlated with the rate of attempted retrievals ($r^2=0.63$, $N=10$, $P=0.006$) and was also significant for the threshold comparison (ANOVA: $F_{1,6}=3.62$, $P=0.01$), but not for the categorical comparison. Experienced family members made more attempts to retrieve infants from other carriers and the substrate than those from Less Experienced families (Fig. 4). We found no significant differences between groups when we examined the roles of parents alone.

Parental effects on infant behaviours

Parental experience was not a significant variable when we examined infant behavioural interactions with parents only. Infants climbed from the substrate to a parent more in later weeks (ANOVA: age: $F_{1,16}=68.25$, $P<0.0001$; experience: $F_{1,16}=0.21$, NS). This same pattern was true for the reverse as well; infants climbed off parents to explore the substrate more in Month 2 than in Month 1 (age: $F_{1,16}=48.34$, $P<0.0001$; experience: $F_{1,16}=2.59$, NS).

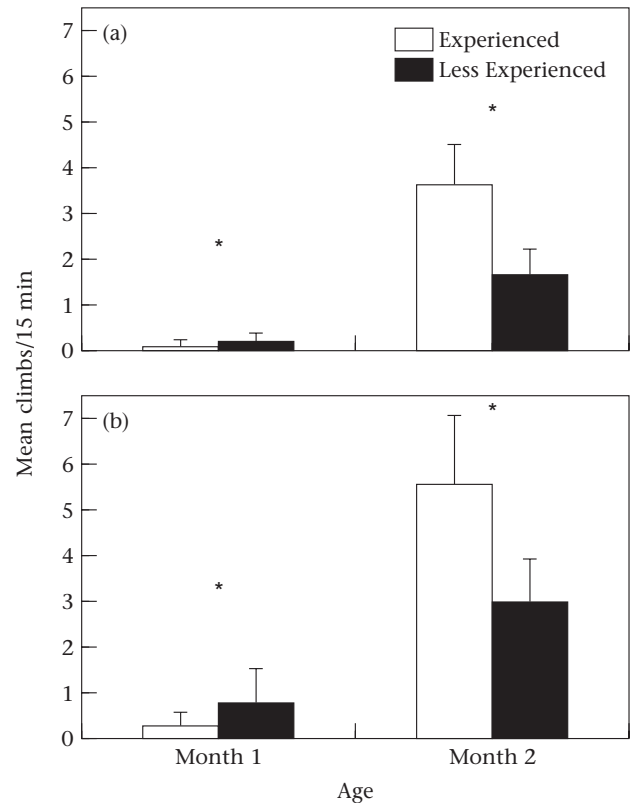


Figure 5. Rate of infant climbs (a) from the substrate to a carrier and (b) from a carrier to the substrate per 15 min. Infants from Less Experienced families climbed from the substrate to all carriers more in Month 1, and those in Experienced families did so more in Month 2 (experience: $F_{1,16}=14.63$, $P=0.001$; age: $F_{1,16}=108.75$, $P<0.0001$, interaction: $F_{1,16}=18.46$, $P=0.0006$). Similarly, infants from Less Experienced families climbed from all carriers to the substrate more frequently in Month 1, while infants from Experienced families climbed to the substrate more in Month 2 (experience: $F_{1,16}=5.92$, $P=0.027$; age: $F_{1,16}=78.71$, $P<0.0001$; interaction: $F_{1,16}=13.53$, $P=0.002$).

Family effects on infant behaviours

Infants in Less Experienced families climbed from a carrier to a substrate more frequently in Month 1 while infants from Experienced families climbed to a substrate more in Month 2 (Fig. 5). Climbing from a substrate to a carrier showed the same pattern. Infants from Less Experienced families climbed to a carrier more in Month 1 and from Experienced families more in Month 2 (Fig. 5).

