



Exaggerated sexual swellings and male mate choice in primates: testing the reliable indicator hypothesis in the Amboseli baboons



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The paradigm of competitive males vying to influence female mate choice has been repeatedly upheld, but, increasingly, studies also report competitive females and choosy males. One female trait that is commonly proposed to influence male mate choice is the exaggerated sexual swelling displayed by females of many Old World primate species. The reliable indicator hypothesis posits that females use the exaggerated swellings to compete for access to mates, and that the swellings advertise variation in female fitness. We tested the two main predictions of this hypothesis in a wild population of baboons (*Papio cynocephalus*). First, we examined the effect of swelling size on the probability of mate guarding ('consortship') by the highest-ranking male and the behaviour of those males that trailed consortships ('follower males'). Second, we asked whether a female's swelling size predicted several fitness measures. We found that high-ranking males did not prefer females with larger swellings (when controlling for cycle number and conception) and that females with larger swellings did not have higher reproductive success. Our study, the only complete test of the reliable indicator hypothesis in a primate population, rejects the idea that female baboons compete for mates by advertising heritable fitness differences. Furthermore, we found unambiguous evidence that males biased their mating decisions in favour of females who had experienced more sexual cycles since their most recent pregnancy. Thus, rather than tracking the potential differences in fitness between females, male baboons appear to track and target the potential for a given reproductive opportunity to result in fertilization.

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The evolution of male mate choice in sex-role-reversed species can easily be understood according to the general principles of sexual selection; when females are mate-limited, they are expected to compete for access to males, and those males, in turn, are expected to be choosy. This phenomenon is well described in some sex-role-reversed species of pipefish (Berglund, Rosenqvist, & Svensson, 1989; Vincent, Ahnesjö, Berglund, & Rosenqvist, 1992) and shorebirds (Székely & Reynolds, 1995). In contrast, when the sex roles are conventional, choosy males will be at a competitive disadvantage and, therefore, male mate choice should be selected against. Exceptions to this prediction have been demonstrated, most notably in those cases where female fecundity varies and choosy males therefore benefit by preferring females with higher fecundity (Servedio & Lande, 2006). Indeed, empirical work across a broad range of taxa indicates that male choosiness in these

scenarios is common. For example, in those species where female body size predicts fecundity, males often demonstrate a preference for larger females (lizards: Olsson, 1993; fish: Sargent, Gross, & Van Den Berghe, 1986; insects: Bonduriansky, 2001).

However, male mate choice is increasingly observed even when direct fecundity benefits for choosy males are not apparent. In some of these cases, males might receive indirect benefits from females, analogous to the 'good genes' models of mate choice that have been developed for female choice (see Chapter 3 in Andersson, 1994). For example, experimental work in barn owls, *Tyto alba*, suggests both that male barn owls prefer females with spottier plumage and that the offspring of those females mount a more effective immune response (Roulin, Jungi, Pfister, & Dijkstra, 2000; Roulin, Riols, Dijkstra, & Ducrest, 2001). That is, males may bias their mating investment toward females whose offspring have superior genetic immunity. In other cases, males may evolve preferences when male investment in mating is so high or costly that mating necessarily limits future mating opportunities, thus imposing opportunity costs. For example, males should choose mates carefully when their

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ability to mate with many females is constrained by intense male–male competition or sperm competition (Owens & Thompson, 1994; Schwagmeyer & Parker, 1990; reviewed by Edward & Chapman, 2011).

The exaggerated sexual swelling displayed by many cercopithecin primates is commonly cited as a trait upon which males base mate choice, and studies in two baboon populations have suggested that, at least in these species, males prefer females with larger swellings (Domb & Pagel, 2001; Huchard et al., 2009). However, the fitness benefits that males might receive as a result of this choosiness based on swelling size are unknown. Therefore, knowledge of the evolutionary forces that have shaped both the behaviour and the trait remain obscure, and the question of what information males may receive from these signals remains open (Deschner, Heistermann, Hodges, & Boesch, 2004; Fitzpatrick, Altmann, & Alberts, 2014; Higham, Semple, MacLarnon, Heistermann, & Ross, 2009; Huchard et al., 2009).

Sexual swellings appear during the follicular phase of the female sexual cycle, are thought to have evolved multiple times in the primate lineage (Dixon, 1983), and are most commonly associated with multimale, multifemale social systems (Nunn, 1999). It has been well established in several species of baboons, in chimpanzees, *Pan troglodytes*, and in two species of macaques that male mating behaviour increases in response to these changes in swelling size within a given cycle (baboons: Bielert & Anderson, 1985; Hausfater, 1975; Higham, Heistermann, Ross, Semple, & MacLarnon, 2008; Huchard et al., 2009; Nitsch, Stueckle, Stahl, & Zinner, 2011; Packer, 1979; chimpanzees: Breaux, Watson, & Fontenot, 2012; Deschner et al., 2004; Emery & Whitten, 2003; Tutin, 1979; macaques: Brauch et al., 2007; van Noordwijk, 1985). In fact, as the understanding of this trait has become more refined over the past decade, researchers have identified three distinct types of variation in swelling size (Zinner, Alberts, Nunn, & Altmann, 2002).

(1) Swelling size varies within each cycle. In many species, maximal size for a given cycle is achieved around the time of ovulation. This within-cycle variation has been demonstrated repeatedly to be a probabilistic indicator of ovulation in baboons and chimpanzees (Dahl, Nadler, & Collins, 1991; Emery & Whitten, 2003; Hendrickx & Kraemer, 1969; Nunn, 1999; Wildt, Doyle, Stone, & Harrison, 1977; reviewed in Alberts & Fitzpatrick, 2012; but see Reichert, Heistermann, Hodges, Boesch, and Hohmann (2002) on bonobos, *Pan paniscus*, and Engelhardt, Hodges, Niemitz, and Heistermann (2005) on longtailed macaques, *Macaca fascicularis*, for examples of limited correspondence between swelling size and ovulation). Furthermore, it has been shown in baboons and chimpanzees that the intensity of male mating behaviour increases during the periovulatory period when females are more likely to conceive (Deschner et al., 2004; Emery & Whitten, 2003; Higham, MacLarnon, Ross, Heistermann, & Semple, 2008; Higham et al., 2012; Noe & Sluijter, 1990; Rigail, Higham, Lee, Blin, & Garcia, 2013).

