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13 Title: Exaggerated estrous swellings and male mate choice in  
14 primates: testing the reliable indicator hypothesis in the  
15 Amboseli baboons.

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17

18

19 INTRODUCTION

20

21           The evolution of male mate choice in sex-role reversed species can easily be  
22 understood according to the general principles of sexual selection. That is, when females  
23 are mate-limited they are expected to compete for access to males and those males, in  
24 turn, are expected to be choosy. This phenomenon is well described in some sex-role  
25 reversed species of pipefish (Berglund et al. 1989; Vincent et al. 1992) and shorebirds  
26 (Szekely & Reynolds 1995). In contrast, when the sex roles are conventional, choosy  
27 males will be at a competitive disadvantage and, therefore, male mate choice should be  
28 selected against. Of course, exceptions to this prediction have been demonstrated, most  
29 notably in those cases where female fecundity varies and choosy males therefore benefit  
30 by selecting females with higher fecundity (Servedio & Lande 2006). Indeed, empirical  
31 work across a broad range of taxa indicates that male choosiness in these scenarios is  
32 common. For example, in those species where female body size predicts fecundity, males  
33 often demonstrate a preference for larger females (lizards; Olsson 1993, fish; Sargent et  
34 al. 1986, insects; Bonduriansky 2001).

35

36           However, male mate choice is increasingly observed even when direct fecundity  
37 benefits for choosy males are not apparent. In some of these cases, males might receive  
38 indirect benefits from females, analogous to the “good genes” models of mate choice that  
39 have been developed for female choice (see Chapter 3 Andersson 1994) For example,  
40 experimental work in barn owls suggests both that male barn owls prefer females with  
41 spottier plumage and that the offspring of those females mount a more effective immune

42 response (Roulin et al. 2000, 2001). That is, males may bias their mating investment  
43 toward females whose offspring have superior genetic immunity. In other cases, males  
44 may evolve preferences when male investment in mating is so high or costly that mating  
45 necessarily limits future mating opportunities, thus imposing opportunity costs. For  
46 example, males should choose mates carefully when their ability to mate with many  
47 females is constrained by intense male-male competition or sperm competition  
48 (Schwagmeyer and Parker 1990; Owens and Thompson 1994; reviewed by Edward and  
49 Chapman 2011).

50

51       The exaggerated estrous swelling displayed by many cercopithecine primates is  
52 commonly cited as a trait upon which males base mate choice, and studies in several  
53 species have suggested that males prefer females with larger swellings (Domb & Pagel  
54 2001; Higham et al. 2009; Huchard et al. 2009). However, the fitness benefits that males  
55 might receive as a result of this choosiness based on swelling size are unknown.

56 Therefore, knowledge of the evolutionary forces that have shaped both the behavior and  
57 the trait remain obscured, and the question of what information males may receive from  
58 these signals remains open (Deschner et al. 2004; Higham et al. 2009; Huchard et al.  
59 2009; Fitzpatrick et al. 2014).

60

61       Sexual swellings appear during the follicular phase of the female sexual cycle, are  
62 thought to have evolved multiple times in the primate lineage (Dixson 1983), and are  
63 most commonly associated with multi-male multi-female social systems (Nunn 1999). It  
64 has been well established in many species that male mating behavior increases in

65 response to these changes in swelling size within a given cycle (baboons, Hausfater 1975;  
66 Packer 1979; Bielert & Anderson 1985; Higham et al. 2008b; Huchard et al. 2009; Nitsch  
67 et al. 2011; chimpanzees, Tutin 1979; Emery & Whitten 2003; Deschner et al. 2004;  
68 Breaux et al. 2012 macaques, van Noordwijk 1985; Brauch et al. 2007). In fact, as the  
69 understanding of this trait has become more refined over the past decade, researchers  
70 have identified three distinct types of variation in swelling size (Zinner et al. 2002).

71

72 1) Swelling size varies within a cycle, generally achieving maximal size for that cycle  
73 around the time of ovulation. This type of variation has been demonstrated  
74 repeatedly to be a probabilistic indicator of ovulation in at least some species  
75 (Hendrickx and Kraemer 1969; Wildt et al. 1977; Dahl et al. 1991; Emery and  
76 Whitten 2003; see Nunn 1999; Alberts and Fitzpatrick 2012 for thorough review)  
77 and it has been shown in baboons that females are more attractive to males during  
78 the period of highest fertility (Noe & Sluijter 1990). Furthermore, it has been  
79 demonstrated in chimpanzees that males both copulate with and compete for  
80 females more actively during the peri-ovulatory period (Deschner et al. 2004).

81

82 2) Swellings vary in size within an individual across cycles. That is, females of most  
83 primate species cycle repeatedly before conceiving and it has been demonstrated  
84 in several species that maximal swelling size increases from cycle to cycle within  
85 one individual (Emery and Whitten 2003; Deschner et al. 2004; Higham et al.  
86 2008b; Fitzpatrick et al. 2014). If the probability of conception increases with  
87 subsequent cycles, this type of variation may signal differences in the probability

88 of conception across cycles. Indeed, although variation in conception probability  
89 across cycles within an individual has not—to our knowledge—been described  
90 empirically, data from our study population suggest that the cycles immediately  
91 following post partum amenorrhea are less likely to result in conception than later  
92 ones (data presented in Fitzpatrick et al. 2014.) Furthermore, it has been shown  
93 that alpha males successfully target conceptive cycles, suggesting that, within a  
94 given female, cycles vary in the probability of conception (Weingrill et al. 2003;  
95 Alberts et al. 2006).

96  
97 3) Finally, swelling sizes may differ between individuals. Because this type of variation  
98 can only be revealed by controlling for the within-cycle and across-cycle variation  
99 exhibited by each female, it is more challenging to demonstrate empirically.  
100 Three studies have been able to do so (Deschner et al. 2004; Huchard et al. 2009;  
101 Fitzpatrick et al. 2014).

102  
103 Thus, it is known that males respond to the first type of variation (within-cycle variation  
104 in swelling size) and that the second type of variation has the potential to signal important  
105 information to males (because swelling size increases as cycle number progresses).  
106 However, it remains unclear whether the third type of variation—variation between  
107 females in sexual swelling size (beyond differences accounted for by within-cycle and  
108 across-cycle variation)—has additional information content for male primates.