Results of analyses of the number of helpers by linear regression and threshold comparisons were significant for climbing on/off carriers (linear regression: $r^2=0.68$, $N=10$, $P<0.01$; threshold: $t_8=3.06$, $P=0.02$), as well as specifically climbing to the substrate ($r^2=0.82$, $N=10$, $P<0.01$; threshold: $t_8=3.02$, $P=0.02$) and climbing onto a carrier ($r^2=0.66$, $N=10$, $P<0.01$; threshold: $t_8=2.75$, $P<0.03$). No climbing behaviour was significant in the categorical comparison.

Ontogeny of behaviour. Markers of development such as the age at which infants were first found independent of a carrier in scan samples, were off a carrier 50% of the

time, first climbed to the substrate in an observation, first crossed a cage division, and first manipulated an object were positively correlated with each other, indicating that infant development was fairly uniform. In addition, these correlations confirm that the behavioural measures of scan sampling and observational methods were comparable.

The more attempts that infants made to get food from the bowl or a family member, the more total food infants consumed across all food tests (linear regression: $r^2=0.898$, $N=31$, $P=0.001$). The earlier infants went to the test bowl, the more food they consumed from the bowl across all tests ($r^2=0.364$, $N=31$, $P=0.0003$). However, infants that approached the food bowl at a younger age received less total food (from the food bowl or from family members) across all tests ($r^2=0.23$, $N=31$, $P=0.006$).

First birth versus combined births

While there were few effects of parental experience on infant behaviour between families, we did find some differences in the first litter of subjects born during this study to Less Experienced parents (for three of the five parents with first surviving infants) compared with those born to Experienced parents. However, when we combined all three sets of infants in Less Experienced families, these results were no longer significant. The following results were significant only for the first-born infants (within this study), except where specifically noted. Regressions for number of helpers may be a nonlinear result as Less Experienced families had no more than one helper present at the first birth and Experienced families all had at least four nonreproductive helpers.

First-born infants from Less Experienced families climbed from a carrier to a substrate earlier (experience: Mann–Whitney U test: $U=1$, $N_1=N_2=5$, $P=0.016$; number of helpers: linear regression: $r^2=0.538$, $N=10$, $P<0.02$), and crossed cage divisions for the first time earlier (experience: $U=2$, $N_1=N_2=5$, $P=0.032$; number of helpers: $r^2=0.690$, $N=10$, $P<0.003$). However, infants from Experienced families and/or families with more helpers crossed more cage divisions across all weeks (experience: $U=2$, $N_1=N_2=5$, $P=0.032$; number of helpers: $r^2=0.514$, $N=10$, $P<0.02$) and ventured to the floor earlier than infants from Less Experienced families (experience: $U=2.5$, $N_1=N_2=5$, $P=0.04$). As this species is arboreal, the floor appears to be an intimidating place where only adventurous infants risk exploring. Infants in families with more helpers were observed off a carrier for the first time significantly later in daily scan sampling ($r^2=0.495$, $N=10$, $P<0.023$).

Although parental experience had no overall effect on climbing from parents to substrate, this study's first-born infants from Less Experienced families climbed from a parent to a substrate more than infants from Experienced families (ANOVA: experience: $F_{1,16}=7.63$, $P=0.014$; age: $F_{1,16}=9.30$, $P=0.008$). Less Experienced parents successfully retrieved their first-born study infants from the substrate more often than Experienced parents ($F_{1,16}=4.35$, $P=0.05$), but this difference did not persist through subsequent births.

Twin Differences

We found no significant differences due to twin or singleton (single births or cases in which birth siblings died) litters for any measures but weight. We calculated the mean and standard deviation of weightings collected per session for the combined infant/carriers and the carriers alone (infant/carrier mean=4.1 weightings, mean standard deviation between weight measures=1.05 g; carrier alone mean=3.7 weightings, mean standard deviation between weight measures=1.40 g). Singletons weighed more than twins at 12 weeks of age (Mann–Whitney U test: $U=20$, $N_1=10$, $N_2=16$, $P=0.02$). However, growth rates did not differ significantly for single subjects versus twins. Neither weight at week 12 nor growth rates differed significantly between infant sexes or for family experience or the number of helpers present.

The mean intraclass correlation between twins for care-taking behaviours was 0.109 ± 0.109 and for infant behaviours was 0.296 ± 0.188 . These results indicate that there was greater variance between behaviour of twins within a family than between litters in different families, and that twins within a litter received similar caregiving.

