



Allonursing in white-faced capuchins (*Cebus capucinus*) provides evidence for cooperative care of infants

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Abstract

Allonursing is a highly cooperative behaviour that may have important fitness consequences for the infant while the benefits to the allomother are less clear. To investigate the function of this behaviour, we compared patterns of allonursing and nursing exhibited by white-faced capuchin monkeys (*Cebus capucinus*). We used a linear mixed model approach to analyse data collected on 21 infants from six social groups in Sector Santa Rosa, Costa Rica. Infants nursed at higher rates and for longer durations from their mothers than from allonurses. They also allonursed at higher rates from lactating and non-lactating parous females than from nulliparous females and at higher rates from maternally related female allonurses than other females. We found no observed effect of adult female rank or infant sex. We conclude that infant white-faced capuchins engage in allonursing as a means to acquire additional milk, and that participating allonurses may benefit from increased inclusive fitness.

Keywords

allocare, infant handling, cooperative breeding, allolactation.

1. Introduction

For mammals, the most energetically expensive reproductive state is lactation, as compared to the states of gestation and cycling (Clutton-Brock et al., 1989; McCabe & Fedigan, 2007). Due to the high energetic demands of lactation, females may be conservative and restrict access of suckling infants who are not their own. Females who cannot or will not restrict access to non-offspring may experience a reduction in the amount or quality of milk

transferred to their own offspring, or may have to increase the amount of time they spend foraging in order to offset the costs of increased suckling, either of which may put the parent or infant at a higher mortality risk (Millar, 1978; Clutton-Brock et al., 1989). Despite these apparent costs, 'allonursing', or the act of nursing the offspring of another female, has been observed in 12 mammalian orders (Packer et al., 1992; König, 1997). The extent of allonursing varies between taxa and is largely based on the number of breeding females within the group, the size of the group, and the average size of a litter (Packer et al., 1992; König, 1997).

Allonursing behaviour in mammals has been explained by several hypotheses (Roulin, 2002). For species that are characterized by large litters but small groups (e.g., lions, meerkats), females may willingly participate in allonursing because there is a possibility of benefiting through kin selection or delayed reciprocity (Pusey & Packer, 1994; MacLeod et al., 2013). Within female philopatric species, individuals in small groups are more likely to be related and females may increase their inclusive fitness by allonursing related non-offspring, especially if it increases the likelihood of infant survival (Hamilton, 1964; Wilkinson, 1987). Reciprocity is also expected to be most advantageous in small groups where there is a greater chance for reciprocation (Boyd & Richerson, 1988). Females can reciprocate through like acts, by giving milk in turn, or they may reciprocate through unlike acts, such as supporting the allonurse in a future agonistic interaction (Muroyama, 1994; Pusey & Packer, 1994; Roulin, 2002). For plural breeding mammal species with a single offspring per litter (e.g., colonial breeders like seals or bats), females may misdirect their care towards another female's offspring because they are unable to identify their own infant among so many, enabling non-offspring to steal milk (Packer et al., 1992; Roulin, 2002). In contrast, animals with small groups and single offspring litters (e.g., primates) are unlikely to be victims of milk theft or misdirected care because females can identify their own young (Fragaszy & Mitchell, 1974; Maestripieri, 2001). Instead, allonursing in taxa such as non-human primates has been predominantly explained by reciprocation, kin selection and/or adoption (Pereira et al., 1987; Vasey, 2007).

Allonursing has been recorded in more than 25 primate species, including humans (Packer et al., 1992; Roulin, 2002; Hewlett & Winn, 2014), and rates vary from occasional observations to over 10% of total nursing bouts in some species (Packer et al., 1992). Capuchins engage in allonursing

quite frequently without restriction, and this has been described as a genus-typical phenomenon (Fragaszy et al., 2004). It has been recently proposed that the genus *Cebus* be divided into *Sapajus* (robust capuchin species) and *Cebus* (gracile capuchin species) (Alfaro et al., 2012; Boubli et al., 2012). Although we are aware of this on-going taxonomic discussion, for the sake of consistency with, and clarity of reference to the previously published literature, we will refer to capuchin species by the generic name used in the original publication. Allonursing accounts for 11% and 13% of total nursing bouts for *Cebus olivaceus* and *Cebus nigrinus*, respectively (O'Brien & Robinson, 1991; Baldovino & Di Bitetti, 2008). O'Brien (1988) describes parasitic allonursing events where juveniles and adults steal milk from adult females. Perry (1996) reports rates of 0.01–0.05 bouts/h for older infants (10+ months) of *Cebus capucinus*. It is described as 'common' in *Cebus apella* (Fragaszy et al., 2004). Two studies specifically investigate the function of allonursing in capuchins (*C. nigrinus*: O'Brien & Robinson, 1991; *C. olivaceus*: Baldovino & Di Bitetti, 2008) but these produced different conclusions regarding its primary function (e.g., soothing infants and reciprocity respectively). More work on allonursing patterns in capuchins is warranted to determine if there are any cross-specific trends.

Few studies have investigated the different allonursing hypotheses in plural breeding mammals characterized by a single offspring per litter. This study provides the first comprehensive analysis of nursing and allonursing in white-faced capuchins (*C. capucinus*) by examining three hypotheses from the allomother's perspective: alliance-enhancement, learning-to-mother, and kin selection, as well as two hypotheses from the infant's perspective: milk acquisition, and parasitic nursing. We hope to provide a new perspective on the conflicting conclusions drawn from previous studies of other capuchin species. We investigate three potential reasons why females engage in allonursing:

- (1) Alliance Enhancement: Allonursing may provide a means for females to strengthen previously established affiliative bonds with important social partners that are based on kinship or on the existing dominance hierarchy. Such alliances, enhanced by allonursing services, may lead to reciprocal agonistic support or exchange of other social services (Maestriperi, 1994; Perry, 2012). High-ranking females are often considered important social partners (Seyfarth, 1977; Perry, 1996) and allonursing is directed

up the hierarchy in other capuchin species (Baldovino & Di Bitetti, 2008), therefore we predict that:

