

Do exaggerated sexual swellings function in female mating competition in primates? A comparative test of the reliable indicator hypothesis

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The reliable indicator hypothesis proposes that exaggerated sexual swellings in female primates serve as honest signals of female quality that function in female–female competition over mates. We examined a version of this hypothesis using interspecific data to test whether exaggerated sexual swellings are associated with female mating competition, as measured using the adult sex ratio, female canine size, and expected female mating synchrony. The ratio of females to males and relative canine size declined over evolutionary transitions in swelling state, thus providing no support for the reliable indicator hypothesis. Expected female mating synchrony increased over evolutionary transitions in swelling state, but this pattern did not approach significance, and the patterns were opposite to predictions when controlling for the number of males in the group. In addition to these comparative tests, we reviewed evidence concerning individual attributes of females relative to characteristics of their swellings. Contrary to the reliable indicator hypothesis, the least fertile females, or those least likely to raise surviving offspring, often have larger swellings. We consider the statistical power of our tests, discuss the theoretical and empirical bases for our comparative predictions, and consider other lines of evidence needed to test the reliable indicator hypothesis. We also discuss an alternative hypothesis, the graded signal hypothesis, which combines the benefits of biasing and confusing paternity through a novel mechanism and is testable in the field and the laboratory. *Key words:* comparative study, communication, honest signaling, independent contrasts, primates, sexual swellings. [*Behav Ecol* 12:646–654 (2001)]

Females of some Old World primates show prominent swelling or conspicuous coloration of their perineal region during the part of their menstrual cycle when they are most likely to ovulate. These exaggerated sexual swellings are found mainly in species where females actually or potentially have multiple mates (Clutton-Brock and Harvey, 1976; Dixon, 1983; Hrdy and Whitten, 1987; Nunn, 1999a), and this prominent signal clearly alters male behavior toward swollen females (e.g., Girolami and Bielert, 1987). A sexual swelling also has been noted in one species of bird with similar mating patterns (the alpine accentor, *Prunella collaris*; Davies et al., 1996; Nakamura, 1990), suggesting that this trait may be more widespread than assumed. Female sexual behaviors in birds and mammals may serve as counterstrategies to male attempts at monopolizing fertile matings and coercing females to mate (Davies, 1985; Gowaty, 1997; Nunn, 1999b; Smuts and Smuts, 1993; van Noordwijk and van Schaik 2000; van Schaik et al., 1999). Hence, the adaptive significance of this probably costly signal is important for understanding intersexual conflict and variation in mating systems.

Several hypotheses have been proposed to account for the evolution of exaggerated sexual swellings in primates (reviewed in Hrdy and Whitten, 1987; Nunn, 1999a). Until recently, two hypotheses were most widely discussed. The best

male hypothesis proposes that exaggerated swellings incite male–male competition so that females can identify, and then mate with, the male with the best genotype (Clutton-Brock and Harvey, 1976). In contrast, the many male hypothesis claims that exaggerated swellings attract multiple males as mating partners (Hrdy, 1981; Hrdy and Whitten, 1987). Mating with multiple males facilitates paternity confusion, which is thought to reduce the risk of infanticide (Ebensperger, 1998; Hrdy, 1979; van Schaik et al., 1999). Some features of exaggerated sexual swellings are consistent with the best male and many male hypotheses, but neither hypothesis can fully account for all aspects of this exaggerated trait (Nunn, 1999a).

Another hypothesis for exaggerated sexual swellings, the reliable indicator hypothesis (Pagel, 1994b), has recently attracted attention. Pagel (1994a) used an evolutionarily stable strategy (ESS) model to show that males should always cue into signals of female fertility that indicate the best time to compete. Even a small swelling would be sufficient for this, and there is no reason to expect a larger swelling to incite greater male–male competition or sexual interest. Thus, to account for the size of these swellings, Pagel (1994a) argued that they are honest, and therefore costly, signals of female quality. Females need to signal quality because, contrary to popular belief, they also face competition for access to mates.

In this study, we tested general predictions of the reliable indicator hypothesis using phylogenetic comparative methods. Ideally, comparative tests of the hypothesis would use quantitative data on female mating competition during estrus across a wide array of species and information on relative variation in male and female quality. Such detailed comparative data,

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Received 16 June 2000; revised 17 January 2001; accepted 26 January 2001.

however, are unavailable. Instead, we tested a broader version of the hypothesis that focuses on aspects of female mating competition, based on the following predictions:

