RESEARCH ARTICLE

Hormonal Correlates of Paternal Care Differences in the Hylobatidae

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Only one of the 15 species of monogamous hylobatids, the siamang (*Symphalangus syndactylus*), demonstrates direct paternal care in the form of infant-carrying, providing a unique model for examining hormonal correlates of paternal care differences between siamangs and gibbons. We used behavioral data and fecal hormone analysis to investigate (1) differences in monthly percent father–infant proximity in relation to monthly fecal androgen metabolite concentrations from infant birth to the late postpartum period between siamangs and gibbons, (2) the pattern of change in fecal androgen and fecal estrogen metabolite concentrations during the 8-week peripartum period between siamangs and gibbons, and (3) the change in mean fecal glucocorticoid metabolite concentrations at 1-month postpartum from individual baseline between siamangs and gibbons. Father–infant proximity increased as androgen concentrations decreased over the postpartum period in siamangs but not in gibbons. Androgen concentrations increased around birth in siamangs during the 8-week peripartum period, but exhibited a decreasing trend around birth in gibbons. Estrogen concentrations increased from pre- to postpartum in siamangs during the 8-week peripartum period, but exhibited a decreasing trend from pre- to postpartum in gibbons. The difference in mean glucocorticoid metabolite concentrations from baseline was greater in siamangs than gibbons. Our data suggest a relationship between specific steroid hormone patterns and differences in paternal care among the hylobatids, warranting further investigation of such proximate mechanisms. Am. J. Primatol. 74:247–260, 2012.   © 2012 Wiley Periodicals, Inc.

INTRODUCTION

Parental involvement during rearing of offspring is crucial for normal development of physical, psychological, and behavioral characteristics of the young in all mammalian species. It has been theorized that the discrepancy in parental investment between the sexes is a result of the energetic costs of internal fertilization and lactation [Trivers, 1972]; however, more recent studies have suggested that there are likely other factors, including opportunities for multiple matings and paternity uncertainty [Magrath and Komdeur, 2003; Møller and Cuervo, 2000], or a combination of several factors including the operational sex ratio within a population [Kokko and Jennions, 2008] that may play a role in the evolution of little or no paternal investment among mammals. Not surprisingly, much of the research that has examined parental care in mammals has focused on maternal behavior and the associated role of hormones [Nelson, 2005].

The potential importance of paternal care, however, has received increasing interest in recent years. Theoretically, males should mate with as many females as possible to increase their individual reproductive success. Factors such as energetic costs, paternity uncertainty, and early infant dependence on nursing, however, may limit the amount of care a male can provide to his offspring [Kokko and Jennions, 2008; Magrath and Komdeur, 2003; Trivers, 1972; Woodroffe and Vincent, 1994]. Nonetheless, direct paternal care is still observed in approximately 5–10% of all mammalian species, occurring predominantly in rodents, carnivores, and some primates [Buchan et al., 2003; Clutton-Brock, 1991; Gubernick and Teferi, 2000; Kleiman and Malcolm, 1981; Woodroffe and Vincent, 1994].

Although, paternal care is rare among primates, it is known to occur in several well-studied genera of New World primates, including *Callicebus*,

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Aotus, *Callimico*, *Callithrix*, *Cebuella*, *Leontopithecus*, and *Saguinus* [Kleiman, 1985; Kleiman and Malcolm, 1981; Ziegler et al., 2004, 2009a]. The only apes that exhibit paternal care, with the possible exception of *Homo sapiens*, are members of the family Hylobatidae. Native to Southeast Asia and parts of India and China, the hylobatids comprise the largest group of apes consisting of four genera (*Nomascus*, *Hylobates*, *Symphalangus*, and *Hoolock*) [Groves, 2001]. All species are believed to be primarily monogamous, form long-lasting pair-bonds, and are typically found in small family groups with one to four offspring [Brockelman et al., 1998; Geissmann, 1991; Leighton, 1987; Macdonald, 2001; Reichard and Barelli, 2008]. Yet, extra-pair copulations have been reported in some hylobatid populations, suggesting that social bonds and reproductive strategies may be more dynamic than originally reported [Palombit, 1994a,b, 1996; Reichard and Barelli, 2008].

The evolution of paternal care in hylobatids has not been extensively researched, but it is known that even within the hylobatids, the form and degree of paternal care varies across species. Male siamangs (*Symphalangus syndactylus*) actively participate in direct infant care through infant carrying that typically begins between 6 and 12 months of infant age. This infant transfer, during which the father does most of the carrying, is known to occur both in the wild [Chivers, 1974; Lappan, 2005] and in captivity [Alberts, 1987; Dielentheis et al., 1991; Dal Pra and Geissmann, 1994]. As the infant develops, mother–infant contact slowly decreases while father–infant contact increases, facilitating the transfer [Alberts, 1987; Chivers, 1974]. In fact, in the wild, the infant learns to move and feed independently and to interact socially with conspecifics while under the care of the male [Chivers, 1974; Lappan, 2005]. In contrast, there is little to no data available suggesting that males of any other gibbon species demonstrate substantial direct paternal care in the wild [Carpenter, 1940; Ellefson, 1974; Palombit, 1996], and it has only been reported exceptionally in captivity [Berkson, 1966]. Instead, paternal investment is exhibited indirectly in the form of territory defense and protection of the female and offspring.

Most research examining paternal care in the hylobatids has focused on ultimate mechanisms related to the evolution of species differences (i.e. socioecological factors; Dunbar, 1988). Palombit [1996], however, investigated differences in the role of proximate behavioral mechanisms of pair bond maintenance between gibbons and siamangs and found that both sexes invest more equally in maintaining the pair bond in siamangs than in gibbons. Still, no studies to date have examined proximate hormonal mechanisms that may be crucial to our understanding of differences in paternal care in the hylobatids. This is surprising, given that in recent years many studies have begun to focus research on hormones as potential mediating factors of paternal care in other biparental primate species, including common marmosets (*Callithrix jacchus*) [Dixson and George 1982, Ziegler et al., 2009a,b, 2011], black tufted-ear marmosets (*C. kuhlii)* [Nunes et al., 2000, 2001], cotton-top tamarins (*Saguinus oedipus*) [Ziegler and Snowdon, 2000; Ziegler et al., 1996, 2004], and humans (*H. sapiens*) [Fleming et al., 2002; Gray et al., 2006, 2007; Storey et al., 2000].