DISCUSSION

Contrary to our predictions, the experience level of a family had little influence over the quality of care an infant received. In fact, we found no difference in infant survival between conditions. When infants survived, it appeared that all families maintained an equal level of care as shown through infant carrying, food provisioning and retrieval behaviour among caretakers despite variation in experience or in the number of helpers available for infant care. Individual roles in infant care varied greatly, but family members compensated for these variations by adjusting their own individual behaviour.

Survival rates were consistent with historical data from this colony. Less Experienced families had a slightly lower rate of survival (50%) than the colony average for parities 1–4, but not unreasonable considering three of the five pairs were first-time parents. From 1978 to 1994, first-time parents in our colony achieved only a 6.7% survival rate, but in the 4 years preceding this study (1994–1998), that rate increased to 45.5%. This increase is most likely due to changes in husbandry as well as the decision not to breed hand-reared tamarins in our colony.

Infants were carried at consistent rates in both Experienced and Less Experienced families, but the carrying responsibility of specific family members varied greatly. As other studies on cottontop tamarins have found (McGrew 1988; Tardif et al. 1990; Price 1992), mothers appear to be maintaining a minimal level of carrying all the time (an average of 15%), although mothers do carry 50% of the time in the first 2 weeks (Ziegler et al. 1990). Their frequency of carrying did not change across conditions. In Less Experienced families, fathers carried much more often. However, in Experienced families, nonparental helpers carried as well. As a result, infants from all families were carried an average of 73.5% of the time over their first 8 weeks. These results contrast with

Ziegler et al. (1990), who found that the number of helpers present in a family influenced the role of carrying for mothers, rather than fathers. However, our results parallel those from the other studies of cottontop tamarins and with Achenbach & Snowdon (2002), who found weight loss in fathers caring for newborns was most severe in groups with no helpers.

Results from food tests also support this notion of division of labour. The presence of helpers directly affected the role fathers had in transferring food with infants. While helpers greatly influenced the role fathers played, mothers in both conditions maintained a limited role in food transfers. Mothers showed no significant change in the amount of food infants received from them, regardless of experience. Fathers were primarily responsible for these caregiving duties unless helpers were present.

When we compared only the parents' care of infants between levels of experience, we found several significant differences in caretaking behaviours such as successful retrieve and rejection rates. However, when we combined the contributions of all group members, these differences disappeared. Helpers contributed to care and this resulted in greater flexibility for parental roles. In later weeks this might be partially attributed to the growing role of the infant in determining its own care, but in early weeks when infants are virtually helpless, this is clearly the communal response of the caretakers themselves.

We found that for a variety of behaviours the number of helpers had significant effects. We analysed the relationship between the number of helpers and rates of behaviour in three ways: as a linear regression, a threshold comparison (0–1 versus 2+ helpers), and on a categorical basis (0–1 versus 2–3 versus 4–5 helpers). We found that there was a positive linear correlation between number of helpers and successful retrievals and also attempted retrievals, but that rejections and transfers as a result of rejection were not affected by the number of helpers in a group. There appeared to be a threshold effect for attempted retrievals indicating that this result is most likely due to the interaction between experience and group size. We suspect that these significant retrieval results were a product of the fact that infants in these groups were also climbing off carriers more, forcing helpers to attempt retrievals more.

Infant development also varied with experience of their parents. All infants demonstrated normal maturation by increasingly displaying behaviours like climbing off a carrier more frequently as they aged. However, the infants in Less Experienced families climbed off carriers more in Month 1 while infants from Experienced families climbed off more in Month 2. At a later age when all infants were developing independence, the infants who had climbed off later, climbed off most. Similar results were evident in food tests. Infants who went to the bowl earlier for food independently did not consume as much total food across tests. This indicates to us that while Less Experienced infants may be developing independence earlier, they are not necessarily benefiting from this independence. This result is consistent with Fairbanks' (1996) findings in vervet monkeys that those infants

treated to a harsher, more independent parenting style were not as secure in potentially stressful circumstances. In our study, infants who were permitted or even forced off earlier and those that obtained food independently earlier were not as confident, as evidenced by decreased total amounts of adventuresome behaviours (e.g. total food obtained independently overall, going to the floor and crossing cage divisions early), later on.