109

110           Despite this gap, a main hypothesis that attempts to explain both the evolution of  
111 exaggerated swellings and the male response to them hinges on the assumption that it is  
112 precisely this variation between individuals that is salient for males. This hypothesis has  
113 become known as “the reliable indicator hypothesis”; it posits both that exaggerated  
114 swellings signal intrinsic differences in female quality (i.e. enduring differences in  
115 phenotypic quality) and that males bias their mating behavior toward females with larger  
116 swellings (Pagel 1994). Thus, the reliable indicator hypothesis makes two main  
117 predictions: 1) males will demonstrate a preference for females with larger swellings, all  
118 else being equal; 2) superior females (with higher lifetime reproductive success) will  
119 have larger swellings. Importantly, the reliable indicator hypothesis proposes that the  
120 type of quality being signaled is a permanent characteristic of a female, and that some  
121 females are consistently superior to others, a superiority that is associated with increased  
122 lifetime reproductive success. One empirical test of this hypothesis reported support for  
123 its predictions; male baboons preferred females with larger swellings and that those  
124 females had higher infant survival (Domb & Pagel 2001). However, a reanalysis of the  
125 data presented in this study showed that it was methodologically flawed in that it failed to  
126 control for differences between baboon groups in food availability (and hence in female  
127 body condition, in the competitive environment for males, and in infant survival), which  
128 could have accounted for the observed results (Zinner et al. 2002).

129

130           Furthermore, no test of the reliable indicator hypothesis has differentiated  
131 between the permanent type of quality it proposes and the more transient type of quality  
132 that is probability of conception. Thus, without controlling for whether a given sexual

133 cycle resulted in a conception, the reliable indicator hypothesis cannot be adequately  
134 investigated. Specifically, if conceptive swellings are larger than non-conceptive ones  
135 (which appears to be true in at least some species, (Emery & Whitten 2003; Deschner et  
136 al. 2004; Gesquiere et al. 2007; Higham et al. 2008a, 2009; Huchard et al. 2009;  
137 Fitzpatrick et al. 2014)) and, given that males of some species are able to identify and  
138 seem to prefer cycles with higher probabilities of conception (Weingrill et al. 2003;  
139 Alberts et al. 2006), then it may appear that males prefer larger swellings when, instead,  
140 they may only be tracking probability of conception. Neither Domb and Pagel (2001) nor  
141 any subsequent studies that examined the reliable indicatory hypothesis were able to  
142 control for this potential confound.

143

144         Despite the absence of resolution about what variation in swelling size can  
145 potentially signal and despite the limitations of Domb and Pagel (2001), it continues to be  
146 cited as having shown that exaggerated swellings are a reliable indicator of female  
147 quality (e.g. Gouzoules & Gouzoules 2002; Paul 2002; Jablonski 2004; Jawor et al. 2004;  
148 Dixson & Anderson 2004; Caro 2005; Preston et al. 2005; Massironi et al. 2005; Veiga &  
149 Polo 2005; Drea 2005; LeBas 2006; Weiss 2006; Polo & Veiga 2006; Pagel & Meade  
150 2006; Gumert 2007; Watson & Platt 2008; Huchard et al. 2009; Huangshan et al. 2010;  
151 Gladbach et al. 2010; Rundle & Chenoweth 2011; Weiss et al. 2011; Haselton &  
152 Gildersleeve 2012). However, no other study has provided clear support for the reliable  
153 indicator hypothesis. One recent study found evidence for the idea that male primates  
154 prefer females with larger swellings, but was unable to control for between-cycle  
155 variation in individual females because of small sample sizes (Huchard et al. 2009).

156 Further, a number of studies have found that males are more responsive to conceptive  
157 cycles than to nonconceptive cycles, highlighting the importance of controlling for  
158 conceptive status in measuring male preferences (Bercovitch 1987; Bulger 1993;  
159 Weingrill et al. 2003; Setchell 2004; Alberts et al. 2006; Gesquiere et al. 2007). The one  
160 study that has successfully made this critical distinction between male response based on  
161 swelling size versus male response based on within-female changes in conception  
162 probability (between cycles) has failed to support the reliable indicator hypothesis  
163 (Deschner et al. 2004). Finally, with respect to the potential for sexual swellings to signal  
164 variation in female fitness, results are also mixed; one reports a relationship between  
165 swelling size and components of female fitness (baboons; Huchard et al. 2009) while  
166 others report an absence of one (mandrills; Setchell 2004; Setchell et al. 2006).

167

168       Thus, the functional significance of male mate choice in response to exaggerated  
169 swellings is still open. Here, we investigate the relationship between swelling size and  
170 male mating behavior as well as components of female fitness. In order to do so, we  
171 take advantage of the most detailed and largest collection to date of swelling size  
172 measurements in an ongoing study of savannah baboons (*Papio cynocephalus*;  
173 Fitzpatrick et al. 2014). This dataset has revealed critical sources of variance in swelling  
174 size; swelling size was shown to be influenced by the number of times a female had  
175 cycled since her most recent pregnancy (*cycles since resumption*), the amount of rainfall  
176 (*days since last wet month*)—which predicts food availability, and female age  
177 (Fitzpatrick et al. 2014). Together, this information accords a more precise test of the  
178 reliable indicator hypothesis than has been possible previously, by allowing us to

179 examine male mating decisions at the same time that we control for several potential  
180 confounds. As such, we address two questions. First, do males bias their mating behavior  
181 toward females with larger swellings? Second, does variation in swelling size predict  
182 female fitness?

183

## 184 METHODS

185

### 186 *Study Population and Data Collection*

187

188 We collected morphological data (swelling size), behavioral data (male mating  
189 behavior), and proxies of female fitness from a natural population of savannah baboons  
190 (*Papio cynocephalus*) that has been under continuous study by the Amboseli Baboon  
191 Research Project (ABRP) for over four decades (Hausfater 1975; Alberts et al. 2006;  
192 Gesquiere et al. 2007; Altmann et al. 2010; Alberts & Altmann 2012). Savannah baboons  
193 exhibit female philopatry and male dispersal, live in multi-male multi-female groups  
194 where both males and females mate multiply, and breed at relatively similar frequencies  
195 year round. The Amboseli baboons occupy a short-grass savannah habitat that has  
196 undergone dramatic ecological change (from acacia woodland to more open savannah).  
197 The ecosystem is subject to extreme variation in both intra-annual and inter-annual  
198 rainfall (Altmann et al. 2002; Alberts et al. 2005).