(2) Swellings vary in size within an individual across cycles. Females of most primate species cycle repeatedly before conceiving. In chimpanzees and baboons, where sexual swellings have been the most intensively studied, maximal swelling size increases from cycle to cycle within one individual (Deschner et al., 2004; Emery & Whitten, 2003; Fitzpatrick et al., 2014; Higham, Heistermann, et al., 2008). This type of variation may signal differences in the probability of conception across cycles. Although variation in conception probability from one cycle to the next has not, to our knowledge, been described empirically for any species, data from our study population suggest that the cycles immediately following postpartum amenorrhoea are less likely to result in conception than later ones (data presented in Fitzpatrick et al.,

2014). Furthermore, in four populations of baboons (three wild and one captive), alpha males were shown to successfully target conceptive cycles, further suggesting that, within a given female, cycles vary in the probability of conception (Alberts, Buchan, & Altmann, 2006; Bulger, 1993; Daspre, Heistermann, Hodges, Lee, & Rosetta, 2009; Gesquiere, Wango, Alberts, & Altmann, 2007; Weingrill, Lycett, Barrett, Hill, & Henzi, 2003).

(3) Finally, swelling sizes may differ between individuals. Because this type of variation can only be revealed by controlling for the within-cycle and across-cycle variation exhibited by each female, it is more challenging to demonstrate empirically. Three studies have been able to document interindividual differences in swelling size (controlling for within-cycle and across-cycle variation), one in chimpanzees and two in baboons (Deschner et al., 2004; Fitzpatrick et al., 2014; Huchard et al., 2009).

Thus, it is known that males in some species respond to the first type of variation (within-cycle variation in swelling size) and that the second type of variation has the potential to signal important information to males (because swelling size increases as cycle number progresses in several species). However, it remains unclear whether the third type of variation, variation between females in sexual swelling size (beyond differences accounted for by within-cycle and across-cycle variation), has additional information content for male primates of any species.

Despite this gap, ‘the reliable indicator hypothesis’, a main hypothesis to explain both the evolution of exaggerated swellings and the male response to them, hinges on the assumption that it is precisely this variation between individuals that is salient for males. The reliable indicator hypothesis posits both that exaggerated swellings signal intrinsic differences in female quality (i.e. enduring differences in phenotypic quality) and that males bias their mating behaviour toward females with larger swellings (Pagel, 1994). Thus, the reliable indicator hypothesis makes two main predictions: (1) males will demonstrate a preference for females with larger swellings, all else being equal; (2) superior females (with higher lifetime reproductive success) will have larger swellings. Importantly, the reliable indicator hypothesis proposes that the type of quality being signalled is a permanent characteristic of a female, and that some females are consistently superior to others, a superiority that is associated with increased lifetime reproductive success. To designate this specific type of difference in swelling size, we refer here to interindividual differences in swelling size.

One empirical test of the reliable indicator hypothesis reported support for its predictions; male baboons preferred females with larger swellings and those females had higher infant survival (Domb & Pagel, 2001). However, a reanalysis of the data presented in this study showed that it failed to control adequately for differences between baboon groups in food availability (and hence in female body condition, in the competitive environment for males, and in infant survival), which could have accounted for the observed results (Zinner et al., 2002). Furthermore, no test of the reliable indicator hypothesis has differentiated between the permanent type of quality it proposes (interindividual differences in quality) and the more transient type of quality that is probability of conception. Thus, without controlling for whether a given sexual cycle resulted in a conception, the reliable indicator hypothesis cannot be adequately investigated. Specifically, if conceptive swellings are larger than nonconceptive ones (which appears to be true in at least some species; Deschner et al., 2004; Emery & Whitten, 2003; Fitzpatrick et al., 2014; Gesquiere et al., 2007; Higham, MacLarnon, et al., 2008; Higham et al., 2009; Huchard et al., 2009) and if males prefer cycles with higher probabilities of conception (as in baboons: Alberts et al., 2006; Bulger, 1993; Daspre et al., 2009; Gesquiere et al., 2007; Weingrill et al., 2003),

then it may appear that males choose mates on the basis of interindividual differences in swelling size when, instead, they may only be tracking probability of conception. Neither [Domb and Pagel \(2001\)](#) nor any subsequent studies that examined the reliable indicator hypothesis were able to control for this potential confound.

Despite the absence of resolution about whether interindividual variation in swelling size can signal enduring aspects of female quality, and despite the limitations of [Domb and Pagel's \(2001\)](#) study, Domb and Pagel's study continues to be cited as having shown that exaggerated swellings are a reliable indicator of female quality (e.g. [Caro, 2005](#); [Dixon & Anderson, 2004](#); [Drea, 2005](#); [Gladbach, Gladbach, Kempnaers, & Quillfeldt, 2010](#); [Gouzoules & Gouzoules, 2002](#); [Gumert, 2007](#); [Haselton & Gildersleeve, 2012](#); [Huangshan et al., 2010](#); [Huchard et al., 2009](#); [Jablonski, 2004](#); [Jawor, Gray, Beall, & Breitwisch, 2004](#); [Preston, Stevenson, Pemberton, Coltman, & Wilson, 2005](#); [LeBas, 2006](#); [Massironi, Rasotto, & Mazzoldi, 2005](#); [Pagel & Meade, 2006](#); [Paul, 2002](#); [Polo & Veiga, 2006](#); [Rundle & Chenoweth, 2011](#); [Veiga & Polo, 2005](#); [Watson & Platt, 2008](#); [Weiss, 2006](#); [Weiss, Kennedy, Safran, & McGraw, 2011](#)). Importantly, no other study has provided clear support for the reliable indicator hypothesis. One recent study found evidence that male baboons prefer females with larger swellings but was unable to control for between-cycle variation in individual females ([Huchard et al., 2009](#)). Furthermore, because male baboons are more responsive to conceptive cycles than to nonconceptive cycles, controlling for conceptive status is essential for measuring males' response to swelling size ([Alberts et al., 2006](#); [Bulger, 1993](#); [Daspre et al., 2009](#); [Gesquiere et al., 2007](#); [Weingrill et al., 2003](#)). The one study that successfully made this critical distinction (between male response based on swelling size versus male response based on changes in conception probability across cycles) was done in chimpanzees, and failed to support the reliable indicator hypothesis ([Deschner et al., 2004](#)). Finally, with respect to the potential for sexual swellings to signal variation in female fitness, results are also mixed; one reports a relationship between swelling size and components of female fitness (baboons: [Huchard et al., 2009](#)) while others report an absence of such relationships (mandrills: [Setchell et al., 2006](#); [Setchell & Wickings, 2004](#)).

