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Parenting costs time: Changes in pair bond maintenance across pregnancy and infant rearing in a monogamous primate (*Plecturocebus cupreus*)

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Abstract

Relationships support social animals' health, but maintaining relationships is challenging. When transitioning to parenthood, new parents balance pair-bond maintenance with infant care. We studied pair-bond maintenance via affiliation in 22 adult titi monkey pairs (*Plecturocebus cupreus*) for 16 months centered around their first offspring's birth. Pair affiliation peaked during pregnancy, decreased across the postpartum period, and rose after reaching minimum affiliation 32.6 weeks postpartum. Pairs in which fathers carry infants more than average had lower affiliation at the infant's birth and return to an increase in affiliation sooner. Parents of infants who were slow to independence had higher rates of affiliation. Titi monkey infants actively prefer their fathers; mothers may avoid their infant-carrying mate, suggesting infants play an active role in parental affiliative decline. Our data supports previous findings that affiliation between partners declines following an infant's birth, but demonstrates new knowledge about the extent and duration of affiliative decline.

Introduction

Relationships are vital to the survival of social species. While social bonds form between a variety of dyadic types, adult romantic relationships—sometimes referred to as adult attachments—are some of the most potent and important bonds individuals can form (Fraley, 2019). In humans, the existence and quality of adult romantic relationships reliably

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predict health, happiness, and longevity (Loving & Slatcher, 2013). Individuals in long-term romantic relationships live longer (Lawrence et al., 2019), recover faster from illness or surgery (Kiecolt-Glaser, 2018), and are overall more satisfied with life (Roberson et al., 2018) than individuals who are not in romantic relationships. However, in order for a relationship to survive and thrive, a pair must engage in active pair-bond maintenance as they navigate the changes that inevitably occur across an individual's lifetime.

Just as an individual is reshaped by a myriad of life events, relationships also change over time, responding to both discrete events and continuous change. One of the earliest and most easily identified transitions is the shift from relationship formation to relationship maintenance (Clark et al., 2019). This considerable milestone attracts much attention in the current relationship science literature as specific neurobiological and behavioral changes mark this transition (Walum & Young, 2018). Both in the human and nonhuman animal literature, individuals reinforce relationships through maintenance behaviors like proximity, affiliation, shared tasks, and pair communication (*humans*: Stafford, 2016; Ogolsky & Bowers, 2013; *nonhuman animals*: Dolotovskaya, Walker, et al., 2020; Singletary & Tecot, 2020). Though the exact behaviors involved in pair-bond maintenance vary depending upon species, the types of behaviors are consistent across taxa. Further, these maintenance behaviors are particularly important not just for regular maintenance of the bond, but also when pairs experience stress or changes to their relationship. Employment of pair-bond maintenance behaviors help ensure the resilience of the bond when energetic and behavioral priorities need to shift, as is the case when a pair becomes parents.

In the transition to parenthood, romantic partners experience large scale changes in their social landscape, which alter their behavior within the relationship. Adding offspring to the existing attachment relationship between partners shifts the dyad into an attachment network, wherein the offspring now require energetic resources previously devoted to the partner. Because infants of many species cannot adequately meet their own thermoregulatory, nutritional, or psychological needs, early caregivers often act as external homeostatic regulators (Hofer, 1994). Parental responsiveness supports secure infant attachment and infants can solicit parental care through vocal and behavioral solicitations (Bell & Ainsworth, 1972). In order to provide this care, new parents experience dramatic changes to their neurobiology and behavior which support infant responsivity and care (for review: Rogers & Bales, 2019). Lactation and infant carrying are the two most costly forms of infant care among mammals (Altmann & Samuels, 1992) and new parents must re-allocate energetic resources toward infant care and energetic maximization or conservation. Sometimes, this shift in energetic resource allocation results in reductions to the frequency of pair-focused social behaviors (Altmann, 1980), though there is an increasing amount of evidence to suggest that social behaviors are conserved as long as possible (*titi monkeys*: Dolotovskaya & Heymann, 2020; *black howler monkeys*: Dias et al., 2011; *gelada baboons*: Dunbar & Dunbar, 1988). As a consequence of allocating less time to social behaviors-- including pair maintenance behaviors--romantic dyads may experience postpartum dips in relationship quality and satisfaction (*humans*: Belsky et al., 1985). Indeed, navigating the new balance required to meet the needs of the infant, the partner, and the self can cause considerable conflict between romantic partners (Adamsons, 2013; Cowan & Cowan, 1992). While these effects have been studied in the immediate postpartum period, most studies do

not evaluate their longevity or what milestones in infant development coincide with changes in the pair relationship.

The current study longitudinally examines the relationship between pair-bond maintenance and infant care as new parents balance the needs of their relationship with the needs of dependent offspring. This work demonstrates a unique perspective on attachment networks between parents and offspring as it focuses on how the presence of additional attachment network members (i.e., offspring) influence the relationship between existing members (i.e., the pair/parents). To investigate whether, and how, pair-focused behaviors change across the time when the dyad cares for their infant, we worked with coppery titi monkeys (*Plecturocebus cupreus*): small-bodied, socially monogamous neotropical primates that form socially monogamous pair bonds (Cubicciotti & Mason, 1976; Dolotovskaya, Roos, & Heymann, 2020; Fuentes, 1998; Kleiman, 1977; Mason, 1966) and provide biparental care to their offspring (Fragaszy, Schwarz, & Shimosaka, 1982; Mason, 1966; Mendoza & Mason, 1986). Pair relationships are maintained with affiliative behaviors (Fernandez-Duque et al., 2000), territorial mate guarding (Mendoza & Mason, 1986), and vocal duets (Lau, Clink, & Bales, 2020; Robinson, 1979). Pairs that have been together longer tend to engage in affiliative behavior more often (Hoffman, 1998; Rothwell, Carp, Savidge, Mendoza, & Bales, 2020). In addition to forming pair bonds, titi monkeys provide biparental care. Males serve as the infant's primary attachment figure and provide the bulk of non-nutritional parental care (Fragaszy et al., 1982). Females provide sustenance via lactation, carry the infant during nursing bouts, and have been observed to actively avoid and reject carrying the infant at other times (Mendoza & Mason, 1986; Reeder, 2001). Titi monkey infants actively solicit and transfer between parents, effectively shaping the frequency with which it is carried by each parent (Mendoza & Mason, 1986).

Thus far, no studies to date have examined the direct impacts of infant care on pair affiliation in a controlled manner. Here, we assess the impacts of the transition to parenthood on intra-pair affiliation. The current study tracks pair affiliation in the eight months prior to the birth of a pair's first infant and across the eight months following the birth to the first surviving offspring in an effort to uncover how and when affiliative social behaviors between pair mates change during this time. Overall, we expected pair affiliation to decline following the birth of the infant and recover as the infant becomes more and more independent. As titi monkey fathers are the primary caregivers of their infants, and mothers may avoid her partner when he is carrying the infant, we expected the proportion of time the father carries the infant to negatively predict the proportion of time the pair spends in affiliative contact. As affiliation may increase with pair tenure, we expected pair tenure to positively predict the rate of affiliation between pair mates. Finally, as infant care decreases with growing infant independence, we expected infant independence to positively predict pair affiliation.

Methods

Selection of Subjects and Housing

We identified 22 pairs of adult coppery titi monkeys (*Plecturocebus cupreus*; hereafter referred to as titi monkeys) for our study. We chose pairs for whom we had collected scan sample data when they gave birth to their first surviving infant. This criterion excluded any

pairs with a first parturition prior to 2008 or after 2019. The infants of all 22 pairs survived past eight months of age. Each focal family consisted of one adult male, one adult female, and their infant. Adult females in this study ranged from 2.17 to 12.81 years of age at the time of the infant's birth (M = 4.97, SE = 0.60). Adult males ranged from 2.41 to 10.96 years of age at the time of the infant's birth (M = 5.25, SE = 0.45). The duration of pair tenure, prior to the infant's birth ranged from 0.37 to 3.57 years (M = 0.97, SE = 0.16).