199

200 The study population consisted of over 300 individuals of both sexes and all ages,  
201 all of which were habituated to human observers, individually identifiable by sight, and

202 distributed across five different social groups during the period of this study. All data  
203 were collected during one field season of 12 months (November 2008 through November  
204 2009) and a second field season of 5 months (February 2010 through June 2010).

205

206 The full analysis for this study included two discrete parts, one for each research  
207 question. Both of these analyses used morphological data as the independent variable  
208 (swelling size) and each then asked how swelling size predicted a response variable. The  
209 response variable in our first analysis was behavioral (male mate choice) and the  
210 response variables in our second analysis were life history measures (proxies of female  
211 fitness.) Because male baboons are rarely presented with an opportunity to truly choose  
212 between two simultaneously cycling females, our use of ‘male mate choice’ in this study  
213 does not necessarily imply simultaneous choice. Rather, we use two measures of male  
214 behavior to assess male mating decisions. Below, we first detail the collection of the main  
215 predictor of interest (swelling size). In subsequent sections, we describe the details of  
216 each of the two analyses, including the data collection for the response variables and the  
217 analytic approaches.

218

219 *Main Predictor Variable of Interest: Maximal Swelling Size*

220

221 We used two different measures of swelling size: swelling width and swelling  
222 length. Swelling sizes were measured from digital images of individual reproductive  
223 females, collected opportunistically during daily observations. Digital images were  
224 collected using a Photoscale-2 and digital caliper, a system that allowed for the

225 conversion of measurement in pixels to an estimate in millimeters (Fitzpatrick et al.  
226 2014).

227

228 In order to control for the *within cycle* variation, we included only those females  
229 for whom we were able to capture maximal swelling size, designated as a size estimate  
230 that was collected within two days prior to the first day of deturgescence (“d-day”). This  
231 designation is justified by previous analyses showing that size estimates gathered on “d-  
232 2” (two days prior to deturgescence) and “d-1” (one day prior to deturgescence) were  
233 statistically equivalent (see Fitzpatrick et al. 2014 for a thorough explanation of this  
234 designation and method). In order to control for the *within individual* variation and the  
235 potential confound of conceptive status, we included only those cycles that resulted in a  
236 pregnancy. That is, this analysis was restricted only to conceptive cycles. Therefore, each  
237 female in the data set was represented only once (N = 34 females). Although spontaneous  
238 miscarriages and stillbirths occur in this population (Beehner et al. 2006; Beehner 2006),  
239 all conceptions represented in this analysis resulted in a live birth.

240

241 *Analysis 1: Male Mate Choice*

242

243 *Selection of response variables (behavioral data)*

244

245 In order to assay whether male preference varied as a function of differences in  
246 swelling size between individuals, we collected behavioral data during the clear bouts of  
247 mate-guarding, or “consortships”, that take place when a female has a swelling. These are

248 unambiguous associations between one estrous female and one adult male (Saayman  
249 1970; Seyfarth 1978; Packer 1979; Bercovitch 1988; Alberts et al. 1996, 2003). During  
250 consortships, the consorting male attends closely to the estrous female, usually  
251 maintaining proximity and displaying vigilance. However, consortship possession is  
252 often overturned because males may fight over them intensively. As a consequence,  
253 females are not only consorted continuously during the five-day window during which  
254 they are most likely to ovulate (Wildt et al. 1977; Higham et al. 2008b; Daspre et al.  
255 2009), but are usually consorted by more than one male during a given cycle.

256

257       We selected our behavioral response variables based on two key features of male-  
258 male competition in the presence of estrous females. First, of all the males in a social  
259 group, the highest-ranking male is the most likely to be able to exercise choice (Bulger  
260 1993; Weingrill et al. 2003; Deschner et al. 2004; Alberts et al. 2006; Gesquiere et al.  
261 2007). Second, consortships often attract male “following,” in which one or more males  
262 that are not the consort partner will trail the consort pair (Danish & Palombit 2014).  
263 Following males are identifiable because they clearly coordinate their movements with  
264 the consort pair, and glance at the consort pair regularly and more often than do other  
265 individuals in the group. Followers sometimes make overt attempts to take over  
266 possession of the established consortships, which usually involves charging, fighting, or  
267 coalitionary behavior with other males. Even in the absence of a clear takeover attempt,  
268 however, following behavior most likely imposes costs on the follower (e.g. limited  
269 foraging opportunities or energetic costs of vigilance, as has been documented for mate  
270 guarding itself; Alberts et al. 1996).

271

272           Thus, our two behavioral measures of male preference were 1) consortship by the  
273 highest-ranking male, and 2) proportion of consortship time that the consorting pair was  
274 trailed by at least one follower. Because males of many species bias their mating  
275 behavior toward peri-ovulatory females, we controlled for the potential effect of swelling  
276 size variation *within cycles* on male behavior by restricting our analysis to only those  
277 behavioral data that were collected during the five-day window prior to “d-day.”

278

279 *Response variable 1: consortship by highest-ranking male*

280

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

293

294 *Response variable 2: proportion of consort time with a follower*

295

296 Data on followers were collected during point samples (instantaneous samples of  
297 behavior collected every two minutes) taken during 30-min focal animal samples  
298 (Altmann 1974). Focal samples were collected on consorting pairs (i.e. one estrous  
299 female and her consort partner during each focal sample). At each point sample we  
300 recorded the number of followers present and then created a proportion of consort time  
301 spent with at least one follower. Field conditions prevented the collection of focal  
302 samples from 2 of the females for which we captured maximal swelling width and length.  
303 Therefore, when using this second response variable (proportion of consort time with a  
304 follower), the sample included only 32 conceptive females. When we performed the  
305 multivariate linear regression (predictors described in *Additional predictor variables* sub-  
306 subsection), the residuals were distributed normally. Therefore, this response variable  
307 remained as a proportion in the multivariate linear regression (see Results section).