Thus, the functional significance of male mate choice in response to exaggerated swellings has been unresolved because a complete test of the reliable indicator hypothesis has been absent. Here, we conduct the first complete test of the reliable indicator hypothesis in a primate population by investigating the relationship between interindividual differences in swelling size and male mating behaviour as well as components of female fitness. To do so, we take advantage of the largest and most detailed collection to date of swelling size measurements in an ongoing study of savannah baboons, *Papio cynocephalus* ([Fitzpatrick et al., 2014](#)). This data set has already revealed critical sources of variance in swelling size; swelling size was shown to be influenced by the number of times a female had cycled since her most recent pregnancy (cycles since resumption), the amount of rainfall (days since last wet month), which predicts food availability, and female age ([Fitzpatrick et al., 2014](#)). Together, this information accords a more precise test of the reliable indicator hypothesis than has been possible previously, by allowing us to examine male mating decisions at the same time that we control for these potential confounds. As such, we address two questions. First, do males bias their mating behaviour toward females with larger swellings independent of what swellings might signal about current condition (i.e. do males respond to interindividual variation in swelling size)? Second, does interindividual variation in swelling size predict female fitness?

METHODS

Study Population and Data Collection

We collected morphological data (swelling size), behavioural data (male mating behaviour), and proxies of female fitness from a natural population of savannah baboons that has been under continuous study by the Amboseli Baboon Research Project (ABRP) for over 4 decades ([Alberts & Altmann, 2012](#); [Alberts et al., 2006](#); [Altmann, Gesquiere, Galbany, Onyango, & Alberts, 2010](#); [Gesquiere et al., 2007](#); [Hausfater, 1975](#)). Savannah baboons exhibit female philopatry and male dispersal, live in multimale, multifemale groups where both males and females mate multiply, and breed at relatively similar frequencies year round. The Amboseli baboons occupy a short-grass savannah habitat that has undergone dramatic ecological change (from acacia woodland to more open savannah). The ecosystem is subject to extreme variation in both intra-annual and interannual rainfall ([Alberts et al., 2005](#); [Altmann, Alberts, Altmann, & Roy, 2002](#)).

The study population consisted of over 300 individuals of both sexes and all ages, all of which were habituated to human observers, individually identifiable by sight and distributed across five different social groups during the period of this study. All data were collected during one field season of 12 months (November 2008–November 2009) and a second field season of 5 months (February 2010–June 2010).

The full analysis for this study included two discrete parts, one for each research question. Both of these analyses used morphological data as the independent variable (swelling size) and each then asked whether interindividual differences in swelling size predicted a response variable. The response variable in our first analysis was behavioural (male mate choice) and the response variables in our second analysis were life history measures (proxies of female fitness). Because female baboons do not cycle synchronously, male baboons are rarely presented with an opportunity to compare two simultaneously cycling females. Thus, our use of 'male mate choice' in this study does not imply simultaneous choice (see [Edward, 2014](#), for relevant discussion on this topic). Rather, we used two measures of male behaviour to assess male mating decisions. Below, we first detail the collection of the main predictor of interest (interindividual differences in swelling size). In subsequent sections, we describe the details of each of the two analyses, including the data collection for the response variables and the analytic approaches.

Main Predictor Variable of Interest: Maximal Swelling Size

We used two measures of swelling size: swelling width and swelling length. Swelling sizes were measured from digital images of individual reproductive females, collected opportunistically during daily observations. Digital images were collected using a Photoscale-2 and digital calliper, a system that allowed for the conversion of measurement in pixels to an estimate in millimetres ([Fitzpatrick et al., 2014](#)). All swelling size measurements were absolute, rather than being scaled to body size. Although relative swelling size may be a biologically relevant signal, technical limitations prevented us from collecting reliable body size measures (see Online Resource 5 from [Fitzpatrick et al., 2014](#), for more detail). Furthermore, previous studies in our population have demonstrated that absolute size does indeed predict important features of individual females ([Fitzpatrick et al., 2014](#)). Finally, studies in other populations of baboons report that absolute measures of swelling size predict several components of a female's reproductive biology ([Higham, MacLarnon, et al., 2008](#); [Huchard et al., 2009](#)). These previous results confirm that differences in absolute interindividual

swelling size have the potential to function as an important indicator.

We restricted our analysis to cycles that resulted in pregnancy (i.e. 'conceptive cycles'). This is an essential restriction because male baboons differentiate between conceptive and nonconceptive cycles (Alberts et al., 2006; Bulger, 1993; Daspre et al., 2009; Gesquiere et al., 2007; Weingrill et al., 2003). The reliable indicator hypothesis posits that, rather than indicating something about the likelihood of conception, swelling size indicates differences in enduring, heritable quality; a test of this hypothesis must therefore control for the likelihood of conception. Furthermore, we wanted to control for the within-individual variation in swelling size that has been demonstrated in this population (Fitzpatrick et al., 2014). Again, this is an important restriction because the reliable indicator hypothesis posits that sexual swellings reveal biologically meaningful differences between individuals rather than between or within cycles. Thus, each female in the data set was represented only once ($N = 34$ females). Although spontaneous miscarriages and stillbirths occur in this population (Beehner, 2006; Beehner, Nguyen, Wango, Alberts, & Altmann, 2006), all conceptions represented in this analysis resulted in a live birth.

Analysis 1: Male Mate Choice

Selection of response variables (behavioural data)

To assay whether male preference varies as a function of inter-individual differences in female swelling size, we collected behavioural data during clear bouts of mate guarding, or 'consortships', when a female had a sexual swelling. A consortship between a cycling female (i.e. displaying a swelling and therefore approaching ovulation) and an adult male is unambiguous (Alberts, Altmann, & Wilson, 1996; Alberts, Watts, & Altmann, 2003; Bercovitch, 1988; Packer, 1979; Saayman, 1970; Seyfarth, 1978). During consortships, the consorting male attends closely to the female, usually maintaining proximity and displaying vigilance. However, consortships are often overturned because males fight over them intensively. As a consequence, females are not only consorted continuously during the 5-day window during which they are most likely to ovulate (Daspre et al., 2009; Higham, Heistermann, et al., 2008; Wildt et al., 1977), but are usually consorted by more than one male during a given cycle.