All coppery titi monkeys in this study were born and housed at the California National Primate Research Center (CNPRC). Titi monkeys were housed in pairs in enclosures measuring either 1.2m × 1.2m × 2.1m, 1.2m × 1.2m × 1.8m, or 1.6m × 1.2m × 0.7m. The environment was maintained at 21 degrees Celsius on a 12-hour light cycle with lights on from 06:00 to 18:00. Titi monkeys were fed monkey chow, carrots, bananas, apples, and rice cereal twice daily. Water was available *ad libitum* and additional edible foraging enrichment was provided twice daily. Subjects were housed in male-female pairs. Subject pairs were recruited eight months prior to the birth of their first infant. After the birth of their infant, the family (male, female, and infant) remained together in the same enclosure for at least eight months. This housing situation is the same as described in previous studies (Mendoza & Mason, 1986; Tardif et al., 2006). All procedures followed NIH guidelines for the ethical treatment of laboratory animals and were approved by the University of California Davis Institutional Animal Care and Use Committee.

Data Collection

The data collected for this study included pair affiliation and parental care behavioral observations for each focal family unit. Each observation type was recorded five days a week in two-hour intervals during daytime hours (6:30 to 16:30) for a total of 16 months centered around the birth of each pair's first surviving infant. These data have been collected since 2008 in our laboratory.

Pair affiliation was recorded for the full 16-month observation period described above. Every two hours, a trained observer recorded whether adult partners were within social proximity of each other, social contact, tail-twining, or none of the above (Table 1). These measures do not include interactions with offspring. For our analyses, social affiliation was measured as the proportion of time a pair spent in proximity, contact, or tail-twining—as opposed to none of these behaviors—out of all of the observations collected on that pair over a particular period of time.

Parental care was recorded for the eight-month period following the birth of the pair's first surviving offspring. Every two hours, a trained observer recorded whether infants were being carried by their father, their mother, or neither ("off") (Table 1). This measure does not include interactions between pair mates. For our analyses, parental care was measured as the proportion of time each parent spent carrying the infant out of all of the observations collected on that infant over a seven-day period of time. Parental care was separated into the proportion of time the father carried the infant, the proportion of time the mother carried the infant, and the proportion of time either parent carried the infant.

We conducted analyses on two sets of data. The first set of analyses examined social affiliation data over a 16-month period, which began eight months before the infant was born, and ended eight months after the infant was born for each pair. Because pair tenure ranged from 0.37 to 3.57 years, not all pairs had the full eight months of data preceding their infant's birth. This happened if the pairs became pregnant immediately after pairing. Of the 22 pairs in this study, 11 pairs had the full set of eight months pre-birth data, 5 pairs had seven of the eight months of pre-birth data, and 6 pairs had five of the eight months pre-birth data. The aim of this first set of analyses was to examine broad changes in social affiliation centered around the birth of the infant. We chose to condense these data into 4 four-month periods in order to examine pair behavior during several key stages: pre-pregnancy (8 to 5 months prior to infant birth), pregnancy (4 to 0 months prior to infant birth), infant dependence (0 to 4 months postpartum), and infant independence (4 to 8 months postpartum). We chose four-month periods for two reasons: 1) pregnancy in titi monkeys is approximately four months (Valeggia, Mendoza, Fernandez-Duque, Mason, & Lasley, 1999), and 2) infants tend to transition to greater behavioral independence after four months of age (Fragaszy et al., 1982). Therefore, our four periods capture the four months directly preceding pregnancy, the entire four months of pregnancy, the first four months of an infant's life when it is highly dependent on parents, and the next four months of an infant's life when it is more independent. The proportion of time pairs spent in affiliative contact was calculated by adding the number of scan samples when a pair was in affiliative contact (tail-twining, contact, proximity) over each four-month period, and dividing by the total number of scan samples recorded during that interval. This gave us 4 four-month period social affiliation scores, with possible values ranging from 0 to 1.

The second set of analyses examined the first eight months after the infant was born with the goal of investigating the effects of parental behavior on social affiliation between partners. We used the pair affiliation scan sample data described above to measure changes in pair affiliation over time in conjunction with the parental care scan sampling described above. While infants are typically observed being carried by one parent during nearly every observation throughout the first four months of their life, the timing of the transition to behavioral independence is variable and typically happens rapidly. We considered an infant "independent" when it was observed "off" for ten consecutive observations. For our sample, mean infant independence occurred at 150.75 (SE = 4.81) days post-birth, ranging from 116 to 193 days. Because this change can occur in a matter of days, we chose to group our data by week. Therefore, we calculated the proportion of time spent in affiliative contact by adding up all of the times a pair was in affiliative contact (tail-twining, contact, proximity) over seven days, and divided by the total number of scan samples recorded during that interval. This gave us a weekly social affiliation score, with possible values ranging from 0 to 1. We then calculated three infant-carry scores: father carry, mother carry, and parent carry. Father carry was calculated by dividing the number of times the father was observed carrying the infant over seven days by the number of total observations recorded for that infant during that interval. Similarly, we calculated mother carry by dividing the number of times the mother was observed carrying the infant by the number of total observations recorded for that seven-day interval. Parent carry was calculated by adding the times either the mother and father were observed carrying the infant over a seven-day period divided by

the total number of observations for that sampling period. These calculations gave us weekly scores of the proportion of time the infant was carried by the father, the mother, or either parent, with possible values ranging from 0 to 1. Data for this study are available via Open Access (http://doi.org/10.5281/zenodo.4480404).

Data Analyses

We first wanted to examine change in parent social affiliation over a 16-month period. In R Statistical Software (version 4.0.3, R Core Development Team, 2020), we performed a Shapiro Wilk test of normality (Royston, 1983), removed two extreme outliers, and used Levene's test using the car package (Fox & Weisberg, 2019) to test for homogeneity of variance (Schultz, 1985). Using the lme4 package (Bates, Mächler, Bolker, & Walker, 2015), we used a general linear mixed model (LMM) to determine whether period of time (fixed effect) predicted the proportion of time a pair spent in affiliative contact. We included pair ID as a random, repeated-measures effect. We performed a log likelihood ratio test to compare the fit of our model to that of a null model. To compare the mean values of affiliation between time points, we conducted a Tukey's Test post-hoc analysis, correcting for multiple comparisons, using the multcomp package (Hothorn, Bretz, & Westfall, 2008). Tests were two-tailed and the significance threshold was set at .05.

We next wanted to determine how parenting behaviors impacted the proportion of time parents spend in social affiliation with each other during the first eight months of an infant's life. Upon visual inspection of the data, it appeared affiliation followed a quadratic trend (Figure 1). To empirically test which trajectory best explained our data, different growth models that included no growth, linear growth, and quadratic growth were applied to the data using SAS 9.4 using PROC NLMIXED (SAS Institute, Cary, NC). These tests were run prior to including model covariates, but determined which growth model we would use to test for the effects of covariates. This model is subject-specific, allowing for a general growth model to characterize the population, but also allowing the coefficients of the growth model to be unique to the individual dyad. Based on a comparison of AIC values, the quadratic growth model best fit our data.

We then compared measures of fit such as log likelihood and the information criterion of Akaike (AIC; Akaike, 1974) to determine whether adding random effects for the intercept, trough value of affiliation (value at which the inflection point occurs in the quadratic trajectory when affiliation begins to increase again), and time to trough value of affiliation. Deviance tests indicated that a quadratic growth model that included a random effect for each of the growth coefficients provided the best relative fit.

We then built on our baseline model by adding time-varying and fixed coefficients. Our time-varying covariates were the proportion of time the father spent carrying the infant each week, proportion of time the mother spent carrying the infant, and the proportion of time either parent was observed carrying the infant during each seven-day interval. We used pair-centering and grand-mean-centering to determine the effect of each time-varying covariate within a pair, controlling for all other covariates, and between pairs, including the effects of the other predictors. The fixed covariates, which remain constant throughout the testing period, were the length of time a pair had been together at the time the infant

was born (pair tenure) and the age at which the infant became independent (defined as the point at which the infant has been observed "off" for ten consecutive observations). Fixed covariates were centered about their respective means. We chose to examine the effects of pair tenure on affiliation because a previous study showed that well-established pairs were more likely to be observed tail-twining during scan samples than newly-formed pairs (Rothwell et al, 2020). We chose to examine infant-specific predictors because the presence of an infant predicts a decrease in proportion of time pairs spend in affiliative contact during the first year that a pair is together (Witczak, Blozis, & Bales, *in prep*).