- (1) Increases in the adult sex ratio (females per male) are expected over evolutionary origins of exaggerated swellings, under the assumption that a higher ratio of females to males indicates greater female mating competition (see also Hemelrijk and Luteijn, 1998). By the same reasoning, losses of exaggerated swellings should be associated with decreases in the adult sex ratio.
- (2) Exaggerated sexual swellings should be associated with increased female canine size. Previous research has shown that canine size is a predictor of contest competition in both sexes (Plavcan et al., 1995). Among males, this competition is over access to mates, whereas among females it is often assumed to be over access to resources. However, females could use their weaponry equally well to compete for access to mates. Thus, assuming that other sources of competition do not obscure or bias the comparative patterns, we use female canine size as a surrogate measure for female mating competition.
- (3) Finally, exaggerated sexual swellings should be associated with increased female mating synchrony because male discrimination among females is more important when females mate synchronously (Pagel, 1994a; Radwan, 1995). Whereas Pagel's (1994a) ESS formulation of male-male competition makes no assumptions regarding mating synchrony (Pagel, 1995), field and laboratory studies have suggested that female competition increases during synchronous mating (Perry and Manson, 1995; Wasser, 1983; Zinner et al., 1994). Moreover, if exaggerated swellings represent a form of spite by reducing the probability that other females conceive through competition over inseminations (Pagel, 1994b), then some degree of mating overlap is needed to make this spiteful behavior possible.

To have comparable information across species, these predictions are necessarily based on indirect measures of competition. Use of such indirect measures, and the related possibility of confounding variables, is a limitation of comparative research. Such limitations, however, are offset by two important benefits of cross-species comparisons. First, a comparative approach is needed to understand why exaggerated sexual swellings have evolved in some species but not in others. Using a broad array of species rather than a single comparison of two closely related species allows for statistically more powerful tests of predictions, which is preferred because we have more confidence that a trait is an adaptation if it has evolved multiple times in association with some other trait rather than just once (Pagel, 1994a). Second, comparative tests can be used to generate and test hypotheses. Thus, such tests inform more detailed experimental studies within species or across closely related species (e.g., Losos, 1995).

The comparative results presented here represent the first quantitative test of the reliable indicator hypothesis using phylogenetic comparative methods. These tests are not necessarily independent of one another, but instead represent different ways of examining female mating competition across species. In addition, we do not test alternative predictions (e.g., for the best male and many male hypotheses) because many of the comparative patterns were used to generate these hypotheses (Nunn, 1999a). Moreover, the reliable indicator hypothesis makes few predictions that overlap with the other hypotheses, reflecting the possibility that multiple factors have influenced the evolution of this exaggerated trait (Nunn, 1999a).

METHODS

To control for fundamental differences in the primate radiations, we restricted our analyses to catarrhine primates (see van Schaik et al., 2000). Identification of species that have exaggerated swellings was based on Nunn (1999a). This source used a three-part definition of exaggerated swellings: (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 (see Dixon, 1983; Rowell, 1972); and (3) the signal is clearly visible by human observers at a distance.

To calculate the sex ratio in test 1, we took information on the number of adult males and females from an unpublished database used in several recent comparative studies (e.g., Nunn and Barton, 2000; Nunn and van Schaik, in press). This database uses major reviews of primate behavior and social organization and is updated by more recent journal articles and by personal communications with experts on particular species (comparative data and information on the computer programs used are available on the Internet at <http://faculty.virginia.edu/charlienunn>). For the fission-fusion bonobo and chimpanzee (*Pan paniscus* and *P. troglodytes*), we calculated group composition based on population group size (i.e., the community), rather than foraging group size (i.e., the party) because females can mate with any community males and therefore potentially compete with other community females for mating partners. We examined patterns using the band for the higher-level societies of the gelada (*Theropithecus gelada*) and the hamadryas baboon (*Papio hamadryas*), as copulations have been documented outside the breeding unit (see Andelman, 1986; for captive populations, see Krebs and Kaumanns, 1999; Smith et al., 1999). We also repeated some analyses with data from Mitani et al. (1996), who used foraging-group size for the gelada and hamadryas baboon.

For test 1, we also examined patterns using the number of potentially fertile females, calculated as the number of females divided by the interbirth interval, rather than as the absolute number of females. Ross and Jones (1999) was the primary source for information on interbirth intervals, with additional data from Dunbar (2000). Interbirth intervals (and mating durations) for *Cercocebus galeritus* were taken from Field and Walker (1995).

To examine comparative patterns of female mating competition using canine size in test 2, we used residual canine size calculated from an isometric line relative to body mass (slope = 0.333 because canine size is a linear measure and body mass is volumetric). Information was taken from Plavcan et al. (1995).

In analyses of mating synchrony in test 3, we used expected female mating overlap, calculated as the probability that two or more females mate synchronously. The expected number of mating females was calculated based on methods in Dunbar (1988, 2000) and Nunn (1999a), with modifications that should provide a more accurate estimate of expected mating synchrony. The probability that two or more females mate simultaneously was based on breeding season duration, number of females, interbirth interval, the duration of mating (i.e., number of days in estrus), presence of postconception matings, and number of cycles to conception. With these values, we used the binomial theorem,

$$P_{(Y \geq 2)} = \frac{k!}{Y!(k-Y)!} p^Y (1-p)^{k-Y},$$

where $P_{(Y \geq 2)}$ is the probability that two or more females (Y)

are mating simultaneously, k is the number of females in the group, rounded to the nearest whole number, and p is the probability that any given female is mating. With information on the duration of mating per cycle in days (m), the number of cycles to conception (c), and the interbirth interval measured in days (I), the probability of a female mating is $p = (mc)/I$. This formula applies to nonseasonally breeding species, in which females mate throughout the year. Breeding seasonality was incorporated by multiplying I by the proportion of the year in which mating can take place, which was calculated in Mitani et al. (1996) as the duration of the breeding season divided by 365.

