



## REVIEW

# The evolution of exaggerated sexual swellings in primates and the graded-signal hypothesis

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Females of some Old World primate taxa advertise their sexual receptivity with exaggerated sexual swellings. Although a number of hypotheses have been proposed, the function of this conspicuous trait remains unsolved. This review updates information on the phylogenetic distribution of exaggerated swellings and identifies aspects of the morphology, physiology and behaviour of species with this conspicuous trait. Some of these patterns represent new information, while other patterns have been previously identified, but not in ways that control for phylogeny. This review shows that exaggerated swellings are correlated with some features that serve to confuse paternity certainty among males, while other features tend to bias paternity towards more dominant males. Hypotheses for the evolution of exaggerated swellings are then reviewed and critically evaluated. Individually, no single hypothesis can account for all the patterns associated with exaggerated swellings; however, a combination of different hypotheses may explain the contradiction between confusing and biasing paternity. I suggest that exaggerated swellings can be viewed as distributions representing the probability of ovulation (the graded-signal hypothesis). In the context of this probabilistic model, exaggerated swellings enable females to manipulate male behaviour by altering the costs and benefits of mate guarding, so that dominant males tend to guard only at peak swelling, but females can mate with multiple males outside peak swelling to confuse paternity. This hypothesis makes testable predictions for future comparative and observational research.

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The females of many primate species signal proceptive and receptive sexual behaviour with changes in the size, shape, turgidity and colour of their perineal skin (Rowell 1972; Dixson 1983). These visual signals are quite varied, and they are found in all primate radiations, including species as diverse as ringtailed lemurs, *Lemur catta* (Jolly 1966), tarsiers, *Tarsius bancanus* (Wright et al. 1986), mantled howler monkeys, *Alouatta palliata* (Glander 1980), patas monkeys, *Erythrocebus patas* (Dixson 1983), and whitehanded gibbons, *Hylobates lar* (Dahl & Nadler 1992).

The focus of this paper is on a derived form of sexual advertisement in which swellings have become exaggerated, most notably in terms of size. These 'exaggerated swellings' are found only in the Old World monkeys and

apes, and the swellings that result are quite substantial. For example, when maximally swollen, female body weight increases by approximately 14% in chacma baboons, *Papio ursinus* (Bielert & Busse 1983), up to 17% in pigtailed macaques, *Macaca nemestrina* (Dixson 1983), and possibly over 25% in some subspecies of red colobus, *Colobus badius* (Struhsaker 1975).

Several lines of evidence suggest that exaggerated swellings are costly for females. First, increased body weight should make travel more costly, especially in an arboreal setting (Schmidt-Nielson 1984). Second, exaggerated swellings are thought to involve intra- and extracellular water retention (Dixson 1983); thus, fluids that could be used in other bodily functions must be diverted to the signal. Finally, swollen females must deal with increased parasites (e.g. bloodsucking flies; F. White, personal communication) and minor cuts to the surface of the swelling (Hausfater 1975), as both of these problems are increased by the smooth, exposed skin that accompanies maximum

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turgidity. Given these costs, exaggerated swellings are usually assumed to confer substantial benefits.

The long history of interest in exaggerated swellings (e.g. Darwin 1876) has resulted in a number of plausible hypotheses for their function (Clutton-Brock & Harvey 1976; Hamilton 1984; Hrdy & Whitten 1987; Pagel 1994). Recently, there has been renewed interest in this trait, and this interest is not restricted to primatologists (e.g. Sillén-Tullberg & Møller 1993; Pagel 1994; Wiley & Poston 1996). In addition, there are now indications of similar traits in at least one nonprimate taxon (alpine accentors, *Prunella collaris*; Davies et al. 1996; Nakamura 1998). Such cases of potential convergence may provide opportunities for comparative tests outside the order Primates.

Despite this widespread attention, however, the function of exaggerated swellings remains enigmatic and controversial (e.g. Hrdy & Whitten 1987; Small 1993; Pagel 1994). One major problem is that existing hypotheses can account for some features of exaggerated swellings, but no single hypothesis can account for all the features common to these species.

In this review, I consolidate our knowledge about this trait and its distribution, and I critically examine the compatibility of existing hypotheses. I show that exaggerated swellings serve seemingly contradictory functions: on the one hand, exaggerated swellings tend to concentrate paternity in one (or a few) dominant males; on the other hand, they tend to blur, or confuse, paternity among males.

I therefore propose a more complex function for exaggerated swellings (the graded-signal hypothesis). This hypothesis combines some of the benefits of previous hypotheses, and so its proposed functions are not entirely new. However, the graded-signal hypothesis provides a novel mechanism for how exaggerated swellings achieve these benefits. This hypothesis can also account for the exaggeration of an ancestrally small sexual signal, and it makes a number of testable predictions. The focus of this paper is the function of exaggerated swellings during fertile cycles; however, I conclude by briefly considering other more derived and possibly deceptive functions of exaggerated swellings, including pregnancy swellings, adolescent exaggeration and 'swellings' in subadult male colobus monkeys.

## METHODS

This paper is primarily a review of existing information and ideas. However, to examine and confirm patterns relevant to exaggerated swellings, several cross-species comparative tests were conducted. Therefore, in this section I present operational rules for assigning character states, and I discuss the phylogenetic comparative methods used in these tests.

### Assigning Character States

#### *Exaggerated swellings*

An operational definition of exaggerated swellings must distinguish this signal from the nonexaggerated

('ordinary') swellings common to all primate radiations (Rowell 1972). The presence of exaggerated advertisement can be scored as a categorical trait with three states (no swelling, ordinary swelling, or exaggerated swelling; Sillén-Tullberg & Møller 1993). Here, however, the first two categories were combined into one state (nonexaggerated).

A species was classified as having exaggerated swellings if the following criteria were satisfied: (1) either adults or adolescents (or both) undergo visible changes in a specialized 'sexual skin' over the course of the female cycle; (2) the sexual skin involves swelling and/or reddening of anatomical parts not directly involved in copulation, such as the circumanal skin, the area around the ischial callosities, or the chest and abdomen (Rowell 1972; Dixson 1983); and (3) the signal is clearly visible by human observers at a distance.

To limit the effects of confounding factors, I restricted comparative analyses to the Old World anthropoid primates (catarrhines), which are considered to be a monophyletic group (Fleagle 1988; Martin 1990; Purvis 1995). Character states (see Appendix) were assigned based on reviews of female sexual behaviour (especially Dixson 1983; Hrdy & Whitten 1987). These reviews are remarkably consistent, indicating that the distinction between exaggerated and nonexaggerated signals is clear to most authors. Nevertheless, some clarifications are required. Rhesus macaques, *Macaca mulatta*, Japanese macaques, *M. fuscata*, and longtailed macaques, *M. fascicularis*, are classified as having exaggerated swellings because young females, but not all adults, have a swelling that changes with ovulatory state (Anderson & Bielert 1994). The gelada, *Theropithecus gelada*, was also classified as having a sexual swelling, mainly because the skin of the female's chest undergoes a cyclical pattern of reddening and swelling (Dunbar & Dunbar 1974). Swellings in pigtailed langurs, *Simias concolor*, are large, but they do not involve nonsexual anatomy (Tenaza 1989). Furthermore, recent field researchers have failed to notice colour and size changes despite observations of sexual activity (L. Paciulli & R. Delgado, personal communication). Whitehanded gibbons have been described as having 'conspicuous' swellings (Dahl & Nadler 1992). However, gibbon swellings are small relative to those observed in other Old World species, and they involve only the vulva (Dahl & Nadler 1992). Finally, it could not be confirmed that black colobus, *Colobus satanus*, possess an exaggerated swelling (Struhsaker & Leland 1979, 1987; Hrdy & Whitten 1987); as a result, swellings in this species were classified as nonexaggerated (see also Sabater Pi 1973; Oates 1994).

