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Female behavioral proceptivity functions as a probabilistic signal of fertility, not female quality, in a New World primate



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ABSTRACT

The interests of males and females in mating contexts often conflict, and identifying the information conveyed by sexual signals is central to understanding how signalers manage such conflicts. Research into the information provided by female primate sexual signals has focused on exaggerated anogenital swellings as either reliable-indicators of reproductive quality (reliable-indicator hypothesis) or probabilistic signals of fertility (graded-signal hypothesis). While these morphological signals are mostly confined to catarrhine primates, these hypotheses are potentially widely applicable across primates, but have not been tested in taxa that lack such morphological signals. Here, we tested these hypotheses in wild black capuchins (*Sapajus nigritus*), a species in which females lack morphological sexual signals but produce conspicuous behavioral estrous displays. Specifically, we examined the proportion of time different females spent producing these signals with respect to measures of female quality (dominance rank, parity, age-related fecundity and cycle type) and in relation to the timing of fertility, as determined by analysis of fecal progesterone. Time spent displaying did not vary across females based on measures of female quality, but increased with the approach of ovulation. Further, male mating effort varied according to the timing of female fertility. Proceptive behaviors in this species thus meet predictions of the graded-signal hypothesis, providing the first support for this hypothesis based solely on behavioral signals.

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Introduction

In contrast with most mammalian taxa, primate sexual behavior is characterized by a relaxation of female sexual activity from impending ovulation. At a proximate level, this is explained by a decreased importance of hormonal regulation on the physical ability of primate females to engage in sexual behavior (Wallen et al., 2003). Human females lay on an extreme of this continuum, by showing continual sexual receptivity and concealed ovulation with a lack of conspicuous signals of fertility (Dixon, 2012). However, rhythmic changes in sexual activity occur in many monkeys and apes, and a number of studies have shown that female fertility periods among non-human primates tend to be associated with a sharp peak in copulations and with an increased sexual interest in males (Deschner et al., 2004; Engelhardt et al., 2005; Heistermann et al., 2008, but see Heistermann et al., 2001). Similarly, in human females, recent studies have challenged the idea of concealed ovulation by providing evidence for subtle, yet perceivable, signals of fertility that appear to trigger men's preferences towards women during

the fertile phase (Bobst and Lobmaier, 2014; but see Havlíček et al., in press). Taken together, these studies suggest that in non-human primates, and to some extent in humans, the degree of interaction between female fertility signaling and male mating response is still a crucial point in understanding the evolution of sexual behavior.

Attempts to explain the inter-specific variability in the extent and precision to which sexual signals provide information on female fertile phase in non-human primates have focused on the selective pressures that favor females advertising versus concealing fertility. In this context, the patterning of fertility signals among primates appears to represent an adaptive response of females to specific features of mating and social systems, such as intensity of male intra-sexual competition, reproductive skew and tenure length (Kappeler and van Schaik, 2004). Importantly, infanticide by males is a strong selective force potentially shaping female sexual behavior in many primate taxa (van Schaik et al., 2004). Less clear is how fitness benefits to females, the accuracy of fertility signaling, and male-imposed constraints interact to determine inter-specific variation in primate sexual signals (but see Higham et al., 2012). To address this point, a wealth of studies have investigated the adaptive function of sexual swellings (i.e., conspicuous enlargement of the female anogenital skin) in several primate species that live in different social systems, from single male

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units to multimale–multifemale groups, where the adaptive advantage of fertility signaling is dictated by the extent to which males constrain female sexual behavior (van Schaik et al., 2004). This body of work has focused on testing two main competing hypotheses: the reliable-indicator hypothesis (Pagel, 1994) and the graded-signal hypothesis (Nunn, 1999).

The reliable-indicator hypothesis suggests that sexual swellings in females are costly handicaps that honestly signal female lifetime reproductive quality, and which incite males to differentially allocate their mating effort to consort females with larger swellings (Pagel, 1994). In contrast, the graded-signal hypothesis (Nunn, 1999) proposes that swellings are probabilistic signals of intra-cycle variation of fertility, with swelling size varying in accordance with the probability of ovulation and peaking in size around the time of ovulation. Following gradual increases in swelling size, dominant males mate-guard females around peak swelling, whereas other males gain access to females when the probability of fertility is lower. The result is that females simultaneously confuse and bias paternity among males, which can act jointly to dissuade infanticide (Nunn, 1999; van Schaik et al., 2004). While support for the reliable-indicator hypothesis has been mixed (Domb and Pagel, 2001; Huchard et al., 2009; Zinner et al., 2002), the graded-signal hypothesis has received growing support in a number of studies of Old World monkeys and apes (e.g., Barelli et al., 2007; Brauch et al., 2007; Deschner et al., 2004; Higham et al., 2008, 2012).