For expected female mating overlap, we took information on female number from Mitani et al. (1996), as this reference also provided matched estimates of breeding season duration needed for these calculations. Mating duration was taken from the literature and previous comparative data sets (Nunn, 1999b; van Schaik et al., 1999). Some values, especially the number of cycles to conception, were difficult to obtain from the literature. Among species for which cycles to conception could be estimated, these values were highly correlated with breeding season duration (nonphylogenetic analysis: $r_s = .80$, $n = 13$, $p = .001$; phylogenetic analysis: all eight increases in breeding season duration were associated with more cycles to conception, $p < .01$ in a sign test). We therefore estimated cycles to conception for some females from congeneric species with similar breeding season durations. Species with post-conception matings (see van Schaik et al., 1999) effectively create greater female mating overlap, provided that males cannot differentiate potentially conceptive from nonconceptive cycles (cf. Gust, 1994; Kinnaird, 1990). We therefore added one cycle to conception for species in which females regularly mate during pregnancy (based mainly on van Schaik et al., 1999).

In our analyses, we first provide general trends using the raw species data. Statistical results are provided only for phylogenetic tests because the ANOVA tests in nonphylogenetic analysis have greatly inflated degrees of freedom (Garland et al., 1993). For example, a nonphylogenetic analysis of test 1 would examine differences in sex ratio in species with and without exaggerated sexual swellings. With our dataset, such a test would seem to have > 60 df, but in fact there have been only five evolutionary transitions in the presence of exaggerated swellings. Thus, the degrees of freedom would be inflated approximately by a factor of 12, making significant results more likely.

To examine the comparative patterns statistically, we used the BRUNCH algorithm, implemented using the computer program CAIC (Purvis and Rambaut, 1995) and based on independent contrasts (Felsenstein, 1985; Harvey and Pagel, 1991), to identify changes in the presence of exaggerated swellings (the independent variable in our analyses). The sign of an independent contrast is arbitrary (Garland et al., 1992), although the BRUNCH algorithm forces contrasts in the independent dichotomous variable to be positive (Purvis and Rambaut, 1995). Thus, we tested whether transitions in the dependent variable were significantly greater than 0 using a t test (Purvis and Rambaut, 1995). Branch lengths were incorporated when calculating contrasts for the dependent variable. To implement these tests, we used the composite estimate of primate phylogeny provided by Purvis (1995).

For expected female overlap, we corrected our estimates for the number of females in the group because female overlap is a function of female number (Nunn, 1999a). Because swellings are found only in multimale groups and the number of females increases with the number of males (Altmann, 1990; Mitani et al., 1996; Nunn, 1999a), failure to control for female number would result in overlap measures simply reflecting

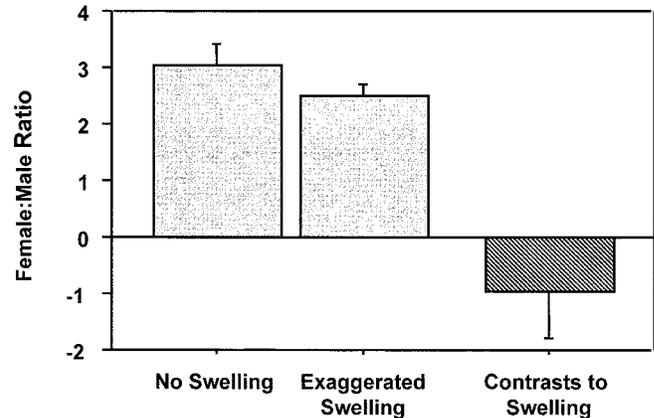


Figure 1

Sex ratio and exaggerated sexual swellings. Shaded bars indicate female:male sex ratio (+1 SE) for species with and without exaggerated sexual swellings. Hatched bar shows results (+1 SE) for evolutionary contrasts (i.e., mean evolutionary change in female:male sex ratio over evolutionary changes in swelling state). With contrasts, the female:male sex ratio is predicted to increase over evolutionary transitions to exaggerated swellings under the reliable indicator hypothesis, but the opposite pattern is found.

the number of females. In a separate set of tests, we also corrected expected female overlap for male number, as in test 1, because males are the objects of female competition assumed by the hypothesis. To correct for either the number of females or males, we calculated the slope of the least-squares regression line of contrasts in expected female overlap on contrasts in female or male number (taken from Mitani et al., 1996). This slope was then used to calculate residuals from the raw species values (see Nunn, 1999a). These residuals were then reentered into CAIC and examined relative to swelling state transitions using the BRUNCH algorithm.