We selected our behavioural response variables based on two key features of male–male competition in the presence of cycling females. First, of all the males in a social group, the highest-ranking male is the most likely to be able to exercise choice (Alberts et al., 2006; Bulger, 1993; Deschner et al., 2004; Gesquiere et al., 2007; Weingrill et al., 2003). Second, consortships often attract male 'following', in which one or more males that are not the consort partner will trail the consort pair (Danish & Palombit, 2014). 'Following males' are identifiable because they clearly coordinate their movements with the consort pair, and glance at the consort pair regularly and more often than do other individuals in the group. Followers sometimes make overt attempts to take possession of established consortships, which usually involves charging, fighting or coalitionary behaviour with other males. Even in the absence of a clear take-over attempt, however, following behaviour most likely imposes costs on the follower (e.g. limited foraging opportunities or energetic costs of vigilance, as has been documented for mate guarding itself; Alberts et al., 1996).

Thus, our two behavioural measures of male preference were (1) consortship by the highest-ranking male and (2) proportion of consortship time that the consorting pair was trailed by at least one follower. We restricted our analysis to behavioural data that were collected during the 5-day window prior to the first day of deturgescence ('d-day'). This controlled for the fact that males of several

species (including baboons) bias their mating behaviour toward periovulatory females, probably reflecting male sensitivity to within-cycle differences in swelling size (Brauch et al., 2007; Nitsch et al., 2011). Analysing only data collected within 5 days of d-day controlled for differences in male behaviour that were attributable to within-cycle differences in swelling size, which allowed us to determine the importance interindividual variation in swelling size. In addition, we included only those females for whom we were able to obtain measures of maximal swelling size, designated as a size estimate that was collected within 2 days of d-day. This designation is justified by previous analyses showing that size estimates gathered 1 day (d-1) and 2 days (d-2) prior to deturgescence are statistically equivalent (see Fitzpatrick et al., 2014, for a thorough explanation of this designation and method).

Response variable 1: consortship by highest-ranking male

To calculate this metric, we used consortship observations that were collected on a near-daily basis as part of the ongoing ABRP data collection protocol. Consortship start time and stop time and the identity of individuals in the consorting pair were recorded ad libitum whenever an observer was monitoring one of the study groups (Alberts & Altmann, 2011). From these data, we created a simple binary variable for each female for whom we had a measure of maximal swelling size: the female either was or was not consorted by the highest-ranking male during a given sexual cycle. We chose a binary categorization rather than a continuous measure such as a proportion (e.g. observed consort time with alpha male/total observed consort time) because when we performed a multivariate linear regression on proportion (predictors described in Additional Predictor Variables, see below), the residuals were non-normally distributed and did not respond to transformation.

Response variable 2: proportion of consort time with a follower

Data on followers were collected during point samples (instantaneous samples of behaviour collected every 2 min) taken during 30 min focal animal samples (Altmann, 1974). Focal samples were collected on consorting pairs (i.e. one cycling female and her consort partner during each focal sample). At each point sample, we recorded the number of followers present and then created a proportion of consort time spent with at least one follower. Field conditions prevented the collection of focal samples from two of the females for which we obtained maximal swelling width and length. Therefore, when using this second response variable (proportion of consort time with a follower), the sample included only 32 conceptive females. When we performed the multivariate linear regression (predictors described in Additional Predictor Variables, see below), the residuals were distributed normally. Therefore, this response variable remained as a proportion in the multivariate linear regression (see Results).

Additional predictor variables

In addition to swelling size, we modelled additional features of each individual female, including 'cycles since resumption', 'female age' and 'female rank'. We included one ecological variable, 'days since last wet month', and one demographic variable, the 'number of adult males in the queue' ('average queue length'), as predictor variables (Table 1). All of these additional predictors were included to control for potentially confounding effects. The correlation coefficients between all predictor variables were less than 0.5, and the variance inflation factors were all less than 2, allowing us to include them all as predictors in the same model.

The predictor variable 'cycles since resumption' was an integer representing the number of times a female had cycled since her most recent pregnancy, so that the first cycle after postpartum amenorrhea was cycle 1 and, if pregnancy did not occur, the next

Table 1
Parameters used in analysis of male mate choice as a function of sexual swelling size in female savannah baboons

Predictor	Description	Range	Mean±SD
Swelling width	Maximal swelling width (mm)	108.24–164.83	127.33±10.85
Swelling length	Maximal swelling length (mm)	121.42–197.74	155.22±17.87
Cycles since resumption	No. of times a female had cycled since her most recent pregnancy	2–8	3.81±1.56
Female age	Female age (to nearest 0.1 year)	7.1–18.3	12.09±3.24
Female rank	Female dominance rank	1–27	11.05±6.56
Days since last wet month	No. of days since the last month in which rainfall occurred (November 2009–February 2010)	0–320	100.43±119.34*
Average queue length	No. of adult males in the queue (no. of adult males in the group minus no. of cycling females), averaged over the 5-day window prior to deturgescence	0.4–17	11.01±4.19

* Days since last wet month showed a bimodal distribution. All other variables conformed to normality.

cycle was cycle 2, and so on. We included cycles since resumption because this predictor varied considerably in our data set and had a large effect on swelling size in our previous analysis (Fitzpatrick et al., 2014). That is, even though we only considered conceptive cycles in this analysis, females conceived anywhere from two to eight cycles after resumption. Therefore, we could not effectively examine the specific effect of swelling size without controlling for an effect of cycles since resumption.

Female age was calculated to the nearest tenth of a year and was included as a predictor because age is a source of variance in swelling size in our study population (Fitzpatrick et al., 2014), indicating that we need to control for the effect of age in attempting to identify any effect of swelling size. Furthermore, fertility declines with age for female baboons (Alberts & Altmann, 2003; Beehner, 2006), but a study in chimpanzees found evidence that male chimpanzees prefer older females (Muller, Emery Thompson, & Wrangham, 2006). That is, males may modify their investment as a function of female age, preferring either younger or older females.

Female rank was calculated from dyadic agonistic interactions between individuals and was represented as an ordinal number so that the highest-ranking female received rank 1, the next highest-ranking female was rank 2, and so on. This variable was included in our analysis because recent studies in this population found evidence of an interaction between male and female rank such that consortships were most likely when both partners were high ranking (Tung, Charpentier, Mukherjee, Altmann, & Alberts, 2012). In addition, some aspects of swelling size appear to be associated with female rank (Fitzpatrick et al., 2014). Thus, we opted to control for female rank because we specifically wanted to examine the effect of swelling size on male behaviour, irrespective of female rank.