- (a) Allonursing bouts involving adult females that are lower ranking than the infant's mother should be more frequent and of longer duration than bouts involving adult females that are higher ranking than the mother.
 - (b) Allonursing bouts should be more frequent and of longer duration for high-ranking infants (regardless of the allomother's rank), and these infants should receive less aggression from potential allonurses.
 - (c) Given that white-faced capuchins are female-philopatric and males disperse, females may regard female infants, but not male infants, as future alliance partners. If so, then allonursing should be preferentially directed towards female infants over male infants.
- (2) Learning-to-Mother: Female allonurses may be participating in allonursing in order to gain valuable 'motherhood' experience (Lancaster, 1971). If this hypothesis holds true, it would be expected that:
- (a) Allonursing bouts involving nulliparous females would be more frequent and of longer duration than bouts involving parous females.
- (3) Kin Selection: Female allonurses may increase their inclusive fitness by preferentially allonursing related infants (Hamilton, 1964). If allonursing patterns are driven by kin-selection, then it would be expected that:
- (a) Allonursing bouts involving kin would be more frequent and of longer duration than bouts involving non-kin.
- (4) Infants are active participants in allonursing interactions, and will typically approach potential females from whom they will then attempt to allonurse. Infants may stand to benefit from allonursing, and we examine this from the perspective of two hypotheses:
- (5) Milk Acquisition: White-faced capuchins are widely dispersed while foraging, and infants may become separated from their mothers. Thus, infants may occasionally seek out allonurses to obtain milk if their mothers are not readily available (Perry, 1996; Roulin, 2002). If infants are seeking allonurses primarily for milk it is expected that:

- (a) Allonursing bouts involving lactating females would be more frequent and of longer duration than bouts involving non-lactating females.
 - (b) Mothers would not be in the vicinity of the infant when allonursing takes place.
 - (c) Infants would allonurse more frequently and for longer durations when they are older and close to being weaned and no longer nurse regularly from their mothers.
- (6) Parasitic Nursing: If infants are engaging in parasitic allonursing by stealing milk then there should be little benefit for females who do participate (Packer et al., 1992). In this case, it would be expected that:
- (a) Infants should initiate most bouts of allonursing and allonurses should attempt to move away from infants who try to suckle, or they should end bouts prematurely (e.g., by hitting or biting the infant).

2. Methods

2.1. Study site and species

We conducted this study from May through August of 2012, and January through May of 2013 in Sector Santa Rosa in the Área de Conservación Guanacaste (ACG), Costa Rica. The research was conducted with permission of the Costa Rican agency MINAE and the ACG, and was approved by the University of Calgary's Life and Environmental Sciences Animal Care Committee (BIOI8R-03, Permit No. AC11-0082). Santa Rosa is a seasonal tropical dry forest, which experiences an annual average of 1472 mm of rain (Fedigan & Jack, 2001). The dry season occurs from mid-Dec to mid-May, and the wet season from mid-May to mid-Dec.

White-faced capuchins live in multi-male, multi-female groups, consisting of natal adult females, their offspring, and immigrant males. Capuchin females are capable of giving birth year-round, but approx. 44% of infants are born in the three month period between May and July, and 80% of the births occur in the six month period between February and July (Carnegie et al., 2011). Study subjects comprised 7 male infants and 14 female infants aged 0 to 17 months from 5 study groups of habituated capuchins. Weaning age is variable and ranges from 9 to 23 months (Weaver, 1999; Fragaszy

et al., 2004). To ensure that infants were sampled throughout the weaning period, we observed infants up to 17 months. During the first field season (May–August 2012: Early wet season), we followed three groups: CP, LV, and GN. During the second field season (January–May 2013: Dry season), we followed five groups: CP-AD, CP-RM, LV, GN and EX. CP experienced a fission event during the autumn of 2012 that resulted in two distinct groups: CP-AD and CP-RM (Table A1). We identified individuals using age–sex class, body size, facial structure, scars, skin pigmentation, hair pattern and colour (Fedigan, 2003).

2.2. Data collection

We followed groups on a 3-day rotational basis and collected behavioural data for 10–12 h/day for 5–6 days/week. We collected behavioural data using a PSION Workabout hand-held computer and conducted 10-min continuous focal animal sampling of infants (Altmann, 1974). We followed eight focal infants during the first field season and thirteen focal infants during the second. Combined, we have 121 data collection days with 1075 contact hours and an average of 17.8 focal hours per infant (range: 3.8–40.5 h) (Table A2). We recorded all affiliative, aggressive, and proximity related behaviours (i.e., approaches and leaves to 5 m) and the identity of the participants. We recorded (allo)nursing bouts in two ways: within 10-min infant focal samples and ad libitum. In each instance, we recorded the identities of the infant and the interactant (mother or allonurse), and the duration of the bout to the second.

A successful nursing (allonursing) bout was defined as an event in which the infant placed its mouth on its mother's (allonurse's) nipple and suckled for more than 10 s. The duration of the suckling bout was recorded from onset until the infant removed its mouth from the nipple (Baldovino & Di Bitetti, 2008). Suckling behaviour is also accompanied by stimulation of the other nipple using a hand, and switching rapidly between nipples after stimulation. We only analysed bouts that were recorded from start to finish. Due to visual constraints, it was not always possible to establish whether or not milk transfer occurred. Only bouts where infants could be clearly seen suckling on a nipple were used in the analysis. The 10-s rule was applied because milk transfer may not begin immediately. There is typically a latency period between nipple stimulation and milk let-down (Bisset, 1974; Cameron, 1998). Attempted bouts occurred when infants failed to establish

contact with the nipple or suckled for less than 10 s. A rejection occurred if the female attempted to move away or bite/hit the infant. Male allonurses were excluded from the analyses as they were infrequent participants ($N = 32$ across all age classes for males) and all bouts with males were less than 10 s long.

2.3. Genetic analysis and determining maternal and paternal relatedness

In order to determine maternal and paternal relatedness, faecal samples were collected from all individuals in each study group including independent infants. Samples were collected using sterile techniques and then stored in a freezer (-20°C) for several months before being shipped to the laboratory for analysis. We used these samples to extract and genotype DNA at 20 short tandem repeat loci: Apm01, Ceb01, Ceb02, Ceb03, Ceb04, Ceb07, Ceb08, Ceb09, Ceb10, Ceb11, Ceb105, Ceb115, Ceb119, Ceb120, Ceb127, Ceb128, Ceb130, d3s1210, d7s794 and pepl4 (Jack & Fedigan, 2006; Muniz & Vigilant, 2008; Cortés-Ortiz et al., 2010). The protocols for the laboratory analyses are described in Wikberg et al. (2014).