These comparative tests are not necessarily independent of one another, but for two reasons we preferred them to multivariate tests (i.e., with a composite estimate of female mating competition constructed from all the surrogate variables). First, information is often lacking for different species in the different tests. This leads to small sample sizes when contrasts are calculated because information is needed for each species in the sample to obtain comparable contrasts (Purvis and Rambaut, 1995). The second reason is related to the first: the diversity of information available for different species in the tests allows us to better evaluate the generality of the comparative patterns across primates, as slightly different sets of species were used to calculate contrasts in the different tests. Because specific directional predictions were tested, we used one-tailed statistical tests with significance level (α) set at 5%.

RESULTS

Test 1: Adult sex ratio and number of fertilizable females

First we examined the adult sex ratio, measured as the number of females per male. The reliable indicator hypothesis predicts that larger values, indicating greater competition, should be found in species with exaggerated sexual swellings. Contrary to this prediction, however, species with exaggerated swellings had only 2.48 females per male, whereas those without exaggerated swellings had 3.05 females per male (Figure 1). Similar results were obtained when using the Mitani et al. (1996) data set for the number of males and females (mean with exaggerated swellings = 2.7, mean without = 5.2; see also Nunn, 1999b). In phylogenetic tests based on independent

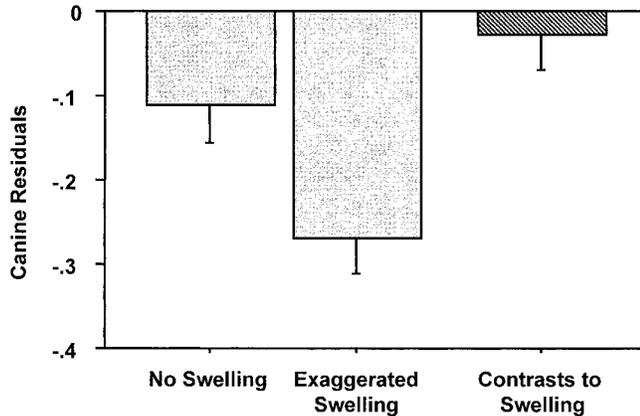


Figure 2

Canine residuals and exaggerated sexual swellings. Bars show mean canine residuals ($+1$ SE) for species with and without exaggerated sexual swellings (shaded bars) and for contrasts (hatched bar). Canine residuals, a proxy variable for female mating competition, were taken from Plavcan et al. (1995), provided as deviations from a fixed isometric line (see Methods); thus, residuals do not sum to zero and the mean in this subsample of catarrhines is negative. Contrary to the reliable indicator hypothesis, species with exaggerated sexual swellings have smaller canines.

contrasts, the reliable indicator hypothesis predicts that evolutionary changes in swelling state are associated with positive increases in the ratio of females to males. Contrary to this prediction, four of the five contrasts were negative (mean = -0.98 ; $t = -1.18$, $n = 5$, $p = .85$; Figure 1). Results remained largely the same when using the Mitani et al. (1996) data set (mean = -1.07 , $t = -1.71$, $n = 5$, $p = .92$).

The number of potentially fertile females may be a more relevant measure of female reproductive competition than the absolute number of females in the group. We therefore repeated the above analyses using the number of potentially fertile females, estimated for each species as the number of females divided by the interbirth interval. Across species, patterns were again opposite to predictions (mean with exaggerated swellings = 1.6, mean without = 2.2). Phylogenetic analysis provided consistent results (four of the five contrasts were negative; $t = -1.14$, $n = 5$, $p = .84$).

Test 2: Female canine size

We examined patterns in female canine size under the assumptions that competition over access to mates influences canine size in females, as it does in males (Plavcan et al. 1995), and that other sources of competition are not systematically correlated with swellings in a way that would confound the analysis. The comparative data did not support predictions of the reliable indicator hypothesis: species with exaggerated swellings had smaller canines (Figure 2). In phylogenetic tests, the trend remained counter to predictions of the reliable indicator hypothesis (3 of 5 contrasts were negative; $t = -0.67$, $p = .73$).

Test 3: Expected female mating synchrony

Finally, we tested whether factors leading to increased mating synchrony are correlated with exaggerated sexual swellings. Species with exaggerated swellings had slightly higher expected female mating overlap after controlling for female number (Figure 3). In phylogenetic analysis, only four of the five possible contrasts in swelling state were available for this test due to insufficient information on the mating variables needed for

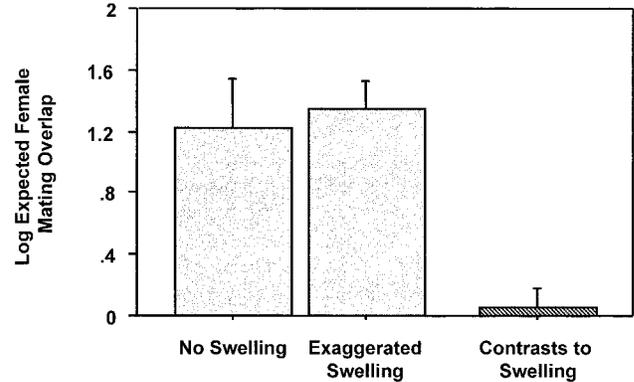


Figure 3

Expected female mating overlap and exaggerated sexual swellings. Bars show mean ($+1$ SE) expected female mating overlap, log transformed, for species with and without exaggerated sexual swellings (shaded bars) and for contrasts (hatched bar). Expected mating overlap was calculated based on Dunbar (1988, 2000) and Nunn (1999b), with several modifications that provide more accurate estimates (see Methods).