Given that a quadratic growth model provided the best relative fit to the social response scores, a version of the model with interpretable parameters was applied to test the effects of covariates (Cudeck & du Toit, 2002). Letting y_{ij} denote the social response for titi monkey pair i at week j, the quadratic growth model was parameterized as

$$y_{ij} = \beta_{yi} - \left(\beta_{yi} - \beta_{0i}\right)\left(\frac{week_{ij} - 1}{\beta_{xi}} - 1\right)^2 + \varepsilon_{ij} \tag{1}$$

where, for titi monkey pair i, β_{0i} represents the response at week 1, β_{yi} represents the trough response, and β_{xi} represents the week at which the trough response occurs. In the model, each of the coefficients is a sum of a fixed effect that relates to the population and a random effect that relates to titi monkey pair i. For example, $\beta_{0i} = \beta_0 + u_{0i}$, where β_0 denotes the expected response for the population at week 1 and u_{0i} is the random effect for titi monkey pair i. Positive values of u_{0i} for an animal pair would indicate that a titi monkey pair's response at week 1 is higher than the expected value of the population, and a negative value indicate that an animal pair's response at week 1 is lower than the expected value of the population. Finally, the residual of the model is denoted by ε_{ij}.

Under the quadratic growth model in Equation (1) the residual was assumed to be normally distributed with a mean of zero and variance σ^2_ε. The variance was assumed to be homogeneous across animal pairs. Specifically, the residual variance $\sigma^2_{\varepsilon i}$ was assumed to follow a lognormal model (c.f.: Hedeker et al., 2008):

$$\sigma^2_{\varepsilon i} = \exp(\tau_0) \tag{2}$$

where τ_0, when exponentiated, is the (geometric) residual variance for a titi monkey pair.

The three quadratic growth coefficients (β_{0i}, β_{yi}, and β_{xi}) were then predicted by the covariates, with each covariate centered about their respective sample mean. First, the effects of covariates were evaluated individually. In evaluating the effects of the length of time a pair had been together, for instance, each of the growth coefficients was regressed as follows:

$$\beta_{0i} = \beta_{00} + \beta_{01} PairTenure_i + u_{0i}$$

$$\beta_{yi} = \beta_{y0} + \beta_{y1} PairTenure_i + u_{yi}$$

$$\beta_{xi} = \beta_{x0} + \beta_{x1} PairTenure_i + u_{xi}$$

where β_{00}, β_{y0}, and β_{x0} represent the expected response at week 1, the trough response, and the week at which the trough response occurs, respectively, for titi monkey pairs whose pair tenure score was at the sample mean. The coefficients β_{01}, β_{y1}, and β_{x1} represent the expected unit change in each of the coefficients for a one-unit increase in *PairTenure_i*. The residuals of the three equations, u_{0i}, u_{yi}, and u_{xi}, denote the random effects conditional on *PairTenure_i*. In each of the models fit to the data, each of the three random growth coefficients could covary.

Next, the full set of covariates were included in a larger model to provide tests of the covariates with the effects being statistically adjusted for other model covariates. Effects that were not statistically significant at the .05 level when tested independently were not included in the larger model and a final, relatively parsimonious version of the model was used for interpretation. It is important to note that the significance of fixed and random effects was only interpreted in this one final model; therefore, post-hoc corrections were not needed for this final model.

Results

We first examined general changes in social affiliation between titi monkey pair mates over the eight months prior to infant birth and the eight months following infant birth. We collected an average of 1030.36 (SE = 71.66) scan samples per pair over this period of time (range = 117 – 1497). Analyses were based on a total of 22,668 observations. Initially, our data were not normally distributed (W = 0.93, p < .001); however, when we plotted our data, we identified two outliers (Figure 1). The same pair spent 80.9% and 79.0% of their observations in affiliative contact during the first period (8 to 5 months pre-birth of the infant) and second period (4 to 0 months pre-birth of the infant), respectively. When we removed those two outliers, our data were normally distributed across each period (Table 2; Figure 2). Levene's test also indicated equal variances (F (3, 82) = 0.82, p = .49). Because our data were normally distributed and did not violate assumptions of homogeneity of variance, we fit a general linear mixed-effects model to our data. The period of time had a significant effect on proportion of time in affiliative contact (X2(3) = 67.23, p < .0001). Tukey's test revealed significant differences between nearly all four-month periods of time (Table 3). Affiliation at pregnancy (4 to 0 months pre-birth of infant; M = 0.39, SE = 0.02) was higher than affiliation at pre-pregnancy (8 to 5 months pre-birth of infant; M = 0.32, SE = 0.02, p < .001), infant dependence (4 to 0 months pre-birth of infant; M = 0.31, SE = 0.02, p < .001) and infant independence (5 to 8 months post-birth of infant; M = 0.21, SE = 0.02, p < .001). Pair affiliation was also lower at infant independence than it was at pre-pregnancy (p < .001; Table 3) and T3 (p < .001).

We next wanted to determine why the proportion of time pairs spend in affiliative contact decreased after the birth of the infant. Data from the first eight months post-birth of the infant were used for analyses, and time was binned into seven-day periods to capture the effects of rapid changes in infant independence. We collected an average of 592.67 (SE = 54.73) observations per pair (range = 168–1429), and analyses were based on a total of 12,374 observations. A Shapiro-Wilk test revealed that data were normally distributed for 26 of the 35 seven-day periods (Table 4; Figure 3), so we decided not to remove any outliers or transform our variables. Levene's test also suggested our data did not violate assumptions of homogeneity of variance (F (34, 641) = 0.83, p = .74). Therefore, we were able to proceed with our nonlinear mixed-effects modeling.

Given the pattern of affiliation over the eight-month period post-infant birth (Figure 3), we first determined whether a no growth, linear growth, or quadratic growth model best fit our data. Deviance tests indicated a quadratic growth model provided best relative fit (Table 5). Additionally, as we fit our no growth, linear growth, and quadratic growth models, residual variance decreased from 0.36, to 0.11, to 0.07, respectively. Therefore, the quadratic model explained the most variance in the data. These findings suggest affiliation declines after the birth of an infant, but then hits an inflection point and begins to rise again after a period of time. We added random effects one by one to determine whether dyads were quantitatively different in their starting levels of affiliation, their trough levels of affiliation, and the time when they reached their trough level of affiliation. Based on a comparison of model fit, the model with all three random effects best fit our data (Table 6) and resulted in the lowest residual variance ($\sigma_{ei}^2 = 0.05$).

We then evaluated the effects of each covariate independently. Our covariates were the length of time a pair had been together (pair tenure), the time at which an infant was considered independent (independent), the proportion of time the father spent carrying the infant (father carry), the proportion of time the mother spent carrying the infant (mother carry), and the proportion of time either parent spent carrying the infant (parent carry). Covariates were entered at all three levels (intercept, trough, and time to trough). Covariates that were statistically significant were added to the final, full model (Table 7). Because including all three measures of father carry, mother carry, and parent carry in our final full model would violate assumptions of independence, we chose to examine residual variance to determine which parameter to include in our final model. Compared to models with the other carrying-related covariates, the model that included father carry as a covariate resulted in the lowest residual variance ($\sigma_{ei}^2 = 0.02$; Table 7). Upon examining the data, father carry also varied more at each time point (Figure 4) than mother carry (Figure 5) and parent carry (Figure 6). For these two reasons, we decided to include the father carry covariates (grand-mean centered and pair-centered) in our final model and did not include the mother carry or parent carry covariates.

