

Original Article

Estrous synchrony in a nonseasonal breeder: adaptive strategy or population process?

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The idea that female mammals can manipulate the duration of each other's estrus in an effort to influence the degree of synchrony between their periods of sexual receptivity is a persistent and popularly held one. It is frequently cited as proof of pheromonal communication in humans and often invoked by models of female reproductive strategies more generally. Yet, to date, no tests of the evolutionary arguments put forward by proponents of the phenomenon have been undertaken. We addressed this deficit with an analysis of the reproductive demography of wild female chacma baboons, where variance in the temporal distribution of female receptivity is known to occur. Specifically, we tested the predictions that this variance will reflect female attempts to minimize 1) the risks of being monopolized by a single male or 2) the intensity of interfemale competition for males. Using model comparison, we found no evidence that male number or operational sex ratio had any influence on the distribution of female receptivity, the number of females in estrus, or the duration of female sexual swellings. Indeed, when modeling estrous overlap and cycling female number, we found that a simple nondeterministic model provided the best fit. We conclude, therefore, that variance in the temporal distribution of female receptivity is indicative of nothing more than a population process and that socially mediated synchrony is not a tangible adaptive phenomenon. *Key words:* female receptivity, population process, sexual selection, socially mediated synchrony. [*Behav Ecol* 23:573–581 (2012)]

INTRODUCTION

The temporal distribution of female fertility is one of the principal factors mediating both intra- and intersexual interaction. It governs not only the intensity of competition within the sexes but also the tenor of the social dynamics between them (Kvarnemo and Ahnesjö 1996). Its effects are most obviously seen at the taxonomic level, where it can reliably predict broad differences in the nature and structure of mating systems (Emlen and Oring 1977; Mitani et al. 1996; Clutton-Brock 2007). It is also the case, however, that the behavior of both sexes is sensitive to temporal variance in female receptivity occurring within a given period of mating (Hausfater 1975; Jirotkul 1999; Clark and Grant 2010). This sensitivity has led some to suggest that selection should favor females who are able to adjust the temporal distribution of their receptive periods facultatively (Ridley 1986; Cowlshaw and Dunbar 1991; Zinner et al. 1994; Stockley 1996; Nunn 1999b). Doing so may enable them to manipulate intra- and intersexual dynamics to their advantage by reducing, for example, the risks of being monopolized by dominant males or the intensity of interfemale competition.

These suggestions invoke the notion of socially mediated estrous synchrony, where females are predicted to use pheromonal communication to manipulate the duration of each

other's estrus in an effort either to induce or avoid entrainment (McClintock 1971). Although a number of studies, on an array of species, claimed to have observed such behavior (e.g., McClintock 1978; Handelsmann et al. 1980; Wallis 1985; French and Stibley 1987; Weller A and Weller L 1993) as well as the pheromonal mechanisms thought to underpin it (Schank and McClintock 1997; Stern and McClintock 1998), the extent to which variance in estrous synchrony reflects the existence of an adaptive strategy appears questionable, however, not least because for nearly every study reporting an effect, there is another that has failed to find one (e.g., Gattermann et al. 2002; Matsumoto-Oda and Kasuya 2005; Tobler et al. 2010). Furthermore, many of the original studies claiming to have observed the phenomenon have been subsequently discredited on methodological grounds (see for e.g., Wilson 1992; Schank 2000, 2001a, 2001b, 2004; Yang and Schank 2006). Ultimately, the current consensus seems to be that socially mediated synchrony, if it exists at all, is likely to be rare. If true, it must also be the case that the models of sexual selection that invoke the phenomenon have limited application. To date, however, no attempts to interrogate these models have been made, and thus, despite their regular invocation, their value remains an open question.

Our objective here then is to provide the first formal test of the 2 prevailing evolutionary accounts of socially mediated synchrony. The first and more popular of these argues that because females typically favor polyandry but are often vulnerable to sexual coercion, they should dynamically adjust levels of estrous synchrony to mitigate the risks of being monopolized by a single typically dominant male (Ridley 1986; Zinner et al. 1994, 2004; Stockley 1996; Nunn 1999a, 1999b). The

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rationale being that by overlapping their receptive periods, females create an opportunity cost which makes it impossible for a single male to monopolize access to all potentially fertile females. As a result, he is forced to choose between mating exclusively with one female or mating with multiple already mated females. Because it is assumed that females will seek a relatively low degree of overlap and ovulation tends to occur in the latter stages of receptivity (e.g., Deschner et al. 2004; Geschiere et al. 2007; for review, see Nunn 1999a), the expectation is that dominant males will elect to compromise paternity certainty for mate number; an expectation borne out by numerous empirical studies (for review, see Nunn 1999a). Following the same logic, the second model we examine predicts that females should seek to avoid estrous overlap precisely because it forces males to choose between them (Pereira 1991; Schank 2004). The argument being that by maintaining a state of asynchrony, females are able to minimize the risks of interfemale competition and thus increase their chances of mating exclusively with the highest quality male, as measured by, for example, dominance.