calculating expected overlap. Among these four contrasts, three were accompanied by positive changes in residual overlap, and the mean was slightly greater than zero (0.06; Figure 2), but this difference was not significant ($t = 0.50$, $p = .32$).

We repeated analyses after controlling for the number of males because this is the putative source of female competition under the reliable indicator hypothesis. Mean residual expected overlap was negative in species with exaggerated swellings (-0.047), but it was positive in those species without exaggerated swellings (0.10). This pattern was therefore opposite to predictions of the reliable indicator hypothesis. In phylogenetic analysis, three of the four contrasts were negative ($t = -1.29$, $p = .86$).

Does swelling size honestly indicate female quality?

For exaggerated swellings to act as honest signals of quality, they must be costly, which is supported by several lines of evidence (Dixon, 1998; Nunn 1999b; Wrangham, 1993). First, exaggerated swellings lead to increased male attention, thus increasing risk of injury through male aggression (Goodall, 1986; Zinner et al., 1994). Second, they increase vulnerability to blood-sucking insects (F. White, personal communication), which represents a significant cost to large mammals such as primates (Dudley and Milton, 1990; Hart, 1990; Rubenstein and Hohmann, 1989). Third, exaggerated swellings change a female's weight and center of gravity, possibly affecting the efficiency of arboreal locomotion (van Noordwijk M, personal communication). Finally, these changes, along with increased conspicuousness of the bright sexual skin, may increase vulnerability to predators (Dixon, 1998).

Other lines of evidence from intraspecific data, however, provide little support for the reliable indicator hypothesis. We examined three predictions that assess whether the size of a female's swelling indicates her quality as a mate. First, females that exhibit infertility, such as repeated cycling without conception, should have smaller swellings, or no swellings at all, if swelling size reliably indicates female quality. A search of the literature revealed that in many cases where females failed to conceive, they had large, sometimes continuous swellings (Table 1). These data may be biased toward finding a pattern that is contrary to the reliable indicator hypothesis because researchers are probably more likely to note larger than smaller swellings, particularly in females that cycle repeatedly with-

Table 1
Repeated cycling

Species (reference)	Description
<i>Papio cynocephalus</i> (W); (Hausfater, 1975)	Female Lulu cycled throughout the 14-month study and developed the largest swelling of all females, but failed to conceive despite normal mating behavior.
<i>Pan troglodytes</i> (W); (Goodall, 1986)	Female Gigi cycled, produced swellings, and menstruated regularly for 12 years, but failed to conceive, despite having large swellings and regular matings.
<i>Papio cynocephalus</i> (W); (Wasser, 1983)	Alpha female had largest swelling and failed to conceive for at least 6 months.
<i>Macaca fascicularis</i> (W); (van Noordwijk M and van Schaik CP, unpublished)	Female Mager in Kb group had unusually large swellings for her age and did not conceive for 3 years.
<i>Pan troglodytes</i> (C); (de Waal, 1982; Muller K, personal communication)	Female Puist, and later Moniek, never conceived but nonetheless produced regular and very large swellings.
<i>Papio hamadryas</i> (C); (Pfeiffer et al., 1985)	One mature female had no conceptions over an 18 month period, but she exhibited a permanent, and large, sexual swelling.

out conceiving. Further research could easily produce refined tests of these predictions, as frequencies of infertile females in wild groups are thought to exceed 10% (Anderson, 1986).

Second, the largest swellings should be found in the female age class characterized by peak fertility. A comprehensive comparative study by Anderson (1986) showed that in the 15 species for which information is available, males prefer older or multiparous females over adolescent or primiparous females. Furthermore, this preference is linked to age correlates of female reproductive success: in all 24 species for which information is available, older females have higher reproductive success, as based on a variety of correlates of reproductive success, including age-specific fertility tables for six of the species (Anderson, 1986; see also Altmann et al., 1988; Fairbanks and McGuire, 1984). With these facts in mind, the reliable indicator hypothesis predicts that swellings of older, multiparous females should be larger if they honestly signal female quality. We can rely on data compiled by Anderson and Bielert (1994) to examine this prediction (see additional examples in Table 2). Contrary to the reliable indicator hypothesis, adolescent females had larger swellings (or more intense perineal coloration) than adult females in 11 species of catarrhines in the Anderson and Bielert (1994) data set. In eight of these species, females are classified as having exaggerated sexual swellings, but in some, such as the *fascicularis* group of macaques, mainly adolescents have the exaggerated trait. The best evidence comes from studies that measured both swelling size and fecundity. For example, Strum and Western (1982) found that adolescent female olive baboons (*Papio anubis*)

had larger swellings but were less fecund. In the same species, however, Scott (1984) found that consortships, an indication of male interest, were of shorter duration and required larger swellings on the part of young females. Thus, not all studies concur in their findings, but numerous patterns run counter to the reliable indicator hypothesis and require explanation.