For all infants and most of the females, maternal kinship was known from long-term census data on births. In cases where maternal kinship was unknown, we used maternity assignments in CERVUS at a 95% confidence level (Marshall et al., 1998; Kalinowski et al., 2007). Using these data, allomothers were classified into two possible relatedness categories based on maternal relatedness: kin ($r \geq 0.25$) and non-kin ($r < 0.25$). We choose this threshold because dyads with a lower degree of theoretical relatedness than $r = 0.25$ no longer show kin-bias in several species of primates, including white-faced capuchins (Kapsalis & Berman, 1996; Chapais, 2001; Kapsalis, 2004; Perry et al., 2008). Paternal relatedness was not taken into account when analyzing the effects of maternal relatedness. Sires were also assigned at a 95% confidence level in CERVUS. If we were unable to determine kinship via demographic records and parentage assignments, we calculated estimated relatedness values to infer whether dyads were more likely to be kin or non-kin (Wikberg et al., 2014). We then constructed pedigrees using both paternal and maternal kinship information (i.e., combined kinship), and classified allomothers into two possible relatedness categories: kin ($r \geq 0.25$) and non-kin ($r < 0.25$). Due to the fact that alpha males father the majority of the group's infants during their short ($\bar{x} = 4$ years) tenure periods (Jack & Fedigan, 2006; Wikberg, unpubl.), infants rarely reside with

adult female paternal kin and paternally related allonurses would be skewed toward nulliparous females. Given the instability of alpha male tenureship prior to and during this study, the likelihood of an adult female being paternally related to a focal infant is reduced even further. To control for parity effects, only adult females were included in the analyses of 'combined' paternal and maternal kinship effects. A few dyads were excluded from the combined analysis because we did not obtain DNA samples from all the focal infants.

2.4. Determining rank

Female capuchins are described as having nepotistic dominance relationships, with a strong, stable linear dominance hierarchy (Bergstrom & Fedigan, 2010). We determined the rank order in each group based on the direction of agonistic dominance interactions. We only included the interactions between mature adult females (>5 years; Carnegie et al., 2006) because younger females have not yet acquired a stable position in the dominance hierarchy (Bergstrom & Fedigan, 2010). We analysed the rank data using Noldus MatMan 1.0. Statistical significance could not be determined for EX, LV, CP-AD and CP-RM owing to a small female sample size (≥ 6 females is needed to test for statistical significance: Appleby, 1983; Bergstrom & Fedigan, 2010). For this reason, females in both seasons were placed into rank categories of high, medium, and low (Table A3). These rank categories are usually apparent during observations in the field, while a female's exact dominance rank is not always discernible.

2.5. Terminology

All female allonurses were classified into one of two parity categories: Nulliparous (immature females and adult females who had not given birth) or Parous (adult females who had given birth at least once). We classified allonurses into two lactational categories: Lactating (females with a nursing infant, or those who recently lost an infant) and Non-lactating (immature females or adult females without an infant). Infants were considered weaned if the rate of nursing consistently dropped below one bout per hour (Weaver, 1999). In analyses involving allonurses, the infant's relative rank was categorized as higher if the infant outranked the allonurse, or lower if the infant was outranked by the allonurse. Infant's ranks (high, medium, low) were based

on their mother's rank for analyses of interactions between infants and allonurses. Thus the infant of a high-rank mother was also given the rank of 'high', and so forth.

2.6. *Analysis of data*

Linear Mixed Models (LMM, Genlinmixed in SPSS v. 21.0) with a normal distribution and an identity link function were used in each analysis. In each case, infant and allonurse identities were incorporated as random factors by nesting the infant and allonurse identities within group identities. Random factors allowed us to take into account repeated measures on individuals (e.g., infants and allonurses/mothers).

Two dependent variables were analysed, the duration (allo)nursing bouts and the rate of (allo)nursing bouts for each infant–allonurse (infant–mother) dyad. For analyses involving the duration of bouts, we included both ad libitum and focal data. The rate of allonursing bouts included only focal data, and excluded infants BM and PE, who were not observed allonursing during focal sampling. There is no evident pattern between these two infants whose defining characteristics differ in age, rank, group, and female mothering experience. Both infants were observed allonursing ad libitum. Rates of (allo)nursing were calculated as: (number of bouts/number of focal hours) per infant–allonurse dyad. For the analysis of rates only, we included dyads into the model that were not observed to interact, and they were given a rate of zero.

The number of potential allomothers available to each infant changed as the season progressed, and these changes were not consistent across groups or categories. In order to account for the number of available females, we calculated proportions of lactating, parous, higher-ranking, and related females available to each infant. For example, the proportion of lactating females available was calculated as follows: (number of lactating females/the total number of females in the group). Females of all age–sex classes, except for infants and the mother of the infant being sampled, were included when calculating the availability proportions for all types of allomothers apart from the proportion of higher-ranking allomothers. Only adult females (>5 years) who had acquired a stable rank within the dominance hierarchy were included when calculating the proportions of higher-ranking females (Bergstrom & Fedigan, 2010). These proportions were included as a continuous covariate into both models (duration and rate) and as an interaction effect

with the fixed effect(s). Sequential Bonferroni analyses were conducted in order to compare the effect between different categorical variables.

We included the following fixed effects: infant age, infant sex, allo-mother’s parity, allomother’s lactational state, maternal kinship, combined kinship, and relative and absolute dominance rank. These fixed effects were analysed in separate LMM models because the way the rate of nursing/allonursing was calculated differed for each fixed effect. For example, an allonurse’s kinship status in relation to a focal infant remained unchanged through a field season, yet her lactation status went from non-lactating to lactating, such that the total number of hours she was available to the fo-cal infant differed for her kinship and lactation status. This resulted in two unique rates for this infant–allonurse dyad — their kinship rate and their lactation status rate.

3. Results

All focal infants and adult females, except for one adult female who went missing during the course of the study, were observed to participate in al-lonursing. A total of 1257 nursing and allonursing bouts were observed during focals and ad libitum (Table 1). Allonursing bouts comprised 12.4% (119/959) of focal nursing bouts. Of a possible 218 infant–allonurse dyads, only 75 (34.4%) were observed allonursing either within a focal or ad libitum sampling period.

Rates of nursing ($\bar{x} + SE = 2.1 + 1.0$ bouts/h, $N = 21$) were significantly higher than the rates of allonursing ($\bar{x} + SE = 0.3 + 1.0$ bouts/h, $N = 159$; $F_{1,178} = 114.774$, $p = 0.001$). Moreover, duration of nursing bouts ($\bar{x} + SE = 55.4 + 1.0$ s, $N = 1041$) was significantly longer than duration of allonursing bouts ($\bar{x} + SE = 21.9 + 0.7$ s, $N = 216$; $F_{1,1255} = 151.850$, $p = 0.001$).

Table 1.
Number of nursing and allonursing bouts per focal and ad libitum sam-
pling methods observed during both field seasons for all focal infants.

