

last argument was intuitively advanced by Aristotle⁹). The discrepancy between the predicted and actual gains in performance can be ascribed to the presence *in vivo* of elastic structures (tendons and ligaments): these can store more elastic energy because of the greater ground-reaction force, which is used successively to boost the power amplification generated by the muscle-tendon complex.

The mass range that enables all of these effects to be optimized (about 2–9 kg) corresponds closely to the actual size range of archaeological halteres specimens (Fig. 1, bottom)^{1,10}, suggesting that athletes in ancient times had worked this out for themselves.

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COMMUNICATIONS ARISING

Evolutionary biology

Significance of primate sexual swellings

Exaggerated sexual signals are likely to be shaped by sexual selection, but few studies have examined signal evolution in females. Domb and Pagel¹ have presented support for the hypothesis that individual differences in exaggerated sexual swellings in female primates are reliable indicators of differences in female quality². However, our re-analysis of their data casts doubt on their conclusions.

In support of the sexual-selection hypothesis that swellings reliably signal enduring individual differences in female quality, Domb and Pagel¹ report that the vertical length of a female baboon's sexual swelling at maximum turgescence is correlated with female fitness. However, they did not demonstrate that variation in fertility between females is reflected in swelling size independently of other variables that might be used by males to predict reproductive output among females.

Female body height explains a significant portion of the variation in swelling size in Domb and Pagel's data³. In particular, taller females had longer swellings ($r^2 = 0.27$, $P = 0.02$, $n = 20$). In addition, the authors

pooled data from five baboon groups³. Their study groups show significant differences in swelling length ($F_{4,17} = 2.96$, $P = 0.05$), in age at first conception ($F_{4,24} = 17.82$, $P < 0.001$) and in number of offspring surviving per year ($F_{4,24} = 3.93$, $P = 0.014$). The groups also differed substantially in food availability³, which markedly affects female fertility⁴, and in adult sex ratio (1.3–2.2 females per male³), which might influence the male competitive regime⁵. Females in groups with higher food quality have 'longer' swellings and mature earlier. In these same groups, adult sex ratio is biased towards males, so males experience more competition per female, particularly when only one female is sexually active.

By pooling across groups, Domb and Pagel make the implicit assumption that a male can choose between females in different groups in the same manner that he chooses between females of the group in which he lives. This assumption is not supported by available data on dispersal^{6–8}. The authors controlled for age and rank in their analysis, but when female height and group membership are also controlled using their data, swelling length is no longer a significant predictor of female quality (Table 1).

The authors claim that males use the size of the sexual swelling to determine mating effort, but they did not control for adult sex

ratio — males may expend more effort simply because they have more competitors. They also analysed only the periods when a single female was receptive, excluding periods when more than one female had a swelling³. However, periods of oestrous synchrony are the best time to test whether males prefer to mate with females with larger swellings.

What do the sexual swellings of female primates indicate? We present three hypotheses that are not mutually exclusive and include that tested by Domb and Pagel. In the first, swellings are probabilistic signals of the timing of ovulation⁹; although they cannot pinpoint it¹⁰, the highest probability of ovulation is at peak swelling, making swelling size a within-cycle indicator of the probability of conception⁹. In the second, swelling size signals cycle-to-cycle variability in the probability that a female will conceive and so is a within-female indicator of the probability of conception across cycles. In the third, swelling size signals enduring differences between females in their individual ability to conceive and raise offspring, as tested by Domb and Pagel¹, and is an indicator of consistent differences in quality between females².

The within-cycle hypothesis is supported by comparative data³. To support the between-females hypothesis and distinguish it from the within-female hypothesis, three lines of evidence are needed: differences between females in swelling size are enduring characteristics of individuals; variation between females in swelling size explains variation in fertility independently of other factors; and males prefer to mate with females with larger swellings.

However, none of this evidence has been supplied by Domb and Pagel. They have few repeated measures of female swelling size^{1,3}, precluding an analysis of whether between-female differences are consistent. Even in their small sample of repeated measures, the coefficient of variation of swelling length ranged up to 11%, which is as large as between females (11.4%; ref. 3).

We suggest that the correlation found by Domb and Pagel between swelling length and female fitness might not be due to males using individual differences in sexual swellings as an indicator of female quality, but that instead it could result from confounding variables that are correlated with swelling size. Additional information is required before alternative explanations can be ruled out. We contend that there remains no convincing empirical support for the reliable-indicator hypothesis to account for this striking signal in some primates.

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Table 1 Correlations between female fitness and characters

Female character	r_{length}	r_{age}	r_{rank}	r_{height}	F_{group}
Age at first conception	-0.53	0.04	0.46	0.21	6.40*
No. of offspring per year	0.39	0.26	0.24	0.11	1.27
No. of surviving offspring per year	0.46	0.48	-0.59	0.05	0.45
Proportion of offspring surviving	0.34	0.45	-0.68*	0.03	0.53
No. of offspring per year surviving ≥ 6 months†	0.25	0.29	-0.59	-0.27	2.29
Proportion of offspring per year surviving ≥ 6 months†	-0.09	0.07	-0.64*	-0.32	3.19

Correlations are shown between female fitness measurements and female characters in analyses that control for age, rank, female body size and group membership (General Regression Model, Statistica 6.0, Statsoft 2001).