Finally, the evidence suggests that exaggerated swellings deceptively manipulate male behavior, which also contradicts the hypothesis because this supposedly honest signal does not reliably indicate female quality or even ovulation. In addition to adolescent exaggeration, for example, females of many of these species also exhibit swellings during pregnancy, when fertilization is impossible. Although some studies have suggested that swellings during pregnancy are less attractive to males than swellings during potentially fertile cycles (Gust, 1994), in other studies, males were found to initiate more matings with pregnant than with cycling females (Wallis, 1982). Other forms of potential manipulation in the form of situation-dependent swellings have been documented. For example, females often exhibit swellings after male takeovers in hamadryas baboons (Colmenares and Gomendio, 1988; Zinner and Deschner, 2000). Hence, the above observations lead us to reject the central assumption that exaggerated swellings are honest, which critically weakens the hypothesis.

DISCUSSION

The comparative tests failed to support the hypothesis that exaggerated sexual swellings function in female intrasexual

Table 2
Adolescent exaggeration (supplementing Anderson and Bielert, 1994)

Species (reference)	Description
<i>Macaca fascicularis</i> (C); (Nawar and Hafez, 1972)	Only adolescents ($n = 1$) show cyclical changes in sex skin.
<i>Macaca maurus</i> (W); (Matsumura, 1993)	Adolescents are swollen for a longer duration of ovulatory cycle but have more irregular cycles (suggesting infertility).
<i>Macaca mulatta</i> (W); (Kaufmann, 1965)	Sex skin changes more evident in young females.
<i>Pan paniscus</i> (W); (Furuichi, 1987, 1992)	Adolescent females have irregular swellings, but frequently reach maximum swelling size and firmness.
<i>Pan paniscus</i> (C); (Dahl, 1986)	Adolescents had longer pre- and swelling phases, as did females in their first cycles following pregnancy.
<i>Pan troglodytes</i> (C,W); (Wallis and Lemmon, 1986; Wallis and Goodall, 1993)	During pregnancy, younger females exhibit swellings for a greater proportion of time than older females.
<i>Theropithecus gelada</i> (W); (Dunbar and Dunbar, 1974)	Only juvenile females have swollen chests, although coloration of sex skin is not as intense as in adults.

W, wild or semi-wild; C, captive.

competition for mates. Exaggerated swellings were not associated with increased female mating competition, as measured using the adult sex ratio, residual canine size, and expected female mating overlap. These comparative tests relied on assumptions regarding the source of female competition, but we have no evidence that other sources of competition, such as resources, vary in a way that would bias or obscure the results. In addition, the results are from independent contrasts and so may be affected by errors in phylogenetic topology and branch lengths. In nonphylogenetic tests, however, the trends remained opposite to predictions in most cases; thus, alternative phylogenies, when they become available, are unlikely to change the conclusions. Finally, a review of the published literature showed that although exaggerated sexual swellings may be costly, the least fertile females, and those least likely to raise offspring to maturity, often have the largest swellings.

The predictions may have been unsupported due to low statistical power in our comparisons, as these tests were based on a small number of contrasts (Thomas and Juanes, 1996). Several factors make this explanation unlikely, including our use of one-tailed tests that increase power (Cohen, 1988; Sokal and Rohlf, 1995) and the fact that five of the six comparative results were opposite to predictions of the hypothesis. Nonetheless, we calculated statistical power. With five contrasts, a significance criterion of 0.05, and a medium effect size ($= 0.25$; see Cohen, 1988; Erdfelder et al., 1996), the statistical power of the one-tailed t tests was indeed low ($= 0.12$, calculated using G*Power, version 2.0; see Erdfelder et al., 1996). Power considerations are most relevant to the one test that was in the predicted direction (test 3, without correcting for the number of males; see Cohen, 1988). We therefore computed the ratio of Type 1 and 2 error rates that would achieve significance (i.e., α and β , where power $= 1 - \beta$). For this compromise power analysis (Erdfelder et al., 1996) of four contrasts, significance would be attained if $\beta = 1.48\alpha$ (effect size $= 0.25$, $n = 4$ contrasts, one tailed). The high probability of rejecting a true null hypothesis in this case, however, does not provide very convincing support ($p < .33$), especially in view of the other results that run counter to predictions.

Another issue involves the predictions that we used to test the reliable indicator hypothesis. Our measures of female mating competition make the best use of the available data, but they are indirect. Moreover, it might be argued that we tested a broader interpretation of the hypothesis than was originally proposed by Pagel (1994a). For example, we included single-male groups in our analysis, but Pagel (1994a) argued that competition in such groups is not relevant to the hypothesis because the harem male, freed from direct competition for access to females, “will always mate with each of the females” (p. 1338–1339), regardless of variation in their intrinsic quality.