The predictor variable 'days since last wet month' was an integer that captured the extent to which the Amboseli basin was experiencing drought or wet conditions. It was especially important to account for this predictor because our two study periods spanned nearly unprecedented ecological extremes of drought (June–October 2009) and heavy rainfall (November 2009–February 2010). In addition, days since last wet month constrained swelling size in our previous study (Fitzpatrick et al., 2014), and these ecological conditions may also constrain male behaviour.

Finally, we included a variable representing the male competitive environment, 'average queue length', as a predictor in our analysis. Queue length was measured as the number of adult males that were present on a given day minus the number of cycling females in the social group on that day who were within the 5-day window prior to d-day. This measure of the competitive environment is based on the observation that each male can only consort one female at a time, and each female is consorted by no more than one male at a time, resulting in a competitive environment that is a function of both the number of adult males and the number of cycling females in the group. For this metric, we included cycles that were both conceptive and nonconceptive because it is

extremely rare for a cycling female not to be consorted (whether or not she conceives). That is, every female that is cycling will reduce the intensity of the competitive environment. We calculated queue length for each of the 5 days during which behavioural data were collected and then took the average across that period, producing the final predictor variable, average queue length. Because we averaged across the 5-day period, the average queue length was not always an integer.

Information-theoretic analysis

Because several variables (in addition to swelling size) may influence male mating behaviour, we evaluated a candidate set of models using an information-theoretic approach. This method assumes that the researcher has used previous biological knowledge to select appropriate predictors, but allows for different combinations of those predictors that might be equally plausible at the outset (Burnham, Anderson, & Huyvaert, 2011; Garamszegi, 2011; Symonds & Moussalli, 2011). We calculated Akaike's Information Criterion (AIC) (Akaike, 1973) for each model in our candidate set using the statistical software, R. We did this series of calculations twice: once for each response variable. We used an adjusted measure of AIC, AIC_c, which is recommended for smaller sample sizes (Burnham et al., 2011; Symonds & Moussalli, 2011) and then calculated the Akaike weight value (w_i) as a measure of goodness of fit to evaluate each of the model sets. After identifying each of the best models using the AIC approach, we used post hoc analyses to elucidate the effect of swelling size on our two assays of male preference.

Analysis 2: Swellings as an Indicator of Female Fitness

To test the hypothesis that swelling size signals female fitness, we examined the relationship between variation in swelling size and proxies of female fitness. We used a classical null/alternative hypothesis testing approach for this second analysis because we wanted to explicitly test this specific hypothesis. We selected five measures to assess reproductive life span, reproductive rate and early infant survival, all of which contribute ultimately to female reproductive success. Although including offspring survival as a component of parental fitness can sometimes lead to mistaken conclusions about evolutionary outcomes (Wolf & Wade, 2001), we nevertheless employ the common empirical convention of using early infant survival as a reflection of female fitness. This is especially valid for long-lived primates with an extended period of dependency; in Amboseli baboons as in other wild primate populations, early infant mortality can be substantial (Altmann & Alberts, 2003) and maternal characteristics contribute to infant survival (Silk, Alberts, & Altmann, 2003). Therefore, males will generally benefit from mating with a female whose infants are likely to survive. Furthermore, most of our proxies have been used in previous studies (e.g. Domb & Pagel, 2001). Our selected measures were as follows.

(1) Age at first conception. All else being equal, individuals that mature earlier have higher lifetime fitness. In Amboseli baboons, the earliest-maturing females have, on average, a 0.5 infant advantage over their lifetime compared to the latest-maturing females (Altmann, Hausfater, & Altmann, 1988).

(2) Survival to 1 year of age of the individual infant that was conceived during the cycle represented in our data set.

(3) The number of a female's infants that survived to 1 year of age, per reproductive year of the female's life.

(4) The proportion of the female's total offspring born that survived to 1 year of age.

(5) The number of live infants born per reproductive year during the female's life.

RESULTS

Analysis 1

Multimodel inference: predictors of whether a female was consorted by highest-ranking male on a given conceptive cycle

When we modelled the predictors of whether a female was consorted by the highest-ranking male on a given conceptive cycle, four models were produced with $\Delta_i < 2$, indicating that they had substantial and nearly equivalent support. Two of the top models included swelling length as a predictor variable, although none of the top models included swelling width. However, the effect size for swelling length was weak and the direction was opposite that predicted by the reliable indicator hypothesis (ranging from -0.002 to -0.004). That is, females with longer swellings were slightly less likely to be consorted by the highest-ranking male, and this effect was very weak. All of the top models included average queue length, indicating that an increased competitive environment reduced the probability that a given female would be consorted by the highest-ranking male. All but one of the top models included cycles since resumption as an important predictor; females who had experienced more sexual cycles since their most recent pregnancy were more likely to be consorted by the alpha male. Finally, although one of the top models included days since last wet month, the effect size was weak (0.001) (Table 2).

Table 2

Models of fixed effects on the probability of being consorted by the highest-ranking male in the group ($N = 34$ conceptive cycles) and the proportion of time that a consortship was trailed by a follower male ($N = 32$ conceptive cycles)

	Swelling width	Swelling length	Cycles since resumption	Female age	Female rank	Days since last wet month	Queue	AICc	ΔAIC_c	w_i	
Alpha male			0.112				-0.041	43.244	0.000	0.106	
		-0.002					-0.033	43.448	0.204	0.096	
		-0.004	0.093				-0.043	43.613	0.368	0.088	
			0.113			0.001	-0.027	45.135	1.891	0.041	
							-0.025	45.757	2.512	0.030	
							-0.041	45.848	2.603	0.029	
		-0.002		0.119		-0.005		-0.041	45.924	2.680	0.028
				0.116				-0.041	46.005	2.760	0.027
				0.113	0.004			-0.023	46.028	2.783	0.026
			-0.001				0.000	-0.032	46.139	2.895	0.025
		-0.002		-0.011							
Follower male	0.008		0.051					7.531	0.000	0.111	
	0.010							8.295	0.764	0.076	
			0.066					8.679	1.148	0.062	
	0.008		0.061			-0.008		8.918	1.387	0.055	
	0.009						0.014	9.462	1.931	0.042	
	0.008		0.045				0.009	9.827	2.296	0.035	
			0.075			-0.008		10.156	2.625	0.030	
	0.008		0.052		0.002			10.306	2.775	0.028	
	0.008		0.052				0.000	10.314	2.783	0.028	
	0.010					-0.004		10.615	3.084	0.024	

Bolded rows in both candidate sets indicate those models that should be considered equivalent to best model (i.e. $\Delta_i < 2$). Because only the top 10 models for each candidate set are shown, the Akaike weights that are shown (w_i) do not sum to 1.