The main effects in development were only evident for infants born in the first litter of this study. First-born infants in Less Experienced families behaved differently from those born later in Less Experienced families or those born to Experienced parents. The first-born infants in this study performed some behaviours sooner, but they also engaged in them less frequently overall. Since we found no significant variation in overall quality of care provided for this study's first-born versus later-born infants, we could only attribute these behavioural differences to the lack of siblings. Infants of families with no older siblings appeared less mature than those in larger social groups either because they did not experience care from many family members, or because once they were interactive they had no siblings with which to develop socially. Most first-born infants from Less Experienced families were raised as singletons, whereas infants from Experienced families were more often raised with a twin. The absence of older siblings and/or a twin may have influenced the behavioural development of infants. Yamamoto (1993) noted that singleton common marmoset infants are dependent for longer than twins, and Cleveland & Snowdon (1984) found that singletons play less and spend more time in contact with older siblings. Siblings may have an important function in promoting independence in singletons.

Singletons weighed more than twins at an early age, but we found no differences in weights for infants from Experienced or Less Experienced families. Although singletons weighed more at 12 and 20 weeks of age, growth rates did not differ and analysis for weight differences at 20 weeks of age showed that the difference in weight disappeared. Thus, as Johnson et al. (1996) found, there appears to be a simple 'delay' in maturation in the weights. We suspect that early differences in behavioural development are also 'delays' rather than deficiencies, and that these early differences in behaviour dissipate as infants mature. While weight gain and growth rates are one aspect of physical development, measurement of body dimensions and development of genitalia are additional data that would be useful for characterizing physical development. Because of our noninvasive protocols, body measurements and genital dimensions for infants could not be collected. Preliminary data from later months indicate that genital development might be correlated with weight gain in females, but for males, gonad development is linked to pubertal development (also see Ginther et al. 2002).

We could not separate the influence of number of helpers and the experience of a family, except to say that we did not see categorical effects for the number of helpers in a group. This indicates that there appeared to be a threshold effect that correlated with the experience

of the family. From their first litter to their second, parents can move from having no helpers to two, a significant aid in rearing new infants especially for Less Experienced families where even very young helpers may carry newborns. We observed very low levels of rejection or abuse in this study. When severe rejection occurred, it quickly resulted in the death of offspring, thus preventing us from obtaining behavioural data. Experience with siblings while in a family has dramatic results on infant mortality when tamarins become parents. Johnson et al. (1991) reported a negative correlation between low infant survival and level of exposure to infants while parents were in their natal group. Tardif et al. (1984) found that experience while in natal groups was more important for female cottontop tamarins than for common marmosets. We keep members of our colony in their natal groups as long as possible both to aid parents and to let tamarins gain rearing experience of their own. Thus, we rarely have experienced parents with only a few helpers.

We are intrigued by the ability of individual families to produce a consistent level of care, despite a broad variation of experience and helpers. There is an obvious division of labour of infant care (previously noted by Price 1992 for cottontop tamarins and Rothe et al. 1993 for common marmosets) but care can be redistributed as siblings are born to a group and later disperse or are removed to relieve the family's growing numbers. One example of this is that nonreproductive helpers less than 12 months of age in the Less Experienced condition were involved in significantly more infant carrying than their Experienced-condition counterparts. There must be some monitoring and coordination of infant care that allows infant caregivers to respond flexibly to changes in family size.

We do not yet know whether quality of care in infancy has long-lasting developmental effects. The 31 infants from this study are being followed through puberty into adulthood. Hormonal and sexual development as well as relationships with parents, peer siblings and newborns are being monitored. Will early developmental environment influence later behaviour and physiology? Do these effects fade as these infants grow fully independent and enter puberty? Do these effects influence the manner in which they raise their own offspring? These are questions we hope to answer in the future.

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