Our decision to test a broader interpretation of the hypothesis was based on the biology of the species involved. In the first place, it may be incorrect to argue that harem males face less competition (Pagel, 1994a), as extragroup males represent a nearly constant threat to the resident male’s control through attempted takeovers and extrapair copulations. Moreover, even in single-male groups, males make decisions to mate with a female, particularly when more than one female is potentially fertile. Thus, while harem males may experience lower costs in direct competition within the group, they still face opportunity costs when mating with a female, including vigilance directed toward extragroup male competitors.

A related consideration involves female competition and whether (1) it is greater in single-male groups, which is an empirical question and (2) whether such an increase would

fall within the formulation of the reliable indicator hypothesis, which is a theoretical question and relevant to the issue of including these species in the tests. For the empirical question, female mating competition is better documented in single-male groups (gelada baboons: Dunbar, 1980; lion-tailed macaques, *Macaca silenus*: Kumar, 1987; hanuman langurs, *Presbytis entellus*: Sommer, 1989; captive hamadryas baboons: Zinner et al., 1994; captive rhesus macaques in single male groups, *Macaca mulatta*: Zumppe and Michael, 1985), although comparable data are needed to make meaningful comparisons to multimale groups (e.g., baboons, *Papio cynocephalus*: Wasser, 1983). In terms of theory, the model underlying the reliable indicator hypothesis first examines competition among males and then applies this model to females to show that they should also compete for mates (see Pagel, 1994a). As noted by Pagel (1994a, 1995), male competition in this model does not depend on female number; thus, applying the same logic to females, competition among females for mates should exist in both single-male and multimale groups. Females in single-male groups may not compete for the best male because there is generally only one male available, but they may compete for sperm (Radwan, 1995; Sommer, 1989; Sommer et al., 1992). Based on these considerations, there are good reasons to expect swellings to occur in species with single-male groups under the reliable indicator hypothesis, but they are found almost exclusively in species characterized by multimale groups.

The reliable indicator hypothesis: a reevaluation

By focusing on the size of the swelling and by framing this issue quantitatively, Pagel (1994a) identified serious shortcomings with the best male and many male hypotheses. In particular, his ESS model showed that swelling size under the best male hypothesis should not incite greater male-male competition. Overall, Pagel’s (1994a) reliable indicator hypothesis is plausible; it identifies an overlooked hypothesis for this exaggerated trait, and it draws attention to the possibility of a sex-role reversal regarding primate mate choice.

The analyses presented here are only a first step toward testing the reliable indicator hypothesis comparatively, and they rely on a number of assumptions. Our results therefore highlight the need for additional tests, including experiments, but several factors suggest that the reliable indicator hypothesis is unlikely to be the primary explanation for the evolution of exaggerated sexual swellings in primates. First, in the permanent social groups that characterize most primates, males have information on a female’s quality in addition to the size of her swelling. For example, males will have information on a female’s quality by observing how many immature offspring she has, by noting her age (e.g., through nipple condition or body size), or by identifying the amount of competition she generates among longer-term residents. Thus, costly quality indicators should be less common in species with long-term individualized relationships, such as primates, and only common in species without such relationships, if females vary in quality, and when males accrue nontrivial costs from each mating (e.g., Polak et al., 1998).

Second, a female’s capacity to access resources, and thus to generate a daily energy surplus, may be more important than her current condition (i.e., the state of her energy stores). This capacity may be a function of experience and dominance rank, which are not always translated into larger swelling size (Anderson and Bielert, 1994). Thus, females with relatively short interbirth intervals and many successfully weaned offspring may be in relatively poor physical condition and also support small swellings, yet these are the females that generate the greatest competition among males (van Noordwijk,

1985). Such a phenomenon would explain why the least fertile females often have the largest swellings.

Third, female reproductive competition in primates may involve resources rather than mates (Sommer, 1989; cf. Dunbar and Sharman, 1983; Hemelrijk and Luteijn, 1998). For example, the amount of female competition in baboons was found to increase with the number of females that were mating (Wasser, 1983), which at first would seem to support the reliable indicator hypothesis. A closer look reduces that support, however, because the second most attacked class of females were those in the first trimester of pregnancy, and they were most likely to be attacked by estrous females or those in later stages of pregnancy. Thus, it appears that in baboons, which do not generally exhibit postconception matings (van Schaik et al., 1999), female competition involves the timing of reproduction with respect to lactation and weaning resources.

