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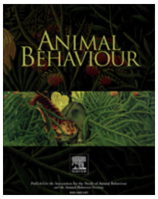

No evidence for ovarian synchrony or asynchrony in hamadryas baboons

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The tendency for females to have synchronous or asynchronous ovarian cycles has been reported in several species, including hamadryas baboons, *Papio h. hamadryas*. Both fitness benefits and costs have been postulated for each condition; however, these remain to be demonstrated. Moreover, uncertainty remains about whether these ovarian cycle patterns are 'real' or an artefact of sampling and statistical design. We used a null model incorporating a bootstrap randomization procedure to examine whether ovarian cycles were more synchronous or asynchronous than expected by chance in a large captive hamadryas colony. Male contraception meant that all female colony members underwent repeated ovarian cycling throughout the 1-year study. No pairing or group of females had synchronous or asynchronous ovarian cycles. Rather, females oscillated between pseudosynchronous and pseudoasynchronous states, because ovarian cycle length varied between and within females. We outline why the absence of synchrony and asynchrony and variation in cycle length in this and other studies are explicable when one considers (1) the brief ovarian cycle bouts typical of natural fertility populations and (2) the type of synchrony or asynchrony measures that were employed. Furthermore, we demonstrate that while variation in ovarian cycle length appears to be ubiquitous among animals with these cycles, this does not rule out the possibility of synchrony and asynchrony occurring in natural fertility populations. Further research on this phenomenon in hamadryas and other species is justified, therefore, albeit with a focus on natural fertility populations and employing null-model techniques similar to that used here.

Ovarian synchrony, the tendency for group-living females to coordinate the timing of consecutive ovarian cycle events, has been reported in a number of species including humans (e.g. McClintock 1971; Weller & Weller 1993, 1997) and other primates (chimpanzees, *Pan troglodytes*: Wallis 1985; gold lion tamarins, *Leontopithecus rosalia*: French & Stribley 1987). Ovarian synchrony is purported to benefit females by synchronizing their receptive periods to limit the degree to which they can be monopolized by dominant males (Emlen & Oring 1977; Ridley 1986; Colinshaw & Dunbar 1991; Paul 1997; Soltis et al. 2001; Shuster & Wade 2003; Kutsukake & Nunn 2006). This may enable females to pursue alternative mate choices, facilitate an anti-infanticide strategy or cryptic female choice, or increase paternal investment by decreasing the probability of males obtaining multiple mates (Knowlton 1979; Eberhard 1996; Hrdy 2000).

Ovarian synchrony can also lead to situations in which males become the limiting sex (i.e. a female-biased operational sex ratio, OSR; Emlen & Oring 1977). In such cases male choice and female–female competition are expected to determine which females are able to mate (Trivers 1972; Kvarnemo & Ahnesjo 1996), thereby compromising female mate choice as well as paternity confusion and cryptic choice strategies. Additionally, female-biased OSRs may also result in higher incidences of coercive copulations involving lower ranked males because such males are less likely to be excluded from the breeding pool by oversubscribed dominant males (Matsumoto-Oda et al. 2007).

Females may actually be better served, therefore, by avoiding ovarian synchrony in situations where OSRs are female biased (Ims 1990; Dixson 1998; Schank 2004). Indeed, ovarian asynchrony, the staggering of consecutive ovarian events, has also been reported in several mammals, including golden hamsters, *Mesocricetus auratus* (Gattermann et al. 2002), chimpanzees, *P. t. schweinfurthii* (Matsumoto-Oda et al. 2007) and ring-tailed lemurs, *Lemur catta* (Pereira 1991). Furthermore, it has been suggested that relatively lengthy and variable ovarian cycles that are typical of mammalian species may have evolved primarily to allow females to avoid ovarian synchrony and the high costs associated with it (Schank 2001b, 2004; Yang & Schank 2006).

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Adult female baboons exhibit cyclic changes in perineal turgescence during the ovarian cycle, which are positively correlated with the timing of ovulation (Hendrickx & Kraemer 1969; Wildt et al. 1977; Shaikh et al. 1982) and coincide with increased sexual receptivity (Tobler 2009). Female hamadryas baboons, *Papio h. hamadryas*, from the same one-male unit (OMU; i.e. a single adult, resident male and one or more adult females) were found to have a higher degree of overlap in the turgescent phase of their ovarian cycles (i.e. ovarian synchrony) than could be explained by chance alone in one captive (Schwibbe et al. 1992; Zinner et al. 1994) and one wild (Kummer 1968) population. Ovarian synchrony may assist hamadryas females by confounding resident male control and enabling intra-OMU mating opportunities (Zinner et al. 1994, 2006; Kummer 1995; Smith et al. 1999), but any benefits remain to be demonstrated.

Increases in the number of simultaneously oestrous females in an OMU also result in lower rates of conception (Zinner et al. 1994) and higher rates of interfemale aggression (Plowman et al. 2005). Increases in the intra-OMU OSR are expected to lead to intensified interfemale competition for access to an increasingly limited resident male sperm supply (hamadryas baboons have smaller testes than other baboons; Jolly & Phillips-Conroy 2003, 2006). The relative merits of ovarian synchrony, therefore, may decrease as the number of simultaneously oestrous females in an OMU increases. Hence, asynchrony may generally represent a better strategy for hamadryas females in larger OMUs where OSRs are expected to be higher.