Ultimately, then, both models argue that females will actively adjust levels of estrous synchrony in response to changes in the potential for individual males to secure exclusive mating access. As such, they both make clear and testable predictions about the covariance between changes in estrous overlap and factors governing the intensity of intermale competition, most notably the operational sex ratio (OSR: the ratio of males to sexually receptive females; Emlen and Oring 1977) and the size of the male cohort. Model 1 (reduce monopolization risk) predicts that levels of overlap should be a negative function of the intensity of intermale competition; specifically, overlap should increase in response to a decrease in male number (MN) and/or an increase in the OSR. This is because as MN decreases and/or the OSR increases, so the intensity of intermale competition for mating access decreases, and concomitantly, females become increasingly vulnerable to monopolization. At its most basic, Model 2 (reduce interfemale competition) predicts that females should seek a permanent state of asynchrony, simply because estrous overlap always forces males to choose between females. A more nuanced prediction, however, is that, because the quality of the best male should increase with the size of the male cohort, female efforts to avoid overlap should increase with MN.

It has been suggested that variance in estrous cycle length undermines the evolutionary potential for socially mediated synchrony because it prevents consistent phase matching (Schank 2000, 2001b). Therefore, we begin our analysis with an examination of both inter- and intrafemale variance in cycle length. We assess the ability of models incorporating the effects of monopolization risk and interfemale competition to account for this variance. Following this, we then determine the value of these models in describing variance in the occurrence of estrous overlap and the number of cycling females. The reason for modeling cycling female number is that in nonseasonal breeders, the system on which models of synchrony typically focus, females are not guaranteed to resume cycling at the same time. Therefore, if they are able to manipulate levels of entrainment, then they must also be able to influence each other's return to estrus. In order to determine the relative merits of the available deterministic models, we pit them against those considering nondeterministic effects. Specifically, within our candidate model set, we include models predicting that changes in estrous overlap and cycling female number are the result of 1) stochastic shifts in female reproductive condition (population process models) and 2) environmental seasonality (ecological models). We detail these as well as the rationale underlying them in the MATERIALS AND METHODS.

MATERIALS AND METHODS

Study species and site

We pursue our objectives using a longitudinal analysis of the reproductive demography of wild female chacma baboons (*Papio hamadryas ursinus*). Chacma baboons, like all savanna baboons, are characterized by a multimale multifemale mating system in which numbers can vary widely, but where there are typically more adult females than adult males (Bulger 1993; Weingrill et al. 2003). Breeding is nonseasonal, and virtually, all mating occurs in the context of mate guarding, which occurs throughout a female's period of receptivity (Clarke, Henzi, et al. 2009). A period that lasts around 10 days and is clearly signaled by the achievement of maximum tumescence in the exaggerated sexual swellings females develop during each of their estrous cycles (Clarke, Barrett, et al. 2009). Chacma baboons are particularly well suited to the objectives of this study for 2 reasons. First, their mating system is characterized by profound intersexual conflict over polyandry: Females have clearly been selected to pursue matings with multiple males per period of receptivity and in response males have evolved strategies aimed at preserving mating exclusivity (Clarke, Henzi, et al. 2009; see also Clarke, Pradhan, et al. 2009). In addition, it is also characterized by sufficient variance in the ratio of sexually mature males to sexually receptive females to make interfemale competition biologically relevant (Clarke et al. 2010).

Data come from a 7-year continuous census (1998–2004) of one troop (Table 1) of wild chacma baboons located at the De Hoop Reserve, South Africa (for details, see Barrett et al. 2004). During this period, the number of adult males and females and the reproductive condition of all sexually mature females were, where possible, recorded on a daily basis (see also Clarke et al. 2008). Only data from sexually mature nonnatal males and parous females are presented.

Response variables

Duration of swelling

We used the duration of swelling turgescence to assess intra- and interfemale cycle variability. Our rationale was that because the duration of the follicular phase and, concomitantly, the duration of sexual swelling are the primary source of variance in cycle length in primates (Stern and McClintock 1998; Tobler et al. 2010), facultative adjustments in the timing of receptivity should be most evident in this phase.

Estrous overlap and cycling female number

When modeling both the degree of estrous overlap and the number of cycling females, we used the change in their value across months, $x_t - x_{t-1}$, lagged onto the immediately preceding month's values for all explanatory variables as the response variable (see also Clarke et al. 2008). By doing so, we were able to model the temporal association between changes in explanatory and response variables explicitly and thus clearly distinguish between deterministic and nondeterministic effects. We quantified the degree of estrous overlap in

Table 1
Details of study group over the period May 1998 to September 2003

	Mean \pm SD	Minimum	Maximum
Group size	38.340 \pm 3.177	31	49
MN	5.701 \pm 2.219	1	11
Female number	10.442 \pm 1.650	6	15

a given month as the proportion of that month that the receptive periods of 2 or more females overlapped.