Despite the almost singular focus on sexual swellings for testing the reliable-indicator and graded-signal hypotheses, it is clear that animal communication often occurs in multiple modalities (Higham and Hebets, 2013; Liebal et al., 2013; Partan and Marler, 1999). For instance, along with (or instead of) morphological components, females may signal their reproductive state via proceptive behaviors that include non-morphological sexual displays characterized by, for example, gestural or vocal components. Studies of species in which females provide both morphological and behavioral sexual displays have produced inconsistent results. In particular, in contrast to the widespread evidence that sexual swellings serve as graded signals of female fertility, the link between proceptive behaviors and the female fertile phase is more equivocal (Aujard et al., 1998; Brauch et al., 2007; Deschner et al., 2004; Engelhardt et al., 2005; Higham et al., 2009, 2012; Reichert et al., 2002). Most support for such a link comes from species in which swellings are less conspicuous or absent, with frequencies of female socio-sexual behaviors increasing around the time of ovulation, and thus potentially providing some information about female fertility to males (Engelhardt et al., 2005; O'Neill et al., 2004; Wallen et al., 1984; but see Fürtbauer et al., 2011; Heistermann et al., 2001). While on a proximate level it is clear that proceptive behaviors are to some extent associated with changes in the secretion of estrogen and progesterone during the ovarian cycle (Engelhardt et al., 2005; Wallen et al., 1984; Zehr et al., 1998; but see Wallen, 2001), the information that these displays potentially convey and their impact on male mating behavior in the absence of additional morphological displays remain unclear. Examining the extent that proceptive behaviors conform to predictions of the reliable-indicator or graded-signal hypothesis may prove illuminating in this respect.

Species characterized by female behavioral proceptivity but lacking confounding morphological signals of fertility provide an ideal study system to investigate the function of proceptive behaviors. Importantly, a test on such species may provide a stronger test of the graded-signal hypothesis, as morphological signals are likely physiologically constrained such that their waxing and waning are necessarily graded, whereas behavioral signals can quickly transition from a total lack of production to high intensity production. However, no study has yet attempted to test these two competing hypotheses in a species that advertises fertility exclusively through non-morphological signals.

Robust (or tufted) capuchin monkeys (genus *Sapajus*, formerly *Cebus apella*) represent an ideal study model in which to test the two hypotheses, as females of these species lack morphological signals of

fertility but are highly sexually proceptive via conspicuous displays that consist of persistent and prolonged visual (gestures and facial expressions) and vocal signals (Carosi and Visalberghi, 2002; Di Bitetti and Wheeler, in press; Janson, 1984). Previous studies of female proceptive displays in a captive group of robust capuchins have shown a strong relationship between progesterone levels and female sexual behavior, and have initially pointed to proceptive displays as functionally equivalent of sexual swellings (Carosi et al., 1999; Carosi and Visalberghi, 2002). Further, these primates are characterized by stable multimale–multifemale groups, and a high risk of infanticide by males following within-group male takeovers (Izar et al., 2007; Janson et al., 2012; Ramirez-Llorens et al., 2008), suggesting that females would likely benefit by confusing paternity among group males. At the same time, females have been suggested to gain direct benefits for themselves and their offspring, in terms of access to monopolisable food resources, by concentrating paternity to the alpha male (Janson, 1984, 1986). Females may therefore compete with one another for access to these preferred males, thus potentially benefitting from signaling their reproductive quality. These signals of female proceptivity seem to be plausible candidates for an honest signal of female quality, given that their production appears to affect their daily activity budget by increasing energy expenditure while decreasing energy intake via reduced foraging time (Janson, 1984). As a consequence, higher quality females should be able to afford to spend more time engaged in production of these signals. Further, while it is unclear how costly their production is relative to that of sexual swellings, recent theoretical work has proposed that reliable/honest signals can evolve even with low or close to zero signal costs (Higham, 2014; Számadó, 2011). Thus although the adaptive significance of these intense displays of female proceptivity remains unclear, both the reliable-indicator and graded-signal hypotheses provide potential explanations for the evolution of these signals.

The present study aimed to, first, assess the association between proceptive displays and ovulatory cycle phase (i.e., pre-perioovulatory, perioovulatory and post-perioovulatory phase) in wild female black capuchins (*Sapajus nigritus*, synonymous with *C. apella nigritus*) (aim 1). Second, we tested whether between-female variation in the intensity of proceptive displays is related to aspects of female reproductive quality (as predicted by the reliable-indicator hypothesis; Pagel, 1994) (aim 2) or whether within the perioovulatory period, the intensity of proceptive displays gradually increases in accordance with the timing of ovulation (as predicted by the graded-signal hypothesis; Nunn, 1999) (aim 3). Further, given support for one or both of these two hypotheses, we were interested in the male responses to these signals, and thus tested whether males showed increased mating effort in response to either the approach of ovulation, or females of higher reproductive quality (aim 4).