308

309 *Additional predictor variables*

310

311 In addition to swelling size, we modeled additional features of each individual  
312 female including *cycles since resumption*, *female age*, and *female rank*. We included one  
313 ecological variable, *days since last wet month*, and one demographic variable, the number  
314 of adult males in the queue (*queue length*), as predictor variables (Table 1). All of these  
315 additional predictors were included to control for potentially confounding effects. The

316 correlation coefficients between all predictor variables were less than .5 and the variance  
317 inflation factors were all less than 2.

318

319 **Table 1:** Parameters used in analysis of male mate choice as a function of swelling  
320 size.  
321

Predictor	Description	Range
Swelling width	Maximal swelling width (mm)	108.24 - 164.83
Swelling length	Maximal swelling length (mm)	121.42 – 197.74
Cycles since resumption	Number of cycles since resumption	2 - 8
Female age	Female age (to nearest tenth of a year)	7.1 - 18.3
Female rank	Female dominance rank	1 - 27
Days since last wet month	Number of days since last wet month	0 - 320
Queue length	Average number of adult males in the queue (number of adult males in the group - number of cycling females)	0.4 - 17

322

323

324 *Cycles since resumption* was an integer representing the number of times a female  
325 had cycled since her most recent pregnancy so that the first cycle after post-partum  
326 amenorrhea was cycle 1 and, if pregnancy did not occur, the next cycle was cycle 2, and  
327 so on. We included *cycles since resumption* because this predictor varied considerably in  
328 our data set and had a large effect on swelling size in our previous analysis (Fitzpatrick et  
329 al. 2014). That is, even though we only considered conceptive cycles in this analysis,  
330 females conceived during anywhere from 2 to 8 cycles after resumption. Therefore, we  
331 could not effectively examine the specific effect of size without controlling for an effect  
332 of *cycles since resumption*.

333

334 *Female age* was calculated to the nearest tenth of a year and was included as a  
335 predictor because age is a source of variance in swelling size in our study population

336 (Fitzpatrick et al. 2014), indicating that we need to control for the effect of age in  
337 attempting to identify any effect of swelling size. Furthermore, fertility declines with age  
338 for female baboons (Alberts & Altmann 2003; Beehner 2006), but a study in  
339 chimpanzees found evidence that male chimpanzees prefer older females (Muller et al.  
340 2006). That is, males may modify their investment as a function of female age, either  
341 preferring younger or older females.

342

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

352

353 *Days since last wet month* was an integer that captured the extent to which the  
354 Amboseli basin was experiencing drought or wet conditions. This predictor was  
355 especially important to account for because our two study periods spanned nearly  
356 unprecedented ecological extremes of drought (June-October 2009) and heavy rainfall  
357 (November 2009-February 2010). In addition, *days since last wet month* constrained

358 swelling size in our previous study (Fitzpatrick et al. 2014.), and these ecological  
359 conditions may also constrain male behavior.

360

361 Finally, we included a variable representing the male competitive environment,  
362 *queue length*, as a predictor in our analysis. *Queue length* was measured as the number of  
363 adult males that were present on a given day minus the number of cycling females in the  
364 social group on that day who were within the five-day window prior to d-day. This  
365 measure of the competitive environment is based on the observation that each male can  
366 only consort one female at a time, and each female is consorted by no more than one  
367 male at a time, resulting in a competitive environment that is a function of both the  
368 number of adult males and the number of cycling females in the group. For this metric,  
369 we included cycles that were both conceptive and non-conceptive because it is extremely  
370 rare for a cycling female not to be consorted (whether or not she conceives). That is,  
371 every female that is cycling will reduce the intensity of the competitive environment. We  
372 calculated *queue length* for each of the five days during which behavioral data were  
373 collected and then took the average across that period.

374

375 *Information theoretic analysis*

376

377 Because several variables (in addition to swelling size) may influence male  
378 mating behavior, we evaluated a candidate set of models using an information theoretic  
379 approach. This method assumes that the researcher has used previous biological  
380 knowledge to select appropriate predictors, but allows for different combinations of those

381 predictors that might be equally plausible at the outset (Burnham et al. 2011; Garamszegi  
382 2011; Symonds and Moussalli 2011). We calculated Akaike's Information Criterion  
383 (AIC) (Akaike 1973) for each model in our candidate set using the statistical software, R.  
384 We did this series of calculations twice: once for each response variable. We used an  
385 adjusted measure of AIC,  $AIC_C$ , which is recommended for smaller sample sizes  
386 (Burnham et al. 2011; Symonds & Moussalli 2011) and then calculated the Akaike  
387 weight value ( $w_i$ ) as a measure of goodness of fit to evaluate each of the model sets. After  
388 identifying each of the best models using the AIC approach, we used *post hoc* analyses to  
389 elucidate the effect of swelling size on our two assays of male preference.

390

### 391 *Analysis 2: Swellings as an Indicator of Female Fitness*

392

393 To test the hypothesis that swelling size signals female fitness, we examined the  
394 relationship between variation in swelling size and proxies of female fitness. We used a  
395 classical null/alternative hypothesis testing approach for this second analysis because  
396 we wanted to explicitly test this specific hypothesis. We selected five measures, each of  
397 which is a measure of reproductive lifespan, of reproductive rate, or of early infant  
398 survival, all of which contribute ultimately to female reproductive success. Although  
399 including offspring survival as a component of parental fitness can sometimes lead to  
400 mistaken conclusions about evolutionary outcomes (Wolf & Wade 2001), we nonetheless  
401 employ the common empirical convention of using early infant survival as a reflection of  
402 female fitness. This is especially valid for long-lived primates with an extended period of  
403 dependency; in Amboseli baboons as in other wild primate populations, early infant

404 mortality can be substantial (Altmann & Alberts 2003) and maternal characteristics  
405 contribute to infant survival (Silk et al. 2003). Therefore, males will generally benefit  
406 from mating with a female whose infants are likely to survive. Furthermore, most of our  
407 proxies have been used in previous studies (e.g., Domb and Pagel 2001). Thus, our  
408 selected measures are: 1) Age at first conception. All else being equal, individuals that  
409 mature earlier have higher lifetime fitness. In Amboseli baboons, the earliest-maturing  
410 females have on average a ½ infant advantage over their lifetime compared to the latest-  
411 maturing females (Altmann et al. 1988). 2) Survival to one year of age of the individual  
412 infant that was conceived during the cycle represented in our data set; 3) The number of a  
413 female's infants that survived to one year of age, per reproductive year of the female's  
414 life; and 4) The proportion of the female's total offspring born that survived to one year  
415 of age. 5) The number of live infants born per reproductive year during the female's life.