Several studies of biparental primate species have supported an association between androgens and the degree of paternal care, but the nature of this relationship varies greatly and can generally be positive or negative. A positive relationship, characterized by androgen-facilitated paternal care, has been demonstrated in *Sa. oedipus*, in part by the aromatization of testosterone to estrogen [Ziegler and Snowdon, 2000]. In contrast, a negative relationship characterized by androgen interference with paternal care, is evident when low or decreased androgen concentrations are associated with increased paternal care, a pattern that has been demonstrated in several callitrichid species. For example, Dixson and George [1982] not only found a reciprocal relationship between testosterone and prolactin in *C. jacchus*, but they also discovered that males had lower testosterone concentrations after infant carrying. Also in *C. jacchus*, Prudom et al. [2008] and Ziegler et al. [2009a, 2011] found a similar relationship between lower testosterone concentrations in fathers and direct infant stimuli. Similarly, in *C. kuhlii*, Nunes et al. [2000, 2001] found that testosterone concentrations were lower among males who carried infants at high rates than males who carried infants at low rates. Ziegler et al. [2004] demonstrated that testosterone concentrations in *Sa. oedipus* fathers decreased during the postpartum period, except around the time of postpartum estrus. Studies with human fathers have also revealed that fathers have lower testosterone concentrations than men who are not fathers [Gray et al., 2006, 2007].

The influence of estrogen on paternal behavior in mammals has not been studied extensively; however, recent research has provided evidence for a variable role of estrogen in mediating paternal care. Estrogen clearly plays a priming role in mediating maternal behavior, as has been demonstrated in female rats (*Rattus norvegicus*) [Rosenblatt et al., 1994], and it can stimulate paternal behavior in castrated male rats primed with both estrogen and progesterone. Similarly, when estrogen is administered directly to the medial preoptic area of the brain, paternal behavior is promoted [Rosenblatt and Ceus, 1998]. Estrogen also appears to be obligate to paternal care in some naturally paternal rodent species, such as the California mouse (*Peromyscus californicus*) [Trainor and Marler, 2001]. In many naturally nonpaternal rodent species, however, estrogen, and

its aromatization from testosterone, interferes with paternal behavior [Cushing et al., 2004, 2008]. Similarly, in some naturally paternal primate species, such as *C. kuhlii*, estrogen may also interfere with the expression of paternal behavior, likely as a result of its aromatization from testosterone [Nunes et al., 2000]. Conversely, in human fathers, Berg and Wynne-Edwards [2001] demonstrated a positive relationship between estrogen and the expression of paternal care. In general, estrogen's role in mediating paternal behavior in mammals remains unclear.

The relationship between glucocorticoids and the regulation of paternal care in biparental primate species is similarly unclear. There is more consensus over the role of glucocorticoids in mediating maternal behavior, as several studies with nonhuman primates and humans have shown that mothers with elevated glucocorticoid concentrations during the peripartum period demonstrate a greater degree or higher quality of maternal care than mothers with low glucocorticoid concentrations [Fleming et al., 1997; Maestripieri et al., 2009; Nguyen et al., 2008]. In one callitrichid species, *C. kuhlii*, cortisol concentrations were found to be lower among males that carried their infants at high rates as opposed to those who carried infants at low rates, but cortisol increased in fathers after the birth of their first litter [Nunes et al., 2001]. In human fathers, on the other hand, Storey et al. [2001] demonstrated that cortisol concentrations in fathers increased prior to the birth of an infant, suggesting a relationship between glucocorticoids and the promotion of paternal care.

Regardless of causality, the pattern of change in hormones across pregnancy and the postpartum period likely also varies between siamang males and males of other gibbon species, but this has not been previously investigated. In the current study, our objective was to examine the relationship between differences in paternal care between siamangs and gibbons and patterns of androgens, estrogens, and glucocorticoids around birth and in the postpartum period. The relationship between changes in these hormone patterns in other biparental primates, and the lack of information on this in the only biparental ape species, supports an investigation of this relationship in the hylobatids. We examined the pattern of change in father–infant proximity relative to the change in androgens over the postpartum period and predicted that siamangs, but not gibbons, would exhibit an increase in percent of time in proximity to infants and a decrease in androgen concentrations across the postpartum period as a mechanism to facilitate infant-carrying behavior [Alberts, 1987]. We also examined patterns of androgens, estrogens, and glucocorticoids around infant birth. We predicted that androgens would decrease in both siamangs and gibbons surrounding birth to facilitate infant tolerance, and that if estrogens facilitate paternal care in hylobatids, only siamang males would exhibit an increase in concentrations from pre- to postpartum. Finally, we predicted that there would be a greater increase in glucocorticoids from individual baseline concentrations in the first month following birth in siamangs than in gibbons, based on previous studies that have shown a relationship between elevated glucocorticoids and paternal care [Reburn and Wynne-Edwards, 1999; Storey et al., 2000], as well as maternal care [Fleming et al., 1997; Maestripieri et al., 2009; Nguyen et al., 2008].

METHODS

Subjects

Six adult (mean: 22.5 ± 3.4 years old, range: 12 to 37 years old) male hylobatids were studied at institutions in North America (Table I). Subjects included three white-cheeked gibbons (*Nomascus leucogenys*), one white-handed gibbon (*Hylobates lar*), and two siamangs (*Sy. syndactylus*). Data for white-cheeked gibbon #0223 consisted only of father–infant proximity data. All subjects were housed in pairs or family groups (including juveniles present in each siamang group) at institutions accredited by the Association of Zoos and Aquariums (AZA). Exhibit sizes were comparable across all institutions and for all subjects. This study was conducted with approval by each zoo's research committee and from the University of Chicago IACUC (ACUP 71848). Additionally, all research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. Information, including age and breeding and rearing history, for each male is shown in Table I.

Behavioral Observations

Behavioral data were collected on each subject using 1-min scan-sampling methods [Altmann, 1974] during observation sessions that lasted 15 min. Data were collected three times per week on average (range: 1–5 times/week; see Table I for number of observations per individual), and sampling began approximately 1 month prior to the birth of an infant and lasted through 6 to 8 months postpartum (between June 2006 and November 2009; range of data collection: 6 to 10 months). All behavioral data were collected using a hylobatid ethogram modified from a preexisting ethogram developed for the Etho-Trak software program [Atsalis et al., 2005], and observers were trained by one of the authors (MR) until they reached greater than 90% interobserver reliability [Crockett, 1996]. Contact between individuals was defined as the focal animal physically touching another individual, whereas proximity was defined as the focal animal being within one arm's length (approximately 0.5 m) of another individual, but not physically touching that individual. Observed

TABLE I. Hylobatid Males Included in the Study

Male	Institution	Species	Age (years)	No. of Infants Fathered	Rearing History	No. of Behavioral Observations
No. 0168	Toledo Zoo	*Nomascus leucogenys*	18	2	Parent	158
No. 0176	Brookfield Zoo	*Nomascus leucogenys*	25	3[a]	Hand	60
No. 0223	Lincoln Park Zoo	*Nomascus leucogenys*	20	2	Hand	121
No. 847	Little Rock Zoo	*Hylobates lar*	23	2	Parent	95
No. 97	Great Plains Zoo	*Symphalangus syndactylus*	37	4[b,c]	Parent	54
No. 467	Cheyenne Mountain Zoo	*Symphalangus syndactylus*	12	2[c]	Hand	60

[a]Second infant died at approximately 3 months old.
[b]Fathered twins during study; one twin died the day after birth, while the other twin was successfully raised by parents; a second infant was also born during study.
[c]A juvenile was also present in the family group.

father–infant contact data were insufficient to include in analyses alone; therefore, proximity and contact data were combined as a measure of overall father–infant proximity for analyses. Father–infant proximity data included father–infant–mother proximity data for 1 and 2 months postpartum, after which measured proximity included proximity of the father to the infant alone (3 through 7 months postpartum).