Our final full model included the effects of father carry (grand-mean centered and pair-centered) on the intercept, the effects of infant age of independence and pair tenure on the trough value, and the effects of infant age of independence, pair tenure, and father carry (grand-mean centered and pair-centered) on the time to trough response (Table 8). The population mean proportion of time spent in affiliative contact when infants are born is

0.40 (SE = 0.21), the population mean affiliation score at the trough (or inflection point) is 0.17 (SE = 0.11), and the population mean time to trough is approximately 32.60 weeks (SE = 5.80 weeks). Between pairs, including the effects of the other covariates in the model, fathers who spend more time carrying their infant than the mean time fathers carry infants have lower initial levels of time spent in affiliative contact (β_{01a} = −2.21, SE = 0.86, p = .02). This effect size is medium (D = −0.55, Hedges, 1982). If an infant becomes independent at an age that is later than the mean time infants become independent, then the proportion of time parents spend in affiliative contact at the trough (or inflection point) is higher (β_{y1} = 3.94, SE = 1.59, p = .02, D = 0.53). These findings suggest that these pairs would not drop as low in affiliation as pairs whose infants become independent earlier. Pairs who have been together for longer than the mean pair tenure have a lower trough value than the mean population (β_{y2} = −0.38, SE = 0.12, p = .004, D = −0.69). The results of this model suggest these pairs who have been together longer would be expected to drop lower than 17.1% time in affiliative contact at their trough. Between pairs, including the effects of the other covariates in this model, fathers who spend more time carrying the infant than the mean time fathers carry infants hit their trough sooner (β_{x3a} = −3.46, SE = 1.49, p = .03, D = −0.50). While this effect is small, this suggests that pairs with fathers who spend a lot of time carrying infants will switch to an increase in affiliation sooner than pairs with fathers who generally don't carry infants as much when we account for the other covariates in the model. Interestingly, within a pair, when we control for the effects of the other covariates, pairs with fathers who spend more time carrying their infants reach that time to trough later (β_{x3b} = 1.09, SE = 0.51, p = .05, D = 0.46). These findings suggest that, excluding the effects of the other covariates, pairs with fathers who spend more time carrying their infant than the population mean take a longer time to hit that inflection point where affiliation begins to rise again.

All of our random effects were significant with the exception of the trough value, suggesting pairs may not differ significantly in that trough value of social affiliation (φ_y = 0.11, SE = 0.16, p = .49, D = 0.15). Pairs did significantly vary in their initial levels of affiliation (φ_0 = 1.27, SE = 0.26, p < .001, D = 0.98) and their time to trough affiliation value (φ_x = 0.84, SE = 0.17, p < .001, D = 1.09). Individual levels of affiliation and trough values are positively correlated ($\rho_{0,y}$ = 1.00, SE = 0.01, p < .001, D = 36.88), suggesting pairs who are more affiliative at the beginning of the sampling period have a higher trough value than those who are less affiliative initially. Initial levels of affiliation and the time to trough are also positively correlated ($\rho_{0,x}$ = 0.78, SE = 0.33, p = .03, D = 0.50), meaning if a pair starts off higher in affiliation, then it will reach that inflection point later and therefore take a longer time to begin the increase in affiliation. The trough value and the time to trough were also positively correlated ($\rho_{x,y}$ = 0.81, SE = 0.33, p = .02, D = 0.53), meaning those with a higher trough value also take longer to reach that trough point at which they would make the switch to increasing in affiliation.

Our final full model also had lower residual variance than the models without covariates and any of the models that only included one covariate (σ_{ei}^2 = 0.02). Deviance tests also indicated that this model fit better than our quadratic model that included all three random effects but did not include any covariates ($X^2(8)$ = 39.2, p < .001). AIC was also smaller for this full model (AIC = 2135.0) than it was for the quadratic model with three random effects

and zero additional covariates (AIC = 2194.3). Therefore, compared to all other models tested, this final full model best explained our data.

Discussion

Our exploration of intra-pair affiliation across the 16 months centered on the birth of a pair's first infant revealed important changes in pair affiliation associated with this major life history event. First, our analyses revealed temporal differences in pair affiliation across time. Affiliation between pair mates was highest in the second time period, during pregnancy 4 to 0 months prior to the birth of the infant. There are important potential biological reasons for this. It is possible that there is something unique about pregnancy, such as decreased mobility for the female that supports increased affiliation within pairs during this period. Within titi monkey pairs, females control proximity between pair mates—both in terms of approaching and withdrawing (Dolotovskaya, Walker, et al., 2020). With restricted mobility and lower energy during pregnancy, females may withdraw less often simply by virtue of being more sedentary, leading to higher calculations of affiliation using our sampling method. It is also possible that lower levels of affiliation at other time points drives the pattern of pair affiliation. The pregnancy period coincides with longer relationship tenure relative to pre-pregnancy, and titi monkey pairs may simply increase in affiliation across pair tenure. There is limited data on intra-pair affiliation across time, but Rothwell et al., (2020) found that well-established pairs were more likely to be observed tail-twining during scan samples than newly-formed pairs, suggesting that at least this measure of affiliation may increase with pair tenure. Titi monkey rates of affiliative behaviors (e.g., grooming, proximity) are low at the time of pairing and increase dramatically during the first week, at which point they become stable across the next month (Hoffman, 1998). Other studies have not examined average levels of affiliation between pair mates across time in this way and indeed it would be difficult to examine such behavior without including the influence of infant presence as titis with unrestricted reproduction tend to give birth within the first year of pairing (Valeggia et al., 1999).

We expected to see reductions in pair affiliation following birth (infant dependence and infant independence) as a consequence of energetic re-allocation toward infant rearing. Our findings align with previous research in titi monkeys which found reductions in social behavior and affiliation (Dolotovskaya & Heymann, 2020; Dolotovskaya, Walker, et al., 2020) and humans, which found reductions in relationship quality (Richter, Krämer, Tang, Montgomery-Downs, & Lemola, 2019) and relationship functioning (Doss, 2009) following the birth of an infant. While we expected lower rates of affiliation postpartum relative to prepartum, we did not expect lower rates of affiliation in the infant independence period compared to the infant dependence period. Our model estimated an average time to trough of 32.6 weeks (approximately 228 days), which demonstrates a longer amount of time of decreasing affiliation than we expected. We predicted that affiliation between parents would begin to increase close to the time when infants transition to behavioral independence, which was approximately 150 days for our sample. Given these results, it is unclear when and whether intra-pair affiliation fully rebounds after partners become parents, especially given that titi monkeys reproduce annually (Valeggia et al., 1999). Future research should expand

the postnatal window of interest to include the birth of a subsequent infant in order to better understand how affiliation changes across this interim.

In order to examine how pair affiliation changes in response to the demands of infant care, we used nonlinear mixed effects modeling, specifying a quadratic trajectory, and included the time-varying fixed effect of paternal carry as well as the time-invariant fixed effects of pair tenure and age of infant independence. Our model also included three random effects, allowing for estimates of initial levels of affiliation, trough values of affiliation (or the lowest value of affiliation before affiliation increases again), and time to trough values of affiliation to be independently estimated across pairs. The model identified several effects. As predicted, affiliation between pair mates decreased following the birth of an infant, but affiliation over the first week of pairing (intercept), length of the decline in affiliation (time to trough), and depth of the decline in affiliation (trough) were statistically significantly affected by our predictor variables (pair tenure, infant date of independence, and the time the father spent carrying the infant). During the first week following their infant's birth, new parents spent an average of 40.4% of their time in affiliative proximity or contact with their pair mate, but over the course of an average of 32.6 weeks, time spent in affiliative contact decreased to an average of 17.1%. There was significant variation between pairs in the time pairs spent in affiliative contact during the first week of pairing and this initial time spent in affiliative contact was related to both the time to, and value of, the trough. Pairs with a high rate of initial affiliation also had higher minimum rates of affiliation and arrived at their lowest rates later. In other words, pairs that spent more time in affiliative contact during the first week after their infant was born did not decrease their time spent in affiliative contact with their mate as much across the infant's development compared to pairs that started off spending less time in affiliative contact, but these pairs also took longer to eventually switch from a decline in affiliation to an eventual increase in affiliation. Pairs did not significantly differ in their minimum proportion of time spent in affiliative contact at the point of the trough, but there was significant variation in the time it took for pairs to reach their minimum rate of affiliation and transition from decreasing to increasing in affiliation. Interestingly, pairs with higher time spent in affiliation at the trough took longer to reach that value, meaning they had a longer, slower decline in affiliation over the study period.