Following others (Hausfater 1975; Bulger 1993; Gesquiere et al. 2007), in the absence of hormonal data, we defined a female's receptive period as the 10 days prior to the last day of sexual swelling tumescence. Although the norm in studies of savannah baboon mating systems has been to use a 7-day window of receptivity, we considered 10 days because available evidence suggests that female receptivity is more protracted in chacma than compared with their East African counterparts (Clarke, Barrett, et al. 2009; Clarke, Henzi, et al. 2009). To be conservative, however, we also ran all analyses using receptive windows ranging from 14 to 7 days and found no difference in results.

Analysis

Model comparison

Although popular throughout the behavioral sciences, null hypothesis testing and the attendant use of *P* values were developed for the analysis of randomized controlled experimental data and have well-known limitations when applied to observational data (e.g., Cohen 1994; Anderson et al. 2000; Garamszegi et al. 2009). Consequently, we used an information-theoretic approach, which aims to quantify the relative ability of multiple models to approximate a true and complete description of a process (Burnham and Anderson 1998). With this approach, the emphasis then moves away from identifying "significant" covariates and instead centers on distinguishing between a range of plausible models that embody a number of potentially competing hypotheses.

We used Akaike's information criteria (AIC) with small sample size correction, AIC_c , which provides an estimate of a model's explanatory power, while controlling for its complexity (Burnham and Anderson 1998; Johnson and Omland 2004), where the smaller the value obtained the better the fit. We assessed the probability that a model's ranking within the candidate model set was robust by calculating Akaike weights, w_i (Burnham and Anderson 1998). Rather than take measures of effect size and precision from only best-fit models, we based inferences on estimates taken from all models, using model averaging. Model-averaged parameter estimates, β , are found by devaluing parameter estimates from each model by the model's associated Akaike weight and then summing estimates of a particular variable across all models (Burnham and Anderson 1998). To assess the precision of these estimates, we used unconditional variances, which incorporate standard sampling variance from a particular model and variance in model selection uncertainty (Burnham and Anderson 1998). Model selection uncertainty is given by the difference between an individual model's estimate of a parameter and the model-averaged estimate. Adding this to the sampling variance from the model, devaluing by the Akaike weight and summing across all models yields an unconditional variance estimate. From this, standard errors and 95% confidence intervals (CI) can then be calculated as normal.

Candidate model set

We formulated a suite of models aimed at identifying whether observed variance in the response variables was a function of deterministic processes driven by male demography, seasonal changes in habitat quality, or stochasticity in female reproductive condition. We explicitly define and number these models in the text below, where + denotes the inclusion of a variable as a main effect alone.

Deterministic effects. Current theory argues that females should facultatively adjust estrous overlap in response to changes in their susceptibility to monopolization by a single

male and/or variance in the intensity of competition for mates. Therefore, we considered models containing the effects of MN and OSR: (i) MN, (ii) OSR, and (iii) OSR + MN. We defined MN as the number of males present in the troop for at least 15 days of a given month (see also Clarke et al. 2008) and OSR as the ratio of adult nonnatal males to adult (non-nulliaprous) females with swellings in the phase D-10 to D-1, where D refers to days before detumescence, so that D-10 to D-1 is the 10-day period prior to this event (see also Clarke, Henzi, et al. 2009).

Environmental effects. We considered the effects of mean monthly rainfall (MR) and temperature (MT), with models (iv) MR, (v) MT, and (vi) MR + MT. The rationale for considering these variables was that the development of exaggerated sexual swellings in female baboons is reliant on an edema that is known to be sufficient to affect a female's water consumption (Clarke 1940). Consequently, the ability to commence and maintain tumescence may be contingent on seasonal fluctuations in water availability, which are profound at our study site. When modeling the duration of swelling, in cases where a turgescence phase occurred within the confines of a single calendar month, we used the monthly mean for temperature and rainfall. If, however, a period of swelling bridged 2 calendar months, the mean across these months was used.

Population effects. To assess population effects, when modeling estrous overlap and cycling female number, we considered models containing measures of background female reproductive demography. The most basic of these predicts that monthly changes in overlap and cycling female number were simply the product of a classic population process, where overlap across months represents a Markov chain and the degree of change observed in 1 month (DG_t) is dependent only on the degree of change seen in the previous month: (vii) $DG_t - 1$. In addition, we also considered the effects of cycling female number (CF) when modeling estrous overlap and absolute female number (AF), when modeling cycling female number: modeling estrous overlap, model (viii) CF, and modeling cycling female number, model (viii) AF. The rationale being that changes in female reproductive condition may reflect nothing more than stochasticity in broader underlying measures of female demography.

When modeling swelling duration, we considered all of the above models, except those including population effects (i.e., i to vi). Instead of these, we included models accounting for potential sources of inter- and intrafemale variance. First, we numbered the cycle from which a given swelling duration was recorded relative to the number of cycles experienced before the female in question conceived, (vii) CC, where CC denotes cycles to conception. In addition, we included models considering the effects of female rank (viii) FR, age, in years, as a linear effect (ix) FA and as a polynomial (x) $FA + FA^2$ and all their possible combinations. The female hierarchy was calculated on the basis of approach and supplants within dyads and was found to be linear and transitive. We treated rank as a 3-level categorical variable—high, mid, and low rank (see also Clarke, Barrett, et al. 2009; Clarke, Henzi, et al. 2009).