The final issue concerns spite, which is an important feature of the reliable indicator hypothesis. Although the spitefulness of exaggerated swellings is controversial (Radwan, 1995), exaggerated swellings may reduce the probability that other females conceive if the signal is maintained longer than needed to signal ovulation and if males have limited sperm supplies. The circumstantial evidence for sperm depletion, however, comes from species without exaggerated swellings: single-male groups, some of which are large (e.g., Sommer, 1989; Sommer et al., 1992), where sperm depletion is expected (Radwan, 1995; Small, 1988). In captive hamadryas baboons, for example, females that cycle more synchronously have a lower probability of conception (Zinner et al., 1994). There are also theoretical objections to exaggerated swellings as spiteful because such traits can spread only if they reduce the actor's fitness less than the recipient's (Knowlton and Parker, 1979; see also Radwan, 1995). This condition is more difficult when the spiteful signal is very costly, as is likely the case with exaggerated swellings (Dixon, 1998; Nunn, 1999b). Finally, there is no statistical association between patterns of exaggerated swellings and female dispersal from their natal groups ($p = .49$, concentrated changes test; Maddison, 1990). Thus, the high relatedness of females in many catarrhines make the conditions for the spread of spite more stringent, as females would often be spiteful to their kin.

Future directions

As with other comparative studies, the tests presented here are correlational and cannot deal with all possible confounding variables, including alternative sources of female competition. In addition, our tests have low statistical power, although most patterns were opposite to predictions. One way to increase the power is to use quantitative information on swelling size, as continuous variables generally provide higher statistical power in comparative tests (Garland et al., 1993; Purvis and Rambaut, 1995; Nunn and Barton, in press). Such quantitative information, however, is not yet available for a sufficient number of species.

In addition to comparative tests, observational and experimental tests of the reliable indicator hypothesis are needed, both in the field and laboratory. One issue involves documenting the proximate link between female quality and the expression of exaggerated sexual swellings (e.g., Mori et al., 1997; Wallis, 1995). In addition, swelling size may indicate aspects of a female's cycle relative to other cycles in that same female, rather than the intrinsic quality of one female relative to other females. For example, estrogens influence swelling size (e.g., Dixon, 1983, 1998); thus, swellings may signal the likelihood that the cycle is ovulatory (i.e., the "competence" of a particular cycle; Emery MA, Whitten PL, personal com-

munication). This means that in addition to tests among females, experiments should disentangle the effects of resource availability on swelling size and how swelling size might signal fertility among cycles within a particular female.

Female mating synchrony is particularly relevant for testing the reliable indicator hypothesis with behavioral data (Radwan, 1995). Although the ESS model provided by Pagel (1994a) does not rely on synchrony of mating for its main conclusions, as clarified by Pagel (1995), male discrimination among females becomes more important when synchrony exists (this point was originally noted by Pagel, 1994a). Predictions based on synchrony may also distinguish between the reliable indicator and other hypotheses, as breeding seasonality, which is expected to lead to greater mating synchrony (Nunn, 1999a; Ridley, 1986), is associated with losses of exaggerated swellings in species with multimale mating systems (van Schaik et al., 1999). Thus, cases of synchrony, either occurring naturally in the wild or experimentally induced in captivity (Zumpe and Michael, 1989), may provide critical tests of the hypothesis.

If the reliable indicator hypothesis cannot account for the evolution of exaggerated sexual swellings, then what hypothesis is left? Nunn (1999b) showed that aspects of some previous hypotheses could be combined into a graded signal hypothesis (see also Noë and Sluiter, 1990; van Schaik et al., 1999). This hypothesis operates through a novel mechanism by proposing that exaggerated swellings represent the probability of ovulation for an individual female, with a higher probability indicated by a larger swelling. In this way, females can alter the costs and benefits of male mate guarding, so that dominant males guard females only when their swellings achieve some threshold size and coloration. Females are thus able to confuse paternity by mating with multiple males below this threshold, when ovulation is less likely but still possible, because the threshold is expected to vary among males according to their ability to defend a female. Nunn (1999b) provides a mechanism for how such thresholds might operate, although this mechanism has yet to be modeled mathematically. Important issues for future research include tests of how closely swelling size indicates the probability of ovulation (e.g., Wildt et al., 1977), documentation of the benefits of biasing versus confusing paternity in wild primate groups, and consideration of other sensory modalities exhibiting gradations that are correlated with fertility (e.g., copulatory calls; O'Connell and Cowlshaw, 1994).

In conclusion, our results do not support the reliable signal hypothesis as the origin and main benefit of exaggerated sexual swellings in primates. We cannot rule out, however, the potential for confounding variables and the possibility that swelling size secondarily indicates aspects of female quality. Existing data suggest that females obtain multiple benefits from exaggerated sexual swellings (Nunn, 1999b). Thus, hypotheses focusing on a single benefit are unlikely to explain all aspects of this exaggerated trait.

We thank M. Emery, K. Hodges, P. Kappeler, S. Patek, M. van Noordwijk, D. Westneat, and two anonymous reviewers for helpful discussion or comments on the manuscript. During the writing of this paper, C.L.N. was supported by a National Science Foundation Postdoctoral Research Fellowship in Biological Informatics and D.Z. was supported by a Deutsche Forschungsgemeinschaft (DFG) grant (Ga342/7-1). C.P.v.S. acknowledges the support of a Forschungspreis of the Alexander von Humboldt Foundation.

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