Material and methods

Field site and subjects

The data for this study were collected in Iguazú National Park, Argentina (25°40' S, 54° 30' W). Black capuchins (*S. nigritus*) live in stable multimale–multifemale groups of 7 to 44 individuals, characterized by female philopatry and male dispersal (Janson et al., 2012). Alpha males are both socially and spatially central in the group, maintaining feeding and mating priority (Janson, 1984, 1990; Tiddi et al., 2011, 2012). Black capuchin females at the study site can be sexually receptive throughout the year, but show high seasonality in reproduction, with proceptive displays and mating activity occurring mainly between May and early September (Janson et al., 2012). Females rarely conceive in two consecutive years if the previous year's infant survives to the next mating season, making infanticide by males a viable reproductive strategy (Ramirez-Llorens et al., 2008). Male–female sexual relationships are characterized by female initiation of consortships with males (mainly the alpha male; Janson, 1984, 1986; Lynch Alfaro, 2005). Even

with some degree of variation across populations, females mate promiscuously and copulations with lower-ranking males are common (Janson, 1984; Lynch Alfaro, 2005), although the temporal relation between copulations with different males and female ovulation is largely unknown.

This study was carried out over four consecutive mating seasons (2010 to 2013) from early May until late August each year. Subjects were 20 sexually mature, individually-recognized females belonging to three habituated groups (Macuco, Rita, and Spot groups); among these, 16 females were observed cycling during at least one mating season (see Table S1 in the supplement). Long-term demographic records on female reproductive outcome are available (Janson et al., 2012), which were used to quantify some aspects of female quality.

Behavioral observations

Behavioral observations were conducted daily by BT and several assistants from approximately 7:00 to 18:00 using focal animal and ad libitum sampling (Martin and Bateson, 2007). Instantaneous focal sampling was used at 1 min intervals to note the occurrence of “proceptive displays”, consisting of visual (facial expressions, body postures, and manual gestures) and/or vocal signals (Carosi et al., 1999; Carosi and Visalberghi, 2002; Janson, 1984). Visual signals included eyebrow raising, chest rubbing, head cocking, and grinning, and were defined in accordance with the species-specific behavioral repertoire (for an example, see the video link in the online supplement; for a complete list and detailed definitions of the behaviors sampled, see Carosi et al., 1999; Carosi and Visalberghi, 2002). Two types of vocalizations have been described as being highly specific to female estrus, both of which are easily discernable from non-estrous vocalizations by ear (Di Bitetti and Wheeler, *in press*; see also Carosi and Visalberghi, 2002; Janson, 1984). Both are characterized by a series of short notes, with one (“piripipi”) being a high frequency call given nearly continuously by proceptive females following a male, while the second (“raspy estrous call”) is a noisy, lower-frequency, higher-amplitude call in which the notes blend to form a single noisy sound (Di Bitetti and Wheeler, *in press*) (see Fig. S1 for spectrograms and the video link in the online supplement). For the current study, we distinguished these call types from other call types (but not from one another) by ear and refer to them both as “estrous calls”. These calls are invariably uttered in association with visual displays (with at least grins always produced simultaneously with these calls; Carosi and Visalberghi, 2002), while visual displays are sometimes produced without simultaneous production of calls. Further, visual displays are perceivable only to individuals in close range to the signaler owing to vegetation density, whereas estrous calls are potentially perceivable by individuals out of visual contact. We thus differentiated between instances in which females showed proceptive displays consisting of 1) visual signals only and 2) both visual and vocal signals.

During observation days when no females were proceptive, focal samples lasted 5 min and were randomized across female subjects using a permutation schedule of at least 1 h between consecutive samples of a given female. Focal samples on proceptive females lasted for 30 min, and a concerted effort was made to sample females in both the morning and afternoon on days in which they were proceptive. A total of 263 h of focal observation were conducted on 16 cycling females (mean = 8.2 h; range: 3.2–16.5 h).

Outside of focal samples, we attempted to follow proceptive females continuously from dawn to dusk in order to ensure adequate hormone sampling through the period of behavioral proceptivity, and to record the occurrence of any copulations and solicitations by females directed to males. At least two observers monitored the group simultaneously in order to maximize the likelihood of observation of these events. A copulation was defined as a heterosexual single or multi-mount sequences that include repeated male thrusts occurring within a 1 hour period (single ejaculation pattern, with mounting activity resumed usually

after an hour from the previous ejaculation: Carosi and Visalberghi, 2002). The dense habitat made it impossible to observe all copulations, although our protocol of closely following females throughout their proceptive period minimized this effect and should have eliminated any biases associated with missing copulations involving certain males.

Fecal sample collection, hormone analysis, and assessment of female fertile phase

In total, 1740 fecal samples were collected opportunistically (between 7:00 and 18:00) for monitoring reproductive state in the 20 study females, including samples collected from non-cycling, cycling, and pregnant females. The current analyses are based on 409 samples collected with sufficient frequency to allow a reliable determination of the timing of ovulation.