We controlled for the repeated sampling of females by allowing intercepts to vary by "Female ID" (Gelman and Hill 2007). Initially, we considered models that included both individual intercepts and individual slopes across age for each female. However, examination of the variance components and likelihoods revealed that the inclusion of individual slopes provided no additional insight. Therefore, all model comparisons are based on models allowing only individual intercepts. For all response variables, in addition to the models detailed above, we also included a model containing only the intercept. All models included an intercept except the population process model, which predicts that change occurs at random.

We used generalized linear models with Gaussian errors and an identity link function when modeling estrous overlap and cycling female number and a generalized linear mixed model with Gaussian errors and an identity link function when modeling swelling duration. We tested the underlying assumptions of normality, homogeneity, and independence of errors. Although the independence and homogeneity of residuals were satisfied in all models, the assumption of normally distributed errors was not. This is, however, not a concern if the objective, as was ours, is the estimation of effect size and precision and the sample size is reasonably large, which ours was (Gelman and Hill 2007; See also Fox 1991); although, it must be noted that not all texts would agree with this position (e.g., Crawley 2007). Generalized linear mixed models carry the additional assumption that the sample of the group-level effect is drawn from a normal distribution and requires that estimates of the group means (best linear unbiased predictors or Bayesian Shrinkage estimates) are normally distributed. Diagnostics confirmed that this was true for all hierarchical models run. Details of all diagnostics for all models are provided in the Supplementary Material.

We present results for only those top models that collectively accounted for 95% of the available Akaike weight (Burnham and Anderson 1998). All analyses were carried out using the freely available R statistical software (R Development Core Team 2009) with the “bbmle” (Bolker 2010) and “lme4” (Bates et al. 2008) packages.

RESULTS

Cycle variability

We were able to determine the length of the swollen period for a total of 66 estrous cycles from 12 females, yielding 5.5 cycles per female. On average, females experienced 3.538 ± 0.364 estrous cycles per interbirth interval. For any given cycle, females were swollen for 19.643 ± 0.449 days, with 12 days being the shortest period of swelling observed and 32 days the longest. Although some of this variance was associated with interfemale differences, most appeared to stem from intrafemale variation (interfemale variance = 1.129; intrafemale variance = 12.719; see also Figure 1).

Model comparison revealed that variance in swelling duration was best described by a model containing the number

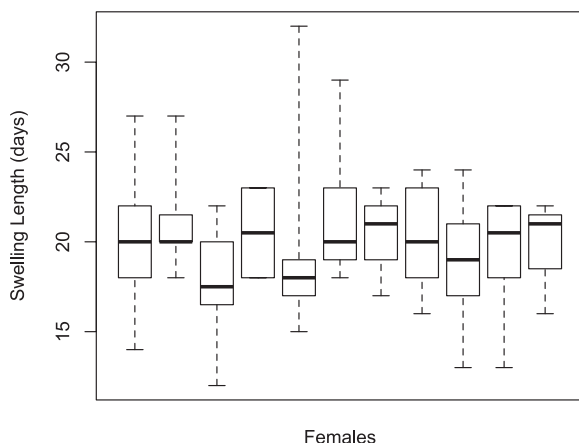


Figure 1

Box-and-whisker plot of variance in swelling duration exhibited by each female in the sample. Ends of whiskers indicate minimum and maximum observed values, tops and bottoms of boxes indicate upper and lower quartiles, and horizontal lines within boxes describe the median.

of cycles until the conceptive cycle was experienced (Table 2). Model-averaged parameter estimates indicate that this variable had only a negligible effect (CC: $\beta \pm$ unconditional 95% CI = -0.010 ± 0.522), despite being present in all top models (Table 2). The effects of MN ($\beta \pm$ 95% CI = 0.057 ± 0.420), OSR ($\beta \pm$ 95% CI = 0.076 ± 1.032), female age (FA: $\beta \pm$ 95% CI = 0.009 ± 0.032 ; FA²: $\beta \pm$ 95% CI = 0.00001 ± 0.0005), and rank (high rank: $\beta \pm$ 95% CI = 0.068 ± 0.138 ; mid rank: $\beta \pm$ 95% CI = -0.021 ± 0.155 ; and low rank: $\beta \pm$ 95% CI = 0.021 ± 0.155) were all weak.

The occurrence of overlap

We were able to calculate the proportion of the month that the receptive periods (D-10 to D-1) of 2 or more females overlapped for a total of 51 consecutive months (Figure 2a). Levels of overlap exhibited a spiking pattern, with positive and negative changes occurring with near equal frequency (positive = 17, negative = 18) and alternately (Figure 2b). Periods of stasis were rare, and there was never any cumulative increase or decrease in levels of overlap across months (Figure 2b). Overlap between conceptive cycles was observed in only 4 of the 51 months, yielding an average overlap of 0.951 ± 0.494 days per month.