Collection method	Nursing	Allonursing	Total
Focal	840	119	959
Ad libitum	201	97	298
Total	1041	216	1257

3.1. Infant age

The rates of nursing decreased as infants aged ($F_{16,72} = 4.016$, $p = 0.001$). Rates were highest for infants aged zero ($N = 5$) and one month ($N = 5$) and lowest for infants aged 16 months ($N = 2$; Figure 1). In contrast, the duration of nursing bouts did not differ significantly as the infant aged ($F_{16,1024} = 1.513$, $p = 0.088$; Figures 1 and 2). We rarely observed an older infant, aged 9 to 17 months, receiving hits or bites from its mother in an attempt to discourage a nursing bout. Rather, nursing seemed to terminate on its own accord, through mutual disassociation of the infant–mother pair. Rates of nursing were recorded for eight infants during the expected weaning period (9+ months). Only one of these eight infants (NP) showed a consistent decrease of one bout/hour during each month between the ages of 14 and 17 months. NP did not allonurse during this period either, indicating that she had likely been fully weaned by 14 months. Two infants, aged 9 to 12 months showed variability, with some months being below 1 bout/hour, and some well above. The remaining four infants, aged 9 to 14 months, did not show any decrease in nursing rates. The oldest focal infant recorded to nurse regularly from his mother was 23 months, and she was likely still lactating because milk-transfer was observed at 21 months.

We observed two instances of allonursing in infants as young as one month, who were unable to move independently of their mothers. Al-

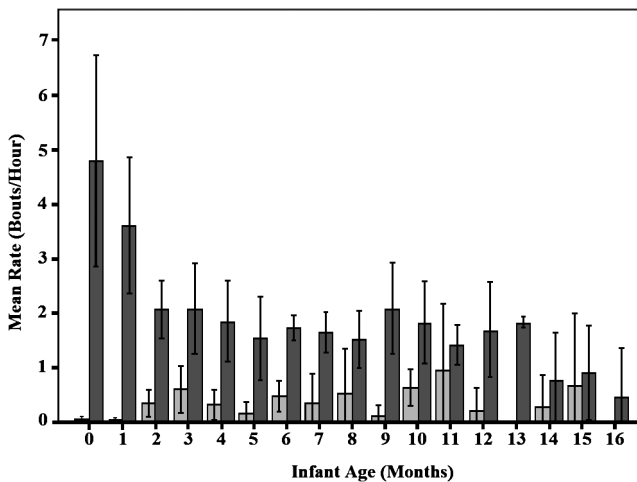


Figure 1. Mean rate (bouts/h \pm SE) of nursing (dark grey) and allonursing (light grey) bouts across infant age (months).

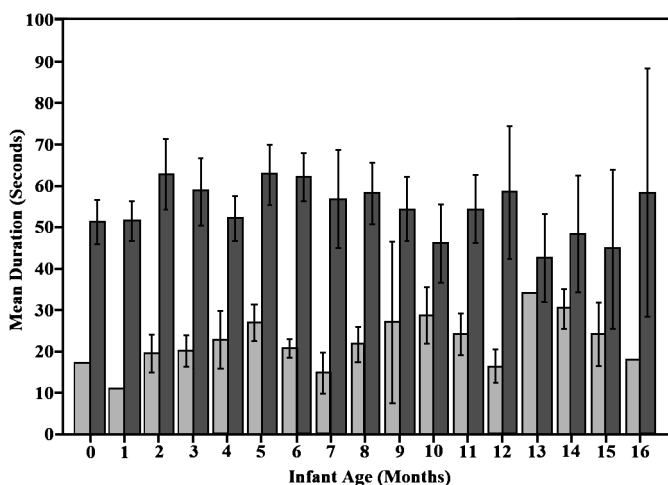


Figure 2. Mean duration ($s \pm SE$) of nursing (dark grey) and allonursing (light grey) bouts across infant age (months).

lonursing became more frequent when the infant gained independence (3+ months), and continued to be a common occurrence until they were weaned. Infant age was not related to the rates of allonursing ($F_{17,72} = 1.386$, $p = 0.169$), nor was it related to the duration of allonursing bouts ($F_{16,199} = 1.492$, $p = 0.105$; Figures 1 and 2).

3.2. Infant sex

There was no statistically significant difference among male and female infants for nursing rates (Female infants (FI): $\bar{x} + SE = 2.0 + 0.2$ bouts/h, $N = 15$; Male infants (MI): $\bar{x} + SE = 2.5 + 0.5$ bouts/h, $N = 6$; $F_{1,19} = 1.148$, $p = 0.297$), or in the duration of nursing bouts (FI: $\bar{x} + SE = 53.2 + 1.1$ s, $N = 710$; MI: $\bar{x} + SE = 60.5 + 2.1$ s, $N = 331$; $F_{1,1039} = 2.617$, $p = 0.106$). Allonursing bouts followed the same pattern, and there was no difference in rates (FI: $\bar{x} + SE = 0.04 + 0.01$ bouts/h, $N = 150$; MI: $\bar{x} + SE = 0.03 + 0.1$ bouts/h, $N = 61$; $F_{1,209} = 1.139$, $p = 0.287$), or duration of bouts (FI: $\bar{x} + SE = 22.3 + 0.9$ s, $N = 162$; MI: $\bar{x} + SE = 20.0 + 1.3$ s, $N = 54$; $F_{1,214} = 0.828$, $p = 0.364$) among male and female infants.

3.3. Proximity and aggression

Typically, infants initiated the allonursing bout by approaching and then attempting to suckle from a prospective allonurse. In 65.5% (78/119) of allonursing focal cases, infants approached the allonurse to contact. Mothers

were usually more than 5 m away from their infant when the infant approached another female to allonurse (77.3% cases (92/119)). We observed allonurses rejecting (e.g., moving away, hit or bite infant) an infant's allonurse attempt 8 times. These occurred prior to, or during an allonursing bout. Of these 8 rejections, 5 were from lower-ranking females and 3 were from higher-ranking females; 2 were from unrelated females and 6 were from related females; and 4 females were non-lactating and 4 females were lactating. Only high-ranking infants received a hit or bite, medium and low-ranking infants were not observed receiving hits or bites from an allonurse. Of the 119 allonursing bouts recorded during a focal follow only 8 occurred immediately after a stressful event (e.g., intergroup aggression or intragroup aggression) to which the infant was in proximity (i.e. within 10 m of the event).