#### *Social system*

A species was classified as multimale if a mean of more than 1.5 males were typically present in the social group. Information on male number was taken from a data set used in other ongoing comparative projects (van Schaik et al., in press). Species living in higher-level organizations (Stammach 1987), such as hamadryas baboons, *Papio hamadryas*, geladas, and possibly mandrills, *Mandrillus sphinx*, are not easy to classify in this scheme. These

species were classified as multimale because one-male units are typically in close contact during daily foraging and sleeping, and extragroup copulations have been observed or are possible (Kummer 1968; Dunbar & Dunbar 1975; Stambach 1987; Lahm 1997; White 1997). The number of males in hamadryas, gelada and mandrill groups was set at a low value of 1.5. This is a conservative assumption because these species all possess exaggerated swellings, which are thought to be associated with multiple breeding males (Clutton-Brock & Harvey 1976).

### Mating duration

Values for median duration of sexual activity and cycle lengths were taken from van Schaik et al. (in press). Only species with well-defined periods of sexual activity were used in the analysis; thus, because their mating durations matched cycle lengths in van Schaik et al. (in press), vervets, *Cercopithecus aethiops*, and stump-tailed macaques, *Macaca arctoides*, were excluded from the analysis of mating duration.

### Comparative Methods

I used phylogenetic comparative methods to deal with problems associated with the nonindependence of species data points (Harvey & Pagel 1991; Martins & Hansen 1996). All analyses involve either two discrete characters, or a combination of one continuous and one discrete character. In the case of two discrete variables, I used Maddison's (1990) concentrated changes test to calculate statistical significance levels (using MacClade version 3.01; Maddison & Maddison 1992). This test calculates the probability of obtaining the observed distribution of *Y* character states by chance, taking into account the observed pattern of *X* character states on the hypothesized phylogeny. The two swelling states were also traced phylogenetically using MacClade.

When one variable was continuous and the other discrete, I determined whether transitions to or from exaggerated advertisement were associated with consistent changes in the continuous variable. For this, I used a variant on the method of independent contrasts (Felsenstein 1985), as implemented by the BRUNCH algorithm in the computer program CAIC (Purvis & Rambaut 1995). I calculated statistical significance using a *t* test to determine whether the mean of these contrasts differed significantly from zero (Purvis & Rambaut 1995).

I used the Old World anthropoid clade of Purvis' (1995) phylogeny. This tree provides estimates of branch lengths using a combination of fossil and molecular evidence and is thus well suited to phylogenetic comparative methods that require this information. The concentrated changes test requires a fully bifurcating phylogeny; therefore, polytomies in Purvis' (1995) phylogeny were randomly resolved in order to implement this test. An alternative phylogeny with branch lengths is not presently available; however, alternative topologies are mentioned below when this information is relevant. Phylogenetic sensitivity analyses (e.g. Donoghue & Ackerly 1996; Mitani et al.

1996) are beyond the scope of the present review; however, it is possible to re-examine these patterns on alternative phylogenies when they become available.

## CORRELATES AND CHARACTERISTICS OF EXAGGERATED SWELLINGS

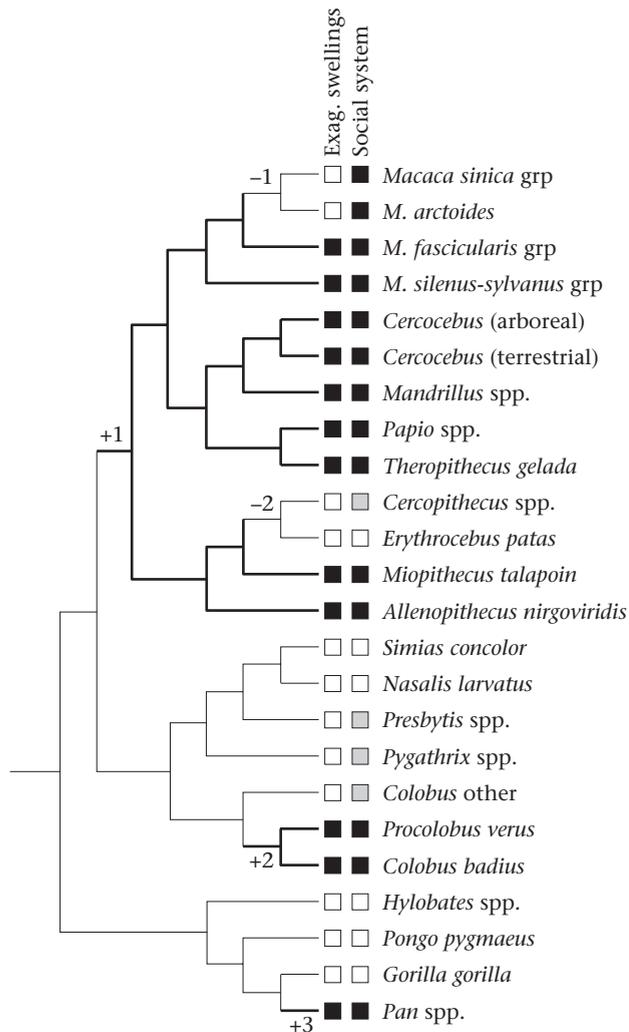
### Phylogenetic Distribution

I begin by considering general patterns in the evolution of exaggerated swellings (see also Sillén-Tullberg & Møller 1993). The phylogenetic mapping in Fig. 1 supports Dixson's (1983) hypothesis that exaggerated swellings have evolved at least three times in the Old World anthropoids. This figure also reveals two losses of exaggerated swellings (both in the cercopithecines). This result is probably robust to alternative phylogenies: the relevant taxa are not likely to be related such that fewer than three gains have occurred (e.g. see alternative phylogenies in Disotell 1996).

In Fig. 1, the reconstructed gains and losses of exaggerated advertisement are numbered (although this numbering is not meant to reflect the temporal order in which exaggerated swellings were gained or lost). Gain 1 takes place at the base of the cercopithecine clade: swellings are present in all baboons and their close relatives, the talapoin, *Miopithecus talapoin*, and Allen's swamp monkey, *Allenopithecus nigroviridis*. In addition, many macaques possess swellings, although loss 1 takes place in this genus (leading to the clade containing *Macaca arctoides* and the *sinica* group, which includes *Macaca sinica*, *M. radiata*, *M. thibetana* and *M. assamensis*; Fooden 1976). Given different phylogenies, it is possible that more than one loss may have occurred in the macaques. Loss 2 takes place in the lineage leading to the guenons, specifically in the transition from *Miopithecus* to *Erythrocebus*. However, bootstrap values for Purvis's (1995) phylogeny near loss 2 indicate uncertainty, and alternative phylogenies (e.g. Disotell 1996) may therefore give a more ambiguous pattern. Gain 2 takes place in the colobines and is associated with only three extant species: red colobus, Zanzibar red colobus, *Colobus kirkii* (possibly a subspecies of red colobus; Oates et al. 1994), and the olive colobus, *Procolobus verus*. Gain 3 takes place in the apes, and here only in the two species of chimpanzee (*Pan troglodytes* and *P. paniscus*). No losses are reconstructed in these latter two lineages. Because I assume three gains and two losses, five contrasts will be available for comparative tests involving a combination of discrete and continuous values.

### Multimale Social Systems

Clutton-Brock & Harvey (1976) originally noted that species with exaggerated swellings live in multimale social systems. Consistent with this observation, species with exaggerated swellings have, on average, over twice as many males per breeding unit (4.3 versus 1.8). Furthermore, 71% of Old World primate taxa classified as multimale show exaggerated swellings, while none that is classified as single-male possesses this trait (Fig. 1). While



**Figure 1.** Phylogenetic reconstruction of exaggerated swellings. Phylogeny from Purvis (1995), with some clades collapsed to facilitate presentation of data. The presence of exaggerated swellings is indicated by dark boxes for the distribution across species and wider internode branches for reconstructed values. Gains (+) and losses (-) are indicated, but the numbering does not reflect the actual temporal order of gains and losses. Social systems are indicated in the second column of boxes. Multimale taxa are indicated by dark boxes, single-male taxa are indicated by white boxes, and taxa with both single-male and multimale species are indicated by grey boxes (data for individual species are available in the Appendix).

this pattern is not contested, it has yet to be documented using statistical methods that control for phylogeny (Harvey & Pagel 1991).