We examined whether synchrony or asynchrony occurs at the colony, OMU and pairwise levels within a captive hamadryas baboon colony where all adult females underwent repeated cycling owing to resident male contraception. We used a null model that incorporates a bootstrap randomization procedure to test for both conditions simultaneously. We obtained 12 months of continuous ovarian cycle data, which represent the longest uninterrupted data set to examine this question in hamadryas baboons and one of the longest for any mammal in the literature at present. Moreover, a controlled feeding regime meant that food abundance did not change within the colony. By removing food availability as a potential causal agent, we could conduct a more conservative test for socially mediated ovarian synchrony and asynchrony than that expected for data from natural settings.

METHODS

Study Population

At the time of the study, the Wellington Zoo colony comprised three adult males, 10 adult females, and six subadult or juvenile members (Table 1). The colony resided in a 0.25 ha naturalistic outdoor enclosure containing a number of trees, rocks, logs and open grassed areas and was surrounded on all sides by a chain-link fence 3 m tall. A sleeping den (6 × 6 m) adjoined the northwestern section of the enclosure. Access to the sleeping den was restricted between the daily feeding times, which occurred at approximately 1000 and 1500 hours unless it was wet or cold. The public viewing area was located on the western side of the enclosure, with a glass wall, 7 m long, forming part of the perimeter fence at this point to assist in viewing. The eastern perimeter of the enclosure adjoins a public park, with the remainder being bordered by other zoo exhibits. The baboons were fed a selection of fruits, vegetables and grains twice daily, as well as boiled eggs and cooked chicken two or three times a week. Two permanently available water sources were located inside the enclosure.

All adult females were members of one of the two OMUs, which comprised six and four females, respectively. Membership of the OMUs remained the same throughout the study period. A member of Rameses's OMU, Tina, did not undergo ovarian cycling during the study and is omitted from all analyses. Additionally, another female, Macey, began exhibiting regular perineal swellings from August 2007 but remained unattached to any OMU during the study. Consequently, Macey is omitted from all OMU-based analyses.

Table 1
The demographic profile of the Wellington Zoo hamadryas baboon colony at the time of the study

Name	Sex	Date of birth	OMU	Age class
Rameses	M	11 Oct 1995	Rameses	Adult
Tina[*,‡]	F	18 Apr 1979	Rameses	Adult
Sinead	F	29 Jan 1993	Rameses	Adult
Beth	F	4 Jun 1994	Rameses	Adult
Kito	F	21 May 2002	Rameses	Adult
Albert	M	24 Jun 1995	Albert	Adult
Jackie[*]	F	17 Oct 1986	Albert	Adult
Grit[†]	F	1 Jan 1988	Albert	Adult
Helen[†]	F	3 Oct 1992	Albert	Adult
Zara	F	21 Sep 1994	Albert	Adult
Greet[†]	F	16 Sep 1996	Albert	Adult
Ayisha	F	4 Sep 2001	Albert	Adult
Carter	M	14 May 1993	None	Adult
Taila	M	2 Oct 2001	None	Subadult
Les	M	19 Sep 2002	None	Large juvenile
Rafiki	M	24 Sep 2003	None	Medium juvenile
Macey	F	13 Mar 2004	None	Medium–large juvenile
Habib	M	7 Dec 2004	None	Medium juvenile
Abeba	F	24 Dec 2004	None	Medium–large juvenile

Resident males are indicated by bold text. The list is organized by OMU affiliation, with OMU-affiliated females and individuals not affiliated to an OMU arranged from oldest to youngest in descending order. All animals were born in Wellington Zoo unless otherwise noted. Age classes for hamadryas baboons are taken from Swedell 2006, having previously been adapted from the descriptions in Sigg et al. 1982.

[*] Introduced from Dierenpark Emmen, the Netherlands, on 7 June 2001.

[†] Introduced from Melbourne Zoo, Australia, on 12 January 1988.

[‡] Postmenopausal at time of study.

To control population growth within the colony, the two resident males were vasectomized in October 2004. This procedure does not alter normal hormone or sperm production and the mating patterns of resident males were not observed to change thereafter (Wellington Zoo staff, personal communication). No pregnancies or births were observed in the colony from March 2005 to the end of the study period in February 2008. Hence, with the exception of Tina, all adult females in the colony had been undergoing repeated ovarian cycling from at least March 2005 until the end of the present study.

Ethical Note

R.T. collected all information from the public viewing area where the baboons were accustomed to people being present. Data collection required no direct contact with the animal subjects. The study was approved by the Victoria University of Wellington Animal Ethics committee.

Ovarian Cycles

Observations on the status of perineal turgescence (inflating, deflating or flat) were made daily for all mature, fertile females in the Wellington Zoo colony over a 366-day period between 2 February 2007 and 2 February 2008. The turgescent phase of the ovarian cycle consisted of the period beginning on the first day of perineal turgescence and ending the day prior to the subsequent first day of perineal deturgescence (i.e. the day of deturgescence, DoD). The nonturgescent phase of the ovarian cycle coincided with the period beginning on the DoD and ending the day prior to the