416

## 417 RESULTS

418

### 419 *Analysis 1*

420

#### 421 *Multi-model inference: predictors of whether a female was consorted by highest-ranking* 422 *male on a given conceptive cycle*

423

424 When we modeled the predictors of whether a female was consorted by the  
425 highest-ranking male on a given conceptive cycle, four models were produced with  $\Delta_i <$   
426 2, indicating that they had substantial and nearly equivalent support. Two of the top

427 models included *swelling length* as a predictor variable, although none of the top models  
428 included *swelling width*. However, the effect size for *swelling length* was both weak and  
429 in the opposite direction than predicted by the reliable indicator hypothesis (ranging from  
430 -0.002 to -0.004). That is, increased swelling length decreased—rather than increased—  
431 the probability that a female was consorted by the highest-ranking male and, even then,  
432 the effect was weak. All of the top models included *number of males in the queue (queue*  
433 *length)*, indicating that an increased competitive environment reduced the probability that  
434 a given female would be consorted by the highest-ranking male. All but one of the top  
435 models included *cycles since resumption (csr)* as an important predictor; females who  
436 had experienced more sexual cycles since their most recent pregnancy were more likely  
437 to be consorted by the alpha male. Finally, although one of the top models included *days*  
438 *since last wet month (dslwm)*, the effect size was weak (0.001) (Table 2a).

439

440 *Multi-model inference: predictors of the proportion of time that a consorting pair had a*  
441 *follower*

442

443       When we modeled the proportion of time that a consorting pair had a follower  
444 (considering only conceptive cycles), a total of five top models produced a  $\Delta_i < 2$ . In  
445 contrast to the previous analysis, *swelling width*—but not *swelling length*—predicted the  
446 proportion of time that a consortship was trailed by a follower male, and in the predicted  
447 direction (increased swelling width was associated with more time with a follower).  
448 *Swelling width* appeared in four of the five top models, and the effect size ranged from  
449 0.008 to 0.010. *Cycles since resumption* was also an important predictor of following; it

450 was included as a predictor in three of the five top models. Only one of the five best  
451 models included *queue length* as a predictor, indicating that the competitive environment  
452 did not influence the proportion of time that a consortship attracted a follower as much as  
453 it did the probability that a female would be consorted by the highest-ranking male.  
454 Again, one of the top models included a small effect of *days since last wet month* (Table  
455 2b).

456

457       Taken together, the multi-model inference indicates that both measures of male  
458 preference were influenced by *cycles since resumption*. As cycle number increased, a  
459 given female was more likely to be consorted by the highest-ranking male and a given  
460 consortship was more likely to be trailed by a follower male. The effects of *queue length*  
461 and *swelling size* on male preference were more equivocal. To further examine the effects  
462 of these three variables (cycles since resumption, competitive environment, swelling size)  
463 on male mate choice, we performed *post hoc* analyses. We report only  $R^2$  values for  
464 these, rather than P-values, because as *post-hoc* analyses, these are subject to Type 1  
465 errors due to multiple testing. Because the effects of *age*, *days since last wet month*, and  
466 *rank* were either negligible or absent, we did not investigate their effects on male mate  
467 choice any further.



473

474 *Consortship by highest-ranking male*

475

476 A bivariate analysis confirmed that females were less likely to be consorted by t

477 highest-ranking male in groups where *queue length* was longer (i.e., where male

478 competition was more intense; Fig. 1a). In addition, the probability of consortship by th

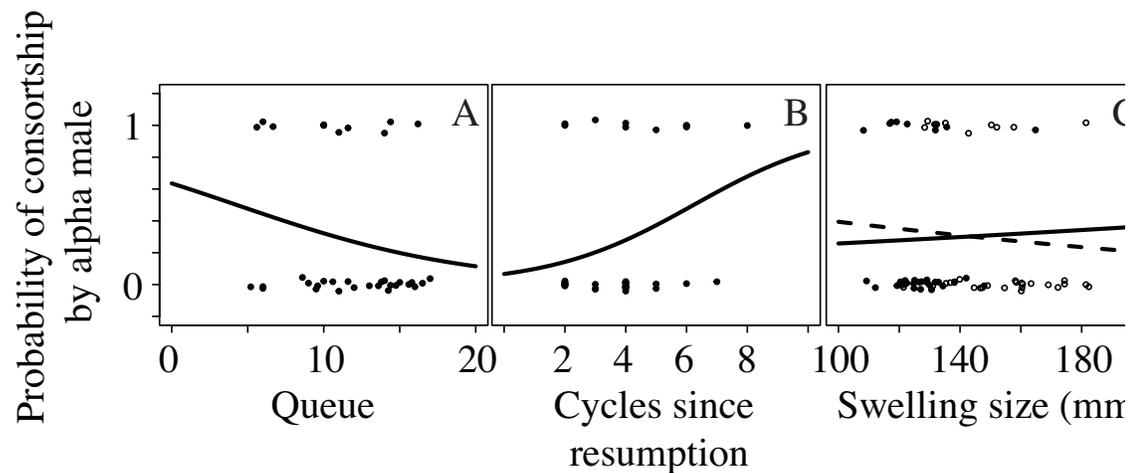
479 highest-ranking male increased with the number of *cycles since resumption* (Fig. 1b) an

480 neither measurement of swelling size predicted consortship by the alpha male in a

481 bivariate analysis (Fig. 1c).

482

483



484

485

486 **Figure 1.** Expected probability of being consorted by the highest ranking male at any  
487 time during the five day window prior to d day a) as a function of the length of the queu

488 b) as a function of cycles since resumption, and c) as a function of maximal swelling siz

489 Each trend line was generated using coefficients generated from a bivariate logistic

490 regression with single predictor. Observed data points plotted and jittered to facilitate

491 visibility.

492

493

494 *Proportion of consort time with a follower*

495

496 The proportion of time that a consortship was trailed by at least one follower was  
497 influenced both by *cycles since resumption* and *swelling width* (see above).

498 Consequently, we performed a simple linear regression of our response variable  
499 (proportion of consort time with a follower) on each of these two predictors separately.