Given the small number of evolutionary transitions in swelling states (three gains and two losses), statistical power is likely to be low. The probability that three gains are found on branches of the phylogeny characterized as multimale approaches statistical significance (Maddison's concentrated changes test:  $P=0.06$ ). I also tested this relationship by using information on the number of males. In four of the five evolutionary transitions in swelling state, changes in the number of males go in the predicted direction (i.e. male number increases with the

gain of swellings, and decreases with their loss). However, the mean of these contrasts is not significantly greater than zero ( $t$  test, two-tailed:  $t_4=1.32$ ,  $P=0.26$ ; just using gains:  $t_2=1.98$ ,  $P=0.19$ ). The one contrary contrast occurs at loss 1: the number of males increases in the clade containing *Macaca arctoides* and the sinica group. These patterns are therefore generally consistent with a relationship between multimale and exaggerated swellings.

### Nonseasonal Breeding

van Schaik et al. (in press) showed that nonseasonal breeding is a further correlate of exaggerated swellings: when examined phylogenetically, exaggerated swellings are lost in multimale lineages following evolutionary transitions to nonseasonal breeding. Thus, of 25 species with exaggerated swellings and information on breeding seasonality in the Appendix, 20 species (80%) are nonseasonal breeders. For example, exaggerated swellings are found in baboons, which are nonseasonal, but not in the multimale vervet monkey, which is strongly seasonal in its reproduction but also multimale. Similarly, more seasonal macaques tend to lack exaggerated swellings (e.g. the sinica group of macaques), and those with intermediate swellings (the fascicularis group) tend to be relatively more seasonal than those with fully exaggerated swellings, such as the Sulawesi macaques. Nevertheless, some exceptions to this pattern exist, including Barbary macaques, *Macaca sylvanus*, and the talapoin monkey (Rowell & Dixson 1975).

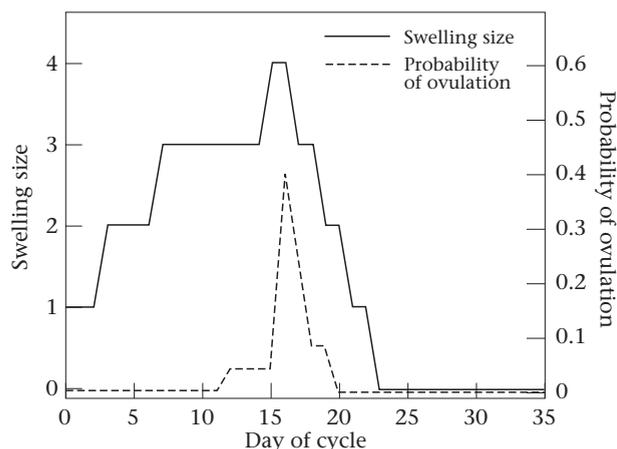
### Gradual Increase in Size

Exaggerated swellings tend to increase in size gradually from their resting state (Zuckerman 1930; Saayman 1970; Dahl 1986). The sexual skin of species with exaggerated swellings begins to swell shortly after menses and can take up to 2 weeks to reach maximum tumescence. For example, Fig. 2 shows that in a captive population of baboons, the average swelling increased in size gradually over 14 days, reached a peak for 2 days, and then subsided to a resting state within 6 days (Wildt et al. 1977). However, it should be noted that experimental manipulations of hormone levels can change swelling levels relatively quickly (e.g. Saayman 1973).

Exaggerated swellings may increase in size gradually because it takes longer to express fully such a large signal. However, even if this feature is the result of a physical constraint owing to the size of the signal, the gradual increase may have important consequences for the type of information that is conveyed. In particular, exaggerated swelling may qualify as graded signals, where subtle morphological changes convey information on a continuous or probabilistic scale.

### Ovulation is Most Likely at Peak Swelling

Endocrinological studies suggest that exaggerated swellings are controlled hormonally (Dixson 1983) and



**Figure 2.** Relationship between swelling size and ovulation in baboons. Ovulation tends to occur at peak swelling, immediately prior to sex skin detumescence, but with some error. The pattern shown here comes from Wildt et al. (1977), and is a composite of ovulation relative to swelling size among 12 adult female baboons (66 cycles). Thus, error in the timing of ovulation in this generalized baboon reproductive cycle is not due to variance in female cycle length, but to true deviations in ovulatory timing relative to swelling characteristics.

that the highest probability of ovulation occurs at peak swelling, just prior to sex skin detumescence (Fig. 2; e.g. Gillman & Gilbert 1946; Graham 1981; and references in Table 1).

Females are more sexually active when they are swollen; thus, exaggerated swellings honestly signal female receptivity. Together with the association between swelling size and ovulation, this suggests that exaggerated swellings are also generally honest signals of fertility. Male behaviour is consistent with exaggerated swellings as generally honest signals (discussed below).

Although olfactory cues may also play a role in signalling female fertility (Michael & Keverne 1968; Dixson et al. 1973), experiments involving models of the female sexual skin demonstrate that male baboons respond to visual cues of receptivity in the absence of olfactory information (Girolami & Bielert 1987; Bielert et al. 1989). In any case, visual, olfactory, and even vocal signals may operate simultaneously without invalidating the patterns and hypotheses discussed here (see below).

### Ovulation Commonly Occurs with Some Error Relative to Peak Swelling

Although ovulation tends to occur immediately prior to sex skin detumescence, this association is not perfect, and ovulation has been regularly documented at other times in the female cycle (Dixson 1983; Martin 1992; Small 1993). For example, Fig. 2 shows that ovulation tends to occur just prior to detumescence in baboons, but individual females actually ovulate anytime within an 8-day window around maximum swelling (Wildt et al. 1977). Table 1 reviews the range of days relative to swelling characteristics in which ovulation has been

documented in other studies. The final two species in this table have 'ordinary' rather than exaggerated swellings and therefore provide important comparisons regarding error in the timing of ovulation. For example, ovulation in the gibbon occurs within 6 days of peak swelling (Nadler et al. 1993), which, compared with species with exaggerated swellings, is in the low range of values for ovulatory error. The comparison is more striking in the gorilla: LH peaks always occurred exactly 1 day after peak labial tumescence (Nadler et al. 1979), as expected if ordinary swellings are more precise indicators of ovulation than exaggerated ones.

### Longer Duration of Peak Sexual Activity

Among species of Old World primates in which females confine their sexual activity to a limited portion of the reproductive cycle, females of species with exaggerated swellings are sexually active for approximately 6 days longer than those without swellings (exaggerated swellings: 10.6 days,  $N=19$ ; no exaggerated swellings: 4.6 days,  $N=8$ ). A longer duration of sexual activity probably allows females to mate with more males (van Schaik et al., in press). Of the five evolutionary changes in swelling state, evolutionary changes in mating duration are in the predicted direction in four cases (i.e. an increase in the duration of mating in gains of exaggerated swellings, and a decrease in losses). The one negative contrast is close to zero and occurs in the contrast between grey langurs, *Presbytis entellus*, and red colobus (about which little quantitative mating data is available), and the mean of these five contrasts was not significantly greater than zero ( $t=1.86$ , two-tailed  $P=0.14$ ).

### Dominant Males Mate-guard at Peak Swelling

Within the multimale social groups in which exaggerated swellings are found, males usually compete most intensely for females that are maximally swollen (Dixson 1983). Dominant males usually win this competition, which gives them greater access to swollen females (e.g. Kaufmann 1965; Hall & DeVore 1965; Rowell 1972; Struhsaker 1975; Tutin 1979). Part of this increased access involves consortship behaviour, defined here as a sexual association between a male and female that involves synchronized patterns of activity (Seyfarth 1978; Packer 1979; Smuts 1985; Bercovitch 1991; see also Manson 1997). Males also perform more perineal inspections and increase mating attempts when females are maximally tumescent (Dixson 1983), and male-male competition and wounding peak at this time (Wilson & Boelkins 1970; Hausfater 1975; Shefferly & Fritz 1992).