Additionally, although data were collected on all aspects of paternal behavior [Rafacz, 2010]; many behavioral measures were recorded too infrequently to include in analyses. Only father–infant proximity data are presented here as an appropriate measure of paternal behavior, as previous research has demonstrated that a key factor involved in the infant transfer in male siamangs, resulting in infant-carrying behavior, is the development of closer father–infant proximity and contact over the postpartum period (beginning around 3–4 months postpartum and lasting through 6 to 12 months postpartum) [Alberts, 1987; Dal Pra and Geissmann, 1994; Dielentheis et al., 1991].

Fecal Sample Collection and Processing

Fecal samples were chosen for their ease of collection and the benefit of noninvasive hormonal monitoring. Fecal samples were collected concurrently with behavioral data, approximately 2 to 5 times per week, beginning approximately 1 month prior to birth and continuing for at least 7 months postpartum. Each institution collected samples in the morning, usually prior to daily exhibit cleaning, and sampling procedures were comparable across all zoos. To identify fecal samples from study males and discriminate them from other individuals, zoos used either green liquid food-coloring (Gordon Food Service, Tampa, FL) or blue gel food-coloring (Americolor, Placentia, CA) as fecal markers administered inside food items. Fresh fecal samples were uncontaminated by urine or substrate.

Each fecal sample was placed into a sealed plastic bag, labeled, and stored at –20°C until shipped to the endocrinology laboratory at Lincoln Park Zoo's Davee Center for Epidemiology and Endocrinology for processing and analysis. Fecal steroid metabolites were extracted from fecal samples using 5.0 ml of 90% ethanol:distilled water by a method modified from Brown et al. [1994] to include agitation on a Glas-col mixer (Glas-col, Terre Haute, IN) on setting 60 for 30 min instead of boiling samples. Samples were then diluted for each specific hormone assay (1:250 for androgens, 1:100 for estrogens, 1:20 for glucocorticoids) in dilution buffer ($0.2M$ NaH_2PO_4, $0.2M$ Na_2HPO_4, NaCl) prior to analysis by enzyme-immunoassay (EIA) for hormone metabolite concentrations.

Enzyme-Immunoassay (EIA)

Fecal androgen metabolites (FAM), fecal estrogen metabolites (FEM), and fecal glucocorticoid metabolites (FGM) were measured using testosterone, estradiol-17β, and cortisol EIA, respectively. All EIAs were validated for fecal extracts of each hormone for each species by demonstrating (1) parallelism between binding inhibition curves of fecal extract dilutions (1:2–1:2,048); and (2) significant recovery (>90%) of exogenous hormone added to fecal extracts. Percent recoveries of testosterone, estradiol-17β, and cortisol are shown in Table II for all three hylobatid species. Assay sensitivity was 0.98 pg/well for all EIAs, and to maintain measures of quality control intra- and interassay coefficients of variation were kept under 10% and 15%, respectively, for each EIA. Cross-reactivities for assays have been previously described [see Brown et al., 1994; Santymire and Armstrong, 2010; Young et al., 2004].

Statistical Analyses

All statistical analyses were performed using JMP Version 7.0.2 (SAS Institute Inc., Cary, NC) and SigmaPlot Version 11.0 (Systat Software Inc., Chicago, IL). Data were collected consistently for every male through 7 months postpartum, so only

TABLE II. Percent recoveries for EIAs for each hylobatid species (appropriate dilutions are in parentheses).

Species	Testosterone EIA (1:250)	Estradiol-17β EIA (1:100)	Cortisol EIA (1:20)
Nomascus leucogenys	$y = 0.787x + 7.104$, $R^2 = 0.969$	$y = 1.005x + 1.485$, $R^2 = 0.999$	$y = 1.081x + 17.546$, $R^2 = 0.9444$
Hylobates lar	$y = 1.026x + 8.778$, $R^2 = 0.925$	$y = 1.014x + 1.011$, $R^2 = 0.999$	$y = 1.0419x + 12.335$, $R^2 = 0.9864$
Symphalangus syndactylus	$y = 0.943x + 5.967$, $R^2 = 0.993$	$y = 0.903x + 2.010$, $R^2 = 0.989$	$y = 1.02x + 12.464$, $R^2 = 0.9977$

these data were analyzed. Mean (±SE) percent of time spent in proximity to an infant over the 7 month post-partum period was calculated for siamangs and gibbons and compared between groups using a *t*-test. The first 2 months post-partum included proximity to both the infant and the female, whereas proximity to the infant only was used to calculate this measure from 3 through 7 months postpartum. A Kolmogorov–Smirnov test was used for normality assumption testing. When data were not normally distributed, a Mann–Whitney Rank Sum Test was used to compare values between the two groups. A repeated-measures analysis of variance (ANOVA) was used to assess the change in monthly percent father–infant proximity for gibbons and siamangs over a 7-month postpartum period. Linear regression trend lines were used on scatter plots of all data points to demonstrate the overall pattern of change in father–infant proximity over time. For all analyses, $P < 0.05$ was considered significant.

A repeated-measures ANOVA was also used to assess the change in monthly mean FAM concentrations in gibbons and siamangs beginning at 1-month prepartum through 7-month postpartum. Linear regression trend lines were again used on scatter plots of all data points to demonstrate the overall pattern of change in FAM concentrations over time. This timeframe was chosen because infant-carrying responsibilities begin to transfer to male siamangs around 6 to 8 months post-partum [Alberts, 1987; Chivers, 1974; Dal Pra and Geissmann, 1994; Dielentheis et al., 1991]. A repeated-measures ANOVA was used to compare monthly mean FAM and FEM concentrations from 4 weeks pre- to 4 weeks post-partum, and linear regression trend lines were used on scatter plots of all data points to demonstrate the overall pattern of change in these hormones surrounding birth. This timeframe was chosen because it mirrored methods of previous studies with callitrichids [black tufted-ear marmoset, *C. kuhlii*, Nunes et al., 2000] that have investigated the role of estrogen in facilitating paternal care immediately following birth and research investigating the relationship between peripartum male androgens and paternal care in biparental primates [*C. kuhlii*, Nunes et al., 2000; humans, Berg and Wynne-Edwards, 2001] and rodents [*P. californicus*, Trainor and Marler, 2001]. General patterns of father–infant proximity and FAM over the postpartum period and peripartum FAM and FEM concentrations were

then compared between siamangs and gibbons to determine whether differences were apparent. For all significant repeated-measures ANOVA results, Holm–Sidak post-hoc tests were used to determine pair-wise differences between months.