Subscripted r values: length, length of swelling (swelling size); age, female age; rank, rank of family; height, height of female (body size); group, female's group.

* $P < 0.05$, two-tailed. †Analysed in ref. 3 but not included in ref. 1.

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Domb and Pagel reply — Zinner *et al.* question our finding that the size of a female wild baboon's sexual swellings predicts her lifetime reproductive success, suggesting that we should have controlled for female height in our analyses of female fitness. But the issue is not whether a female's fitness is independent of her height, but whether males draw inferences about her fitness from her sexual swelling, and do so independently of her height. Our results indicate that they do^{1,2}, supporting the hypothesis that sexual swellings advertise female reproductive value.

There is no record to suggest that male baboons, or male primates of any species, prefer taller females. We have shown that males base their costly mating behaviours on the female's swelling size and not on female height, age or social rank. The amount of aggression from other males that a male must tolerate to consort a female (the key male behavioural trait³) is positively correlated with the size of her swelling (swelling length), statistically controlling for the effects of female height, age and rank ($r=0.59$, $n=13$). By comparison, males do not receive more aggression for consorting taller females ($r=0.41$, $n=13$; $r=-0.069$, $n=13$, controlling for swelling size; $r=-0.25$ controlling for swelling size, female age and female family rank). Contrary to the claim by Zinner *et al.*, we did control for troop differences in these analyses^{1,2}, and in a way that normalized the variances, unlike their approach, which neglects this statistical assumption.

The suggestion of Zinner *et al.* that we should have analysed male interest in females' swellings when more than one female was in oestrus is based on a misinterpretation of our results. We followed an individual focal female, and not all oestrous females simultaneously. Focal females were

not selected according to their swelling size. If two females were simultaneously in their maximally swollen phase, male interest towards the focal female at any given period would be influenced by the presence of the other female; if the other female's swelling was larger than that of the focal female, then male interest in the focal female could be very low.

From our results, this could be incorrectly inferred as failing to support our hypothesis. The only way to untangle such effects is to investigate all possible pairs (triples and so on) of females, following males and females simultaneously. We therefore limited our tests to those situations in which a single female was in oestrus. This procedure automatically controls for other effects and tests the hypothesis.

Zinner *et al.* repeat an earlier idea^{3,4} that swellings are probabilistic signals of the timing of ovulation, which has since fallen out of favour^{5–7}. Nunn has pointed out⁸ that females in species with sexual swellings are attractive and mate for many more days than females in species without sexual swellings, casting further doubt on whether swellings accurately signal ovulation — in fact, they may function to confuse the timing of ovulation^{9,10}. We tested the second hypothesis of Zinner *et al.* but have found no support for it². This leaves the third hypothesis (ours): that swelling size signals enduring differences between females in their ability to conceive and raise offspring.

The contention of Zinner *et al.* that the reliable-indicator hypothesis is unsupported is therefore based on a misunderstanding of this hypothesis and of our results. Males endure higher costs to mate with females with larger sexual swellings², but not with those that are taller¹. Females with larger sexual swellings also have higher lifetime reproductive success². Baboons provide little or no paternal care, and male–male aggression over females is costly. It is important for males to direct their mating efforts towards the females of the highest fitness, and male selectivity, in turn, makes it advantageous for females to advertise their quality. The size of the sexual swelling seems to do just this.

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COMMUNICATIONS ARISING

Magnetic properties

Parasitic ferromagnetism in a hexaboride?

Surprisingly for a compound with no magnetic element, Young *et al.*¹ have observed ferromagnetism in calcium hexaboride (CaB₆) doped with lanthanum (La) — the system has a ferromagnetic Curie temperature as high as 600 K, which is comparable to that of transition-metal ferromagnets such as iron (Fe). Here we show that high-temperature ferromagnetism in this CaB₆ system is not intrinsic but that it is instead due to alien phases of iron and boride.

Our CaB₆ and LaB₆ samples were synthesized in a solid-state reaction² using three types of crucible (BN, ZrO₂ and MgO). We used an acid cleaning procedure to remove magnetic ions, such as iron, from each sample. Samples were immersed in dilute HCl and the amount of soluble iron was measured using an inductively coupled plasma instrument (Varian). The magnetization of each sample was determined before and after acid treatment by using a magnetic balance magnetometer (Cahn).

Figure 1a shows the temperature dependence of the magnetization $M(T)$ of CaB₆ synthesized using a BN crucible. Before acid treatment, a ferromagnetic feature is evident at around 600 K and 1,000 K; however, this disappears after acid treatment. This disappearance may be due either to an inherent ferromagnetism in CaB₆, with the surface state being altered by acid treatment, or to the removal from CaB₆ of ferromagnetic atoms such as iron (M. Sato *et al.*, unpublished results) by the acid cleaning procedure. As iron is detected in the acid, the second possibility is more probable.

Figure 1b shows the corresponding $M(T)$ curves measured for LaB₆. The sample that was synthesized using a BN crucible exhibits diamagnetic and temperature-independent behaviour. However, the sample synthesized using a ZrO₂ crucible shows ferromagnetic behaviour similar to that evident in Fig. 1a. The Curie temperature of LaB₆ coincides with that of CaB₆. Again, acid treatment reduces the ferromagnetic magnetization (Fig. 1b, middle curve). These results indicate that the ferromagnetism is not inherent to CaB₆ but is