The energy spent by males in mate guarding is expected to correlate with the benefits they receive. Because males prefer to guard females that are close to peak swelling, it appears that males regard swellings as generally honest indicators of female fertility. As a result, exaggerated swellings tend to bias paternity towards dominant males.

Table 1. Error in the timing of ovulation relative to peak swelling

Species	Duration over which ovulation can occur (days)*	Type of data	Sample size	References
<i>Cercocebus torquatus</i>	12	Hormonal: serum oestradiol relative to onset of peak swelling	4 females, 7 cycles total	Whitten & Russell 1996
<i>Macaca mulatta</i>	≥6	Artificial inseminations relative to colour breakdown†	218 artificial inseminations (87 pregnancies) in 109 females near peak coloration	Czaja et al. 1975
<i>Macaca nemestrina</i>	5–7	Hormonal: plasma progesterone peak (5) or rise (7) relative to peak tumescence	8 females, 8 cycles total	Bullock et al. 1972
<i>Macaca nemestrina</i>	13	Timed matings relative to peak tumescence; some laparoscopy	21 cycles total	Blakley et al. 1981
<i>Macaca nigra</i>	6	Hormonal: LH peak relative to beginning of maximum swelling	5 females, 10 cycles total	Thomson et al. 1992
<i>Macaca tonkeana</i>	6–20	Hormonal: significant PdG rise relative to deturgescence (6) or onset of swelling (20)	4 females, 8 cycles total	Thierry et al. 1996; see also Aujard et al. 1998
<i>Papio cynocephalus+anubis</i>	≥7	Timed fertile matings relative to detumescence‡	32 females, 195 timed matings during only last half of maximum tumescence	Hendrickx & Kraemer 1969
<i>Papio cynocephalus+anubis</i>	8–10	Laparoscopic examination relative to detumescence	12 females, 66 cycles total	Wildt et al. 1977
<i>Papio cynocephalus+anubis</i>	6	Laparoscopic examination relative to detumescence	55 females, 57 cycles total	Shaikh et al. 1982
<i>Pan paniscus</i>	21	Hormonal: urinary E1C peak relative to onset of peak swelling	4 females, 9 cycles total	Heistermann et al. 1996
<i>Pan troglodytes</i>	≥6	Timed matings relative to detumescence‡	13 females, 207 cycles total	Elder & Yerkes 1936
<i>Pan troglodytes</i>	9	Hormonal: LH peak relative to first day of labial occlusion (i.e. the swollen phase)	9 females, 31 cycles total	Dahl et al. 1991
<i>Hylobates lar</i> ‡	6	Hormonal: LH peak relative to peak genital tumescence	4 females, 6 cycles total	Nadler et al. 1993
<i>Gorilla gorilla</i> ‡	1	Hormonal: LH peak relative to maximum labial tumescence	3 females, 4 cycles total	Nadler et al. 1979

\*Restricted to studies that contained information on the onset of peak swelling or some other morphological correlate of peak swelling that is easily identifiable. Ranges given when exact number of days is unclear, or when multiple hormonal or swelling characteristics were available.

†Results obtained from circumscribed period of female cycle and may therefore underestimate the total duration over which ovulation occurs.

‡Species without exaggerated sexual swelling.

**Table 2.** Compatibility of features and hypotheses

Hypothesis	Correlates and characteristics of exaggerated swellings							
	Bias paternity		Confuse paternity			Other features		
	Ovulation close to peak swelling	Dominant male mating success	Error in the timing of ovulation	Longer duration of receptivity	Subordinate male mating, fertilization success	Multimale social systems	Nonseasonal breeding	Gradual onset*
Best male	✓	✓	No	No	No	✓		
Reliable indicator	✓	✓		(v†)		No	No	
Obvious ovulation	✓	✓	No	No	No	✓		
Male services	✓	✓		✓		✓		
Many male			✓	✓	✓	✓		

\*For all hypotheses, the gradual increase in swelling size may represent a constraint associated with the larger absolute size of this signal (see text).

†Possibly a form of spite in Pagel's (1994) hypothesis.

### Subordinate Males Tend to Mate Outside Peak Swelling

Dominant males are usually capable of excluding subordinate males from mating. However, in the multimale setting where exaggerated swellings are found, dominant males do not typically guard over each female's entire duration of sexual activity. For example, in yellow baboons, *Papio cynocephalus*, Hausfater (1975) found that consortships by dominant males (but not necessarily the same males) occur over an average of 6.8 days of a 9.4-day period of sexual activity. Similarly, consortships were observed for 7 out of 19 days of swelling in olive baboons, *Papio anubis*, (Smuts 1985), and for 5.6 days (Bercovitch 1991) and 6.4 days (Packer 1979) in other studies of olive baboons.

Subordinate males are thus able to mate with females outside peak swelling, when dominant males have shifted their attention to other, more swollen females (Rowell 1972). Matings outside peak swelling may occasionally involve consortships, but are more likely to be opportunistic and to involve reduced mate guarding (Hall 1962; Saayman 1970). In baboons, subordinate males mate with females when dominant males are not interested, either before or after peak swelling is achieved (Hall 1962; Hall & DeVore 1965; Saayman 1970; Hausfater 1975; Packer 1979; Smuts 1985; Rasmussen 1987; Altmann et al. 1988; Bercovitch 1991). Subordinate males are also able to mate in macaques, including rhesus macaques (Southwick et al. 1965; Manson 1992), moor macaques, *Macaca maurus* (Matsumura 1993), longtailed macaques (van Noordwijk 1985; de Ruiter et al. 1992), and pigtailed macaques (Oi 1996). In red colobus, dominant males do the majority of mating, although subordinate males also achieve some matings (Struhsaker & Leland 1985). Subordinate male chimpanzees (Tutin 1979) and bonobos, *Pan paniscus* (Kano 1992) also regularly mate.

The focus on males in this and the previous section ignores the often active involvement of females in the mating process. Examples of relevant female behaviours include solicitations or following of certain males (e.g. Hall 1962; Michael & Welegalla 1968; Manson 1992;

Bercovitch 1991, 1995) and vocalizations that attract male attention and thus influence the outcome of male-male competition and mating behaviour (Hamilton & Arrowood 1979; Hauser 1990; O'Connell & Cowlshaw 1994; Semple 1998). Females also engage in 'sneak' matings with subordinate males when dominant males are not paying attention (Smuts 1987). Finally, females actively participate in consortship behaviour, for example by maintaining (or terminating) consortships with certain males (e.g. Tutin 1979; Taub 1980; van Noordwijk 1985; Bercovitch 1991; Manson 1992; see also Manson 1997). Active consortship behaviour suggests that females also benefit from the consort relationship.

As mentioned above, ovulation occurs with some error relative to sex skin tumescence. Thus, even though subordinate males are generally excluded from mating with fully swollen females, they should occasionally sire offspring. Paternity studies confirm that subordinate males do fertilize females in both natural (de Ruiter et al. 1992; Altmann et al. 1996) and semifree-ranging populations (e.g. Berard et al. 1993; Paul et al. 1993).

### Summary

This review suggests that exaggerated swellings serve contradictory purposes for females. On the one hand, features of exaggerated swellings increase paternity certainty: laboratory studies indicate that the probability of ovulation correlates with swelling size, and field studies show that male-male competition increases as females become more swollen. On the other hand, features of exaggerated swellings confuse paternity: ovulation does not always occur precisely at peak swelling, the duration of sexual activity is longer in species with exaggerated swellings, and females often mate with multiple males at the times when they are potentially fertile.

The contradiction between confirming and confusing paternity can be explained if females are attempting to solve a combination of problems rather than just one. To investigate this possibility, in the next section I review hypotheses for the evolution of exaggerated swellings.

These hypotheses are then evaluated by considering whether the features listed above are consistent, inconsistent, or neutral with respect to these hypotheses (Table 2). Because these hypotheses were partly based on the patterns just presented, this exercise does not represent a case of strong inference (Platt 1964). Nevertheless, these patterns can be used to examine the general consistency and compatibility of the various hypotheses. From this process, new predictions can be tested with independent comparative data sets, in other taxa, in the field, or in the laboratory.