Mean (± SE) change in FGM concentrations from individual baseline was calculated at 4 weeks (~1 month) postpartum for siamangs and gibbons. This parameter was used because it is similar to the window of time used in previous studies with humans and nonhuman primates [Almond et al., 2008; Fleming et al., 1997; Nguyen et al., 2008]. A baseline FGM concentration was calculated for each individual male using an iterative process, in which high values exceeding the mean plus 1.5 standard deviations (SD) are excluded [Brown et al. 1994; Moriera et al. 2001]. For each iteration, the mean is recalculated and the elimination process is repeated until no values exceed the mean plus 1.5 SD, representing baseline hormone values. Mean (±SE) baseline concentration and mean (±SE) change from baseline were calculated and then compared between siamangs and gibbons using a Mann–Whitney Rank Sum Test.

RESULTS

Father–Infant Proximity and FAM Concentrations Over the Postpartum

There was no difference (*t*-test, $t_{33} = -1.466$, $P = 0.152$) in mean percent father–infant proximity over the entire 7 month postpartum period between siamangs (22.1 ± 8.1%) and gibbons (33.3 ± 3.2%). Infant carrying was never observed in gibbon males; however both siamangs did exhibit infant-carrying behavior. The first instance of infant carrying was observed in siamangs #467 and #97 at approximately 4.5 and 7.5 months postpartum, respectively.

As explained in the methods, the percent father–infant contact alone was not sufficient in either group to test for species differences; therefore, contact and proximity were combined into one overall measure of father–infant proximity for analyses. There was a significant monthly change in father–infant proximity over the postpartum period in siamang males (repeated-measures ANOVA: $F_{7,18} = 13.771$, $P < 0.001$). A Holm–Sidak post-hoc test revealed significantly greater father–infant proximity during 6 and 7 months postpartum ($P < 0.001$) than 1 through

5 months postpartum, demonstrating an increase in male proximity to the infant over the postpartum period. Figure 1A shows a scatter plot of all data points and a linear regression trend line of father–infant proximity over the 7-month postpartum period, further showing an increase in father–infant proximity over this time period. In contrast, there were no significant monthly differences in father–infant
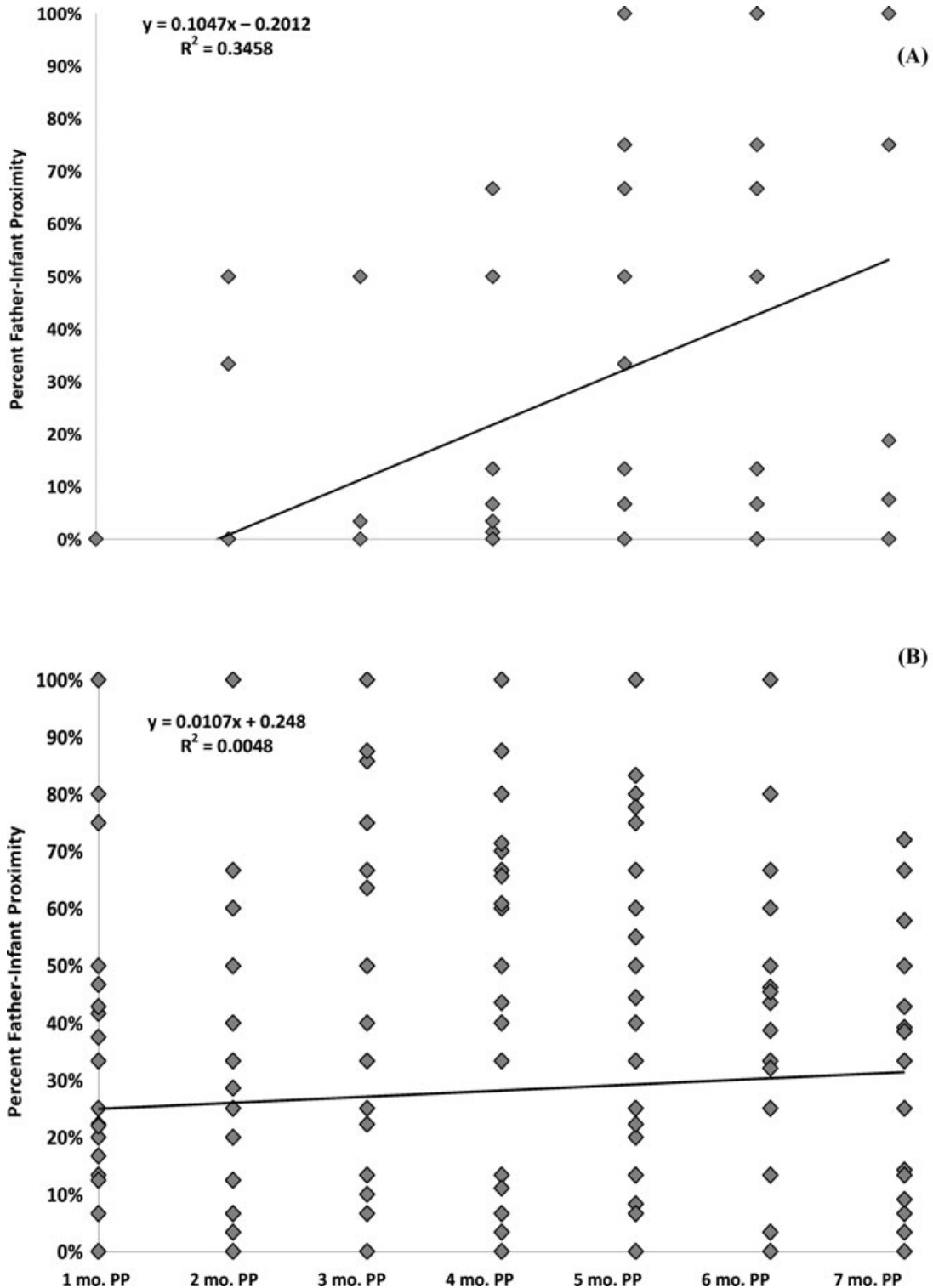

Fig. 1. Change in percent father–infant proximity from birth to 7-month postpartum period (PP). Scatter plots show every data point (closed diamonds) representing daily percent father–infant proximity values within each month postpartum, and the pattern of change over time is indicated by linear regression trend lines (solid black lines) for (A) siamangs (n = 2) and (B) gibbons (n = 3).

proximity in gibbon males (Fig. 1B; repeated-measures ANOVA: $F_{6,10} = 1.437$, $P = 0.201$), and there was no apparent trend in proximity over the postpartum period.