Model comparison revealed that the degree of monthly change in estrous overlap (conceptive + nonconceptive cycles) was best characterized by a model containing only the degree of change observed in the previous month (AIC_c = 310.960, K = 2, w_i = 0.974). The extremely high weight of this model indicates that it could be considered the best fit, within the context of the candidate set, with reasonable certainty. Model-averaged parameter estimates suggest that the degree of change observed in the previous month was a negative predictor of the degree of change observed in the current month (DG_{t-1}: $\beta \pm$ 95% CI = -0.429 ± 0.303). That is, if there was an increase in overlap in 1 month, then there was likely to be a decrease in the next and vice versa (Figure 3). In addition, all models predicted that the OSR ($\beta \pm$ 95% CI = -0.002 ± 0.589) and MN ($\beta \pm$ 95% CI = 0.003 ± 0.133) had no discernible effect on subsequent changes in levels of estrous overlap (Figure 4).

Cycling female number

Over a 77-month period (May 1998 to September 2004), the number of cycling females varied widely from month to month (Figure 5a). As with estrous overlap, positive and negative changes in this number occurred both with equal frequency (positive = 21; negative = 21) and alternately across months (Figure 5b).

Model comparison revealed that changes in cycling female number across months were best characterized by a model containing the degree of change observed in the previous month (Table 3). As with estrous overlap, model-averaged estimates predict that the degree of change observed in the previous

Table 2

Parameter number, K, log-likelihood, log \mathcal{L} , AIC_c, and Akaike weights, w_i , for those models of the duration of sexual swelling tumescence collectively carrying 95% of the available Akaike weight

Model	K	log \mathcal{L}	AIC _c	w_i
CC	4	-133.854	275.708	0.557
CC + FA	5	-133.602	277.204	0.222
CC + FR	6	-133.262	278.524	0.093
CC + FA + FA ²	6	-133.583	279.166	0.067
CC + FR + FA + FA ²	7	-133.089	280.177	0.032

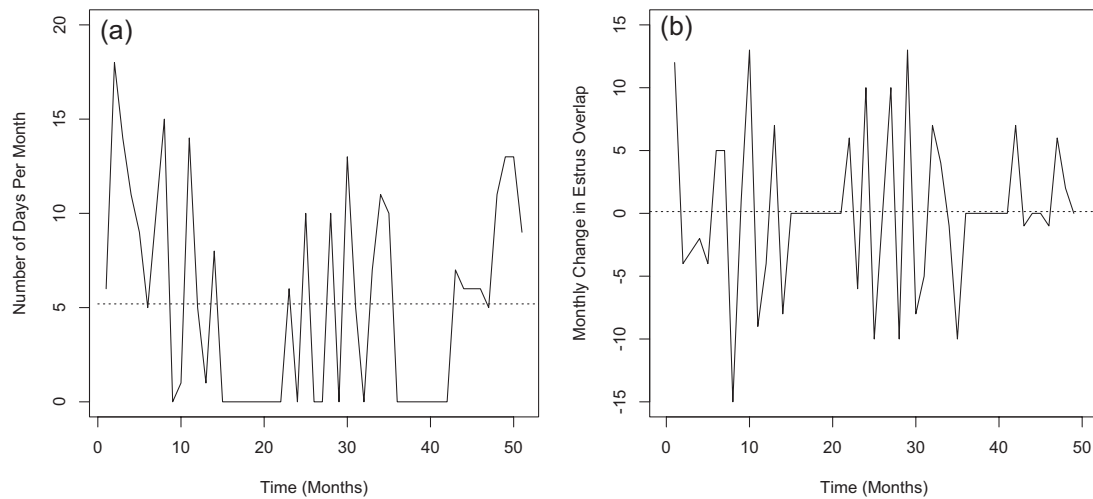


Figure 2

(a) Number of days estrous overlap per month for the period May 1998 to August 2003. Dashed horizontal line indicates mean overlap (5.196 ± 0.751) across entire period. (b) Monthly change in estrous overlap. Dashed horizontal line indicates mean monthly change (0.001 ± 0.028) across entire period.

month was a negative predictor of the degree of change observed in the current month (DG_{t-1} : $\beta \pm 95\% \text{ CI} = -0.294 \pm 0.288$; Figure 6). The high weight of this model indicates that the probability of it being the best fit within the context of the candidate set was extremely high (Table 3). This was further attested to by the very weak effects of MN ($\beta \pm 95\% \text{ CI} = -0.001 \pm 0.029$) and OSR ($\beta \pm 95\% \text{ CI} = -0.003 \pm 0.316$), variables invoked by the second- and third-ranked models (Table 3; see also Figure 7).

DISCUSSION

Our data show that female chacma baboons exhibit substantial variation in the relative timing of both their periods of sexual receptivity and their return to estrus. An examination of

possible covariates revealed that none of this variation could be accounted for by changes in the potential for females to become monopolized by a single male nor in the intensity of interfemale competition for mates. Specifically, we showed that monthly changes in the degree of estrous overlap and cycling female number were not meaningfully associated with variance in MN nor OSR. Indeed, the best predictor of both was the degree and direction of change in their own value observed in the preceding month, suggesting that the occurrence of estrous overlap was simply a product of nondeterministic changes in female reproductive condition. Ultimately then, using over 6 years of demographic data, we fail to find any evidence of females facultatively adjusting the relative timing of their sexual receptivity.