500 Next, we regressed the residuals from each of these models on the other predictor, in  
501 order to isolate the effect on male behavior of each predictor independent of the other  
502 one. As both *cycles since resumption* and *swelling width* increased, consortships were  
503 more likely to attract a follower male (Fig. 2a-b; *cycles since resumption*,  $R^2 = 0.06$ ;  
504 *swelling width*,  $R^2 = 0.13$ ). That is, for a given cycle number, females with wider  
505 swellings were more likely to have a follower. Similarly, for a given *swelling width*,  
506 females who had increased *cycles since resumption* were more likely to have a follower.

507

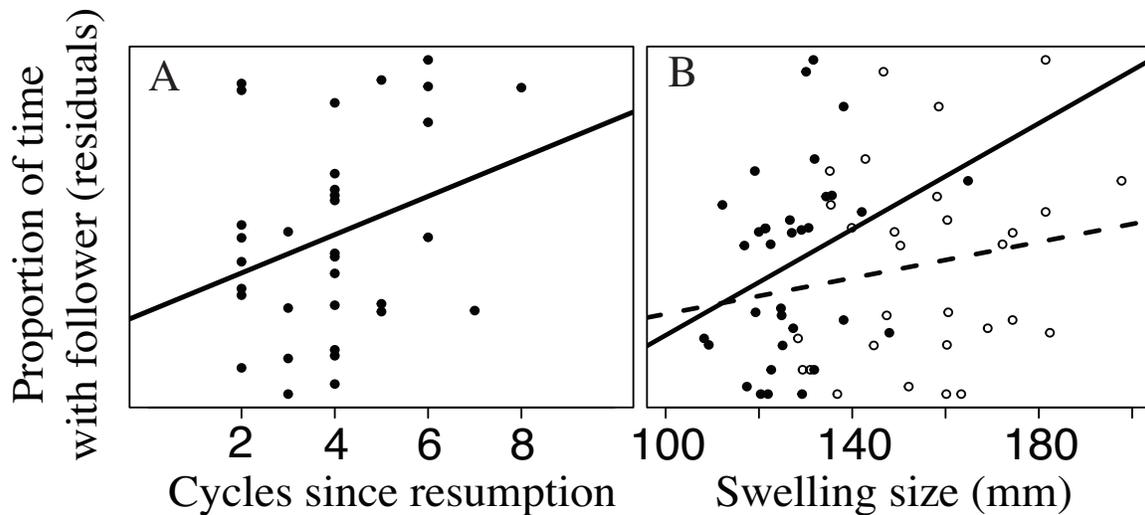
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514

515 **Figure 2.** Proportion of consort time with a follower male as a function of a) cycles since  
516 resumption and b) maximal swelling size. The y axes are the residuals from a) a linear  
517 regression of *proportion of time with a follower* on *swelling width* and *swelling length*  
518 and b) a linear regression of *proportion of time with a follower* on *cycles since*  
519 *resumption*. 2b) Closed circles represent swelling width (solid regression line) and the  
520 open circles represent swelling length (dashed regression line).

521

522

523 *Analysis 2*

524

525 We found no relationships between swelling size and any measure of female  
526 fitness. We fit five generalized linear models (GLM), one for each fitness proxy. In each  
527 of the five models, we included *female age* and *female dominance rank* as additional  
528 predictors to control for their potentially confounding effects on female fitness proxies.  
529 Neither maximal *swelling width* nor maximal *swelling length* were significant positive  
530 predictors of any of the five measures of female fitness (Table 3). Only the relationship  
531 between *swelling length* and *Proportion of total offspring surviving to year 1* was  
532 significant. However, in contrast to the prediction of the reliable indicator hypothesis,

533 that coefficient (between *swelling length* and *Proportion of total offspring surviving to*  
534 *year 1*) was negative, indicating that, if anything, this female fitness proxy was reduced  
535 for those females with longer swellings.

536

537

538

539

540 **Table 3:** Coefficients and p values for relationships between swelling size (*swelling width* and *swelling length*) and each of the  
541 five proxies for female fitness.  
542

Model	Female Fitness Proxy	GLM distribtion	Coefficient		P Value	
			Swelling Width	Swelling Length	Swelling Width	Swelling Length
A	Age at first conception	Poisson	0.003	-0.001	0.711	0.814
B	Survival of infant to year 1	Binomial	-0.068	-0.006	0.225	0.861
C	Infants born per reproductive year	Gaussian	-0.002	0.001	0.152	0.186
D	Infants surviving to year 1 per reproductive year	Gaussian	0.000	-0.001	0.807	0.332
E	Proportion of total offspring surviving to year 1	Gaussian	0.003	<b>-0.004</b>	0.448	<b>0.045</b>

543 DISCUSSION

544

545 *Male Mate Choice for Cycles Since Resumption vs. Swelling Size*

546

547         We examined male behavior during female sexual cycles that resulted in offspring  
548 conception, and found not only that *cycles since resumption* predicted male baboon  
549 behavior, but that it was a stronger predictor than swelling size. Specifically, females in  
550 our study who conceived after experiencing more *cycles since resumption* were both  
551 more likely to be consorted by the highest-ranking male on the conceptive cycle, and  
552 were more likely to attract at least one follower male, even when controlling for multiple  
553 potential confounds, including swelling size. In other words, cycles became more  
554 valuable from a male's perspective as a female progressed further and further away from  
555 her previous pregnancy, perhaps because females become more physiologically able to  
556 support another pregnancy as time passes. This finding provides support for the  
557 hypothesis that males can detect the number of times a female has cycled in the recent  
558 past.

559

560         A potential adaptive explanation for this pattern emerges from the fact that each  
561 sexual cycle has some probability of *not* resulting in offspring. Thus, primate males are  
562 presented with mating opportunities that vary considerably in their fitness pay offs. Males  
563 should therefore experience selection to distinguish female sexual cycles that have a low  
564 probability of conception from those with a higher probability of conception. Indeed,  
565 previous studies both in our study population and others suggest that male baboons are

566 able to do just that (Bercovitch 1987; Bulger 1993; Weingrill et al. 2003; Alberts et al.  
567 2006; Gesquiere et al. 2007). Our study builds upon those results by demonstrating that  
568 males respond differently to earlier conceptive cycles (closer to a recent pregnancy) than  
569 they do to conceptive cycles that are later (further from a recent pregnancy). Indeed, our  
570 results suggest that the apparent ability of males to differentiate conceptive from non-  
571 conceptive cycles might simply reflect males' sensitivity to the number of *cycles since*  
572 *resumption* that a given female has experienced, and that *cycles since resumption* may be  
573 a highly salient indicator of conception probability.

