BEHAVIOR

Subtle, Secret Female Chimpanzees

Richard W. Wrangham

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Better on top. Among female chimpanzees, as among males, rank in the dominance hierarchy determines reproductive success.

Around three decades ago, the myth of the passive female primate was at its height, bolstered by two assumptions. All females were assumed to be uniformly successful at reproduction, because "all females breed." And social evolution was thought to proceed mainly by sexual selection, in which female-female relationships played a small part. So when female cercopithecines—animals such as baboons and macaques—were found to have highly variable levels of success in breeding, correlated with an individual's lifelong rank in the female hierarchy (her dominance status), the myth took a beating (*1*). From then on, female strategies were seen to have their own logic independent of males, and the ecology of female primate relationships became a vigorous research area that was crucial to understanding social evolution. But there were a few holdouts. In some well-studied species—the great apes, for example—there seemed to be little variance in female reproduction. Selection on female reproductive strategies appeared particularly weak in these species, allowing females to be considered as relatively passive pawns of male maneuvering. A new study on page 828 of this issue suggests that this view was simply the result of our ignorance (*2*) and that dominant female chimpanzees are indeed more reproductively successful than their lower-ranked associates.

Pusey, Williams, and Goodall (*2*) show that female chimpanzees in Gombe National Park, Tanzania, vary in their fitness and that fitness is correlated with dominance. If it seems odd that it has taken 37 years for Jane Goodall's Gombe studies to yield data on female reproductive success, consider that the chimpanzee social community contains only 10 to 15 females at any one time, with a mean interbirth interval of 5 years between surviving offspring. Half of the breeding females are immigrants, often of unknown age. Many females meet each other rarely, and even then clear-cut dominance interactions are infrequent, so that it can take several years for observers to detect the dominance relationship of any given pair. But by indexing the dominance ranking of the females over 2-year periods, Pusey *et al.* found that status correlated with at least three measures of fitness for breeding females. The effects are weak enough that if an infertile female is included in the data, the correlations disappear. Nevertheless the results gain strength from parallel correlations of female rank with infant production, infant survival, and offspring maturation rate. Indeed, the rate of production of weaned offspring by dominant females was almost twice as fast as by subordinate females, for whom it was 9 to 10 years.

The author is in the Department of Anthropology, Harvard University, Cambridge, MA 02138, USA. E-mail: wrangham@fas.harvard.edu

It is too early to say why rank has these effects, or why, if rank is as important as the new data suggest, females challenge each other so little. At Gombe, each mother's foraging is concentrated in her own core area within a larger community range defended by natal males. Escalated aggression among females is rare, but Pusey *et al.* speculate that such competition as there is, including infanticide by high-ranking females, may serve to acquire or retain the best core areas. What makes this reasonable is that in extreme circumstances female chimpanzees can compete as intensively as males. Thus captive females, meeting for the first time as adults, can use male-like behavioral strategies to gain rank, including opportunistic coalitions and frequent reconciliations (*3*). It may be that occasional female tactics, still seen too rarely for observers to assess their significance, stabilize ranks in adolescence and underwrite a lifetime of covert rivalry.

Covert behavior by female chimpanzees may be important in the sexual realm as well. In the most substantial analysis yet of chimpanzee paternity, Gagneux *et al.* (*4*) genotyped 13 infants in Taï National Park, Ivory Coast, together with their mothers and all the males of their community. Seven of the infants (54%) proved to have been fathered outside the community, a proportion far higher than anyone anticipated. In Taï, although females normally sleep together with the whole community, individual females sometimes disappear for days or weeks at a time. One of the cuckolding females was unseen by observers for only 1 day and another for 2 days during the months in which they conceived. Intense territorial competition means that male intrusions occur only in large subgroups, with fights but no matings, and are therefore rarely surreptitious. Gagneux *et al.* accordingly believe that extra-group paternity is a result of females visiting neighboring communities. The implication: Females are highly motivated to travel a long distance in search of the neighboring males.

Again, the small sample size implies caution. But even if the rate of extra-group paternity proves generally lower than 54%, a detectable rate of cuckoldry is remarkable and raises two significant points. First, female chimpanzees typically copulate several hundred times per baby, and only a small proportion of their copulations can occur with the neighbors. The data imply that females can select fertile times to cuckold their home-group males, suggesting they are choosing genes.

Second, the costs to females of sneaky matings appear substantial, implying that they bring major benefits. Females risk severe aggression not only from the neighboring males, but also from males who are known to kill infants fathered from other communities. Yet it is hard to imagine how the genetic benefits can be very high, because females mate multiply. This means that even when a fecund female chooses to mate in a neighboring community, she could not, so far as we know, select a specific male as father. The phenotypic benefit thought to account best for multiple mating in chimpanzees is infanticide prevention, on the theory that males forgo aggression toward infants of mothers with whom they remember mating (5). In the Taï case, mating with the neighbors could provide an insurance against future encounters with them when she is accompanied by her offspring.