Pairs in which the father carried the infant more often than the population mean spent less time in affiliative contact during the first postpartum week. Pairs in which the father provides a higher amount of care may shift their energetic resources away from pair-focused activities toward infant-focused activities early on. Dolotovskaya & Heymann (2020) found that female wild coppery titi monkeys prioritized eating over rest and some social activities (likely to support the metabolic price of lactation), while males prioritized resting over eating. Perhaps in pairs in which the father provides more paternal care, the female is free to engage in foraging and feeding activities early on and it is her reprioritization of her time budget that leads to decreased time spent in affiliative contact with her mate. Furthermore, female titi monkeys act as the primary initiator of social proximity and contact (Dolotovskaya, Walker, et al., 2020) and will avoid being in proximity to their mate if he is carrying the infant (Reeder, 2001). Given this information in conjunction with our data, females may avoid affiliating with their partner if he is carrying the infant in an effort to prioritize feeding and/or avoid proximity with the infant—an effect which would

be exacerbated by high levels of male infant carrying. In turn, titi monkey infants have a preferential attachment to their fathers and actively solicit moving from their mother to their father following the end of a nursing bout (Mendoza & Mason, 1986). This highlights to potential role of the infant's attachment to the father as a potential impetus for changes in affiliation and relationship maintenance between new parents.

A within-pairs comparison revealed that pairs in which the father carried the infant more often than the mean took a longer time to reach their lowest point in affiliation before shifting to an increase in affiliation. While this measure excludes the effects of our other covariates (i.e., pair tenure and infant age at independence), it does signal that paternal infant carrying takes a toll on the time a pair spends in affiliative contact. When examining between-pairs effects, we found the opposite effect: pairs in which the father carried the infant more often than the mean switch to an increase in affiliation sooner, signaling that these pairs may recover their rate of affiliation faster than pairs in which the father carries the infant less than the mean. As only the male and female are available to carry the infant, pairs in which the male carries the infant less often are also pairs in which the female carries the infant more often. Perhaps a high rate of maternal carrying in addition to supporting the infant through lactation results in the pair taking longer to increase their affiliation as the female further prioritizes eating to sustain this heavy energetic load.

Finally, infant independence and pair tenure affected the time spent in affiliative contact at the point of the trough value. Pairs whose infants became independent later than the population mean spent more time in affiliative contact at the nadir. While studies in several primate species support the theory put forth by Altmann (1980) that new mothers direct energy away from social activities in favor of eating, they also propose more nuance. Among black howler monkeys (Dias et al., 2011) and coppery titi monkeys (Dolotovskaya & Heymann, 2020), females maintain time allocated to social activities (e.g., grooming) for as long as possible, preferring to reduce resting time prior to reducing social time. Perhaps having an infant that is dependent on its parents for longer impacts the way in which the mother allocates her time budget such that more social activity is preserved. Another explanation may be that fathers promote infant independence in order to obtain greater social access to their partner. Thus, mothers who are more tolerant of being in proximity to their partner while he carries the infant may have infants who are carried longer because the father has less cause to hasten their independence. In reference to pair tenure, pairs that had been together longer than the mean had lower levels of affiliation at the trough. Perhaps pairs that have been together longer do not need to employ these behaviors, or are employing different behaviors, in order to maintain their pair bond.

Broadly, this work supports previous findings in both titi monkeys and humans and continues the narrative that the birth of offspring initiates a decline in relationship maintenance behaviors such as intra-pair affiliation. But the implication that relationship partners allocate their energy away from relationship maintenance to prioritize infant care may over-simplify this phenomenon. The impact of paternal care, length of relationship, and infant independence all play various roles in shaping the timing and degree of the decline in affiliation and though our research illustrates the pattern of change across time, the underlying mechanism behind such change remains theoretical.

Limitations

There were some limitations of the current work. First, our measure of pair mate behavior was conditional, meaning that both animals needed to participate in order for the behavior to be scored. Since the measure is not individual-specific, we cannot know which animal initiated or refused affiliative contact and steered these interactions. Second, some pairs in our sample did not have a complete dataset for the pre-pregnancy period because they became pregnant less than four months after being paired. Due to our small sample size, it is possible that the exclusion of these pairs from the pre-pregnancy period meant that the pairs that were included may have biased the estimated population time spent in affiliative contact at that time point.

Future directions

Overall, these analyses tell us that caring for an infant is costly—and one of the things it costs new parents is time spent together, specifically time spent maintaining their pair bond. This decline may be due to active avoidance by one parent when the partner is carrying the infant or simply a casualty of prioritizing other activities (e.g., eating). Given the length of time in which affiliation continues to decline, further study is needed to identify what factors co-occur with the nadir in affiliation and spur increases in affiliation rates. One mechanism that may contribute to the length of time in which affiliation declines is parental sleep. In humans (Bayer, Hiscock, Hampton, & Wake, 2007; Lee, Zaffke, & McEnany, 2000; Yamazaki, Lee, Kennedy, & Weiss, 2005) and nonhuman primates (Fite et al., 2003), parental sleep declines following the birth of an infant. Decreased sleep is associated with impaired affective processing, namely difficulty in perspective-taking (Shapiro, Gottman, & Carrère, 2000), perceiving events to have a negative bias (Tempesta et al., 2010), and an increased tendency to assign blame (Kahn-Greene, Lipizzi, Conrad, Kamimori, & Killgore, 2006). It is little wonder then, that new parents experience more negative communication and higher problem intensity as well as decreased conflict management (Doss, 2009). Postpartum decrease in sleep is typically more severe for mothers compared to fathers and can persist even after the infant attains nutritional independence (Fite et al., 2003; Richter et al., 2019). Parental sleep has not yet been investigated in titi monkeys, but exploration of the timing of postpartum sleep recovery could provide insight into the recovery of affiliative behavior between pair mates.

Future research should also investigate how other behaviors implicated in pair-bond maintenance are affected by the birth of an infant, going beyond affiliation to include other species-typical behaviors. For instance, vocal duetting is a hallmark behavior of titi monkeys (Robinson, 1979) and has been shown to convey information about individual identity (Lau et al., 2020), pair tenure (Clink, Lau, & Bales, 2019), age (Clink et al., 2019), and kinship (Clink et al., *in review*). Given the complexity of these territorial duet vocalizations (Robinson, 1981) and their importance in daily titi life (Mason, 1966), titis may alter aspects of their duets with changes in parental status.

Given the duration during which pair affiliation decreased following the infant's birth, dyads may become pregnant prior to regaining pre-partum rates of affiliation. Using archival data on subsequent births, it is possible that half of the females in our study became pregnant

in the final month of our postpartum study window. While it was not possible to isolate the effects of subsequent pregnancies on pair affiliation, further research in this area could investigate the extent to which the rebound in affiliation at the end of our research period is attributable to infant development and independence versus the next pregnancy. Future research should also seek to understand whether recovery of pair affiliation occurs, what effect the birth of a second infant has on intra-pair affiliation, and whether there is a cumulative effect of subsequent births on adult affiliation.

Finally, the next chapter to this work should focus directly on the impact of caregiving experience (i.e., paternal care, maternal care) and the quality of the parental pair relationship on the pairing and parenting success of these infants in adulthood. Tracing multiple generations of parenting behavior and pair affiliation would allow us to form a more complete picture of how titi monkeys become the social animals they are and form the attachment network that is the hallmark of their species. Compelling research in humans demonstrates that early social interactions between infant and caregiver shape cross-generational transmission of social affiliation (Feldman, Gordon, & Zagoory-Sharon, 2010). While the implications of this cross-generational transmission of social affiliation has been studied in connection with infants' social behavior, it would be interesting to assess these infants' performance in future pair bonds, specifically in regards to pair bond maintenance behaviors.