## HYPOTHESES FOR THE EVOLUTION OF EXAGGERATED SWELLINGS

### The Best-male Hypothesis

The best-male hypothesis proposes that exaggerated swellings incite male–male competition, which would benefit the female by enabling her to identify and mate with the male that has the best genotype (Clutton-Brock & Harvey 1976). Under the best-male hypothesis, properties associated with success in male–male competition are assumed to be heritable and should thus be passed to a female's offspring. These heritable properties may include the male's competitive ability itself, or indirect features that are correlated with competitive ability, such as disease resistance. Female choice under this hypothesis is a form of 'indirect' mate choice (Wiley & Poston 1996) in which female advertisement results in mating with a genetically superior male.

A generally honest sexual signal would be necessary to incite males to compete. Therefore, the best-male hypothesis can account for features of exaggerated swellings that serve to increase paternity certainty (Table 2). However, the best-male hypothesis is incompatible with features of exaggerated swellings that confuse paternity, including the longer duration of sexual activity, error in the timing of ovulation, and evidence that subordinate males sire offspring. Furthermore, the best-male hypothesis cannot explain why swellings are gradual in their onset (although this aspect of exaggerated swellings could be a functional constraint on the expression of such a large signal, as discussed above).

A mechanism such as the best-male hypothesis is probably most applicable to species in which females are not able to judge male quality in the course of frequent association, as when the sexes are spatially segregated. However, sexual segregation of this type does not commonly occur in primate species that display exaggerated swellings; instead, males and females are typically members of relatively permanent, bisexual social groups (van Schaik & Kappeler 1997). Furthermore, male life histories are characterized by short periods of high rank and high reproductive success (e.g. Altmann et al. 1988; van Noordwijk & van Schaik 1988). This life history pattern means that most males would be deemed 'best' at some point in their lives (Dunbar 1988; although male tenure lengths may differ: Martin 1992). It is thus not clear why females would need such a costly signal to determine male genetic quality. Finally, no evidence suggests that females choose

males on the basis of good genes, which might be assessed through the age of the male (and thus his survivability) rather than his current dominance status.

Pagel (1994) criticized the assumption that a larger swelling should incite male–male competition. Using a mathematical model, Pagel (1994) argued that male–male competition is an evolutionarily stable strategy (ESS) whenever females signal their fertility; thus, larger swellings should not incite greater male–male competition. Pagel's (1994) assertion is supported by species that lack prominent sexual signals yet still display intense male–male competition. For example, male–male competition is well documented in ringtailed lemurs (Jolly 1966; Koyama 1988), where it may be among the most intense of any primate species (Smuts 1987). While female ringtailed lemurs do signal fertility with an ordinary swelling, they lack exaggerated swellings. In other cases, field researchers have noted that female proceptivity alone can incite male–male competition, for example in red howlers, *Alouatta seniculus* (Crockett & Sekulic 1984), grey langurs (Sommer 1988) and lions, *Panthera leo* (Pusey & Packer 1994).

The best-male hypothesis predicts a signal that identifies the optimal time for males to compete. This would likely be a small signal of short duration that signals ovulation very accurately, such as the ordinary signals discussed above. Thus, the best-male hypothesis can explain why female primates would signal fertility, but it cannot account for the exaggeration of these signals. Combining the best-male hypothesis with other hypotheses does not rescue it because actively mating with less-preferred males, and occasionally being fertilized by them, runs directly counter to the genetic benefits proposed under this hypothesis.

### Reliable Quality Indicator Hypothesis

Pagel (1994) proposed that swellings reliably indicate female quality, which is hypothesized to function in female–female competition for preferred males. Under this hypothesis, females are again seeking the genetic benefits of 'good genes'. However, in this case females are using swellings as a signal to males of their current physical condition (and thus genetic quality), with the goal of attracting preferred males that have the option of mating with another female. Pagel's (1994) hypothesis assumes that females differ in their quality, that swellings honestly reflect these differences, and that females compete for access to mates. Males are predicted to prefer females with the largest, most tumescent, and most brightly coloured swellings.

While theoretically plausible, Pagel's (1994) hypothesis is not supported by the available data (Radwan 1995; Wiley & Poston 1996; D. P. Zinner & C. P. van Schaik, unpublished data). First, if swellings function as proposed, they should be honest indicators of female quality. However, several studies have noted that the least fertile females have the largest swellings. For example, adolescent females, which are less likely to conceive in a given cycle, tend to have larger swellings in at least 10 non-human primate species (Anderson & Bielert 1994). In

addition, females that have cycled multiple times without conceiving, and are therefore more likely to be infertile or unable to acquire the resources necessary for reproduction, also tend to have larger (or longer-lasting) swellings (e.g. Zuckerman 1930; Rowell 1970, 1972; Bernstein et al. 1982).

Second, Pagel's hypothesis cannot adequately explain the distribution of swellings across primate species. The reliable quality indicator hypothesis predicts that exaggerated swellings will be found in species where female–female competition for mates is most intense. Thus, exaggerated swellings are expected when the sex ratio is more female biased. However, the opposite pattern is observed: exaggerated swellings occur in multimale social groups, where the female-to-male ratio is lower (Wiley & Poston 1996). Thus, in the Old World anthropoids, single-male taxa have an average of 3.7 females per male, while multimale taxa have 2.3 females per male (data from unpublished comparative database). Female–female competition is also expected to increase in seasonally breeding species because females are more likely to come into receptivity simultaneously when breeding seasons are short (Mitani et al. 1996), and so Pagel's (1994) hypothesis predicts that swellings should be more common in seasonal species. However, as noted above, swellings are instead correlated with nonseasonal breeding (van Schaik et al., *in press*).

Pagel's (1994) hypothesis is therefore not supported by the available evidence, and it is not likely to be the primary selective force responsible for the evolution of this trait in primates. However, once exaggerated swellings have evolved for other reasons, a revised version of Pagel's hypothesis could operate.

### The Obvious-ovulation Hypothesis

Hamilton (1984) proposed that exaggerated swellings pinpoint the timing of ovulation and thus increase paternity certainty, a frequently proposed prerequisite to male care (Clutton-Brock 1991). To assure males of paternity, the obvious-ovulation hypothesis predicts an honest signal of ovulation much like the ordinary swellings described by Rowell (1972). Thus, features of exaggerated swellings that pinpoint ovulation are generally consistent with predictions of the obvious-ovulation hypothesis.

However, features of exaggerated swellings that confuse paternity are inconsistent with the obvious-ovulation hypothesis because paternity uncertainty is not expected to favour male care (Table 2). In addition, extensive male care is not observed in most species with exaggerated swellings (cf. Anderson 1992), and when it is, some of this 'care' can instead be attributed to direct benefits that accrue to males that use infants in social interactions for which past paternity certainty is not needed, such as agonistic buffering (Whitten 1987) or male mating effort (Smuts & Gubernick 1992; van Schaik & Paul 1996).

Nevertheless, given that dominant males are the most likely fathers in species with exaggerated swellings, it may benefit them to protect infants in times of extreme danger, such as during attacks by infanticidal

males (e.g. Palombit et al. 1997). Thus, some benefits under the obvious-ovulation hypothesis are possible, but this hypothesis cannot explain all the correlates of exaggerated swellings.

### The Male Services Hypothesis

As mentioned above, males and females of many species with exaggerated swellings tend to form consortships at peak swelling. Consortships can serve a number of functions for both males and females, including mate guarding, mate assessment and courtship (Manson 1997). Under the male services hypothesis, females can benefit in a direct way from consortship behaviour by dominant males: because these males should be most effective at excluding other individuals or predators, females may gain direct benefits in the form of increased protection from conspecifics or predators (van Noordwijk 1985). These males could also provide assistance in territorial defence (Takahata et al. 1994).