Multimodel inference: predictors of the proportion of time that a consorting pair had a follower

When we modelled the proportion of time that a consorting pair had a follower (considering only conceptive cycles), a total of five top models produced a $\Delta_i < 2$. In contrast to the previous analysis, swelling width, but not swelling length, predicted the proportion of time that a consortship was trailed by a follower male, and in the predicted direction (increased swelling width was associated with more time with a follower). Swelling width appeared in four of the five top models, and the effect size ranged from 0.008 to 0.010. Cycles since resumption was also an important predictor of following; it was included as a predictor in three of the five top models. Only one of the five best models included queue length as a predictor, indicating that the competitive environment did not influence the proportion of time that a consortship attracted a follower as much as it did the probability that a female would be consorted by the highest-ranking male. Again, one of the top models included a small effect of days since last wet month (Table 2).

Taken together, the multimodel inference indicates that both measures of male preference were influenced by cycles since resumption. As cycle number increased, a given female was more likely to be consorted by the highest-ranking male and a given consortship was more likely to be trailed by a follower male. The effects of average queue length and swelling size on male preference were more equivocal. To further examine the effects of these variables (cycles since resumption, competitive environment, swelling width and length) on male mate choice, we performed post hoc analyses. We report only R^2 values for these, rather than P values, because as post hoc analyses, these are subject to type I errors due to multiple testing. Because the effects of age, days since last wet month and rank were either negligible or absent, we did not investigate their effects on male mate choice any further.

Consortship by highest-ranking male

A bivariate analysis confirmed that females were less likely to be consorted by the highest-ranking male in groups where average queue length was longer (i.e. where male competition was more intense; Fig. 1a). In addition, the probability of consortship by the

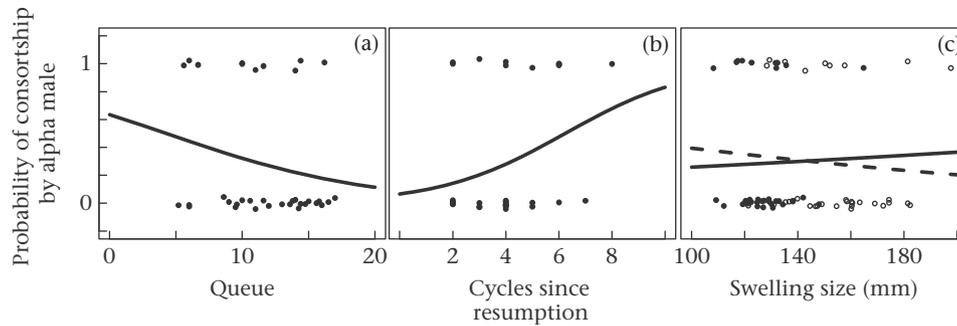


Figure 1. Expected probability of being consorted by the highest-ranking male at any time during the 5-day window prior to deturgescence as a function of (a) average length of queue, (b) cycles since resumption and (c) maximal swelling size. Each trend line was generated using coefficients from a bivariate logistic regression with a single predictor. Observed data points are plotted and jittered to facilitate visibility.

highest-ranking male increased with the number of cycles since resumption (Fig. 1b) and neither measurement of swelling size predicted consortship by the alpha male in a bivariate analysis (Fig. 1c).

Proportion of consort time with a follower

The proportion of time that a consortship was trailed by at least one follower was influenced both by cycles since resumption and swelling width (see above). Consequently, we performed a simple linear regression of our response variable (proportion of consort time with a follower) on each of these two predictors separately. Next, we regressed the residuals from each of these models on the other predictor, in order to isolate the effect on male behaviour of each predictor independent of the other one. As both cycles since resumption and swelling width increased, consortships were more likely to attract a follower male (cycles since resumption: $R^2 = 0.06$; swelling width: $R^2 = 0.13$; Fig. 2a, b). That is, for a given cycle number, females with wider swellings were more likely to have a follower. Similarly, for a given swelling width, females who had more cycles since resumption were more likely to have a follower.

Analysis 2

We found no relationships between interindividual differences in swelling size and any measure of female fitness. We fitted five generalized linear models (GLM), one for each fitness proxy. In each of the five models, we included female age and female dominance rank as additional predictors to control for their potentially confounding effects on female fitness proxies. Neither maximal swelling width nor maximal swelling length was a significant

positive predictor of any of the five measures of female fitness (Table 3). Only the relationship between interindividual differences in swelling length and the proportion of total offspring surviving to year 1 was significant. However, in contrast to the prediction of the reliable indicator hypothesis, that coefficient (between swelling length and proportion of total offspring surviving to year 1) was negative, indicating that, if anything, this female fitness proxy was reduced for females with longer swellings.

DISCUSSION

Male Mate Choice for Cycles since Resumption versus Interindividual Differences in Swelling Size

We examined male behaviour during female sexual cycles that resulted in offspring conception, and found not only that cycles since resumption predicted male baboon behaviour, but that it was a stronger predictor than differences in swelling size between individuals. Specifically, females in our study who conceived after experiencing more cycles since resumption were both more likely to be consorted by the highest-ranking male on the conceptive cycle and were more likely to attract at least one follower male, even when controlling for multiple potential confounds, including swelling size. One explanation for this result is that females display exaggerated proceptive behaviour on conceptive cycles, which drives the male response. Although we did not test this hypothesis directly and cannot conclusively rule it out, previous work on baboons does not support it; in populations where high-ranking males typically monopolize conceptive cycles, new immigrants fail to do so, even if they attain high rank (Weingrill et al., 2003).