Fecal samples not contaminated with urine were collected within 30 min of defecation and stored in polypropylene tubes. Samples were stored in an ice bag for up to 6 h, and were then stored at -15°C until hormone metabolites were extracted (normally within one to seven days) in the field laboratory following the procedure described in Wheeler et al. (2013). Specifically, an aliquot of between 0.4 and 0.6 g of wet, homogenized feces was vortexed with 5 mL of 80% ethanol for 5 min. In cases in which less than 0.3 g of feces were available, only 3 ml of ethanol was used for extraction in order to keep the ethanol-to-feces ratio consistent across samples (see Palme et al., 2013). Samples were then centrifuged at 2000 RPM for 10 min and 1 ml of the supernatant was removed and stored in a 2 ml polypropylene tube wrapped with laboratory film. The fecal sample was then dried completely and its dry weight measured. Extracts were stored in a refrigerator (for samples collected in 2010) or freezer (for samples collected during subsequent years) until transported at ambient temperatures to the German Primate Center, where they were stored at -20°C until hormone analysis.

Fecal extracts were analyzed for concentrations of progesterone metabolites (5α -reduced-20-oxo pregnanes, 5-P-3OH) by enzyme-immunoassay (EIA). The measurement 5-P-3OH has previously been applied successfully to monitor female ovarian function and to assess the timing of ovulation in numerous primate taxa (Barelli et al., 2007; Heistermann et al., 2001, 2004; Higham et al., 2012; Möhler et al., 2005). Because a previous study on female capuchins showed that estrogen profiles appeared to match those of progestogens, and because no clear pre-ovulatory estrogen peak was detectable in fecal samples of cycling animals (Carosi et al., 1999), the timing of ovulation was solely based on progestogen measurements. Fecal extracts were diluted 1:150 to 1:2000 (depending on concentration) with assay buffer before being measured by EIA as described by Dehnhard et al. (2010). Sensitivity of the assay at 90% binding was 2.4 pg. Intra- and inter-assay coefficients of variation (CV), calculated from replicate determinations of high- and low-value quality controls, were 6.9% and 14.8% (high) and 7.7% and 16.0% (low), respectively.

Ovulation in robust capuchins has been shown to occur on the same day as the rise in urinary progesterone (Nagle et al., 1979). In addition, the rise in fecal progesterone metabolites occurs within 0 to 24 h of the urinary progestogen rise (Carosi et al., 1999). Taken together, these findings allowed us to conservatively define a 2-day window in which ovulation was most likely to occur, consisting of the day of the defined rise in fecal 5-P-3OH levels (Day 0; the rise being defined as an increase in levels above a threshold value of 2 SDs above the preceding mean baseline level; see Engelhardt et al., 2004; Heistermann et al., 2001) and the day before (also labeled Day 0). Accordingly, and in agreement with numerous other studies (e.g., Deschner et al., 2004; Engelhardt et al., 2004; Heistermann et al., 2001), the fertile phase (perioviulatory period, POP) in each ovarian cycle was defined as the period comprising the 2-day ovulation window and the two preceding days (Day -1 , and -2) in order to consider sperm life span (Brauch et al., 2007). Based on this, days preceding (day -5 to -3) and following (day 1 to 3) the

fertile phase in which females showed sexual displays were defined as the pre-fertile period (pre-POP) and post-fertile period (post-POP), respectively. Conception and non-conception cycles were differentiated based on the presence of elevated luteal phase progesterone levels maintained for periods longer than 4 weeks (Heistermann et al., 2008).

Over 70 periods of proceptivity were observed over the study period. Among these, we were able to match behavioral data with hormone profiles for 42 cycles from 16 females. However, we restricted our analyses based on the timing of ovulation and female fertile phases to those 29 cycles from 14 females in which daily fecal samples during the periovulatory period were available, allowing for determination of ovulation with the highest degree of precision.

Data analysis

Data on behavioral proceptivity were transformed into daily proportion of instantaneous points (i.e., proportion of time) in which each study female showed proceptive displays. Prior to testing the reliable-indicator and graded-signal hypotheses, we investigated how closely the production of proceptive displays follows cyclical variations in female ovarian function. We addressed this point with two regression models based on within-subject centering, where proportion of time producing proceptive displays (visual and/or vocal signals) or estrous calls only were entered as the dependent variable, and female cycle phases (pre-POP, POP and post-POP) as the independent categorical variable. Within-subject centering allowed us to exclude between-subject effects from within-subject effects by centering repeated observations around the specific subject mean value, discounting between-subject variation (van de Pol and Wright, 2009). Observation points here were daily values of proceptive displays for each female ($N = 210$ observation days on 14 females) during pre-POP, POP and post-POP days within 29 ovarian cycles. Female identity was entered in the models as a fixed effect.

