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Exaggerated sexual swellings in female nonhuman primates are reliable signals of female fertility and body condition

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In some species of Old World monkeys and apes, females exhibit exaggerated swellings of the anogenital region that vary in size across the ovarian cycle. Exaggerated swellings are typically largest around the time of ovulation, and swelling size has been reported to correlate positively with female quality, supporting the hypothesis that exaggerated swellings are honest signals of both female fecundity and quality. However, the relationship between swelling size and timing of ovulation is weak in some studies, and the relationship between swelling size and female quality has also not been consistently reported. Here, we collated empirical studies that have reported either swelling size and estimated timing of ovulation ($N = 26$) or swelling size and measures of individual quality ($N = 7$), to assess the strength of these relationships using meta-analytical methods. Our analyses confirmed that the period of maximal swelling size is closely associated with the most fertile period of the ovarian cycle and that a large proportion of ovulations occur during the maximal swelling period. A small, positive effect size was also found for the relationship between swelling size and body condition. In contrast, the relationships with age and social rank were not significant. Swelling size, therefore, potentially signals both female condition and timing of the fertile phase. Males are likely to benefit from allocating mating effort according to swelling size, while females with large swellings potentially benefit from exerting control over matings in species in which female control is compromised by male mating strategies.

Exaggerated swellings of the female anogenital region occur in around 30 species of Old World monkeys and apes (Dixson, 2012; Sillén-Tullberg & Møller, 1993). These swellings have been described as female ornaments (Clutton-Brock, 2007, 2009), defined as elaborate traits that function to attract males. The tissues of the anogenital region swell as a result of water retention and become red in coloration through distention of the capillaries (Dixson, 2012). Experimental studies have shown that swelling size and coloration increase in response to oestrogen during the follicular phase of the ovarian cycle (Dixson, 2012). The tissue then rapidly detumesces and returns to normal coloration after ovulation (e.g. Brauch et al., 2007). Females potentially benefit from displaying swellings through attracting a preferred mating partner and/or multiple partners, while males potentially benefit from strategically allocating mating effort in relation to within- and between-female variation in fertility status (Nunn, 1999; Pagel, 1994).

Observational studies have shown that maximally swollen females receive the highest levels of mating interest from males (e.g. Gesquiere, Wango, Alberts, & Altmann, 2007), and experimental studies have demonstrated that male baboons are sexually aroused by artificial swellings (Bielert & Anderson, 1985; Girolami & Bielert, 1987). Females are also most likely to approach males and solicit copulations when maximally swollen (Higham et al., 2012). In most species with exaggerated swellings, females mate with more than one male during an ovarian cycle (Clutton-Brock & Harvey, 1976; Pagel & Meade, 2006), and low-ranking males tend to mate earlier in the swelling period than high-ranking males (Emery Thompson, 2005; Gesquiere et al., 2007). These observations are consistent with exaggerated swellings functioning as 'graded' signals of the probability of ovulation that provide females with the benefits of mating with multiple males, such as protection from infanticide, while also biasing paternity towards high-quality males (Alberts & Fitzpatrick, 2012; Nunn, 1999).

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Researchers have also suggested that exaggerated swellings are relatively unreliable signals of fertility at least in some species (van Schaik, Hodges, & Nunn, 2000; Zinner, Nunn, van Schaik, & Kappeler, 2004), given that swellings are often reported to reach a large size several days before ovulation (Deschner, Heistermann, Hodges, & Boesch, 2003; Reichert, Heistermann, Hodges, Boesch, & Hohmann, 2002). For example, a study of bonobos, *Pan paniscus*, reported that females were maximally swollen for an average of 16 days (Reichert et al., 2002), while the fertile window is likely to last around 4 days (Dunson, Baird, Wilcox, & Weinberg, 1999; Wilcox, Weinberg, & Baird, 1995). The same study reported that 30% of ovulations occurred outside the maximal swelling period (Reichert et al., 2002), further supporting the idea that swellings are an unreliable signal of fertility in this species. Selection has thus been suggested to favour mechanisms that make ovulation unpredictable relative to swelling characteristics (van Schaik et al., 2000), with the null hypothesis being that some error in signalling occurs by chance.

Exaggerated swellings have also been reported to vary in maximal size both between individuals and across cycles within individuals (Fitzpatrick, Altmann, & Alberts, 2014). For instance, maximal swelling size increases with the number of cycles since resumption of cycling following a previous birth (Higham, MacLarnon, Ross, Heistermann, & Semple, 2008; Huchard et al., 2009). Exaggerated swellings are costly in terms of increased body weight and risk of tissue damage (Bielert & Busse, 1983; Matsumodo-Oda, 1998), and females receive greater amounts of physical harassment from both male and female group members when maximally swollen (Feldblum et al., 2014; Huchard & Cowlishaw, 2011). Thus, swelling size is potentially indicative of a female's current physical condition and ability to raise an offspring (Pagel, 1994). While this 'reliable indicator' hypothesis has received some support (Domb & Pagel, 2001; Huchard et al., 2009), other studies failed to find a correlation between swelling size and measures of female quality (Möhle et al., 2005; Setchell & Wickings, 2004), where quality is broadly defined as any property of an individual that influences the cost of expressing the exaggerated trait (Johnstone, Rands, & Evans, 2009).