The main objective of our analysis was to evaluate the prevailing evolutionary model of socially mediated synchrony. By demonstrating a lack of any temporal association between the risks of monopolization and subsequent changes in the degree of estrous overlap, we provide the first direct evidence that this model may be of limited utility. This finding may be unique to chacma baboons, but, given that the chacma social system exemplifies that in which socially mediated synchrony is expected to evolve—nonseasonal breeder, multimale multifemale, and highly social cohesive groups—this seems unlikely. It seems reasonable therefore to ask, given the clear benefits that females could derive from being able to manipulate the intersexual dynamic, why such an ability may not have evolved?

Prevailing critiques emphasize the role of constraints, highlighting in particular the difficulty of maintaining entrainment in the face of inter- and intrafemale variability in cycle length (Wilson 1992; Schank 2001a; Yang and Schank 2006; Tobler et al. 2010). In support, we found substantial within- and between-subject variance in swelling duration and by association follicular phase length. It has also been suggested that socially mediated synchrony is unlikely to evolve in a nonseasonal breeder because females will rarely be at the same point in their interbirth interval (Graham 1991). Again, our data support this. We found that females returned to estrus at random to each other and, as testified to by the infrequency of overlap between conceptive cycles, were generally at different points in their interbirth interval. Therefore, although on average, 3 females were cycling at any one time, they were in

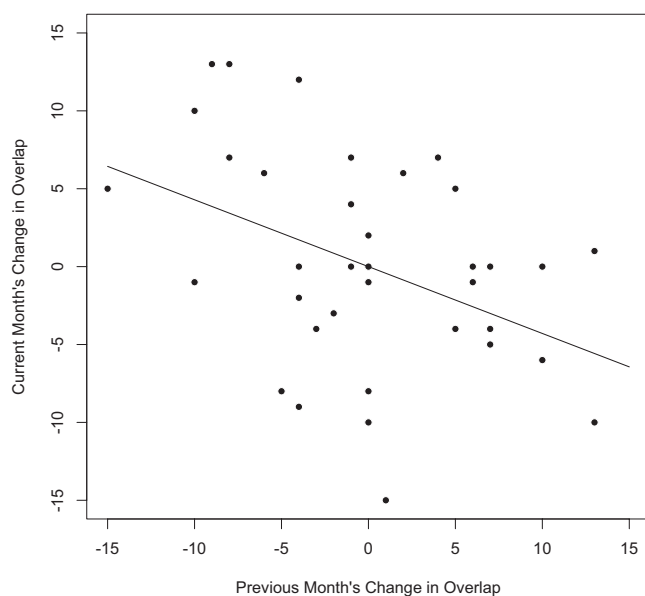


Figure 3

The relationship between monthly change in estrous overlap observed in current month and the previous month. Line describes effect predicted by model-averaged estimates.

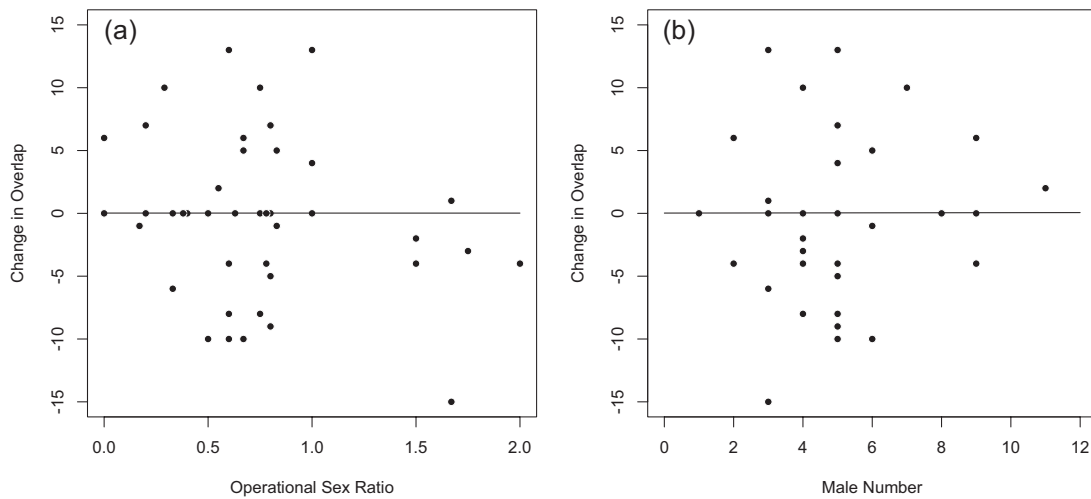


Figure 4

The relationship between the monthly change in estrous overlap and (a) the OSR and (b) the number of males. Lines describe effect predicted by model-averaged estimates.

a position to synchronize with each other for only one or, at best, 2 of the 3 cycles they experienced per interbirth interval.