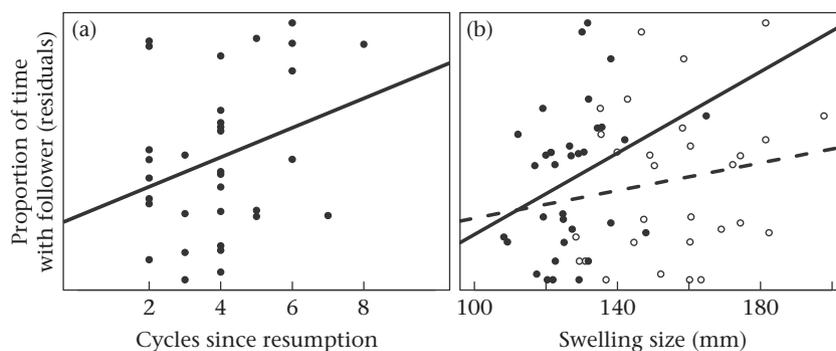


Figure 2. Proportion of consort time with a follower male as a function of (a) cycles since resumption and (b) maximal swelling size. Residuals are from linear regressions of the proportion of time with a follower on (a) swelling width and swelling length and (b) cycles since resumption. In (b), closed circles represent swelling width (solid regression line) and the open circles represent swelling length (dashed regression line).

Table 3
Coefficients and *P* values for relationships between interindividual differences in swelling size (swelling width and swelling length) and each of the five proxies for female fitness

Model	Female fitness proxy	GLM distribution	Swelling width		Swelling length	
			Coefficient	<i>P</i>	Coefficient	<i>P</i>
A	Age at first conception	Poisson	0.003	0.711	−0.001	0.814
B	Survival of infant to year 1	Binomial	−0.068	0.225	−0.006	0.861
C	Infants born per reproductive year	Gaussian	−0.002	0.152	0.001	0.186
D	Infants surviving to year 1 per reproductive year	Gaussian	0.000	0.807	−0.001	0.332
E	Proportion of total offspring surviving to year 1	Gaussian	0.003	0.448	−0.004	0.045

Significant *P* values are shown in bold.

This discrepancy suggests that, male baboons use longitudinal information in order to make decisions about how to invest mating energy. That is, our results provide support for the hypothesis that males use information about the number of times a female has cycled in the recent past in order to identify cycles likely to result in conception, although the exact mechanism by which they do so remains unknown.

A potential adaptive explanation for this pattern emerges from the fact that each sexual cycle has some probability of not resulting in offspring. Thus, primate males are presented with mating opportunities that vary considerably in their fitness payoffs. Males should therefore experience selection to distinguish female sexual cycles that have a low probability of conception from those with a higher probability of conception. Indeed, previous studies both in our study population and in others suggest that male baboons are able to do just that (Alberts et al., 2006; Bercovitch, 1987; Bulger, 1993; Gesquiere et al., 2007; Weingrill et al., 2003). Our study builds upon those results by demonstrating that males respond differently to earlier conceptive cycles (closer to a recent pregnancy) than they do to conceptive cycles that are later (further from a recent pregnancy). Indeed, our results suggest that the apparent ability of males to differentiate conceptive from nonconceptive cycles might simply reflect males' sensitivity to the number of cycles since resumption that a given female has experienced, and that cycles since resumption may be a good indicator of conception probability.

The first prediction generated by the reliable indicator hypothesis is that males should prefer females with larger swellings, even after controlling for within-cycle and within-individual variation in size. That males respond to variation in cycles since resumption does not negate the possibility that they may also have preferences based on differences in swelling size independently. However, our results provide only equivocal support for this first prediction. Although consortships with females that had larger swellings were more likely to attract a follower male, there was no evidence that the highest-ranking males (and those most likely to exercise choice) biased their mating behaviour toward the females with larger swellings. An alternative interpretation of this result is that alpha males are less able to monopolize females with larger swellings, perhaps precisely because followers challenge them more frequently. However, despite the presence of followers, high-ranking males do successfully retain consortships with females who have experienced more cycles since resumption, suggesting that they are, on average, able to mount the energetic resources required to maintain high-value consortships. In other words, the lack of an effect of swelling size on the behaviour of alpha males suggests a lack of (or reduced) motivation rather than a lack of ability. This difference between alpha males (whose behaviour was not influenced by interindividual differences in swelling size) and follower males (whose behaviour was) points to the possibility that alpha males and follower males may not have access to the same signal information, may prioritize that information differently, may be differently constrained, or may have different opportunities.

For instance, follower males might attend more closely than alpha males to swelling size if they tend to be newly immigrated males that would not have the information necessary to assess a female's reproductive history or her number of cycles since resumption (Weingrill et al., 2003). In that case, naïve males might benefit by using swelling size as a proxy for cycles since resumption. However because follower males in our sample were almost entirely males who had been in the social group for longer than 6 months, it is unlikely that these males had less information than alpha males about the number of times that a female had cycled since her last pregnancy.

Alternatively, the differences in the costs associated with following behaviour relative to those of being the primary consort partner may result in this difference in male behaviour. Consorting males incur costs by forgoing foraging opportunities (Alberts et al., 1996; Packer, 1979). In addition, alpha males (who are typically the most active mate guarders among adult males in a baboon group) have higher glucocorticoid levels than other males, indicating considerable energetic stress (Gesquiere et al., 2011). Therefore, successful consortship behaviour requires good energetic and physiological reserves. In contrast, following behaviour requires little or no special skill and the risks are presumably relatively low. Because cycles since resumption is likely to be a good indicator of the probability of conception, males may greatly increase their chances of capturing good reproductive opportunities (i.e. a conceptive cycle) by tracking it; furthermore, those benefits are likely to outweigh both the higher costs of being the primary consort partner and the relatively low costs of being a follower. In contrast, swelling size may provide some information about the quality of a reproductive opportunity (if females with larger swellings have superior physiological reserves and are therefore more likely to conceive or more able to sustain a pregnancy to term), but may not be as reliable as cycles since resumption. Thus, if the benefits to potential sires of larger swelling sizes are lower than the benefits of cycles since resumption, those benefits may not justify paying the higher costs of primary consortship but still outweigh the low costs of engaging in following behaviour (see Fig. 3).