Acknowledgements

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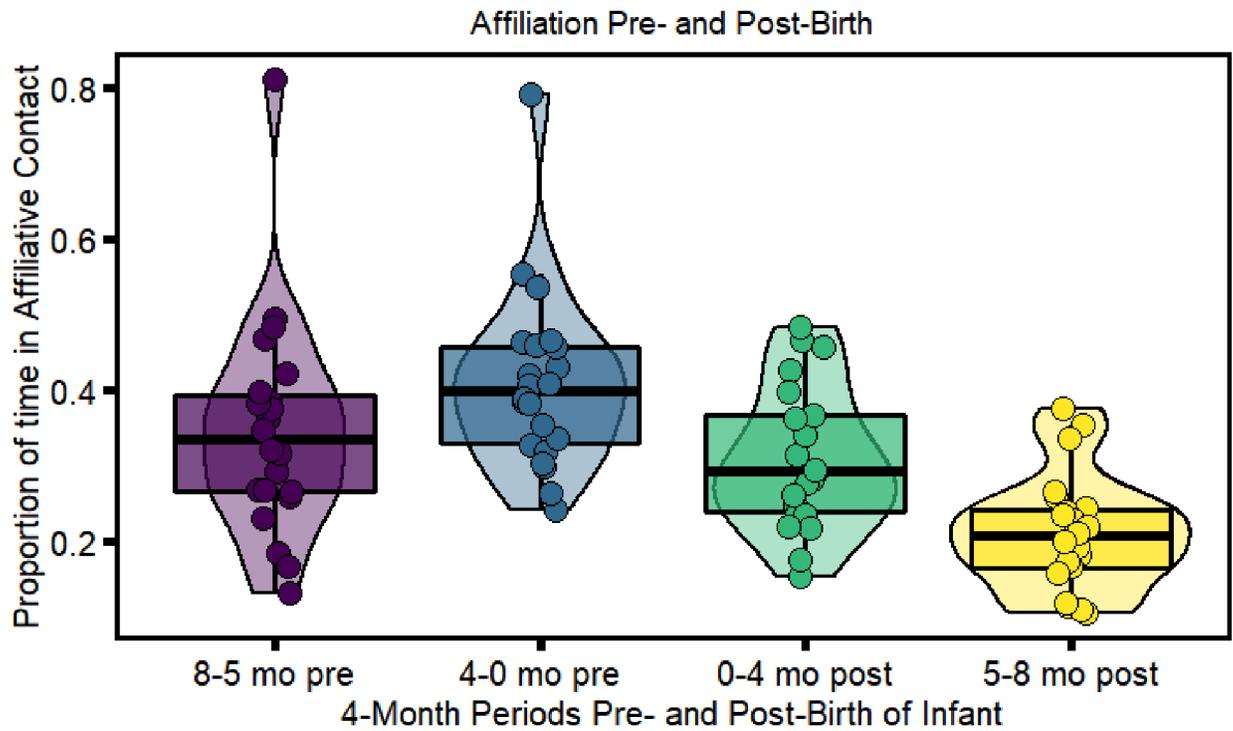
Figure 1.
Proportion of time pairs spend in affiliative contact over 4 four-month periods. Outliers included in the figure. Each point is an observed score for an individual pair at each time point. Boxplots represent median value of affiliative contact with lower and upper hinges corresponding to the first and third quartiles. A violin plot overlays the data for each time period, illustrating the distribution of the variables.
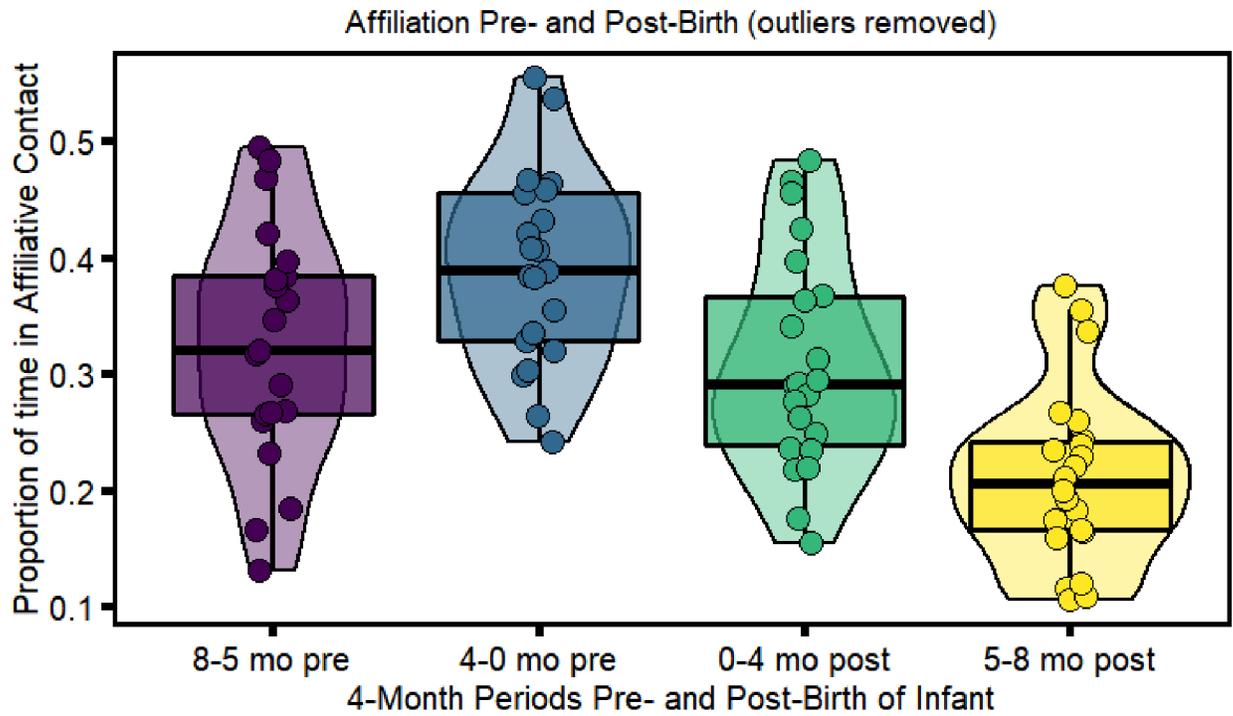
Figure 2.
Proportion of time pairs spend in affiliative contact over 4 four-month periods. Outliers were excluded in figure. Each point is an observed score for an individual pair at each time point. Boxplots represent median value of affiliative contact with lower and upper hinges corresponding to the first and third quartiles. A violin plot overlays the data for each time period, illustrating the distribution of the variables.
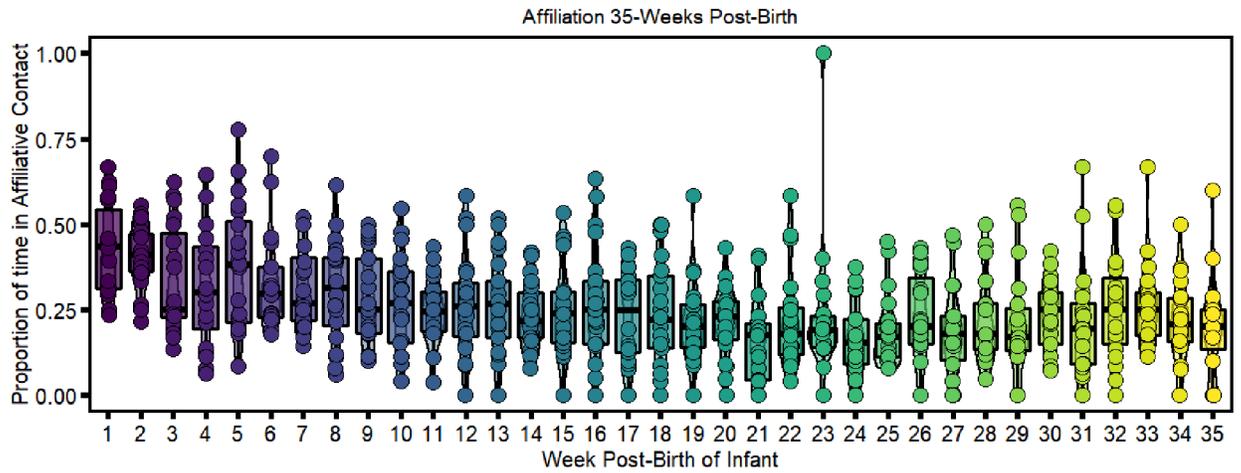
Figure 3.