After assessing the relationship between proceptive displays and ovarian function, we tested predictions of the main hypotheses. First, to test the reliable-indicator hypothesis, we determined whether the proportion of time producing proceptive displays was positively associated with indicators of female reproductive value by running two linear multilevel mixed-effects regressions. These models allow multiple data points from the same subjects to be used but avoid aggregation bias stemming from data organized in nested structures on different levels of aggregation (Raudenbush, 1988). In these models, proceptive displays or estrous calls only were entered as the dependent variable, while indicators of female quality (i.e., dominance rank, parity, age-related fecundity and cycle type) were entered as independent variables. Female dominance ranks were included as ordinal values and were calculated by entering all observed agonistic interactions including aggressions, spatial displacements and submissive behaviors into a dominance matrix to generate a dominance hierarchy using Matman 1.1 (Noldus Information Technology 2003) (De Vries et al., 1993). Data on parity and fecundity were obtained using long-term reproductive records available on the study population. Specifically, age-related fecundity was obtained using long-term reproductive data and was expressed as a function of both female birth rate (infants/year) and female age class (as in Janson et al., 2012). In addition, whether or not a given cycle resulted in conception was entered as an independent variable. Female identity nested inside group identity was entered into this model as a random effect. Because this analysis did not require detailed timing of ovulation, data points ($N = 135$) were daily observations of proceptive displays for 16 females during POP from 42 profiled cycles.

To test the graded-signal hypothesis, we examined whether females tended to gradually increase the proportion of time producing proceptive displays in accordance with the days relative to ovulation. We ran two within-subject linear regressions with either the proportion of time spent producing proceptive displays or producing estrous calls

only as the dependent variable, and the day relative to ovulation as the independent variable (from day -2 to day 0 from ovulation). Observation points were daily proportions of time producing proceptive displays during POP. This analysis was restricted to those 29 cycles (93 observation days from 14 females) with daily hormone sampling during POP.

Finally, we explored male mating behavior and its relationship with female cycle phases based on the occurrence of observed copulations for each observation day. First, we focused on determining if copulations were associated with female fertile phases using a within-subject logistic regression with the occurrence of copulations as the dependent variable and female cycle phase (pre-POP, POP, and post-POP) as the independent variable. Data points ($N = 215$) were daily observations on 14 females during all cycle phases associated with the 29 profiled cycles. In addition, we tested whether the timing of copulations by males depended on their dominance status using a similar logistic regression model in which the occurrence of copulation by alpha males relative to other males (i.e., whether the group's alpha male copulated on a given day with a copulation by any male) was the categorical dependent variable, and day relative to ovulation the independent variable. Data points ($N = 60$) in this analysis were observation days associated with copulations by these two classes of males during the 29 profiled cycles.

Mixed models were run using Stata 10.0 (StataCorp, College Station, TX.). Significance was set at $P < 0.05$ and all reported probabilities are two-tailed.

Results

Sexual behavior and hormone profiles in cycling females

Periods of behavioral proceptivity lasted 3.68 ± 1.63 days (mean \pm SD, $n = 70$) ranging from 1 to 8 days (Fig. S2). Fecal progesterone metabolite profiles in the 42 cycles studied showed a clear cyclical pattern with clearly distinguishable follicular and luteal phases (Fig. S3), allowing for identification of cycle phases (pre-POP, POP and post-POP).

The proportion of time females spent producing proceptive displays was significantly associated with female fertile phase, being higher during POP than pre- or post-POP (for all proceptive displays, $N = 210$ observation days on 14 females: POP vs. Pre-POP: $\beta = -0.47$, $t = -10.84$, $P < 0.001$, POP vs. Post-POP: $\beta = -0.40$, $t = -8.40$, $P < 0.001$; for estrous calls only, $N = 210$ observation days on 14 females: POP vs. Pre-POP: $\beta = -0.29$, $t = -6.90$, $P < 0.001$, POP vs. Post-POP: $\beta = -0.22$, $t = -4.68$, $P < 0.001$).

Sexual behavior as a signal of female quality

Female proceptive displays were not associated with any of the analyzed parameters of female reproductive quality; this was true for both proceptive displays overall and when considering only estrous calls (see Table 1).

Sexual behavior as a probabilistic signal of ovulation

Within POP, the time spent by females showing proceptive displays gradually increased with the approach of ovulation ($N = 93$ observation days on 14 females; $\beta = 0.07$, $t = 2.28$, $P = 0.023$; Fig. 1), although the same did not hold true when considering only the production of estrous calls ($N = 93$ observation days on 14 females, $\beta = 0.02$, $t = 0.56$, $P = 0.525$; Fig. 1).

Male mating patterns in relation to female cycle phases

Copulations were significantly more likely to occur on days associated with POP compared to pre- and post-POP (POP vs. Pre-POP: $N = 215$ copulations among 14 females, $\beta = -2.23$, $t = -4.70$, $P < 0.001$; POP

Table 1

Results of multilevel mixed-effects models testing the reliable-indicator hypothesis for capuchin female proceptive displays using measures of female quality as the independent variables and daily proportion of time producing either a) all proceptive displays, or b) estrous calls only as the dependent variable.