3.4. Rank

In 24% (52/216) of allonursing focal and ad libitum cases, we observed infants to allonurse from females that were higher-ranking than their own mothers. The dominance rank of the infant in relation to the allonurse was not associated to the duration of allonursing bouts (Higher: $\bar{x} + SE = 20.6 + 1.4$ s, $N = 53$; Lower: $\bar{x} + SE = 23.0 + 0.9$ s, $N = 134$; $F_{1,185} = 1.353$, $p = 0.246$), nor was it related to the rate of allonursing bouts (Higher: $\bar{x} + SE = 0.05 + 0.02$ bouts/h, $N = 82$; Lower: $\bar{x} + SE = 0.06 + 0.01$ bouts/h, $N = 105$; $F_{1,185} = 1.353$, $p = 0.246$). The absolute rank of the infant was not related to the duration of allonursing bouts (High: $\bar{x} + SE = 22.1 + 0.2$ s, $N = 90$; Med: $\bar{x} + SE = 20.9 + 0.1$ s, $N = 84$; Low: $\bar{x} + SE = 21.3 + 0.1$ s, $N = 41$; $F_{2,212} = 1.109$, $p = 0.332$), nor was it related to the rates of allonursing bouts (High: $\bar{x} + SE = 0.4 + 0.1$ bouts/h, $N = 45$; Med: $\bar{x} + SE = 0.23 + 0.1$ bouts/h, $N = 21$; Low: $\bar{x} + SE = 0.3 + 0.1$ bouts/h, $N = 24$; $F_{2,87} = 0.494$, $p = 0.612$). Finally, mother's rank was not related to the duration of nursing bouts (High: $\bar{x} + SE = 55.8 + 1.3$ s, $N = 610$; Med: $\bar{x} + SE = 50.1 + 2.2$ s, $N = 168$; Low: $\bar{x} + SE = 57.3 + 2.3$ s, $N = 263$; $F_{2,1038} = 0.489$, $p = 0.613$), nor the rate of nursing bouts (High: $\bar{x} + SE = 2.3 + 0.2$ bouts/h, $N = 45$; Med: $\bar{x} + SE = 1.8 + 0.3$ bouts/h, $N = 25$; Low: $\bar{x} + SE = 2.4 + 0.4$ bouts/h, $N = 20$; $F_{2,87} = 0.494$, $p = 0.612$).

3.5. Parity and lactation

Infants allonursed from parous females in 93.1% (201/216) of allonursing focal and ad libitum cases, and they allonursed from lactating females in

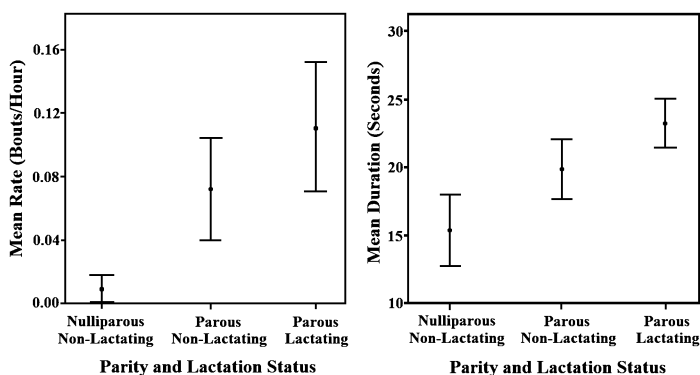


Figure 3. Mean rate (bouts/h \pm SE) and the mean duration (s \pm SE) of allonursing behaviour for nulliparous non-lactating, parous non-lactating and parous lactating females.

70% (152/216) of the cases we observed. These preferences were statistically significant; infants allonursed at higher rates from parous lactating females ($N = 58$), and parous non-lactating females ($N = 51$), than from nulliparous, non-lactating females ($N = 93$; $F_{2,199} = 3.018$, $p = 0.05$; Figure 3). Furthermore, allonursing bouts were significantly longer from parous lactating females ($N = 153$), and parous non-lactating females ($N = 48$), than from nulliparous, non-lactating females ($N = 15$; $F_{2,213} = 4.789$, $p = 0.005$; Figure 3).

3.6. Kinship

We observed infants allonurse from maternal kin in 50.5% (109/216) of allonursing focal and ad libitum cases. We found that maternal kin allonursed at higher rates compared to non-kin (Kin: $\bar{x} + \text{SE} = 0.08 + 0.01$ bouts/h, $N = 56$; Non-kin: $\bar{x} + \text{SE} = 0.02 + 0.01$ bouts/h, $N = 178$; $F_{1,232} = 7.780$, $p = 0.006$, Figure 4). However, the maternal kinship of the infant–allonurse pair was not related to the duration of allonursing bouts (Kin: $\bar{x} + \text{SE} = 21.1 + 0.9$ s, $N = 108$; Non-kin: $\bar{x} + \text{SE} = 22.8 + 1.1$ s, $N = 108$; $F_{1,214} = 0.164$, $p = 0.686$, Figure 4). When we took into account both maternal and paternal kinship, we found that kinship was not related to the rate (Kin: $\bar{x} + \text{SE} = 0.06 + 0.02$ bouts/h, $N = 32$; Non-kin: $\bar{x} + \text{SE} = 0.05 + 0.01$ bouts/h, $N = 73$; $F_{1,103} = 0.605$, $p = 0.439$), or duration (Kin: $\bar{x} + \text{SE} = 22.3 + 1.2$ s, $N = 74$; Non-kin: $\bar{x} + \text{SE} = 22.3 + 1.0$ s, $N = 104$; $F_{1,176} = 0.575$, $p = 0.449$) of allonursing bouts.

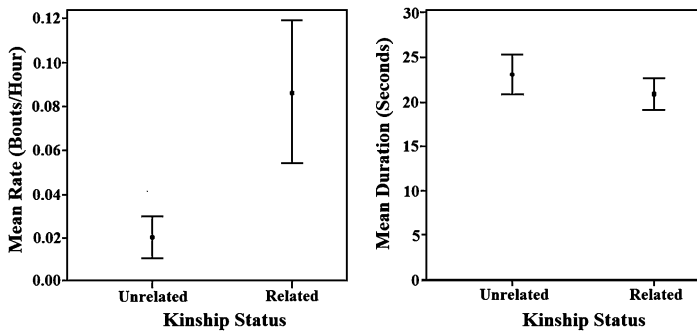


Figure 4. Mean rate (bouts/h \pm SE) and the mean duration (s \pm SE) of allonursing behaviour for maternally unrelated and related infant–allonurse dyads.