Siamang males also demonstrated a significant change in monthly mean FAM concentrations over the postpartum period (repeated-measures ANOVA: $F_{8,41} = 8.040$, $P < 0.001$), and a Holm–Sidak post-hoc test revealed lower FAM concentrations during 6 and 7 months postpartum ($P < 0.001$) than during 1 through 4 months postpartum. Figure 2A shows a linear regression trend line demonstrating a decrease of FAM concentrations from 1 month prepartum through 7 months postpartum. Conversely, no monthly differences in FAM concentrations were observed in gibbon males over the postpartum period (repeated-measures ANOVA: $F_{8,67} = 1.753$, $P = 0.086$), and this lack of relationship is further supported by the linear regression trend line shown in Figure 2B.

Hormonal Patterns Surrounding Infant Birth

Siamang males demonstrated significant weekly differences in peripartum FAM concentrations (repeated-measures ANOVA: $F_{7,10} = 4.884$, $P < 0.001$), and a Holm–Sidak post-hoc test revealed significantly higher FAM concentrations during 1 week prepartum than both 4 weeks prepartum and 4 weeks postpartum ($P < 0.001$) and similar FAM concentrations during both 4 weeks prepartum and 4 weeks postpartum ($P > 0.05$). Figure 3A shows the resulting pattern of change in FAM concentrations in the 8 weeks surrounding birth, as demonstrated by an inverted U-shaped nonlinear regression trend line. In contrast, there were no significant weekly differences in FAM concentrations in gibbon males (repeated-measures ANOVA: $F_{7,17} = 0.853$, $P = 0.547$), although a nonlinear regression trend line shows somewhat higher FAM concentrations during 4 weeks prepartum and 4 weeks postpartum than 1 week prepartum, resulting in a slight U-shaped pattern (Fig. 3B).

For siamang males, there were differences in weekly FEM concentrations surrounding birth (repeated measures ANOVA: $F_{7,9} = 2.407$, $P = 0.036$), and a Holm–Sidak post-hoc test revealed differences in FEM concentrations during 4 weeks prepartum and 3 and 4 weeks postpartum ($P = 0.029$). Figure 4A shows a linear regression trend line indicating an increase in FEM concentrations from the prepartum to postpartum period. Gibbon males, on the other hand, did not show significant weekly differences in FEM concentrations surrounding birth (repeated measures ANOVA: $F_{7,17} = 1.878$, $P = 0.084$); however, as suggested by the linear regression trend line in Figure 4B, there appears to be a slight decrease in FEM concentrations from the prepartum period to the postpartum.

Baseline FGM concentrations for the two siamangs were 54.15 ± 2.34 ng/g dry feces and 63.38 ± 3.75 ng/g dry feces, whereas for the three gibbons, baseline FGM concentrations were 34.43 ± 2.16 ng/g dry feces, 56.32 ± 3.24 ng/g dry feces, and 77.71 ± 4.12 ng/g dry feces. The mean ($\pm$SE) change in FGM concentrations from baseline for 4 weeks ($\sim$1 month) postpartum was greater (Mann–Whitney Rank Sum Test, $U = 405.000$, $P = 0.009$) for siamangs (15.99 ± 3.44 ng/g dry feces) than for gibbons (0.31 ± 1.22 ng/g dry feces).

DISCUSSION

Logistical constraints, namely the low number of offspring produced each year from breeding recommendations in North American zoo-housed populations over the last 5 years, limited the sample size for this study. However, despite small sample size, the animals included here are representative of the population, and the present study was justified in that it was the first investigation designed to determine whether specific patterns of steroid hormones were associated with differences in paternal care between siamangs and gibbons. We recognize that because the overall sample size for this study was small, we must be cautious when interpreting these results. However, in spite of limited sample size, noticeable differences between siamangs and gibbons did emerge, suggesting that patterns may biologically relevant.

Significant differences were found between siamangs and gibbons both in the pattern of change in percent father–infant proximity and the pattern of change in FAM concentrations over the postpartum period. Similarly, the pattern of change in both FAM and FEM concentrations during the 8-week postpartum period differed between siamangs and gibbons. Finally, the change in FGM concentrations from individual baseline during 1-month postpartum also differed between the two groups. We suggest these findings are related to differences in paternal care between siamangs that exhibit direct paternal care (infant carrying) and gibbons that are not known to demonstrate direct paternal care.