Variables	Coefficient	SE	z	P
<i>a)</i>				
Female rank	−0.01	0.02	−0.57	0.566
Female fecundity	−0.13	0.79	−0.17	0.866
Parity	−0.04	0.05	−0.22	0.824
Cycle type ^a	0.03	0.07	0.36	0.717
<i>b)</i>				
Female rank	−0.03	0.02	−1.54	0.124
Female fecundity	−0.28	0.79	−0.35	0.725
Parity	−0.01	0.05	−0.17	0.868
Cycle type ^a	0.01	0.07	0.11	0.835

N = 135 observations (42 cycles from 16 females); female ID nested inside group ID entered as a random effect.

^a Conceptive or non-conceptive cycle.

vs. Post-POP: N = 168, $\beta = -1.93$, $t = -4.02$, $P < 0.001$; Fig. 2a). Further, compared to other group males, copulations by alpha males increased significantly with the approach of ovulation (N = 60 observation days on 14 females, $\beta = -0.47$, $t = -2.41$, $P = 0.016$; Fig. 2b).

Discussion

This study is the first to test the reliable-indicator and graded-signal hypotheses in a species lacking morphological signals of female fertility. By combining behavioral observations with endocrinological measures, we found a significant correlation between female proceptive displays and the periovulatory phase (POP) of the female ovarian cycle. These findings support the idea that such behavioral signals function as indicators of female ovarian activity in this species, consistent with a previous study with captive robust capuchins (Carosi et al., 1999). Specifically, our data show that both visual and vocal components of female proceptive displays cyclically follow the onset of POP. The broad repertoire of sexual displays in black capuchin females, therefore, functions as

the major component of female proceptivity, and is comparable to behavioral displays in other primate taxa (e.g., Engelhardt et al., 2005; Kendrick and Dixson, 1983).

Our findings demonstrate that capuchin females varied their proceptive displays in accordance with predictions of the graded-signal hypothesis (Nunn, 1999), with rates of production of proceptive displays providing a day-by-day probability of ovulation within the periovulatory period. Considering the multimodal aspects of capuchin female sexual signals, our findings indicate that visual signals tracked variation in the timing of ovulation more closely than did the auditory signals. On a proximate level, behavioral displays of proceptivity (both visual and auditory) in female primates are often closely linked to changes in estrogens associated with approaching ovulation (e.g., Aujard et al., 1998; Engelhardt et al., 2005; Wallen et al., 1984; but see Brauch et al., 2007). Our findings suggest that this may hold true also for the visual displays that female capuchin monkeys show during proceptivity, while the motivation to produce estrus calls seems to be less influenced by the hormonal milieu. However, the relationship between estrogen and female proceptivity is difficult to infer in the present case; in some New World monkeys (including capuchins) patterns of estrogens parallel profiles of progesterones with elevated levels present during the luteal phase, with no clear periovulatory changes in estrogen levels discernible (e.g., Carnegie et al., 2005; Carosi et al., 1999; Ziegler et al., 1993b). Further study is thus needed to determine whether there is a causal relationship between estrogens and the observed behaviors.

While it has been suggested that the combination of facial expressions, body postures and estrous calls are redundant (Carosi et al., 1999), our results suggest that the differential pattern of multimodal composite signals may function to provide males with information about their fertility with different levels of accuracy that vary in accordance with the spatial proximity that females maintain with different males (see Higham et al., 2009). Given the differences in the distances over which visual and auditory signals are propagated in dense forest, it may be that estrous calls provide a crude signal of female fertility to all group males without the more precise information related to the timing of ovulation (see also Pfefferle et al., 2008; Townsend et al.,