4. Discussion

Our study is one of the first to evaluate multiple hypotheses for occurrence of allonursing in a non-colonial breeding species characterized by a single offspring per litter and small groups. Such mammals are predicted to be less likely to engage in allonursing because females can identify their own young (Roulin, 2002). Furthermore, most primate species that are characterized by strict linear dominance hierarchies seldom engage in frequent or extensive allonursing (McKenna, 1979; Maestripieri, 1994; Paul & Kuester, 1996). Capuchins present a remarkable exception to this pattern. Our results indicate that allonursing is biased toward maternal kin, and it provides the infant with milk during the absence of its mother. Thus, allonursing may lead to inclusive fitness benefits to all three individuals involved. Given the ubiquitous and intense nature of allonursing in capuchins, we suggest that allonursing in these monkeys is more akin to that in communal or cooperative breeding mammals (e.g., meerkats, mongooses) in which animals willingly provide alloparenting services (MacLeod et al., 2013).

4.1. Alliance-enhancement hypothesis: effects of rank and infant sex

We found no evidence to support the three predictions of the alliance-enhancement hypothesis. We did not observe any effect of dominance rank on allonursing. Infants received similar amounts of allonursing regardless if their mother was higher or lower ranking than the allonurse. The mother's absolute rank (regardless of the allomother's rank) did not affect the amount of allonursing that her infant received. In another population of white-faced capuchins, dominant females allonursed at lower rates than did

subordinate females although infants were just as likely to allonurse from a higher-ranking female as a lower ranking female (Perry, 1996). In tufted capuchins, high-ranking infants were allonursed at higher rates compared to low-ranking infants (Baldovino & Di Bitetti, 2008). Conversely, no effect of rank could be discerned among wedge-capped capuchins (O'Brien & Robinson, 1991). Thus, this component of the alliance-enhancement hypothesis receives mixed support from different capuchin species.

We found no support for the second prediction, in that there was no difference in allonursing rates between high and low-ranking infants. If females are trying to form or maintain alliances with each other through allonursing, then one of two resulting patterns are expected: either low-ranking infants should be subjected to aggressive behaviours (e.g., bites, hits) while allonursing from high-ranking females, or high-ranking infants should not receive rejections or aggression from a low-ranking allonurse. We did not observe a low-ranking infant receive aggression or rejection, although we did see high-ranking infants receiving such.

Finally, male and female infants were allonursed at equivalent rates and for equivalent lengths of time. This suggests that the function of allonursing is not for females to establish preferential alliances with female infants. These findings are supported by the study on tufted capuchins; they also found no effect in regards to infant sex (Baldovino & Di Bitetti, 2008). Despite our lack of support for the alliance-enhancement hypothesis, it is nevertheless possible that females engage in allonursing to strengthen bonds with other adult females in the group, regardless of their dominance rank. To evaluate this possibility, future studies should investigate how female social relationships change over time in relation to their participation in allonursing.

4.2. Learning-to-mother hypothesis: effects of parity

A female's parity status is highly correlated to her lactation status, because all lactating females are parous. Perhaps because of this correlation we found that parous females allonursed infants at higher rates and for longer lengths of time, than did nulliparous females. These results contradict what is predicted by the learning-to-mother hypothesis (Lancaster, 1971). Similar conclusions were reached in other studies of capuchins, nulliparous females were either not observed to participate in allonursing (wedge-capped capuchins: O'Brien & Robinson, 1991), or infrequently (white-faced capuchins: Perry, 1996; Manson, 1999; tufted capuchins: Baldovino & Di

Bitetti, 2008). Similarly, mature fallow deer are more likely to engage in allonursing than immature deer (Birgersson et al., 1991). Few studies of mammals, including ours, conclude that the primary function of allonursing is for inexperienced females to improve maternal skills, although we cannot exclude the possibility that immature females may still benefit in this regard (Roulin, 2002).

4.3. *Kin selection hypothesis: effects of kinship*

We found some support for the kin selection hypothesis in that there were significant differences in the rate of allonursing between maternal kin and non-kin. This finding is contrary to other studies conducted on capuchins, in which maternal kinship did not affect allonursing (O'Brien & Robinson, 1991; Manson, 1999; Baldovino & Di Bitetti, 2008). These previous studies mostly used long-term census data and physical characteristics, rather than genetic data, to distinguish individuals and determine matrilineal relationships. It is unclear why allonursing is kin biased in our study population but not in other capuchin populations. It may be that the occurrence of kin-biased allonursing depends on the group size and the variation in kinship between group members, as is the case for female–female grooming relationships (Perry et al., 2008; Bergstrom & Fedigan, 2013). Related female meerkats and dwarf mongooses were more likely to engage in allonursing, suggesting that they may also gain indirect fitness benefits (Rood, 1980; MacLeod et al., 2013). However, these communal breeding species' nests or dens are composed of highly related females, while capuchin groups generally include both related and unrelated females. Lions, like capuchins, live in groups where females are not always closely related, but nevertheless show kin-biased allonursing (Pusey & Packer, 1994). Given our evidence that allonursing is biased to maternal kin, we propose that one important driver for female white-faced capuchin participation in allonursing is to increase their inclusive fitness.

We did not find a similar kinship effect on allonursing when combining maternal and paternal kin. Similarly, a previous study of white-faced capuchins found no evidence for paternal kin bias, while maternal kin did preferentially direct affiliative behaviours towards each other (Perry et al., 2008). It may be that capuchins cannot distinguish paternal kin as well as they distinguish maternal kin (Sargeant et al., in prep.). Female offspring form long-lasting relationships with their mother. Because maternal kin cluster around a common matriarch, they become more familiar with each other

than with other group members (Walters, 1987). This differential familiarity might be the basis for maternal kin recognition in primates (Chapais, 2001), while it is still unclear if and how primates recognize paternal kin (Rendall, 2004).

In order to fully test the kin selection hypothesis, we would need to examine inclusive fitness benefits of allonursing, which would entail examining long-term data on how allonursing affects infant survival. A component of kin selection theory is that the behaviour should favour the reproductive success of the recipient, be it directly to the infant or indirectly to the mother. If allonursing confers a survival advantage to infants, then females benefit by allowing related infants to suckle. For example, house mice exhibited increased milk production, their infants had higher weaning weights, and more offspring were weaned when females nest with kin than when they nest with non-kin (Sayler & Salmon, 1969; Konig, 1993). These studies provide evidence that allonursing in plural breeding species can confer advantages to participants. Four white-faced capuchin infants and one tufted capuchin infant have been reported to survive to the juvenile stage after being orphaned (Perry, 1996; Rose, 1998; Manson, 1999; Baldovino & Di Bitetti, 2008; Sargeant & Janzen, unpublished, 2014). These infants were independently mobile but unweaned, and still relied on milk for survival. Our study infant was four months old when his mother disappeared, engaged in frequent allonursing bouts from other lactating females, and survived past his first year. Although these cases are rare, they suggest that allonursing provides significant survival advantages to infants who are not yet capable of foraging independently.