Father–Infant Proximity and FAM Concentrations over the Postpartum

The most suitable measure of paternal care in this study was whether infant carrying occurred and the percent father–infant proximity over the postpartum period. Data on the percent father–infant contact alone were not sufficient to test between groups, which might have been a result of the greatest amount of contact occurring late in the postpartum period (around 7 months postpartum) for siamang males. As expected, no infant transfer, and therefore, no infant carrying, was observed in any of
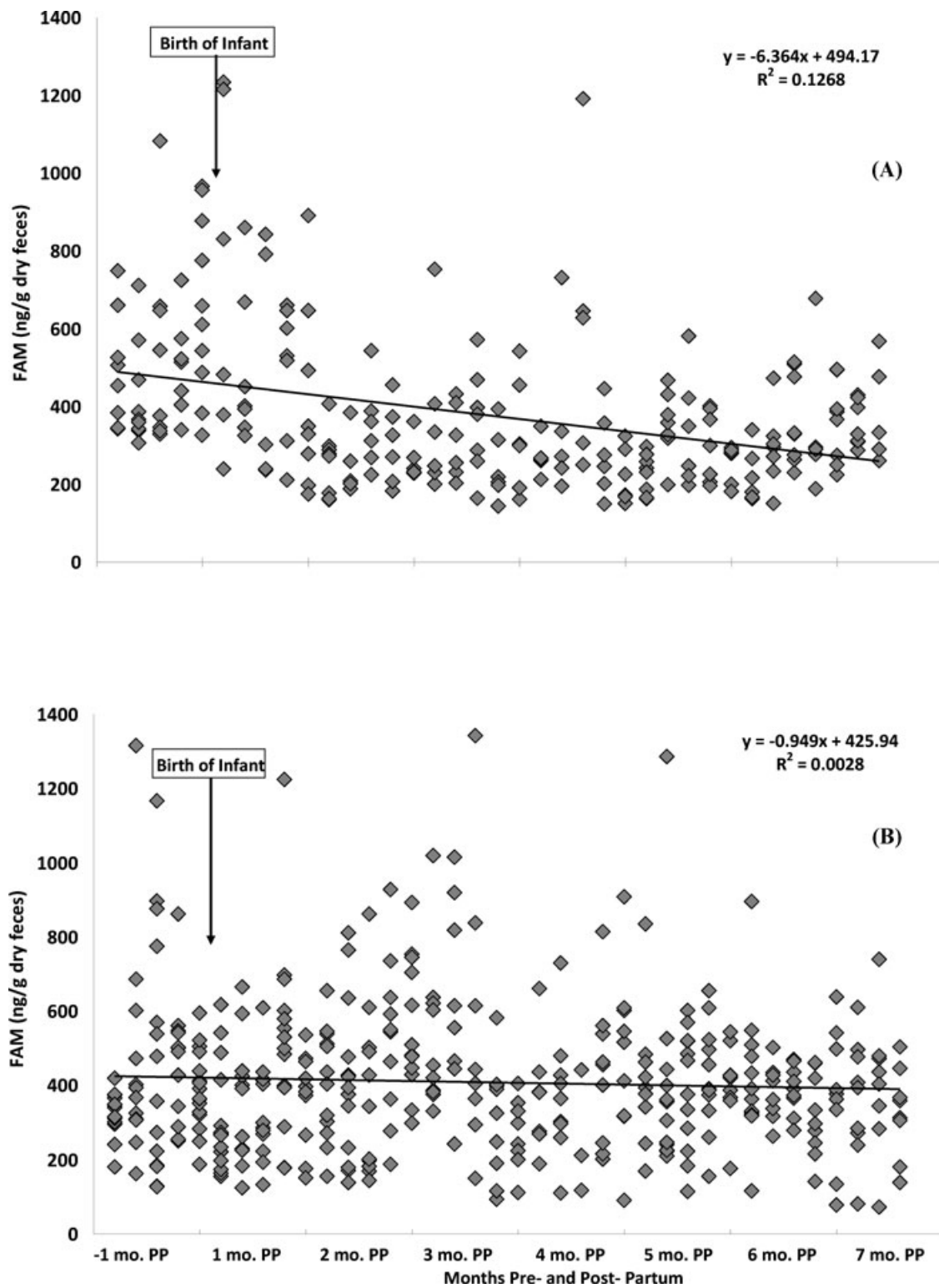
Fig. 2. Change in FAM concentrations from 1 month prepartum through 7 months postpartum. Scatter plots show every data point (closed diamonds) representing daily FAM concentrations within each month pre- or postpartum, and the pattern of change over time is indicated by linear regression trend line (solid black lines) for (A) siamangs (n = 2) and (B) gibbons (n = 3). Birth of an infant is noted on each graph.
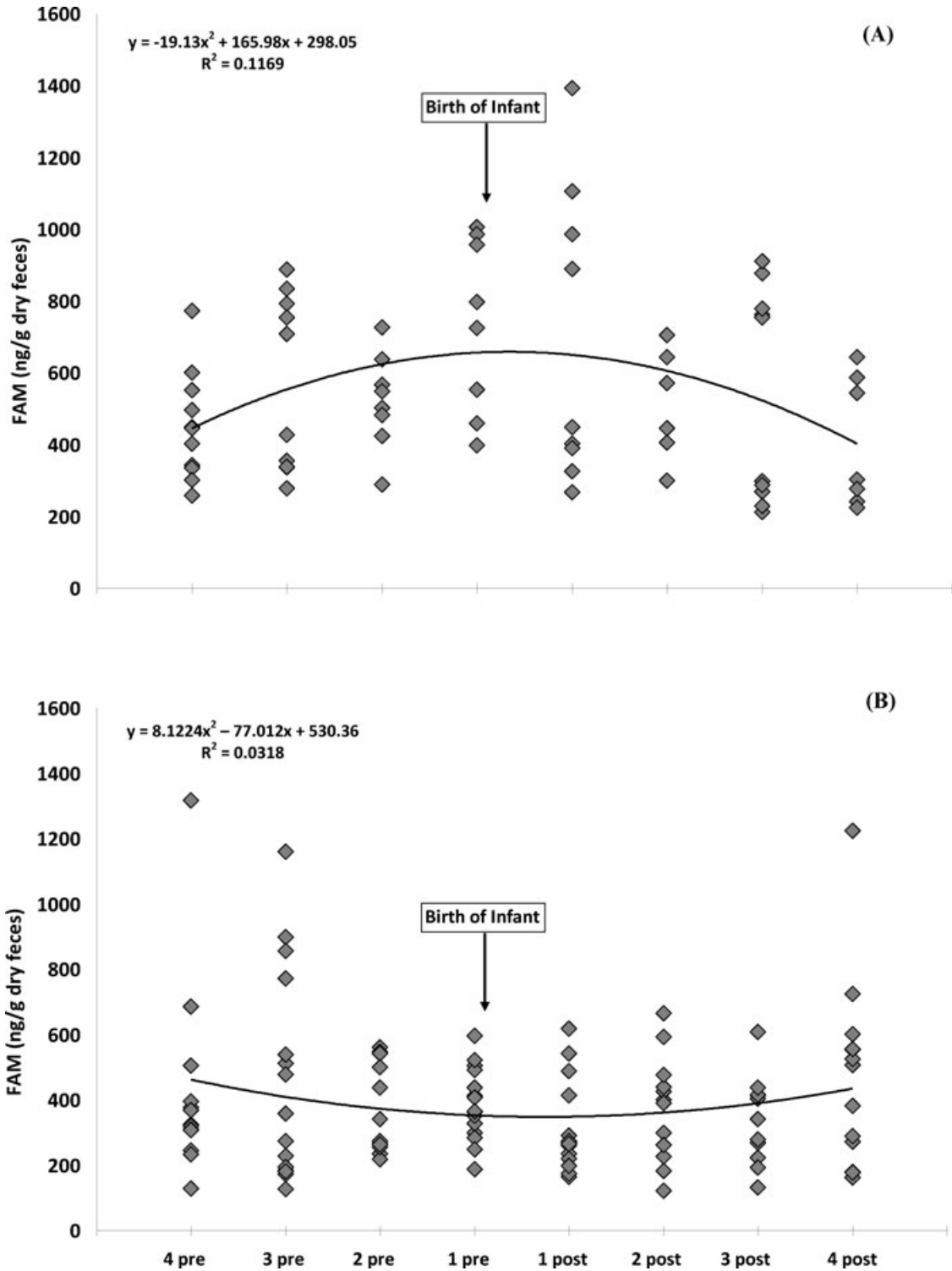
Fig. 3. Patterns of FAM concentrations during the 8-week peripartum period. Scatter plots show every data point (closed diamonds) representing daily FAM concentrations within each week pre- and postpartum, and the pattern of change over time is indicated by nonlinear regression trend line (solid black lines) for (A) siamangs (n = 2) and (B) gibbons (n = 3).