But why should the female ever encounter the neighboring males in the future? Males have been dying at a high rate in the Taï study community. Could the cuckolding copulations be a preemptive safeguard against a take-over by neighbors? This might explain the curious observation that no neighboring females have been seen mating with the males of the study community. If so, the Gagneux *et al.* result may prove to be a rare phenomenon even among chimpanzees, specific to an unusual historical moment. Or is she insuring herself against a bad fruit-season in her own range, when she might need to eat in a neighboring range? That would suggest extra-group matings will be found commonly in other populations. Genetic data are being compiled quickly in other chimpanzee sites and should soon show whether high rates of extra-group paternity are common.

Until this year, no one suspected that female chimpanzees were so active in pursuit of their reproductive interests, yet they are probably doing still more than we appreciate. Chimpanzee and human social systems differ importantly in the characteristics of the female relationships, so there are certainly no direct analogies for human sociobiology. But these studies remind us that even where females interact rarely or subtly, female initiative can be a major force in the evolution of social systems. Selective impact doesn't necessarily correspond with social power.

References

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ISOTOPE FRACTIONATION

Vibrations Under Pressure

Simon M. F. Sheppard

Pressure is one of the key variables in Earth science, ranging from an extremely small fraction of 1 atm in the upper atmosphere (~1 Pa or ~10^{-5} atm) to probably more than 3.5×10^{11} Pa at Earth's center. However, unlike temperature, pressure has rarely played a role in the interpretations of the variations in the stable isotope ratios of elements such as hydrogen (D/H) and oxygen ($^{18}O/^{16}O$) that are observed in natural solids and fluids. Dreisner (1), on page 791 of this issue, and a number of recent studies (2–4) suggest that the pressure dependence of some isotope equilibrium fractionation factors may not be negligible. The results are important from both a theoretical and experimental point of view and for the applied geochemistry community.

Why has the effect of pressure on how isotopes partition themselves among coexisting phases been assumed to be negligible? A pressure effect implies that molar volume changes with isotopic substitution. The zero-point vibrational energy of a molecule plays a critical role in the calculation of isotopic effects based on spectroscopic data and statistical mechanics. Because the zero-point energy decreases to a small extent with increase in the heavier isotope content of the molecule, bond lengths of molecules decrease slightly with an increase in heavy isotope content. These effects are more extreme for hydrogen (as D substitutes for ^1H) than for all other elements, leading to estimated changes of molar volume of up to 0.3% between the pure ^1H and D isotopic end members (5). In natural systems, changes of molar volume for isotope exchange reactions are much smaller because typical isotopic fractionations between phases are only a few percent for hydrogen and a few tenths of a percent for oxygen. Without excluding pressure effects at pressures that reign in Earth's mantle (>1 GPa), the theoretical and experimental study of Clayton *et al.* (5) found no measurable evidence for a pressure effect between 0.05 and 2 GPa for oxygen isotopes in the calcium carbonate–water system.

Dreisner's contribution (1) shows that for isotopic exchange reactions involving a fluid such as water, changes of pressure can measurably influence the fractionation factor. The vibrational frequencies of gases, liquids and solids change with pressure and temperature (*P-T*). Unlike a solid, the density of a fluid varies more rapidly under certain *P-T* conditions than others. The region of strongest density variations is around the critical point of the fluid. This region is also where the vibrational frequencies of water change more rapidly. Thus, at constant temperature, a mineral-water fractionation factor changes with the density of the fluid. The effect for hydrogen isotopes can be large, whereas the maximum effect for oxygen is only slightly larger than the typical measurable precision.

In contrast to Dreisner, who studied a region of relatively low pressure, Polyakov and Kharlashina (2) and Gillet *et al.* (4) explore the pressure effect on the reduced partition coefficient to high pressures and temperatures (<3 GPa, <1200 K). Their calculations showed that the effect is significant for oxygen isotope fractionations, increasing with decreasing temperature for Polyakov and Kharlashina but increasing temperature for Gillet *et al.* These contradictions are probably related to differences in the assumptions.

Importantly, both Dreisner and Gillet *et al.* exploit a much broader experimental data base than has previously been the case, including high-pressure, high-temperature spectroscopic data. To calculate fractionation factors, suitable spectroscopic data have to be incorporated into a model. Since the landmark paper by Urey in 1947 (6) on the calculation of the thermodynamic properties of isotopic substances, the spectral data have been essentially restricted to both ambient *P-T* conditions and molecules with natural isotopic compositions. Except for gases, harmonic or quasi-harmonic assumptions are the rule. Usually little to no data on the shifts of the modes with variations of pressure, temperature, and isotopic composition are available. This information is essential for precise anharmonic calculations, which are needed to evaluate correctly the pressure effect. There may also be a lack of mode assignments.

Natural isotopic compositions for D/H and $^{18}O/^{16}O$ isotope ratios are about 1/7000 and 1/500, respectively. The heavy isotope is very much in the minority. The effect of isotopic substitution of the heavier isotope on the vibration frequencies is usually calculated from some model with its inherent un-

The author is in the Laboratoire de Science de la Terre, Ecole Normale Supérieure de Lyon, 69364 Lyon Cedex 07, France. E-mail: Simon.Sheppard@geologie.ens-lyon.fr