Using currently available data, we first investigated the strength of the evidence that exaggerated swellings are generally reliable signals that peak in size during the period of highest fertility. Given that reliability is defined as the tightness of the correlation with the underlying trait (Searcy & Nowicki, 2005), we predicted that the period of maximal swelling would not, on average, extend greatly beyond the fertile period and that a relatively strong association would be found between swelling size and the probability of ovulation. Because the strength of the association between swelling size and fertility is likely to depend upon how swelling size is measured, we also compared studies that used fine-resolution, continuous measures of swelling size with those that used broad-resolution, categorical measures, with the prediction that studies using categorical measures could underestimate the precision of the relationship between swelling size and ovulation probability. Finally, we conducted meta-analyses on studies that have correlated swelling size with measures of female properties other than current fertility status to test whether exaggerated swellings are reliable indicators of female quality.

METHODS

Literature Review and Inclusion Criteria

Articles were located using keyword searches in Thomson Reuter's *Web of Knowledge* (e.g. 'primate swelling ovulation', 'primate swelling quality') and by checking the reference sections of papers that were identified. To fulfil the inclusion criteria, articles had to contain either (1) data on changes in swelling size across days relative to an independent estimate of the day of ovulation based on ovarian hormone levels (from blood, urine or faecal samples) or laparoscopy, or (2) data on swelling size and any measures of individual female quality (e.g. body condition or social rank). The final data set on swelling size and ovulation consisted of 26 articles (including Deschner, Heistermann, Hodges, & Boesch, 2004, which reported swelling size from the same subjects as Deschner et al., 2003 using a different measure) across 10 species (*Cercocebus atys*, *Macaca nemestrina*, *Macaca sylvanus*, *Macaca nigra*, *Macaca tonkeana*, *Mandrillus sphinx*, *P. paniscus*, *Pan troglodytes*, *Papio anubis*, *Papio cynocephalus*; see Table A1 in the Appendix). A small number of studies were excluded, as data on the day of ovulation in relation to maximal swelling size could not be extracted (i.e. Bullock, Paris, & Goy, 1972; Dahl, Nadler, & Collins, 1991; Fürtbauer, Schulke, Heistermann, & Ostner, 2010; Nyakudya, Fuller, Meyer, Maloney, & Mitchell, 2012; Shaikh, Shaikh, Celaya, & Gomez, 1982; Thomson et al., 1992; Wildt, Doyle, Stone, & Harrison, 1977). As exaggerated swellings are the focus of existing functional hypotheses (e.g. Nunn, 1999; Pagel, 1994), data from species with small swellings (defined as swellings that involve the vulval and clitoral areas only; Dixson, 2012) were excluded (i.e. *Hylobates lar*: Barelli, Heistermann, Boesch, & Reichard, 2007; Nadler, Dahl, & Collins, 1993; *Gorilla gorilla*: Czekala & Sicotte, 2000; Nadler, Graham, Collins, & Gould, 1979), as were data from species with subcaudal swellings (i.e. *Macaca fascicularis*: Engelhardt, Hodges, Niemitz, & Heistermann, 2005). The relationship between swelling coloration and ovulation was not investigated, as few studies with suitable data were available (Higham et al., 2008; Rigaill, Higham, Lee, Blin, & Garcia, 2013; Setchell & Wickings, 2004). The final data set on swelling size and female quality consisted of seven articles across six species (*M. sylvanus*, *M. sphinx*, *P. troglodytes*, *Papio ursinus*, *P. anubis*, *P. cynocephalus*; Table A2).

Data for Swelling Size and Timing of Ovulation Analyses

For studies reporting summary data ($N = 11$ studies), values were directly extracted from the text or figures for (1) the mean day of ovulation relative to the onset of maximal swelling size and (2) the mean duration of the maximal swelling period. For studies that presented data on the timing of ovulation separately for individual cycles ($N = 15$ studies), we calculated mean values across all cycles based on reported values for (1) the day of ovulation relative to the onset of maximal swelling size for each cycle (e.g. if maximal swelling size was reached 3 days prior to ovulation, the value was -3), and (2) the duration of the maximal swelling period, i.e. the total number of days during which the swelling was maximally swollen for each cycle.

Studies were classified as using either a 'categorical' measure (e.g. $1 = $ small to $3 = $ maximal) or a 'continuous' measure of swelling size (e.g. area in cm^2 measured using callipers or estimated from digital photographs). Authors' definitions of maximal swelling size were used throughout, or, where data were presented as graphical representations of averaged swelling size changes across the cycle (e.g. Aujard, Heistermann, Thierry, & Hodges, 1998; Brauch et al., 2007), 'maximal' swelling size was taken as the point at which the peak size was reached. Authors' estimated days of ovulation were used where available. Otherwise, ovulation was assumed to have occurred either 1 day after the serum LH peak, 2 days after the serum oestradiol peak or 2 days after the urinary oestrone peak (Steinetz, Ducrot, Randolph, & Mahoney, 1992), unless otherwise noted. Sample sizes were taken as the number of