Alternatively, reciprocity has been proposed to explain allonursing patterns observed in wedge-capped and white-faced capuchins (O'Brien & Robinson, 1991; Perry, 1996). This pattern can only be maintained if each female's infant has a high probability of being allonursed by another female, as Pusey & Packer (1994) pointed out for social carnivores. Determining the relative contributions of each female is difficult because at any given time, adult females differ in their reproductive states. An inherent restriction of the reciprocal model is that it is difficult to conceptualize when the 'return' of behaviour should occur. Moreover, a recipient can return with a like act or an unlike act. Because females can only return in kind when they are in the lactational state, only a long-term investigation of allonursing among lactating females can determine if certain individuals are contributing more or less

milk. Among mammals, females within a group do not engage in equivalent amounts of allonursing, thus reciprocity in kind does not appear to be part of the mammalian allonursing pattern (Roulin, 2002).

4.4. *Milk acquisition hypothesis: effects of infant age and lactation*

The patterns of nursing and allonursing among white-faced capuchins of Santa Rosa are comparable in certain respects to those previously reported from other capuchin species. Nursing bouts are more frequent and longer in duration than allonursing bouts, and allonursing mimics nursing, in that infants approach potential (allo)nurses, place their mouths on a nipple, and begin to suckle (O'Brien & Robinson, 1991; Manson, 1999; Baldovino & Di Bitetti, 2008).

We found that infant capuchins younger than eight weeks nurse at higher rates than do older infants, and this corresponds to a period of rapid development for infants (McCabe & Fedigan, 2007). If suckling rates are similar across ages (but see Carson & Wood-Gush, 1983; Higgins et al., 1988), infants have almost twice the milk intake during their first two months than at older ages. The onset of weaning was variable among focal infants, and only one infant was weaned by 14 months. The weaning pattern that we observed is similar to what has been described for other capuchin species in that it was relatively benign, variable in age and duration, and dependent on the personalities of both the mother and infant (Fragaszy et al., 2004; Baldovino & Di Bitetti, 2008). Our study supports previously reported trends for capuchins in that allonursing rates peaked at two to three months, which very likely corresponded to an increase in infant mobility rather than an increase in the mother or allonurse's willingness to participate (Pusey & Packer, 1994; Perry, 1996; Manson, 1999; Baldovino & Di Bitetti, 2008).

Infant's allonursed at higher rates from lactating females. However, infants occasionally allonursed from non-lactating females, and they may have done so to 'test' females to determine if they have begun lactating. Once infants located a lactating female, they allonursed from her for longer than from a non-lactating female. We observed a compelling case involving a female who gave birth, and immediately thereafter lost her infant. We observed 5 cases of allonursing prior to the birth, and 26 cases after the birth. Allonursing rates prior to the birth of her infant (non-lactating state) were significantly lower compared to after the birth (lactating state) ($F_{1,4} = 7.746$, $p = 0.05$). We conclude that she became particularly attractive to infants, after the birth

and subsequent loss of her infant, because she was lactating. Based on infants biasing allonursing to lactating females and this case study, we suggest that infants allonurse mainly to acquire milk.

Not all nursing bouts involve milk transfer, and thus may not be nutritive (Japanese macaques: Tanaka, 1992; rats: Kozlov, 2003; pigs: Torrey & Widowski, 2007). Nutritive suckling, defined as a consistent and rhythmic movement of the jaw, is very difficult to establish using visual cues in capuchins because the nipples are located near the armpit, and infants switch rapidly between nipples during a bout (Baldovino & Di Bitetti, 2008; MacDonald, 2011). Cameron (1998) reviewed trends in milk transfer among mammals, and found that the amount of milk transferred during a bout could be highly variable between and within species. This challenges the assumption that milk transfer is always positively correlated with suckling bout length (Festa-Bianchet, 1988) or suckling frequency (Fletcher, 1971). In general, milk composition and quantity delivered can vary between females within the same species and may be due to differences in the condition of the mother (Prentice & Prentice, 1995; Hinde, 2007), or in the mother's reproductive experience (Tardif et al., 2001; Hinde et al., 2009; Hinde & Milligan, 2011). Infant experience and condition may also play a factor in the quantity of milk received (Higgins et al., 1988; Clutton-Brock, 1991). For example, older infant horses and sea lions receive more milk despite suckling for similar amounts of time as compared to younger infants (Carson & Wood-Gush, 1983; Higgins et al., 1988). Owing to this variation, it is difficult to establish the quantity or quality of milk transferred between capuchin infants and their mothers or allonurses by only measuring the duration of suckling bouts. Thus, our suggestion that infants prefer to allonurse from lactating females because of an increase in milk acquisition needs to be confirmed in future studies using more a more accurate measure of milk acquisition.

In Santa Rosa, when infants were engaging in allonursing, mothers were often over five meters or more away from their infants. Thus, infants can access milk even if they cannot immediately locate their mothers. The combination of short term and possible long-term absence of the mother may be one reason why allonursing occurs, especially if allonursing aids in providing a consistent and plentiful milk supply (Perry, 1996; Solomon & French, 1997).

Contrasting findings between species and study sites may result from differences in ecological factors and group spread. For example, milk acquisition may be particularly important to Santa Rosa infants, because of the

extreme nature of the dry season, which may stress milk production in mothers. An interesting venue for further studies is therefore to investigate the seasonal pattern of allonursing behavior at Santa Rosa.

4.5. *Parasitic nursing and soothing hypotheses*

It has also been suggested that infants may be stealing milk from females (Roulin, 2002). When parasitic allonursing has been reported in other mammals, it is usually restricted to species where mothers cannot identify their young, or cannot prevent non-offspring from allonursing (Roulin, 2002). In the latter case, mothers typically display signs of distress and actively discourage or reject non-offspring. Rejection of allonursing attempts is very rarely observed in our study and we have no reason to suspect that mothers cannot identify their young. Overall, there is a lack of evidence for parasitic nursing, or misdirected care in our study. The contrasting parasitic allonursing pattern reported in wedge-capped capuchins is likely because they focused on juveniles and adults, not infants, who tried to steal milk from females (O'Brien, 1988).

Finally, it has been proposed that infants allonurse as a means to soothe themselves after a stressful situation, such as receiving aggression by their mother or another group member (Cameron, 1998; Baldovino & Di Bitetti, 2008; Lappan, 2009). While not mutually exclusive to other hypotheses such as the milk acquisition hypothesis (Baldovino & Di Bitetti, 2008), our study infants were very rarely observed allonursing immediately after a stressful situation. This indicates that soothing is not the primary function of allonursing in our study.