574

575       The first prediction generated by the reliable indicator hypothesis is that males  
576 should prefer females with larger swellings. That males respond to variation in *cycles*  
577 *since resumption* does not negate the possibility that they may also care about swelling  
578 size independently. However, our results provide only equivocal support for this first  
579 prediction. Although consortships with females that had larger swellings were more  
580 likely to attract a follower male, there was no evidence that the highest-ranking males—  
581 those most likely to exercise choice—biased their mating behavior toward females with  
582 larger swellings. An alternative interpretation of this result is that alpha males were less  
583 able to monopolize those females with larger swellings, perhaps precisely because  
584 followers challenge them more frequently. However, despite the presence of followers,  
585 high-ranking males do successfully retain consortships with females who have  
586 experienced more *cycles since resumption*, suggesting that they are, on average, able to  
587 mount the energetic resources required to maintain high-value consortships. In other  
588 words, the lack of an effect of swelling size on the behavior of alpha males suggests a

589 lack of (or reduced) motivation rather than a lack of ability. This difference between  
590 alpha males (whose behavior was uninfluenced by swelling size) and follower males  
591 (whose behavior was) points to the possibility that alpha males and follower males may  
592 not have access to the same signal information, may prioritize that information  
593 differently, may be differently constrained, or may have different opportunities.

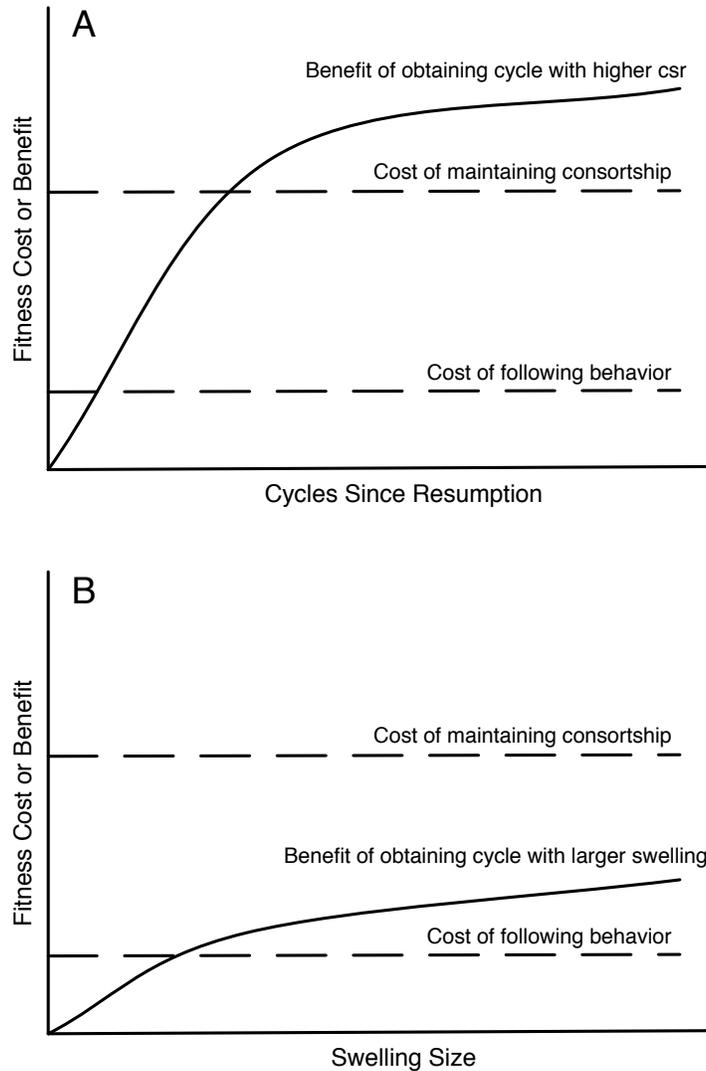
594

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

603

604         Alternatively, the differences in the costs associated with following behavior  
605 relative to those of being the primary consort partner may result in this difference in male  
606 behavior. Consorting males incur costs by forgoing foraging opportunities (Packer 1979;  
607 Alberts et al. 1996). In addition, alpha males (who are typically the most active mate  
608 guards among adult males in a baboon group) have higher glucocorticoid levels than  
609 other males, indicating considerable energetic stress (Gesquiere et al. 2011). Therefore,  
610 successful consortship behavior requires good energetic and physiological reserves. In  
611 contrast, following behavior requires little or no special skill and the risks are presumably

612 relatively low. Because *cycles since resumption* is likely to be a good indicator of the  
613 probability of conception, males may greatly increase their chances of capturing good  
614 reproductive opportunities (i.e. a conceptive cycle) by tracking it; furthermore, those  
615 benefits are likely to outweigh both the higher costs of being the primary consort partner  
616 and the relatively low costs of being a follower. In contrast, *swelling size* may provide  
617 some information about the quality of a reproductive opportunity (if females with larger  
618 swellings have superior physiological reserves and are therefore more likely to conceive  
619 or more able to sustain a pregnancy to term), but may not be as reliable as *cycles since*  
620 *resumption*. Thus, if the benefits to potential sires of larger swelling sizes are lower than  
621 the benefits of *cycles since resumption*, those benefits may not justify paying the higher  
622 costs of primary consortship but still outweigh the low costs of engaging in following  
623 behavior (see Fig 3).