Exaggerated swellings may also enable females to reduce male harassment: by consorting with a powerful male, other, potentially harassing males may be less able to approach the female (Wrangham 1979; Smuts & Smuts 1993; Mesnick 1997). This is true even though the 'protecting' male is actually guarding the female for selfish reasons, namely to maintain exclusive sexual access to the most fertile female in the group (see also Rubenstein 1986). Protection can be active, with the male threatening and attacking other males, but even just the presence of a dominant male can deter other males from harassing the female (e.g. Smuts 1985). By pairing with a powerful male during peak sexual activity, the time when consortships tend to occur (Dixson 1983; Hrdy & Whitten 1987), a female benefits from male protection at the time when harassment is most common (Smuts & Smuts 1993).

The male services hypothesis requires that females honestly signal their fertility in order to stimulate competition and thus elicit consortships with a dominant male; hence, this hypothesis is consistent with features of exaggerated swellings that increase a male's paternity certainty. However, the male services hypothesis does not require the precise signal predicted by the best-male and the obvious-ovulation hypotheses because actual paternity is less important in obtaining the immediate benefits of male services: as long as ovulation tends to occur close to peak swelling, a dominant male will benefit by guarding a female or by providing her with direct benefits in exchange for matings.

In addition, a less precise signal would probably encourage a dominant male to guard the female over a longer period, thus increasing the benefits to the female (van Noordwijk 1985). Furthermore, ovulation tends to occur just prior to detumescence (see above), which can be known by a male only after the fact. Thus, by placing ovulation immediately prior to detumescence, females make it even more difficult for males to predict the precise timing of ovulation, which may also increase the duration of consortship.

## The Many-male Hypothesis

The many-male hypothesis proposes that by signalling receptivity prominently, a female is able to attract multiple males as mating partners (Hrdy 1981; Hrdy & Whitten 1987). By mating with multiple males, a female can confuse paternity, which is thought to reduce the risk of infanticide because males are less likely to kill infants they might have sired (Hrdy 1979; van Schaik et al., *in press*). Evidence from grey langurs (Hrdy 1979), ruffed lemurs, *Varecia variegata* (White et al. 1993) and lions (Pusey & Packer 1994) supports multimale mating as a strategy used by females to reduce the risk of infanticide. Alternatively, mating with multiple males might increase paternal care, as this would increase the number of potential fathers (Hrdy 1981; Hrdy & Whitten 1987). However, mating with multiple males might equally be argued to reduce paternal investment because paternity uncertainty would increase. In any case, male care may represent mating effort rather than paternal investment (Smuts & Gubernick 1992; van Schaik & Paul 1996), which would be unrelated to past paternity. In what follows, I therefore focus on the many-male hypothesis as it relates to preventing infanticide rather than increasing direct male care.

The many-male hypothesis can best account for features of exaggerated swellings that confuse paternity (Table 2). However, the many-male hypothesis cannot account for features of exaggerated swellings that increase the paternity certainty of dominant males. This hypothesis also cannot explain why the ancestrally small signal would become exaggerated. One possibility is that males require a long-distance signal to attract them within range of the female (e.g. Burt 1992). However, this is not likely for primates. First, because of their permanent social groups, it should be possible for male primates to monitor female reproductive condition, irrespective of the type of ovulatory signal used or its degree of exaggeration. Second, as mentioned above, female proceptivity is often sufficient to incite mating in multimale situations, suggesting that males do not need a large visual signal to inform them of mating opportunities. Examples in which females mate with multiple males when these males are available are found in many male-transfer species without exaggerated swellings, including patas monkeys, grey langurs, vervets and redbellied monkeys, *Cercopithecus ascanius* (see Hrdy & Whitten 1987; van Schaik et al., *in press*).

Even if females require a signal in order to elicit mating by males (perhaps owing to some phylogenetic constraint), an exaggerated signal is not expected. Instead, females wishing to confuse paternity would be expected to place ovulation randomly within an ordinary signal of longer duration, which would thus avoid the costs of exaggerated swellings.

Another solution for confusing paternity is for females to conceal fertility as completely as possible (e.g. vervets: Andelman 1987; humans, *Homo sapiens*: Hrdy 1981). In association with concealed ovulation, females could signal their receptivity behaviourally (e.g. grey langurs: Hrdy 1979; vervets: Andelman 1987). As long as the

behavioural signal was usually honest, this combination of concealed ovulation and behavioural cues of receptivity would allow females the greatest flexibility for dealing with male incursions or shifts in dominance (e.g. situation-dependent receptivity; Hrdy & Whitten 1987). However, in practice it may be difficult for females to conceal completely hormonal metabolites associated with ovulatory events (van Schaik et al., *in press*), so that other means of confusing paternity will be more effective.

A related hypothesis for exaggerated sexual swellings concerns cryptic female choice (Eberhard 1985, 1996). Cryptic female choice refers to differential selection of gametes within the female reproductive tract. Thus, a mechanism based on cryptic female choice requires that females mate with multiple males, and so this may provide another benefit under the many-male hypothesis. Cryptic female choice in primates may be especially important in social settings where females are unable to choose their mating partners. Evidence for cryptic choice exists in primates: Dixson & Mundy (1994) showed that the sexual swelling of chimpanzees makes it more difficult for males to deposit sperm near the cervix and that males differ in their ability to do this. While this aspect of sexual swellings has probably influenced the evolution of male genital morphology (Dixson & Mundy 1994), it remains unclear how females benefit from differential selection of male sperm in this case. Further research is therefore needed.

In conclusion, the many-male hypothesis is the most plausible hypothesis to explain features of exaggerated swellings that confuse paternity. However, the many-male hypothesis is not able to explain the conspicuousness of this signal. This hypothesis also cannot explain why features of exaggerated swellings bias certainty towards certain males in the social group. Thus, the many-male hypothesis also cannot stand on its own.

## DISCUSSION

Despite a great deal of attention to the subject, the adaptive significance of exaggerated swellings remains controversial. This review shows that existing hypotheses fail because each focuses on benefits that require either paternity certainty or paternity confusion. However, features of exaggerated swellings both indicate fertility and obscure it (Table 2). A new hypothesis, or a combination of existing hypotheses, is therefore needed to account for the evolution of this trait. Benefits under the male services and the many-male hypotheses appear most plausible. However, it is not presently possible to exclude benefits associated with some other hypotheses (e.g. paternal care by dominant males under the obvious-ovulation hypothesis, perhaps through protection of offspring from potentially infanticidal males).

The patterns discussed above are consistent with van Schaik et al.'s (*in press*) 'female dilemma': on the one hand, females benefit from giving some males a higher probability of paternity (as in male services,

obvious-ovulation, and perhaps even the best-male or reliable-indicator hypotheses); on the other hand, females benefit from confusing paternity (as in the many-male hypothesis). What remains to explain is how exaggerated swellings elicit mate guarding for only part of the female's fertile period, so that females can mate with other males to confuse paternity.

In this section, I provide a mechanism by which exaggerated swellings enable females to both bias and confuse paternity, and I discuss why the ancestrally small sexual signal would become exaggerated. I call this hypothesis the graded-signal hypothesis for exaggerated swellings. This hypothesis posits that exaggerated swellings signal female fertility in a probabilistic manner, so that dominant males tend to mate-guard only at peak swelling, and this allows females to mate with subordinate males outside peak swelling.

### Sexual Swellings as Graded Signals

The hypotheses for exaggerated swellings make incompatible predictions when examined individually; hence, it is not immediately obvious how they could be combined. For example, both the obvious-ovulation and male services hypotheses predict a precise, ordinary signal. However, an ordinary swelling would more likely result in a dominant male monopolizing mating opportunities during a female's entire fertile period, and so this may increase the risk of infanticide by males that did not mate with the female at the time of fertility. In contrast, infanticide risk predicts that females will conceal fertility and mate with many males. However, concealed ovulation may result in less mate guarding (males are less likely to guard a female that fails to signal fertility) and therefore no direct benefits under the obvious-ovulation and male services hypotheses. In addition, truly concealed ovulation may be difficult to achieve (van Schaik et al., in press).