4.6. *Capuchins as cooperative or communal breeders?*

Cooperative breeding refers to a system where individuals other than the biological parents engage in intensive infant care as well as provisioning of non-offspring (Burkart et al., 2009). There is great variety in the form and expression of cooperative breeding behaviours across mammalian species (Solomon & French, 1997). The non-human primates most commonly categorized as facultative cooperative breeders are members of the Callitrichid family (e.g., tamarins and marmosets) (Burkart et al., 2009). A distinguishing behaviour among Callitrichids is the spontaneous provisioning of infants without a prior begging call (Burkart et al., 2009). This differs conceptually from milk provisioning because, while infant capuchins do not beg, neither

do females spontaneously offer their milk to non-offspring. However, the lack of spontaneity does not depreciate the high costs associated with allonursing in capuchins.

Indeed, van Schaik & Burkart (2010) argued that capuchins show elements of cooperative breeding. Traits of cooperative breeders that they list and which apply to capuchins include: extensive alloparental care; communal predator mobbing; sentinel duties (one individual in the group remains vigilant); and a larger brain to body ratio than found in similar-sized independent breeders (Fragaszy et al., 2004). Another trait of cooperative breeders is spontaneous help provided to others, which has been demonstrated in experimental studies of captive capuchins (de Waal et al., 2008). However, since spontaneous food sharing is the key trait often associated with the category of cooperative breeders, we also consider whether capuchins may be better considered as a type of communal breeder. Communal breeders exhibit a plural breeding system where multiple breeding females share the care of the infants born into that group (Clutton-Brock, 2006). As is found in capuchins, communal breeding females do not always breed, and non-breeding juveniles may assist the mother. Unlike capuchins, most other communally breeding species raise offspring within dens or in nests (e.g., rodents: Hayes, 2000; ruffed-lemurs: Vasey, 2007; meerkats: MacLeod et al., 2013). Although the motives of allomothers may vary (e.g., improving social bonds, developing mothering skills), their participation is nonetheless ubiquitous among group members (Clutton-Brock, 2006).

While many primate species might be considered to rear infants communally (e.g., within groups), several behaviours exhibited by capuchin species represent intense investment that is uncommon in other primate species. Such behaviours include carrying and retrieval of infants by non-mothers, and allonursing. Intense communal investment in infants may confer survival advantages that go beyond increased predator detection or counterstrategies to infanticide. If mothers spend long time periods away from their infants (e.g., the dispersed manner in which white-faced capuchins travel and forage), then intense allonursing may supply infants with constant and reliable source of milk (Perry, 1996; Solomon & French, 1997). Although the understanding of cooperative breeders in primates often restricts it to spontaneous food sharing species, capuchins can still be appropriately characterized as cooperative and prosocial communal breeders in which allomothers are likely to enhance infant survivorship (Perry, 2012).

4.7. Conclusions

Allonursing can serve many functions both within and between species (Roulin, 2002). Based on our current data set, the primary driving factor for female participation appears to be inclusive fitness benefits, and for infants is milk acquisition. While individuals may stand to benefit in other ways (e.g., nulliparous females may still gain mothering skills) these motivations do not appear to be driving factors behind allonursing in white-faced capuchins. Finally, allonursing in capuchins is so pervasive and frequent that it measures up to the intense alloparental investment found in communal breeding species.

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Appendix

Table A1.

Age–sex class composition of each group broken down by field season.

Season	Group	AF	AM	SAM	LIM	LIF	SIM	SIF	IM	IF	Total
1	LV	6	2	0	3	3	2	3	0	1	20
1	CP	10	3	3	6	7	1	3	1	1–2	35–36
1	GN	8	1	2	8	3	2	1	1	4	30
2	LV	4–5	3	0	0–3	2	0–2	2	0–2	1	12–20
2	AD	5	2	0–1	1	3	2	1	0	3	17–18
2	RM	5–6	1	1–3	5	3–4	0	0	2	1–2	18–23
2	GN	8	1	1	6	3	1	3	0–1	3	26–27
2	EX	3	1	0	4	1	1	0	1	2	13

A range is indicated where individuals died, emigrated, or aged into a new category. Thus individuals may be represented more than once. AF, adult female; AM, adult male; SAM, sub-adult male; LIM, large immature male; LIF, large immature female; SIM, small immature male; SIF, small immature female; IM, infant male; IF, infant female.

Table A2.

Focal infants and their characteristics, including group membership, group size (including infants), infant sex and age (months), number of nursing and allonursing events observed (combined focal and ad libitum) and focal hours.

Group	Group size	Infant ID	Infant sex	Infant age (months)	Number of nursing events	Number of allonursing events	Focal hours
CP	35–38	CG	M	10–14	34	8	15.3
CP	35–38	MR	F	7–11	44	18	19.8
CP, RM	35–38, 21	MA	F	0–2, 7–11	136	3	40.5
RM	21	DU	F	2–6	44	13	17.4
RM	21	AN	F	0–4	72	19	20.8
AD	17–18	SU	M	4–8	48	21	13.3

Table A2.
(Continued.)

Group	Group size	Infant ID	Infant sex	Infant age (months)	Number of nursing events	Number of allonursing events	Focal hours
AD	17–18	BM	F	3–7	23	1	11.7
AD	17–18	FC	F	3–7	46	24	15.9
AD	17–18	TD	M	3–7	43	19	13.8
LV	17–18	HU	F	9–10	5	1	3.8
LV	12–13	CT	F	3–7	59	18	18.1
GN	27	CC	F	11–16	14	9	12.0
GN	27	HI	F	10–13	22	13	10.8
GN	27	NP	F	4–8, 13–17	24	11	27.4
GN	27	OL	M	0–9	53	3	16.2
GN	27	HT	M	0–3, 8–12	69	8	29.8
GN	27–30	MY	F	0–6	28	11	18.1
GN	27–30	TE	M	0–2	81	1	15.3
EX	13	PE	M	5–9	52	2	18.9
EX	13	EA	F	0–4	75	10	19.4
EX	13	CD	F	0–4	69	3	17.7

Table A3.

Adult female rank categorization (high, medium, or low) by group for each field season.

Season	Group	High	Medium	Low	Total number of adult females
1, 2	GN	2	3	3	8
1	LV	2	2	2	6
1	CP	3	3	4	10
2	LV	2	2	1	5
2	RM	2	1	2	5
2	AD	3	0	2	5
2	EX	1	1	1	3
Total		15	12	15	42

Females were placed into rank categories based on the direction of agonistic dominance interactions.