624

625

626 **Figure 3.** Hypothesized cost-benefit relationships that would result in the pattern  
627 observed in this study. A) Male behavior with respect to *cycles since resumption*; if the  
628 benefit to a male of monopolizing a cycle with a higher cycle number is higher than the  
629 costs of both maintaining the consortship and engaging in following behavior, then high-  
630 ranking males should work harder to obtain those consortships and follower males should  
631 invest in following them. B) Male behavior with respect to *swelling size*; if the benefit to  
632 a male of monopolizing a cycle with a larger swelling size (for a given cycle number) is  
633 higher than the cost of engaging in following behavior, but lower than the cost of  
634 maintaining the consortship, then high-ranking males should not incur the costs of  
635 obtaining those consortships, but follower males should still invest in following them.  
636

637

638

639

640 *Competitive Environment (Number of Males in the Queue)*

641

642       To our knowledge, this study is the first to control for the effect of the competitive  
643 environment (specifically the number of males relative to available females) on male  
644 mate choice with respect to swelling size. The competitive environment only affected one  
645 of our assays of male mate choice; as the number of males in the *queue* increased, the  
646 highest-ranking male was less likely to successfully monopolize a given sexual cycle.  
647 This result is consistent with previous comparative, cross-species reports (Cowlshaw &  
648 Dunbar 1991) as well as results in our study population (Alberts et al. 2003) that male  
649 ability to monopolize estrous females declines with group size. The absence of an effect  
650 of competitive environment on the behavior of follower males in the present study lends  
651 further support to the hypothesis that alpha and follower males may experience different  
652 constraints. Finally, these results highlight the fact that assays of male preference,  
653 including assays other than those we selected, may often only be meaningful if they are  
654 interpreted within the context of the competitive environment.

655

656 *Swelling Size as a “Reliable Indicator” of Fitness*

657

658       Regardless of whether alpha males and follower males respond to—and respond  
659 differently to—variation in swelling size, the question remains, what information is being  
660 signaled by inter-individual variation in swelling size? Does this variation contain

661 information that males care about, beyond probability of ovulation within a cycle and  
662 beyond the probability of conception between cycles? For the reliable indicator  
663 hypothesis to explain variation in male response to sexual swellings, variation in swelling  
664 size should predict some component of female fitness. Our analysis provides no support  
665 for the hypothesis that swelling size (either *swelling width* or *swelling length*) indicates  
666 variation in female fitness. In fact, the relationship between swelling size and female  
667 fitness was, at times, in the opposite direction opposite of that predicted by the reliable  
668 indicator hypothesis. Our study provides the strongest evidence to date that exaggerated  
669 swellings are not signals of enduring differences in fitness between females in baboons.  
670

#### 671 *Summary and future directions*

672

673         We have shown that high-ranking males do not prefer females with larger  
674 swellings (when controlling for cycle number and conception) and that females with  
675 larger swellings do not have higher reproductive success. In doing so, we have tested and  
676 rejected the reliable indicator hypothesis for the function of exaggerated swellings in  
677 cercopithecine primates. Rather than tracking the potential differences in fitness between  
678 females, male baboons appear to track and target the potential for a given reproductive  
679 opportunity to result in fertilization. As the strongest such evidence to date, our results  
680 should shift the discussion about the function and evolution of exaggerated swellings  
681 from one that necessarily invokes intrinsic differences in female quality to one that  
682 focuses on temporal changes in the quality of the reproductive opportunity.

683

684           We emphasize that our test of the reliable indicator hypothesis does not address  
685 the question of whether female baboons experience sexual selection. In fact, testing the  
686 reliable indicator hypothesis cannot, in itself, identify sexual selection on female sexual  
687 swellings because the existence of male mate choice alone does not necessarily exert  
688 sexual selection pressure on female traits. Male mate choice will only exert selection  
689 pressure on swelling size if females with larger swellings receive fitness advantages as a  
690 result of being preferred beyond those that they would receive from being mated at  
691 random (see Equation 6 in Servedio 2007 for mathematical representation of this point).  
692 In other words, the common portrayal of the reliable indicator hypothesis as an  
693 explanation for the evolution of sexual swellings conflates male mate choice as a  
694 *consequence* of selection on males (if females with larger swellings have higher infant  
695 survival and therefore males prefer them) with male mate choice as a potential *cause* of  
696 selection on females. Despite this slip in logic, studies continue to cite Domb and Pagel  
697 (2001) and exaggerated swellings as an example of sexual selection in females (e.g. Paul  
698 2002; Jawor et al. 2004; Deschner et al. 2004; Drea 2005; LeBas 2006; Fernandez &  
699 Morris 2007; Clutton-Brock 2007, 2009; Huchard et al. 2009; Rundle & Chenoweth  
700 2011; Weiss et al. 2011; Davies et al. 2012). We caution the reader against conflating  
701 male mate choice with sexual selection on female traits. Further, in light of this caution,  
702 we highlight the importance of identifying the conditions under which male mate choice  
703 will result in selection pressure on females, versus the conditions under which male mate  
704 choice evolves but is inert as a mechanism of selection on female traits.

705

706 ACKNOWLEDGEMENTS

707

708 We thank the Office of the President of the Republic of Kenya, the Kenya Wildlife  
709 Service and its Amboseli staff and wardens, the Amboseli-Longido pastoralist  
710 communities, Ker & Downey Safaris and Tortilis Camp for their cooperation and  
711 assistance in Kenya. This research could not have been conducted without assistance to  
712 CLF from L. Maryott and the US Embassy in Nairobi during multiple critical times. We  
713 thank the Amboseli Baboon Research Project long-term senior field researchers (R.S.  
714 Mututua, S. Sayialel, and J.K. Warutere) and the research assistants (G.Y. Marinka, C.S.  
715 Mutenkere, and B.O. Oyath) for their invaluable assistance and insight. Many people  
716 have contributed to the long-term data collection and database maintenance; in particular  
717 we thank L. Maryott, T. Fenn, and N. Learn. We thank Jeff Jacobsen for early assistance  
718 with the Photoscale-2 method, Ed Iverson and the Duke University Statistical Consulting  
719 Center for useful discussions about the statistical analysis, and Maria Servedio for helpful  
720 discussions about male mate choice. CLF was supported by Sigma Xi, Duke University  
721 Center for International Studies, Duke Biology, the Princeton Center for the Demography  
722 of Aging (P30AG024361), the Patricia William Mwangaza Foundation, the L.S.B.  
723 Leakey Foundation, an NSF Graduate Research Fellowship, and a Fulbright Fellowship.  
724 Support for the long term research project was provided by the National Science  
725 Foundation (most recently IOS 1053461 and DEB 0919200) and the National Institute of  
726 Aging (R01AG034513 and P01 AG031719). Support data from this project are available  
727 in the Dryad database: doi: XXXXX.

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