the gibbon fathers. In contrast, however, an infant transfer (or the transfer of primary infant-carrying responsibilities from the mother to the father) occurred for both siamangs in this study, although

the timing of the first observation of infant-carrying behavior varied between the siamangs. This variation in timing has been observed in both the wild [Chivers, 1974; Lappan, 2005] and captivity
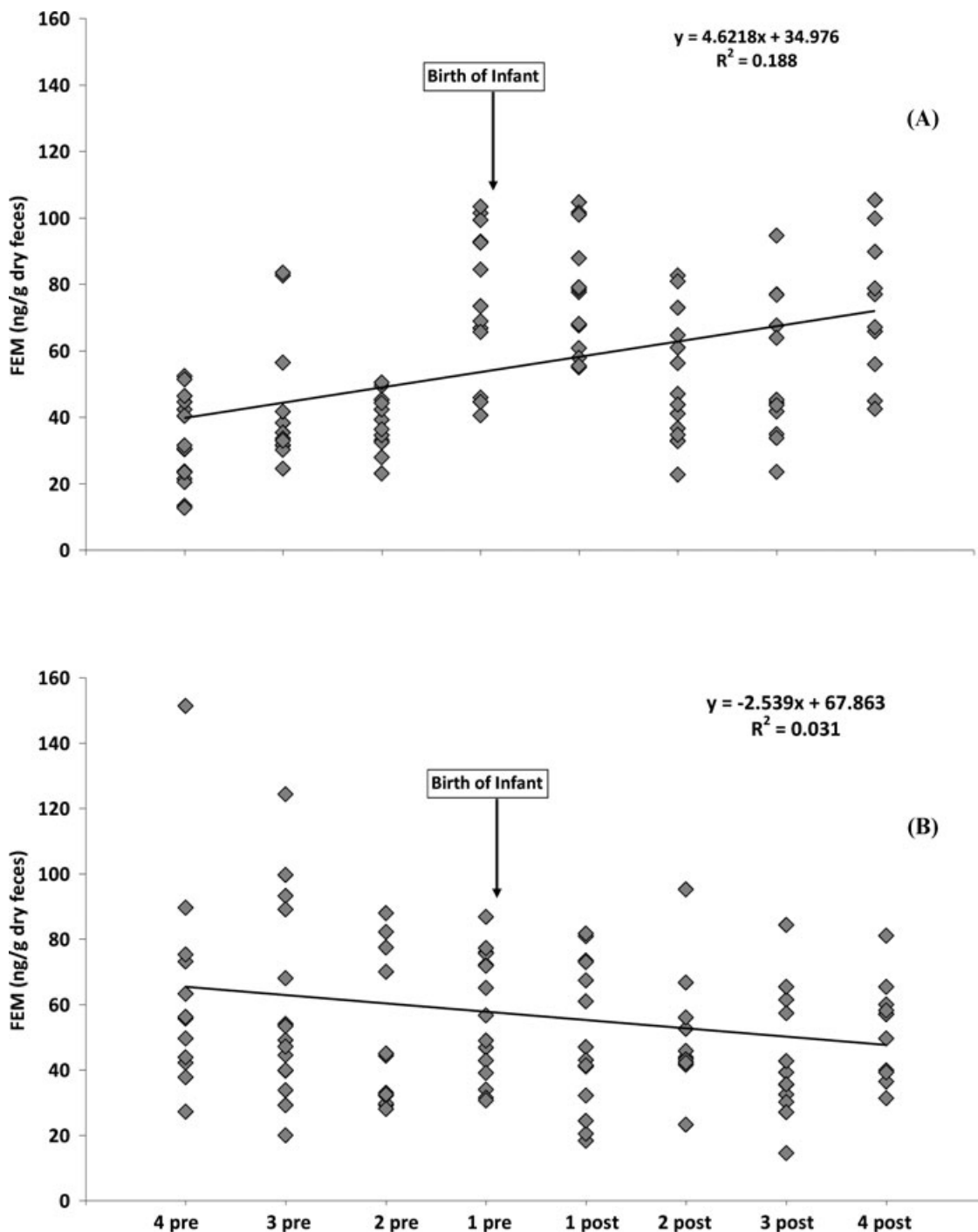
Fig. 4. Patterns FEM concentrations during the 8-week peripartum period. Scatter plots show every data point (closed diamonds) representing daily FEM concentrations within each week pre- and postpartum, and the pattern of change over time is indicated by linear regression trend lines (solid black lines) for (A) siamangs (n = 2) and (B) gibbons (n = 3).

[Alberts, 1987; Dal Pra and Geissmann, 1994; Dielentheis et al., 1991], with male siamangs reportedly beginning to carrying infants anytime between 6 and 12 months postpartum. It has been suggested that the transfer of carrying responsibilities from the mother to the father observed only in siamangs is driven in part by an increase in the percent of time fathers spend in proximity to and interact with infants, along with decreased mother–infant contact and proximity, beginning at about 6 months postpartum and continuing through the second year of infant life [Alberts, 1987; Chivers, 1974; Dal Pra and

Geissmann, 1994; Dielentheis et al., 1991; Lappan, 2005].

Although siamangs and gibbons did not differ in overall mean percent father–infant proximity, an increase in proximity, demonstrated by significantly different monthly measures, was found in siamangs over the postpartum period. Correspondingly, and in contrast, lower FAM concentrations were found in siamangs in the late postpartum, when infant carrying was observed, compared to higher FAM concentrations in the prepartum and early postpartum period. On the other hand, both percent father–infant proximity and FAM concentrations remained relatively constant throughout the postpartum period in gibbons. This finding suggests that in siamangs, low FAM concentrations may be associated with the need to trade aggression, necessary for territory defense or mate guarding, for infant tolerance while developing a relationship that will eventually lead to infant contact once infant carrying begins [Lappan, 2005].

Support for the finding of a reciprocal relationship between increasing proximity and paternal care (infant carrying) and decreasing androgens in the postpartum comes from studies of callitrichids and humans. A similar pattern of change in androgens during the postpartum period in fathers has been demonstrated in *Sa. oedipus*, another biparental primate. Ziegler et al. [2004] demonstrated that testosterone concentrations in fathers decreased during the postpartum period, except around the time of postpartum estrus. It has also been reported that human fathers have lower testosterone concentrations than men who are not fathers [Gray et al., 2006, 2007]. Storey et al. [2000] and Fleming et al. [2002] have reported that androgens decrease with an increase in paternal care several weeks postpartum in human fathers.

Evidence from studies with *C. jacchus*, another biparental primate, suggest a possible causal relationship between paternal care in the form of infant carrying and androgen concentrations. Prudom et al. [2008] and Ziegler et al. [2009a, 2011] found that fathers demonstrate lower testosterone concentrations following direct stimuli from an infant. Similarly, Dixson and George [1982] discovered that males had lower testosterone concentrations after they had carried infants. In *C. kuhlii*, Nunes et al. [2000, 2001] demonstrated that males who carried infants at high rates versus low rates had lower testosterone concentrations males.