Proportion of time pairs spend in affiliative contact over 35 seven-day periods. Each point is an observed score for an individual pair at each time point. Boxplots represent median value of affiliative contact with lower and upper hinges corresponding to the first and third quartiles. A violin plot overlays the data for each time period, illustrating the distribution of the variables.
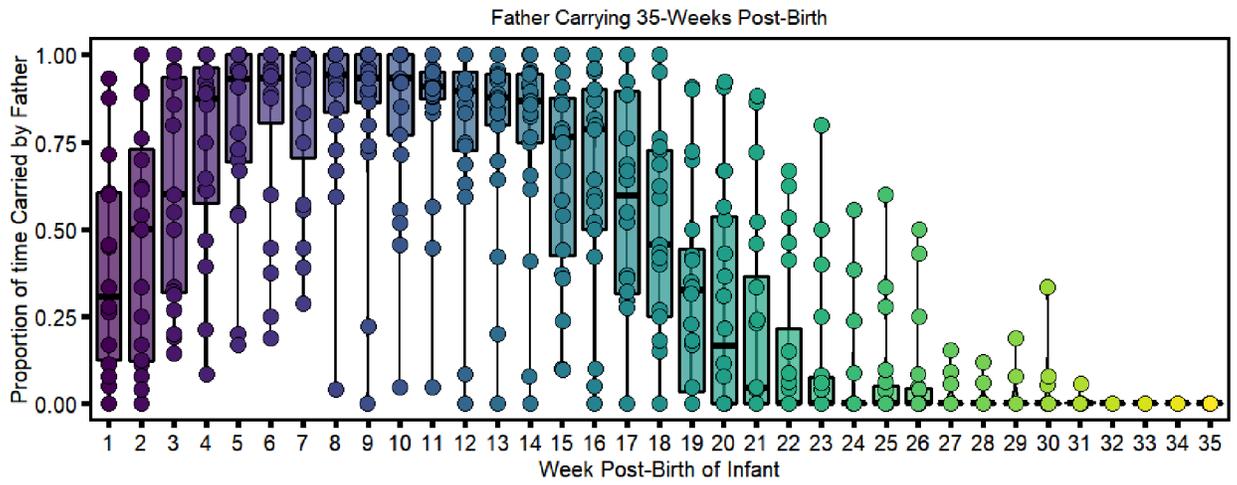
Figure 4.

Proportion of time fathers spend carrying infants over 35 seven-day periods. Each point is an observed score for an individual pair at each time point. Boxplots represent median value of affiliative contact with lower and upper hinges corresponding to the first and third quartiles. A violin plot overlays the data for each time period, illustrating the distribution of the variables.
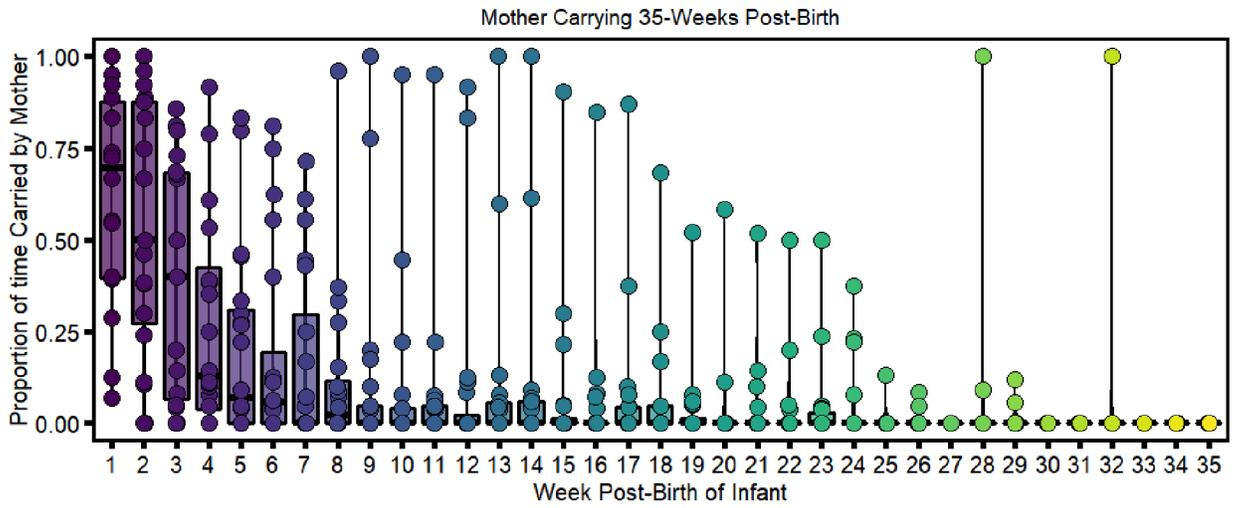
Figure 5.
Proportion of time mothers spend carrying infants over 35 seven-day periods. Each point is an observed score for an individual pair at each time point. Boxplots represent median value of affiliative contact with lower and upper hinges corresponding to the first and third quartiles. A violin plot overlays the data for each time period, illustrating the distribution of the variables.
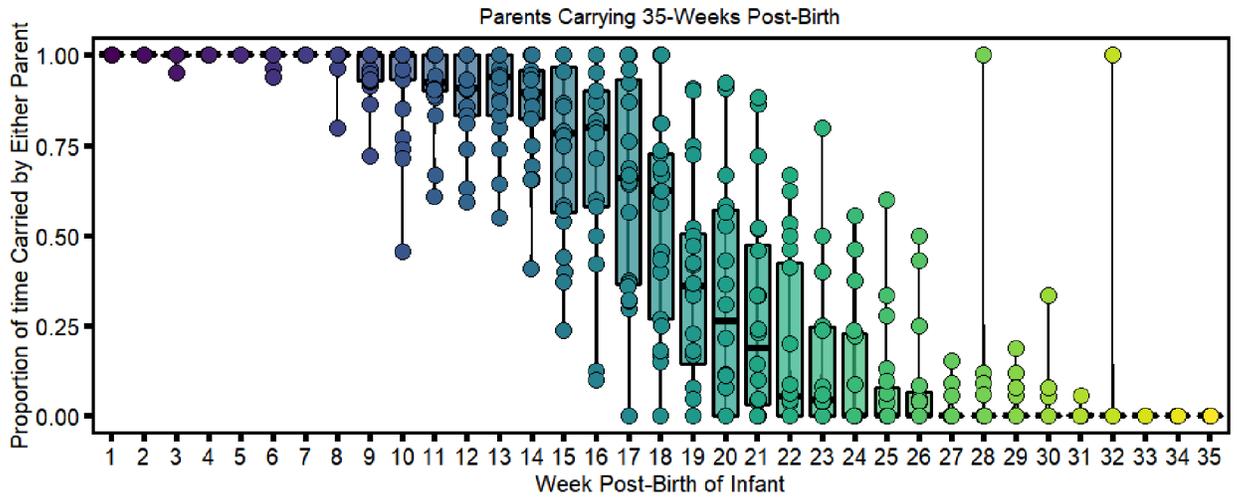
Figure 6.
Proportion of time parents spend carrying infants over 35 seven-day periods. Each point is an observed score for an individual pair at each time point. Boxplots represent median value of affiliative contact with lower and upper hinges corresponding to the first and third quartiles. A violin plot overlays the data for each time period, illustrating the distribution of the variables.

Table 1.

Ethogram for social behaviors.

Behavior	Definition
Affiliative Social Interactions	
Passive Contact	Male's and female's bodies are in physical contact that does not include tail-twining.
Social Proximity	Animal's body (excluding the tail) is within arm's length (approximately 6 inches) of another animal (excluding the tail).
Tail Twine	Male and female tails are intertwined for at least one full turn.
None	Male and female are not in passive contact, social proximity, or tail twining.
Infant Carry Interactions	
Father Carry	Infant is being carried by the father. Needs to have both back feet on the father to count as being carried (can have hands off father but as long as both feet are on father will count as a carry).
Mother Carry	Infant is being carried by the mother. Needs to have both back feet on the mother to count as being carried (can have hands off mother but as long as both feet are on father will count as a carry).
Off	Infant is not being carried by mother or father. If hands are touching a parent but feet are off of the parent this would be scored as "off".

Table 2.

Proportion of time pairs spend in affiliative contact across the 4 four-month periods.