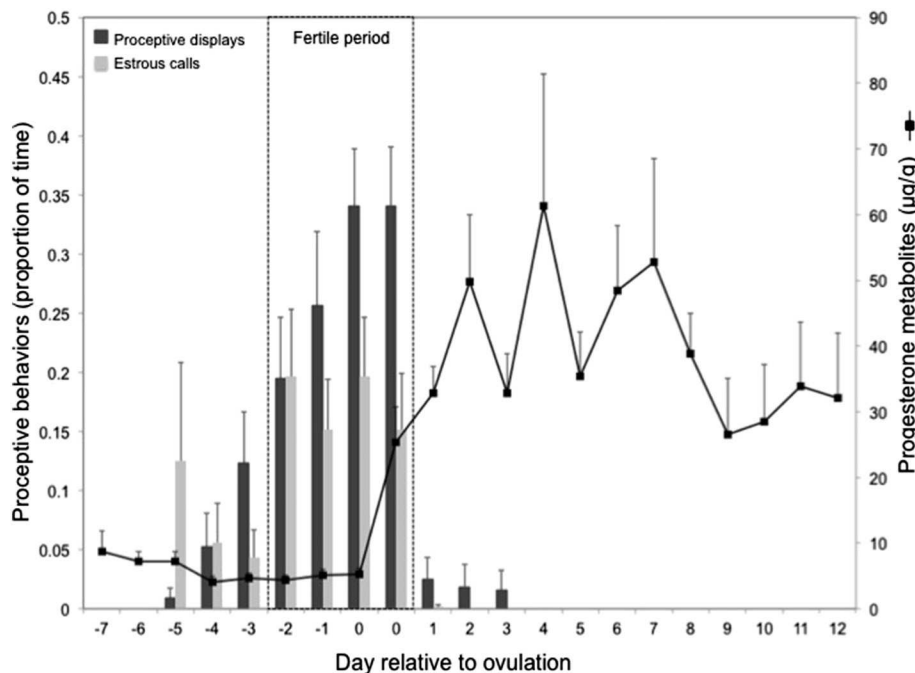


Fig. 1. Composite profiles of progesterone metabolites are shown in association with the daily proportion of female proceptive displays. Dark gray bars represent daily proportion of time producing all proceptive displays; light gray bars depict daily proportions of estrous calls only. Values are derived from 29 ovarian cycles of 14 females and are shown as mean \pm SE.

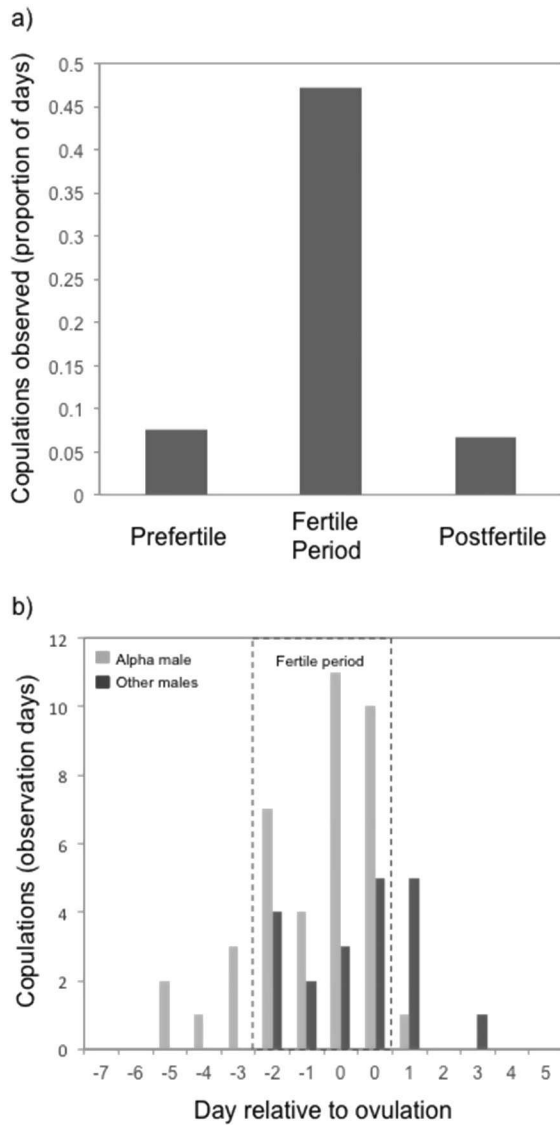


Fig. 2. The occurrence of copulations relative to female cycle phase and to the day relative to ovulation. a) Proportion of days in which copulations occurred during the three different phases: Pre-POP, POP, and Post-POP. b) Distribution of the daily occurrence of observed copulations that included the alpha male or only non-alpha males. Data are derived from daily observations on the three study groups.

2011), with this precise information being received only by males within visual contact. This provides the specific target male with an advantage in terms of the information available to him. Such differing functions of visual and acoustic displays may in fact be advantageous for females that attempt to advertise their fertility to all group males, but at the same time encourage monopolization by dominant males when conception is most likely. Therefore, such a multimodal system may provoke not only an enhanced response by all males, but a modulated response related to the timing of ovulation only in dominant males that more successfully monopolized females during their periovulatory periods. However, it is also possible that the production of the two different estrous call types, acoustic parameters within these call types (e.g., Charlton et al., 2010), or fine aspects of facial expressions or gestures (see Liebal et al., 2013) may vary in a way that is consistent with either the graded-signal or reliable-indicator hypothesis, and future studies should thus address this possibility.

Likewise, signals or cues in additional modalities beyond those examined here may also convey information regarding female reproductive state or quality. For example, chemical signals may play

an important role in between-sex olfactory communication. Although scent marking in New World primates has been mainly investigated in relation to territoriality with little data available regarding its function of advertising female reproductive state (see Heymann, 2006), a study in cotton-top tamarins, a species that lacks behavioral indicators of the periovulatory period, provided evidence for a direct olfactory cue of ovulation that affects male sexual behavior (Ziegler et al., 1993a). Recent studies in both robust and gracile capuchins, however, have found no evidence in support of a potential function of scent marking within socio-reproductive contexts (Carnegie et al., 2005; Schino et al., 2011).