Competitive Environment (Average Queue Length)

To our knowledge, this study is the first to control for the effect of the competitive environment (specifically the number of males relative to available females) on male mate choice with respect to swelling size. The competitive environment only affected one of our assays of male mate choice; as the average queue length increased, the highest-ranking male was less likely to successfully monopolize a given sexual cycle. This result is consistent with previous comparative, cross-species reports (Cowlshaw & Dunbar, 1991) as well as results in our study population (Alberts et al., 2003) that male ability to monopolize cycling females declines with group size. The absence of an effect of competitive environment on the behaviour of follower males in the present study lends further

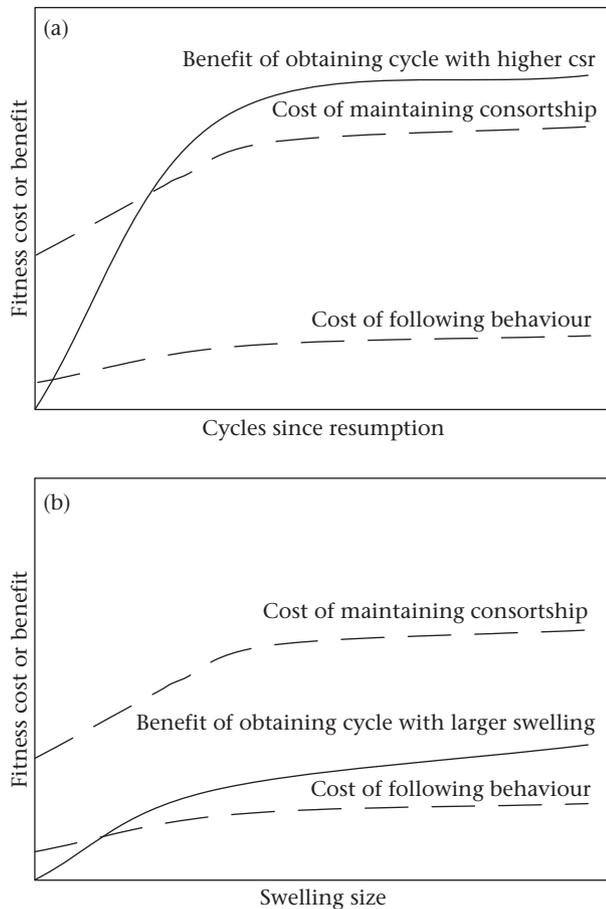


Figure 3. Heuristic of the hypothesized cost–benefit relationships that would result in the pattern observed in this study. (a) Male behaviour with respect to cycles since resumption (csr): if the benefit to a male of monopolizing a cycle with a higher cycle number is higher than the costs of either maintaining the consortship or engaging in following behaviour, then high-ranking males should work harder to obtain those consortships and follower males should invest in following them. Cost functions are increasing because the costs of both male behaviours should increase with cycles since resumption due to the increased presence of followers. (b) Male behaviour with respect to swelling size: if the benefit to a male of monopolizing the cycle of a female with a larger swelling (for a given cycle number) is higher than the cost of engaging in following behaviour, but lower than the cost of maintaining the consortship, then high-ranking males should not incur the costs of obtaining those consortships, but follower males should still invest in following them. Cost functions are increasing because the costs associated with both male behaviours should increase with swelling size due to the increased presence of followers.

support to the hypothesis that alpha and follower males may experience different constraints. Finally, these results highlight the fact that assays of male preference, including assays other than those we selected, may often only be meaningful if they are interpreted within the context of the competitive environment.

Swelling Size as a ‘Reliable Indicator’ of Fitness

Regardless of whether alpha males and follower males respond to, and respond differently to, interindividual differences in swelling size, the question remains, what information is being signalled by variation in swelling size? Does this variation contain information that males care about, beyond the probability of ovulation within a cycle and that of conception between cycles? For the reliable indicator hypothesis to explain variation in male response to sexual swellings, interindividual differences in swelling size should predict some component of female fitness. Our analysis

provides no support for the hypothesis that interindividual differences in swelling size (either swelling width or swelling length) indicate variation in female fitness. In fact, the relationship between swelling size and female fitness was, at times, in the opposite direction of that predicted by the reliable indicator hypothesis. Our study provides the strongest evidence to date that exaggerated swellings are not signals of enduring differences in fitness between females in baboons.

Summary and Future Directions

We have shown that high-ranking males do not prefer females with larger swellings (when controlling for cycle number and conception) and that females with larger swellings do not have higher reproductive success. In doing so, we have tested and rejected the reliable indicator hypothesis for the function of exaggerated swellings in baboons. Rather than tracking the potential differences in fitness between females, male baboons appear to track and target the potential for a given reproductive opportunity to result in fertilization. As the strongest such evidence to date, our results should shift the discussion about the function and evolution of exaggerated swellings from one that necessarily invokes intrinsic differences in female quality to one that focuses on temporal changes in the quality of the reproductive opportunity. We encourage others to replicate this study in other baboon populations, including subspecies that may have different demographic or cycling patterns (such as Kinda baboons, *Papio cynocephalus kindae*, and hamadryas baboons, *Papio hamadryas*).

We emphasize that our test of the reliable indicator hypothesis does not address the question of whether female baboons experience sexual selection for large swellings. In fact, testing the reliable indicator hypothesis cannot, in itself, identify sexual selection on female sexual swellings because the existence of male mate choice alone does not necessarily exert sexual selection pressure on female traits. Male mate choice will only exert selection pressure on swelling size if females with larger swellings receive fitness advantages as a result of being preferred beyond those that they would receive from being mated at random (see Equation 6 in [Servedio, 2007](#), for mathematical representation of this point, also [Fitzpatrick, 2015](#)). In other words, without demonstrating that there is some benefit to females of obtaining more (or better) mates as a result of a given trait, we cannot conclude that the trait is sexually selected. Indeed, in the case of sexual swellings, male mate choice may simply be a consequence of selection on males, if females with larger swellings have higher infant survival and therefore males prefer them. In such a situation, male mate choice will not necessarily cause sexual selection on female sexual swellings, although this causation is assumed by the reliable indicator hypothesis. Despite this slip in logic, studies continue to cite [Domb and Pagel \(2001\)](#) and exaggerated swellings as an example of sexual selection in females (e.g. [Clutton-Brock, 2007, 2009](#); [Davies, Krebs, & West, 2012](#); [Deschner et al., 2004](#); [Drea, 2005](#); [Fernandez & Morris, 2007](#); [Huchard et al., 2009](#); [Jawor et al., 2004](#); [LeBas, 2006](#); [Paul, 2002](#); [Rundle & Chenoweth, 2011](#); [Weiss et al., 2011](#)). We caution the reader against conflating male mate choice with sexual selection on female traits. Furthermore, in light of this caution, we highlight the importance of identifying the conditions under which male mate choice will result in selection pressure on females, versus the conditions under which male mate choice evolves but is inert as a mechanism of selection on female traits.

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