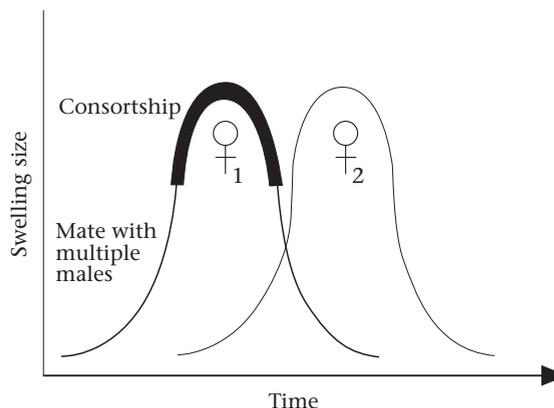
Under the graded-signal hypothesis, two factors are relevant to exaggerated swellings that enable females to overcome the female dilemma: exaggerated swellings are probabilistic signals, and females are sexually active for a longer period.

#### Probabilistic signals

Several features listed above qualify exaggerated swellings as probabilistic, or graded, signals: swellings increase in size gradually, and ovulation tends to occur at peak swelling; however, ovulation occurs with some error relative to peak swelling. Thus, the highest probability of ovulation occurs close to peak swelling, with decreasing probabilities before and after maximum tumescence, so that prominent swellings can be modelled as probability distributions which reflect the likelihood of ovulation (see also Martin 1992). These distributions need not be perfect 'bell-shaped' curves (e.g. Fig. 2).

#### Longer duration

The longer duration of receptivity associated with exaggerated swellings is the second important factor in how



**Figure 3.** Cost trade-offs to mate guarding by males. If exaggerated swellings honestly indicate the probability of ovulation, and if consortships are costly to maintain or females in the group overlap in their receptivity, a dominant male is expected to guard females only at maximum swelling (indicated by the heavy line). In this hypothetical example, the male is expected to leave the first female for a second female that is becoming more swollen (represented by the second probability distribution). This frees the first female to mate with less dominant males while she is still potentially fertile (indicated by the thinner line).

exaggerated swellings can solve the female dilemma. Two factors are relevant here. First is the amount of overlap in female sexual activity, where overlap refers to synchrony in female receptivity. When ovulation is signalled only approximately and females are synchronously receptive, which is more likely when they are receptive for a longer period, males face the opportunity costs of guarding one female when another female is also receptive. Thus, the optimal strategy for a dominant male is to abandon the first female when her swelling begins to subside, and to switch to another female whose swelling is reaching maximum size. In the context of probabilistic signals, this could be viewed as two overlapping probability distributions (Fig. 3). This male strategy has been documented in species with exaggerated swellings (see references and discussion above in Dominant Males Mate-guard at Peak Swelling).

Second, error in ovulation coupled with a longer duration of sexual activity means that a male is required to guard a female for a longer period to exclude other males from paternity. However, mate guarding is costly to males (Alberts et al. 1996), and the longer duration of sexual activity makes it less likely that a male will completely monopolize a female over her entire window of fertility. The longer duration of sexual activity thus enables females to mate with additional males, and this increases the number of males with a nonzero probability of paternity.

This discussion raises issues of female synchrony (McClintock 1981; Nunn, in press). The graded-signal hypothesis assumes that females overlap in the window of probable ovulation, but not necessarily in the precise timing of ovulation itself. Therefore, both active asynchrony of ovulation (Pereira 1991) and randomly distributed ovulations (Noë & Sluifjter 1990) are compatible with the graded-signal hypothesis. In addition, synchrony of

female subgroups within the larger social unit would be allowed under this hypothesis, as long as not all females ovulate in unison. There is no evidence for perfect synchrony in any of the species with exaggerated swellings, which would be readily observed if it existed. Thus, suggestions of moderate female synchrony in primate social groups are fully consistent with the graded-signal hypothesis (e.g. Kummer 1968; Wallis 1985; Nunn, *in press*).

### Relationship between Graded Signals and the Size of these Signals

For a graded sexual signal to evolve from an ancestrally small discrete signal, the ancestral signal would probably have to increase in size in order to facilitate subtle perception of its value by males. In the case of exaggerated swellings, and given primate visual abilities, the ancestrally small sexual signal may have been under strong selective pressure for increased size to allow male visual discrimination of the probability of ovulation. This is especially true in situations of increased group spread, as in many multimale, terrestrial species of primates (Dixon 1983). Therefore, the hypothesis proposed here incorporates Pagel's (1994) theoretical argument that larger swellings should not incite greater male–male competition. Instead, swellings are prominent out of necessity given the ancestrally small 'ordinary' signal and the male receiver's existing sensory apparatus.

### Phylogenetic Distribution of Exaggerated Swellings

Some aspects regarding the distribution of exaggerated swellings remain to be explained. This variation may relate to female control over mating decisions. When females are capable of freely choosing their mates, they can effectively bias paternity while also confusing it (i.e. they can solve the female dilemma without elaborate sexual signals; van Schaik *et al.*, *in press*). However, when female choice is restricted, females are expected to counteract these restrictions, and sexual behaviour, achieved through sexual signals, is a likely female counterstrategy (e.g. Gowaty 1997). This section examines why exaggerated swellings are restricted to the Old World anthropoids, and why expression of this trait is correlated with multimale and nonseasonal breeding.

Compared with their Old World counterparts, females of New World primate taxa are often viewed as having increased power in mating decisions, in that females can more freely mate with subordinate and dominant males (e.g. brown capuchins, *Cebus apella*: Janson 1984; woolly spider monkeys, *Brachyteles arachnoides*: Milton 1985; see also van Schaik *et al.*, *in press*). Part of this increased female power may relate to the more arboreal habits of these taxa, as this may provide females with more escape options from male coercion. For example, in New World monkeys, males seem to be less able to subdue females singly, and so they instead cooperatively mob females (e.g. squirrel monkeys, *Saimiri oerstedii*: Boinski 1987;

spider monkeys, *Ateles geoffroyi*: Fedigan & Baxter 1984). Similar effects may also exist in the three-dimensional habitats of bottlenose dolphins, *Tursiops truncatus*, and birds, where single males are perhaps less able to coerce females (Connor *et al.* 1992; Gowaty 1997). Thus, female primates in the New World may not need elaborate sexual signals to overcome the female dilemma (van Schaik *et al.*, *in press*).

A combination of biased and confused paternity is only relevant when a female can potentially mate with multiple males, and this may explain the correlation between multimale and exaggerated swellings. In addition, however, the form and intensity of coercion probably covaries with social system parameters. In multimale social systems, males are not able to exclude other males from the social unit (Mitani *et al.* 1996). Females therefore have more options for mating partners, and males are expected to use any strategy, including the use of force against females, to increase mating opportunities (Smuts & Smuts 1993; Clutton-Brock & Parker 1995).

Finally, the effect of seasonality on male monopolization potential (and thus on female choice) can explain why exaggerated swellings are found in nonseasonally breeding species. In seasonal species, females are more likely to overlap in their receptivity simply by chance, and so mechanisms to increase overlap, as achieved through exaggerated swellings, are not needed. In nonseasonal species, a single dominant male would be better able to guard each female as she comes into receptivity, and so features of exaggerated swellings would break the dominant male's monopoly by creating female overlap and allowing females to spread paternity among multiple males (see also van Schaik *et al.*, *in press*).

### Directions for Future Research

Additional research is needed to test whether the size of the swelling truly correlates with the probability of ovulation, as predicted by the graded-signal hypothesis. Related to this, research is needed to determine whether exaggerated swellings are indeed more 'probabilistic' than nonexaggerated swellings. Some data are becoming available for species without exaggerated swellings (see Table 1), but more information is needed, including information for New World taxa.

More information is also needed regarding the benefits received by females from mating with dominant males at peak swelling and subordinate males outside peak swelling. What are the costs and benefits associated with consortships in diverse taxa, including those without exaggerated swellings? What happens when females fail to mate with either the dominant male, or with all subordinate males? How much protection, especially from infanticide, is gained by mating with certain males? Some of these questions have already been addressed, although often in different contexts (e.g. Bercovitch 1991, 1995; Anderson 1992; Palombit *et al.* 1997). More information is therefore needed, especially within the signalling framework presented here.