Although we find clear evidence for inter- and intrafemale heterogeneity in the duration of estrous cycles, it is unclear why such heterogeneity should preclude the evolution of socially mediated synchrony. In particular, it is unclear why invariant cycle lengths could not evolve if the benefits of synchrony were great enough. It seems more likely therefore that the reason heterogeneity is still observed is because socially mediated synchrony has never, in fact, been selected for. We would argue that this is because the proximate mechanisms necessary for such an ability to evolve would yield payoff asymmetries that would require participants to engage in an unrealistically long and costly pattern of reciprocity.

It has been suggested that females achieve overlap between their periods of receptivity via a coupled-oscillator system of pheromonal exchange, where one pheromone released by a female prior to ovulation shortens the ovarian cycles of neighboring females, whereas the release of another at ovu-

lation lengthens them (Schank and McClintock 1997; Stern and McClintock 1998). Within a single interbirth interval, this system would lead to some females experiencing repeatedly shorter cycles and others repeatedly longer. That is, some would conceive earlier than would have otherwise been the case and others later. If in accumulation this difference was sufficient to yield differential reproductive output, females would have to take turns in shouldering the costs in order for the strategy to be stable. Furthermore, all else being equal, the female who falls pregnant first is likely to be the one who returns to estrus first during the next interbirth interval. Therefore, in order to reciprocate an individual who bore the costs of synchrony during the last interval, the female who did not incur any cost would have to experience an additional cycle so that she could bear the costs in the current interval. As a consequence, she would have to shoulder not only the costs of synchronization but also the much larger cost of experiencing an additional estrous cycle before conception.

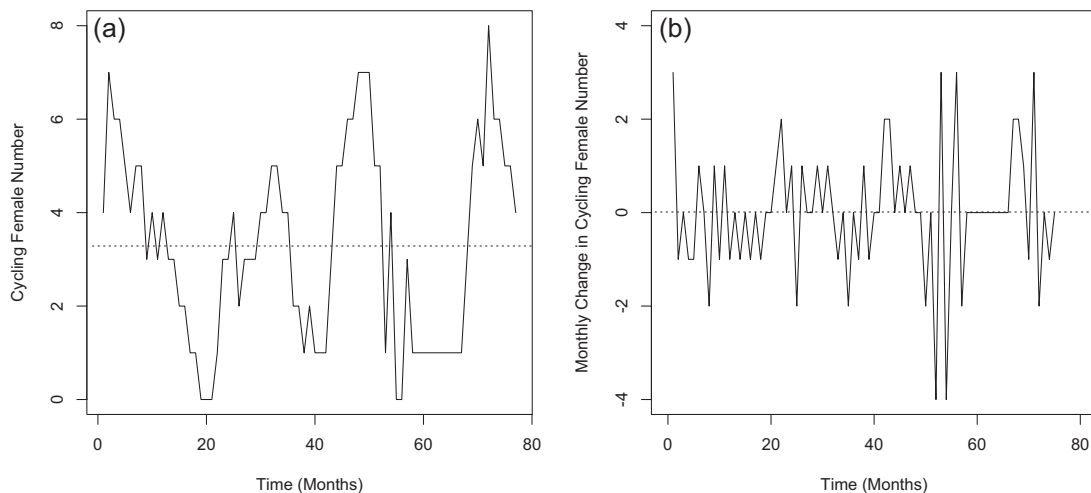


Figure 5

(a) Number of cycling females, per month, for the period May 1998 to September 2004. Dashed horizontal line indicates mean (3.286 ± 0.790) for the entire period. (b) Monthly change in cycling female number. Dashed horizontal line indicates mean monthly change (0.000 ± 0.154) across the period.

Table 3
Parameter number, K , log-likelihood, $\log\mathcal{L}$, AIC_c , and Akaike weights, w_i , for those models of monthly change in cycling female number collectively carrying 95% of the available Akaike weight

Model	K	$\log\mathcal{L}$	AIC_c	w_i
DG_{t-1}	2	-125.071	254.308	0.904
OSR	3	-127.653	261.643	0.023
β	2	-129.010	262.187	0.018
OSR + MN	4	-127.316	263.204	0.011

Although females could theoretically reciprocate in such a manner, the benefits would have to be consistently available and of sufficient value to preclude cheating and ensure stable reciprocity. This, in turn, would require there to be substantial variance in the quality of males and/or substantial benefits to multiple mating and for the benefits of synchrony to be felt equally by all females. Given that a male can assume many different ranks in a group over the course of his residency, direct and indirect genetic effects seem doubtful (Paul 2002). Infanticide and the role of putative fathers in mitigating its risk suggest that there may be sufficient nongenetic gains, however (Nunn 1999a; van Schaik 2000; Clarke, Pradhan, et al. 2009). Although, the extent to which these gains would be sufficient to offset the costs of stable long-term reciprocity between females may be a moot point.