Our findings provide the first evidence for a graded-signal of female fertility based exclusively on behavioral signals. As such, they suggest that proceptive displays, like morphological signals in catarrhine primates, can evolve as a female mating strategy that simultaneously confuses and concentrates paternity among males, which would be advantageous given the risk of infanticide by group males in this population (Janson et al., 2012). Understanding how widespread this phenomenon is awaits further investigation, although some previous studies provide initial evidence (e.g., proceptive tongue-flicking in common marmosets, *Callithrix jacchus*; Kendrick and Dixson, 1983). Such graded behavioral signals of female fertility are potentially interesting because their production, at a proximate level, is largely explained by the central effect of hormones on female behavioral proceptivity (Dixson, 2012; see also above), which may allow for more flexibility in production than those based on a peripheral effect of reproductive hormones (as for sexual swellings). Females may thus have more flexibility to adopt alternative signaling tactics, from concealing ovulation to deceptively signaling its occurrence, based on current social context (but see Zinner and Deschner, 2000 for apparently flexible production of swellings in baboons), ultimately influencing female fitness. Some support for this context-dependent flexibility of female proceptive displays in our study population comes from observations of post-conceptive mating in association with male takeovers (Ramirez-Llorens et al., 2008; B. Tiddi, pers. obs.). Taken together, these findings provide evidence in the study species for some degree of emancipation from hormonal control on the ability to mate and support the occurrence of hormonally modulated sexual displays and interest that flexibly respond to the specific socio-sexual context (Wallen, 2001). Therefore, further studies should aim to investigate via experimental settings how such flexibility affects the production of these behavioral signals across different social contexts (see Wallen, 2001).

In contrast to the predictions of the reliable-indicator hypothesis (Pagel, 1994), we found that female proceptive displays were not associated with measures of reproductive quality in female black capuchins. Specifically, there were no significant relationships between time spent performing proceptive displays and either cycle type (i.e., conceptive vs. non-conceptive cycles) or aspects of female quality (i.e., dominance rank, parity, age-related fecundity), although such information might be conveyed in finer aspects of the signals (e.g., specific acoustic parameters) not examined here. It is important to point out, however, that other aspects of female quality might be actually more important for males when choosing a potential female, such as female resistance to parasite diseases or female genetic richness (Zinner et al., 2002). Therefore, it may be important for future studies to address the importance of alternative measures of female reproductive quality that closely match the current body condition rather than life history parameters of females (see Huchard et al., 2009). Finally, our results may be explained by a lack of an adaptive benefit of male mate choice in our study population. Indeed, female robust capuchins appear to prefer to mate with alpha males (Janson, 1984, 1986), but the low copulation frequency and long periods of male avoidance of female solicitations (Carosi et al., 2005; Lynch Alfaro, 2005) may create a condition where male costs associated with mating with many females might be relatively low, resulting in nearly all females ultimately gaining access to the preferred alpha male during their fertile periods.

According with the prediction that proceptive displays in black capuchin females provide information about the timing of ovulation, males optimized their mating activity by copulating with females almost exclusively during their fertile phase with alpha males in particular intensifying their mating activity as ovulation approached and the likelihood of conception was maximal. As proceptive displays in our study subjects seemed to be highly context-specific (i.e., their occurrence and intensity peaks during their fertile phase) and copulations occurred in association with female fertile phase, it is reasonable to conclude that the production of these displays results in a clear increase in female attractivity for males. Overall, the temporal patterns of male responses suggest that target males are able to use these signals to assess female reproductive phase (i.e., discern timing of ovulation) and in turn to synchronize their mating efforts accordingly.

In conclusion, our study provides evidence in support of the existence of a graded-signal system of female fertility in black capuchin monkeys. This system seems likely to have evolved in response to the risk of infanticide posed by males, especially during periods of group instability (Janson et al., 2012; Ramirez-Llorens et al., 2008). Interestingly, black capuchin females lack two features that have been proposed to play a crucial role for the evolution of female counter-strategy to male infanticide: prolonged periods of mating activity and sexual swellings. Our study suggests that further investigations on the evolution of graded-signals of fertility in primate species should include also species that lack morphological signals, and that behavioral signals should be more widely considered in order to understand the adaptive significance of sexual communication across primate species.

Ethics statement

This study complies the guidelines of the research institutes involved and was approved by of the appropriate authorities in Argentina (Administración de Parques Nacionales, permit #: NEA 158 bis Rnv 4).

Conflict of interest

There are no known conflicts of interest associated with this publication.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yhbeh.2015.07.011>.

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