Patterns similar to those reported above might be expected in other sensory modalities. Thus, in species

with exaggerated swellings, olfactory and vocal signals are also predicted to be graded, probabilistic indicators of ovulation (van Schaik et al., in press). Consistent with the graded-signal hypothesis, O'Connell & Cowlshaw (1994) provide evidence for graded copulation calls in chacma baboons: copulatory call length increases gradually over the female cycle to a peak that coincides with the most likely time of ovulation.

The function (or functions) of exaggerated swellings probably differ among primate clades, and a more fine-grained analysis of species differences should therefore prove interesting. For example, male aggression is possibly reduced in bonobos relative to chimpanzees (Nishida & Hiraiwa-Hasegawa 1987), yet female bonobos are swollen for a greater proportion of their cycles (Dahl 1986). However, the signalling system of bonobos may have been elaborated to function in female sociosexual behaviour (G-G rubbing), as the swelling changes the position of the clitoris to a more ventral position (Dahl 1985, 1986). Patterns should also be examined in nonprimate taxa with similarly conspicuous sexual signals, such as alpine accentors (Davies et al. 1996; Nakamura 1998), as this may provide additional phylogenetically independent data points for evaluating the function of this trait. In addition, such comparisons may highlight other selective factors not readily discernible in analyses restricted to primates.

The focus of this review has been on cross-species patterns. However, individual intraspecific variation in swellings has also been noted (e.g. Rowell 1977), and this variation may be relevant to differentiating between the various hypotheses outlined above. One form of individual variation is related to age: in at least 10 species of nonhuman primates, adolescent females display more conspicuous swellings than adults (see Anderson & Bielert 1994). At present, however, no satisfactory explanation exists for individual differences in patterns of swelling.

Once the link between the signaller and receiver is in place (i.e. male responses to exaggerated swellings), this system is open to further elaboration and possible deceptive functions. Thus, in some taxa, adult females undergo swellings (with matings) at nonfertile times, such as during pregnancy (Hrdy & Whitten 1987; van Schaik et al., in press). Adolescent exaggeration also points to an occasional deceptive function, as these young females are often less fertile.

Swellings may also indicate pre-existing male biases (reviewed in Andersson 1994). Biases of this sort could be detected by placing artificially large 'swellings' on females in species that do not typically have exaggerated swellings to determine how this influences male behaviour (e.g. Girolami & Bielert 1987; Bielert et al. 1989). As a more extreme (but related) example, males of some taxa have possibly also exploited exaggerated sexual signals (see Wickler 1967; Dixson 1983). For example, juvenile red colobus males use pseudosexual signals to appease adult males: juvenile males possess a permanent 'sexual swelling' that is morphologically composed of tissues that are not homologous to those of females (Wickler 1967; Kuhn 1972; see also Hill 1952). As juveniles age, this

'swelling' disappears, and at the same time, harassment by dominant males increases (see Clutton-Brock & Harvey 1976).

Finally, theoretical approaches can be undertaken to model mathematically the benefits and mechanism of the graded-signal hypothesis. This model could then be used to predict parameters for the graded-signal model (e.g. the duration of sexual receptivity and patterns of increase and decrease in swelling size), and these predicted differences could be tested using more detailed cross-species data and field observations.

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## Appendix

### Data used in the comparative tests\*

Species	Exaggerated swelling? (Y/N)	Mean number of males	Social system (S/M)†	Duration of sexual activity (average days)	Seasonal breeding (Y/N)‡
<i>Allenopithecus nigroviridis</i>	Y		M		
<i>Cercocebus albigena</i>	Y	4.3	M	4	N
<i>Cercocebus atterimus</i>	Y	3	M		N
<i>Cercocebus galeritus</i>	Y	2	M		
<i>Cercocebus torquatus</i>	Y		M		N
<i>Cercopithecus aethiops</i>	N	4.1	M		Y
<i>Cercopithecus ascanius</i>	N	1	S	3	Y
<i>Cercopithecus campbelli</i>	N	1	S		
<i>Cercopithecus diana</i>	N	1	S		
<i>Cercopithecus mitis</i>	N	1	S	2	N
<i>Cercopithecus neglectus</i>	N	1	S		N
<i>Colobus angolensis</i>	N	2.4	M		
<i>Colobus badius</i>	Y	4.4	M	5	N
<i>Colobus guereza</i>	N	1.5	S		N
<i>Colobus kirkii</i>	Y		M		
<i>Colobus polykomos</i>	N	2.8	M		
<i>Colobus satanas</i>	N	2.5	M		
<i>Erythrocebus patas</i>	N	1.5	S	1	Y
<i>Gorilla gorilla</i>	N	1.5	S	2	N
<i>Hylobates agilis</i>	N		S		N
<i>Hylobates concolor</i>	N	1	S		N
<i>Hylobates hoolock</i>	N	1	S		N
<i>Hylobates klossi</i>	N	1	S		N
<i>Hylobates lar</i>	N	1	S	4	N
<i>Hylobates moloch</i>	N		S		N
<i>Hylobates muelleri</i>	N		S		N
<i>Hylobates pileatus</i>	N		S		N
<i>Hylobates syndactylus</i>	N		S		N
<i>Macaca arctoides</i>	N		M		N
<i>Macaca assamensis</i>	N	3	M		N
<i>Macaca cyclopis</i>	Y	1.8	M		Y
<i>Macaca fascicularis</i>	Y	4.7	M	15	N
<i>Macaca fuscata</i>	Y	3.4	M	11	Y
<i>Macaca maurus</i>	Y	4	M	15	N
<i>Macaca mulatta</i>	Y	4.5	M	9	Y

## Data used in the comparative tests\* (continued)

Species	Exaggerated swelling? (Y/N)	Mean number of males	Social system (S/M)†	Duration of sexual activity (average days)	Seasonal breeding (Y/N)‡
<i>Macaca nemestrina</i>	Y	2.4	M	13	N
<i>Macaca nigra</i>	Y		M	9	N
<i>Macaca radiata</i>	N	7.3	M	5	Y
<i>Macaca silenus</i>	Y	1.6	M	18	N
<i>Macaca sinica</i>	N	2.7	M	14	Y
<i>Macaca sylvanus</i>	Y	4.7	M	14	Y
<i>Macaca thibetana</i>	N	5.5	M		Y
<i>Macaca tonkeana</i>	Y		M	10	N
<i>Mandrillus leucophaeus</i>	Y		M		N
<i>Mandrillus sphinx</i>	Y	1.5	M		N
<i>Miopithecus talapoin</i>	Y	13	M	11	Y
<i>Nasalis larvatus</i>	N	1	S		N
<i>Pan paniscus</i>	Y	6.7	M	15	N
<i>Pan troglodytes</i>	Y	6.7	M	14	N
<i>Papio anubis</i>	Y	7.2	M	6	N
<i>Papio cynocephalus</i>	Y	7	M	9	N
<i>Papio hamadryas</i>	Y	1.5	M	5	N
<i>Papio papio</i>	Y		M		
<i>Papio ursinus</i>	Y	6.7	M	9	N
<i>Pongo pygmaeus</i>	N	1	S		N
<i>Presbytis cristata</i>	N	1	S		N
<i>Presbytis entellus</i>	N	2.6	M	6	N
<i>Presbytis francoisi</i>	N	1	S		
<i>Presbytis johnii</i>	N	1.3	S		
<i>Presbytis melalophos</i>	N	1.2	S		
<i>Presbytis obscura</i>	N	2.5	M		N
<i>Presbytis pileatus</i>	N	1	S		
<i>Presbytis potenziani</i>	N	1	S		
<i>Presbytis rubicunda</i>	N	1	S		
<i>Presbytis vetulus</i>	N	1	S		N
<i>Procolobus verus</i>	Y	2	M		N
<i>Pygathrix brelichi</i>	N	1.3	S		
<i>Pygathrix nemaeus</i>	N		M		
<i>Simias concolor</i>	N	1	S		
<i>Theropithecus gelada</i>	Y	1.5	M	9	N

\*Sources provided in Methods.

†S: Single male; M: multimale.

‡Breeding seasonality defined as greater than 67% of births in a single 3-month period. Data taken from van Schaik et al. (in press).