A second objective of this study was to assess the possibility that females actively avoid estrous overlap in an effort to mitigate the costs of interfemale competition (Pereira 1991). The fact that estrous overlap was regularly observed and uninfluenced by changes in MN, and the intensity of interfemale competition suggests that this model does not apply to chacma baboons. This was, perhaps, not unexpected, given the importance of interfemale asymmetries in competitive ability within the species. Female baboons, as in many social mammals, form very strict dominance hierarchies that determine the order in which they gain access to vital resources. Consequently, the effects of competition are felt unequally by members of a cohort, with high-ranking females being relatively immune and low-ranking more susceptible (e.g., Palombit et al. 2001). Therefore, although selection may favor low-ranking females who are able to reduce the effects of

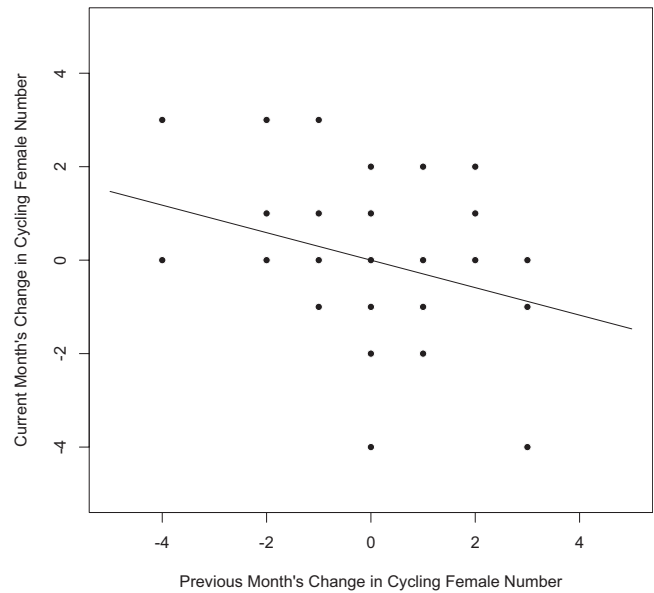


Figure 6
The relationship between monthly change in cycling female number observed in current month and the previous month. Line describes effect predicted by model-averaged estimates.

interfemale competition, high-ranking females will have little to gain from the cooperative maintenance of asynchrony. Consequently, if active desynchronization is costly and requires cooperation between females, it seems unlikely that socially mediated desynchrony will evolve in a species where females form strict dominance hierarchies. Whether this effect of dominance will also preclude selection for heterogeneity in cycle length that serves to increase the stochastic occurrence of asynchrony is less clear, however (Schank 2004). The fact that all females will almost invariably be subordinate for at least some portion of their adult lives may well provide sufficient average advantage to favor the evolution of such heterogeneity.

Whatever the reasons for the ability to manipulate the temporal distribution of sexual receptivity not evolving, the fact that it has not means that female mating strategies are subject

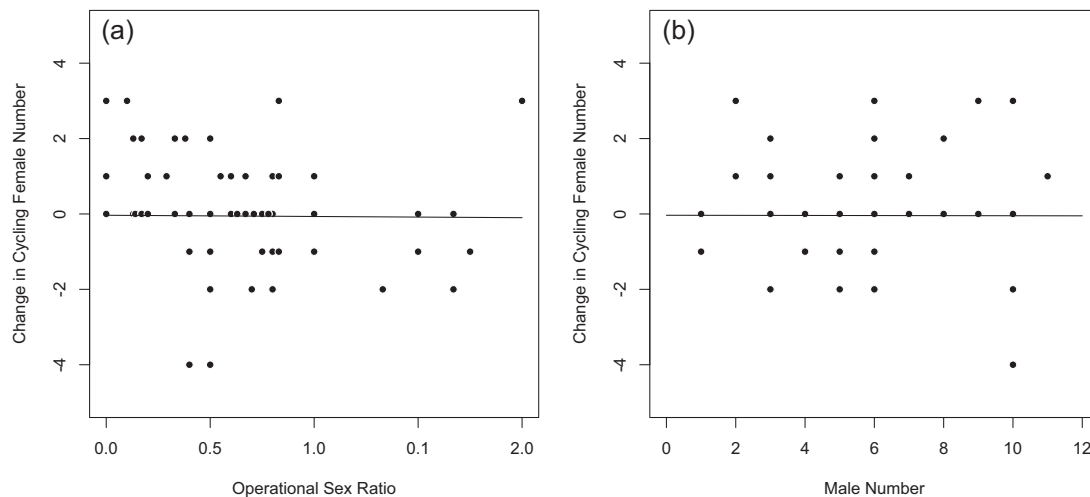


Figure 7
The relationship between monthly change in cycling female number and (a) the OSR and (b) the number of males. Line describes effect predicted by model-averaged estimates.

to variance in the intersexual dynamic. In turn, this means that they must have evolved to cope with stochasticity in the intensity of intermale competition, interfemale competition, and intersexual conflict. Consequently, if we are to identify the effects of sexual selection in a given species accurately, we must move away from microtemporal analyses of the sexes' strategies and instead consider their evolution in the long term (Pjann et al. 2000).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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