Variable	Mean	SE	W	p	skewness	kurtosis
T1 (8–5 months pre-infant birth)	0.32	0.02	0.98	.84	−0.09	−0.96
T2 (4–0 months pre-infant birth)	0.39	0.02	0.98	.92	0.12	−0.82
T3 (0–4 months post-infant birth)	0.31	0.02	0.96	.43	0.35	−0.97
T4 (5–8 months post-infant birth)	0.21	0.02	0.94	.21	0.54	−0.49

Mean and standard error of the mean (SE) are reported with results from the Shapiro-Wilk test (W and p value), as well as measures of skewness and kurtosis.

Table 3.

Results from post hoc analyses using Tukey's post-hoc test.

Comparison	Estimate	SE	p
T2-T1	0.07	0.02	< .001
T3-T1	−0.02	0.02	.68
T4-T1	−0.12	0.02	< .001
T3-T2	−0.09	0.02	< .001
T4-T2	−0.18	0.02	< .001
T4-T3	−0.1	0.02	< .001

Period 1 = 8 to 5 months pre-birth of infant; Period 2 = 4 to 0 months pre-birth of infant; Period 3 = 0 to 4 months post-birth of infant; Period 4 = 5 to 8 months post-birth of infant.

Table 4.

Proportion of time pairs spend in affiliative contact across the 35 seven-day periods.

Week	Mean	SE	W	p	skewness	kurtosis
1	0.43	0.03	0.93	.23	0.28	−1.33
2	0.41	0.02	0.96	.61	−0.35	0.92
3	0.34	0.04	0.89	.03	0.49	−1.36
4	0.32	0.04	0.95	.39	0.30	−1.06
5	0.37	0.04	0.95	.35	0.42	−0.95
6	0.33	0.03	0.85	.01	1.25	0.78
7	0.31	0.03	0.90	.05	0.43	−1.36
8	0.31	0.03	0.96	.58	0.00	0.99
9	0.28	0.03	0.92	.07	0.29	−1.37
10	0.26	0.03	0.97	.75	0.11	−1.08
11	0.25	0.02	0.98	.92	−0.03	0.35
12	0.26	0.03	0.97	.66	0.44	−0.51
13	0.26	0.03	0.98	.84	−0.03	−0.95
14	0.23	0.02	0.96	.48	0.38	1.02
15	0.25	0.03	0.95	.34	0.44	−0.70
16	0.27	0.04	0.96	.46	0.53	−0.48
17	0.23	0.03	0.91	.06	−0.07	−1.58
18	0.24	0.03	0.95	.36	0.33	−1.11
19	0.21	0.03	0.91	.07	1.11	1.71
20	0.21	0.02	0.97	.83	−0.21	−0.37
21	0.16	0.03	0.92	.12	0.41	−0.86
22	0.22	0.03	0.86	.01	1.17	0.39
23	0.23	0.05	0.65	.00	2.56	6.72
24	0.16	0.03	0.95	.34	0.38	−1.01
25	0.19	0.02	0.83	.00	1.18	0.31
26	0.23	0.03	0.94	.22	0.02	−1.15
27	0.19	0.03	0.94	.33	0.51	−0.55
28	0.22	0.03	0.90	.08	0.74	−0.74
29	0.21	0.04	0.89	.04	0.78	−0.25
30	0.24	0.03	0.96	.62	−0.03	−1.31
31	0.21	0.04	0.88	.02	1.20	0.98
32	0.25	0.04	0.97	.74	0.37	−0.70
33	0.26	0.03	0.86	.01	1.43	2.17
34	0.22	0.03	0.98	.92	0.39	−0.29
35	0.20	0.04	0.90	.10	0.76	0.45

Mean and standard error of the mean (SE) are reported with results from the Shapiro-Wilk test (W and p value), as well as measures of skewness and kurtosis.

Table 5.

Indices of model fit, where q is the total number of model parameters.

Model	q	-2lnL	AIC	Models compared	X^2(df)	p
No growth	3	2371.2	2377.2			
Linear	6	2228.3	2240.3	No growth vs linear	142.9(3)	<.001
Quadratic	10	2182.2	2202.2	Linear vs quadratic	46.1(4)	<.001

-2lnL is -2 times the log likelihood. AIC is the Akaike information criterion. Smaller values of the AIC indicate better fitting models. X^2(df) is a deviance statistic for model fit comparisons.

Table 6.

Indices of model fit, where q is the total number of model parameters.

Model	q	-2lnL	AIC	Models compared	X²(df)	p
intercept	11	2244.3	2254.3			
intercept + trough	12	2196.7	2210.7	intercept vs intercept + trough	47.6(1)	<.001
intercept + trough + time to trough	13	2174.3	2194.3	intercept + trough vs intercept + trough + time to trough	22.4(1)	<.001

-2lnL is -2 times the log likelihood. AIC is the Akaike information criterion. Smaller values of the AIC indicate better fitting models. (*df*) is a deviance statistic for model fit comparisons.

Table 7.

Individual covariate effects on the response at week 1, trough response, and time of trough response.

Covariate	β_{01}	β_{y1}	β_{x1}	σ_{ei}^2
Pair Tenure	0.120	−0.421[*]	−0.605[*]	0.048
Independence	7.582	4.685[*]	8.577[*]	0.043
Father Carry (gmc)	−0.649	−0.663	−2.364[*]	0.024
Father Carry (pc)	−0.922[*]	0.165	1.858[*]	0.024
Mother Carry (gmc)	−1.859	1.894	3.688	0.043
Mother Carry (pc)	0.648	−0.108	−1.049[*]	0.043
Parent Carry (gmc)	0.192	−0.003	−4.095[*]	0.025
Parent Carry (pc)	0.762	−0.388	2.445[*]	0.025

gmc = grand-mean-centered; pc = pair-centered;

[*] = $p < .05$.

Table 8.

Parameter estimates from final full model for the effects of each covariate on the proportion of time pairs spent in affiliative contact at week 1 (intercept), trough affiliation score, and time of trough response.

Parameter		Estimate	SE	DF	t Value	Pr > |t|	95% Confidence Limits		D
Fixed Effects									
Mean intercept	β_{00}	4.04	0.21	19	19.59	<.0001	3.61	4.47	4.18
Mean trough	β_{y0}	1.71	0.11	19	15.78	<.0001	1.48	1.94	3.36
Mean time to trough	β_{x0}	3.26	0.58	19	5.61	<.0001	2.04	4.48	1.20
Father carry (gmc; intercept)	β_{01a}	−2.21	0.85	19	−2.59	.02	−4.00	−0.42	−0.55
Father carry (pc; intercept)	β_{01b}	−0.58	0.54	19	−1.08	.29	−1.72	0.55	−0.23
Infant age of independence (trough)	β_{y1}	3.94	1.59	19	2.48	.02	0.62	7.26	0.53
Pair Tenure (trough)	β_{y2}	−0.38	0.12	19	−3.23	.00	−0.63	−0.13	−0.69
Infant age of independence (time of trough)	β_{x1}	5.71	5.31	19	1.08	.30	−5.40	16.81	0.23
Pair Tenure (time of trough)	β_{x2}	−0.24	0.13	19	−1.80	.09	−0.52	0.04	−0.38
Father carry (gmc; time of trough)	β_{x3a}	−3.46	1.49	19	−2.33	.03	−6.57	−0.35	−0.50
Father carry (pc; time of trough)	β_{x3b}	1.09	0.51	19	2.14	.05	0.02	2.16	0.46
Random Effects									
residual variance	τ_0	0.15	0.06	19	2.64	.02	0.03	0.27	0.56
individual (intercept)	φ_0	1.27	0.27	19	4.61	<0.001	0.69	1.84	0.98
individual (intercept, trough)	$\rho_{0,y}$	1.00	0.01	19	172.96	<.0001	0.98	1.01	36.88
individual (trough)	φ_y	0.11	0.16	19	0.70	.49	−0.22	0.44	0.15
individual (intercept, time of trough)	$\rho_{0,x}$	0.78	0.33	19	2.36	.03	0.09	1.46	0.50
individual (trough, time of trough)	$\rho_{x,y}$	0.81	0.33	19	2.49	.02	0.13	1.49	0.53
individual (time of trough)	φ_x	0.84	0.17	19	5.09	<.0001	0.49	1.18	1.08

gmc = grand-mean-centered; pc = pair-centered; D = Cohen's D (effect size)