Although a relationship between infant carrying and decreased androgens implies that androgens may interfere with paternal care in these species, including siamangs, by potentially mediating aggression toward infants and mates and reducing parenting behavior [Hegner and Wingfield, 1987; Ketterson and Nolan, 1992; Wynne-Edwards and Timonin, 2007], one must be cautious when interpreting the causality of the hormone-behavior relationship. The majority of research investigating causality has been unable to produce strong evidence of directionality of the relationship [Wynne-Edwards and Reburn, 2000]. Therefore, it is difficult to determine whether a decrease in FAM concentrations is responsible for infant carrying in siamangs or whether changes in infant and male behavior leading up to the infant transfer may cause a decrease in FAM concentrations.

Hormonal Patterns Surrounding Infant Birth

The pattern of change in FAM concentrations around birth was characterized by an inverted U-shaped pattern, whereas for gibbons, the pattern of change, though not statistically significant, showed the opposite pattern of change in FAM concentrations. Siamangs demonstrated the highest androgen concentrations during 1-week prepartum, which may be related to potentially higher levels of aggression that may be important for protection and defense of mother and infant immediately following birth [Wynne-Edwards and Timonin, 2007]. The decrease in androgen concentrations observed in siamangs by 4-week postpartum, and continuing through the later postpartum period, may become more important to infant care once infant carrying begins. This is again in accordance with other studies of biparental primates [*Sa. oedipus*, Ziegler et al., 2004; human fathers, Fleming et al., 2002; Storey et al., 2000], in which testosterone concentrations decreased several weeks postpartum.

Interestingly, the trend found in the pattern of change in FAM concentrations surrounding birth in gibbon fathers showed a pattern somewhat opposite of that found in siamangs. In these males, the lowest androgen concentrations were found at about 1 month prepartum. For gibbons, maintaining low androgen concentrations and potentially related levels of aggression around birth might help to ensure the safety of the infant. This would be an evolutionarily stable strategy and has been suggested for some biparental species [Wynne-Edwards and Timonin, 2007].

These findings suggest that the role androgens play in male behavior immediately around infant birth may vary between siamangs and gibbons. For siamangs, protection of the infant may be more important than infant tolerance, but then likely changes as the period of infant carrying approaches in the late postpartum. For gibbons, perhaps infant tolerance is more important than infant protection at birth, but then because androgen patterns remain constant in the postpartum, it is possible that androgens may then play a greater role in protection and defense of female and offspring.

Mean FEM concentrations were highest during 4 weeks postpartum and lowest during 4 weeks prepartum in siamang males, resulting in an

increasing linear trend in estrogens surrounding birth. In contrast, there was a trend in gibbons for FEM concentrations to decrease linearly from the pre- to postpartum, with the highest mean concentrations observed during 4 weeks prepartum. The potential role estrogens plays in mediating in paternal care in biparental primates has not been extensively studied, but Berg and Wynn-Edwards [2001] did find that in human fathers, estrogen concentrations increased from before birth to after birth of an infant. Preliminary evidence from nonprimate species (i.e. rodents) suggests that estrogens may promote paternal care of offspring [male rats, castrated and primed with both estrogen and progesterone, Rosenblatt and Ceus, 1998]. It is possible, therefore, that estrogens may also play a role in facilitating paternal behavior in siamangs, though we must again remain cautious when interpreting our results because of small sample size.

In *C. kuhlii*, estrogen may interfere with the expression of paternal behavior [Nunes et al., 2000], and so it is surprising that gibbons showed a similar pattern of change in estrogen, with lower concentrations observed 4 weeks postpartum than at 4 weeks prepartum. However, it is important to note that at 4 weeks prepartum, there was one sample of high estrogen concentration that could have been an outlier (Fig. 4B), suggesting that if removed, the pattern of change in estrogen might have instead remained constant in gibbons during this timeframe. Although it was beyond the scope of the present study, further monitoring of FEM concentrations beyond 4 weeks postpartum through the infant transfer in siamangs is warranted given the observed pattern of change in FAM concentrations during this period. It is also important to note that peripheral estrogen concentrations may not necessarily reflect the role estrogen plays in the brain, especially because of aromatization of testosterone to estrogen (consequently acting on estrogen receptors in the brain), and so, the patterns of FEM concentrations observed in gibbons and siamangs in this study need to be interpreted with caution.

The mean change from baseline FGM concentrations during 1 month post-partum differed between siamangs and gibbons. Siamangs exhibited a greater increase from baseline, suggesting that elevated FGM concentrations following birth may be related to heightened awareness of infant presence or preparedness for future infant-carrying behavior. Previous studies of primates [Fleming et al., 1997; Maestripieri et al., 2009; Nguyen et al., 2008] have determined that moderately elevated glucocorticoids are associated with the quantity or quality of maternal care. It is possible that this pattern emerged in siamangs but not gibbons because infant survival is likely more directly dependent on paternal care (infant carrying) in siamangs. Additionally, previous research with other species that exhibit infant-carrying behavior [nonprimates: male meerkats, *Suricata suricatta*, Carlson et al., 2006 and primates: cotton-top tamarins, *Sa. oedipus*, Almond et al., 2008] has demonstrated that glucocorticoid concentrations increase during the weeks surrounding the birth. Therefore, it is possible that the presence of elevated FGM concentrations during 1 month postpartum for siamangs is related to a need to adapt quickly to a change in the environment (i.e. a newborn infant) by mobilizing energetic reserves to facilitate a response to infant cues [Sapolsky et al., 2000]. A contrasting relationship between glucocorticoids and paternal care has also been reported in *C. kuhlii*, in which fathers exhibited a decrease in glucocorticoids immediately following the birth of an infant [Nunes et al., 2000].

The presence of juveniles in both siamang family groups represents an additional variable that must be taken into consideration when interpreting these findings. However, despite the presence of a juvenile requiring care from its father, both siamangs in this study exhibited infant-carrying behavior. Although Wynne-Edwards and Timonin [2007] conclude from their research and from previous studies of rodents, nonhuman primates, and humans that there are insufficient published data to suggest a causal role for steroid hormones in paternal behavior, the results from this study present an intriguing possibility that there is at least an association between differences in hormone patterns in siamangs and gibbons and differences in paternal care.

CONCLUSION

Siamangs and gibbons are closely related taxa, sharing very similar ecological constraints and selective pressures. However, they also differ substantially from each other when it comes to paternal care. A few researchers have hypothesized about this key difference and examined possible causal factors, but this is the first investigation of the potential role of hormonal proximate mechanisms leading to paternal care differences between siamangs and gibbons. In this study, we determined that there may be a relationship between androgens, estrogens, and glucocorticoids, and paternal care differences in hylobatids. A decrease in androgens corresponding to an increase in father–infant proximity in the late postpartum, along with an increase in estrogens surrounding birth, and an increase in glucocorticoids during 1-month postpartum, in siamangs but not in gibbons, suggests that differences in paternal care could be hormonally mediated. In conclusion, these results highlight the need for additional research to determine proximate and ultimate determinants of differences in paternal care among the Hylobatidae to further elucidate factors driving the evolution of paternal care in the only biparental apes.

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