PERSPECTIVES: BEHAVIORAL ECOLOGY

Dividing Up the Kids

Walter D. Koenig and Joseph Haydock

Why is it that in a typical ant colony only a small number of females (the queens) reproduce, whereas in some communally breeding birds and mammals all females share reproduction? More than 20 years ago, Vehrencamp proposed a model to explain such variation (reproductive skew) in the sharing of reproduction (*1–4*). Vehrencamp's reproductive skew model—an extension of Hamilton's kin selection theory (*5*)—highlights the ecological and genetic factors that shape the evolution of animal societies. Testing reproductive skew theory in the field has proved difficult, particularly in vertebrates. However, this has not deterred Clutton-Brock *et al.* (*6*), who, on page 478 of this issue, present a 7-year field study of the reproductive habits of the meerkat (*Suricata suricatta*), a cooperative-breeding mongoose (see the figure). They provide the most extensive analysis yet of reproductive skew in a colony of mammals.

In her model, Vehrencamp began with the assumption that one individual (the dominant) controls the reproduction of all other individuals of the same sex (subordinates) in the group. She predicted that certain factors would enhance reproductive skew, that is, the control of the dominant over the subordinates. Such factors might include increases in: the benefits of group living, constraints on independent reproduction, and the relatedness of subordinates to the dominant. The reason for these not-entirely intuitive predictions is straightforward—with increases in each of these three factors, the fitness benefits of staying in the group become greater for subordinates. For example, if individuals are susceptible to predation when on their own, then subordinates are likely to benefit by remaining in the group even if the dominant does not allow them to reproduce. The dominant can then monopolize most of the group's reproductive capacity before subordinates decide to "throw in the towel," leave the group and attempt to breed on their own. In contrast, if the benefits of remaining in the group are few, subordinates may fare better if they leave the group, unless, of course, the dominant allows them to breed.

Despite the solid theoretical foundation of Vehrencamp's theory, testing of the model had to wait for nearly a decade until the arrival of molecular methods (such as DNA microsatellite analysis) that provided exact information on parentage. It was then primarily students of social insects who took up the torch (*7*), generating strong support for reproductive skew in several taxa, particularly leptothoracine ants and *Polistes* wasps (*8*, *9*). Concurrently, there was a stampede of theoretical papers that extended the ideas of the original model (*10–16*).

Enter Clutton-Brock *et al.* into the fracas with a careful evaluation of reproductive cooperation and conflict in a meerkat population in the Kalahari desert of southern Africa. Meerkats live in groups of up to 30 individuals that include a dominant female and male, which parent the majority of offspring. Some groups also contain subordinate females that are physiologically capable of reproduction but do not always breed.

A mongoose dominatrix? A dominant female meerkat with her litter. Contrary to the predictions of the optimal skew model, dominant female meerkats can only partially control the breeding habits of subordinate females.

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Applying Vehrencamp's skew model to meerkat colonies, one assumes that a dominant female completely controls group reproduction and that opportunities for subordinate reproduction are only given as inducements, or concessions, to entice disgruntled subordinates to remain in the group (*17*). The amount of the concession is adjusted in a way that maximizes the fitness of the dominant (personal reproduction plus the kin-selected benefits of breeding by genetically related subordinates). Thus, Vehrencamp's theory is also known as the "optimal skew" or "concessions" theory.

Intriguingly, the patterns of breeding behavior documented by Clutton-Brock *et al.* fail to support the key assumption of this optimal skew model. Subordinate female meerkats are more likely to breed when conditions are in their favor rather than when they are about to leave the group. For example, they are more likely to breed when they are bigger than (or the same age as) the dominant, or just after the dominant has been replaced by a new, less powerful female, or when the availability of an unrelated male in the group means that they can avoid the detrimental effects of inbreeding. Although these observations do not specifically reject the optimal skew model, they better support a limited control model in which dominants have only partial control over subordinate reproduction.

The predictions of Vehrencamp's model fare particularly poorly when applied to the results of the meerkat field study. Although dominants gain by retaining subordinates only if the group is small, Clutton-Brock and colleagues found that subordinate female meerkats bred in groups both large and small. Production of litters by subordinates did not dictate whether they assisted in raising the litters of the dominant female or whether they eventually left the group. Apparently, even if the dominant female does offer reproductive opportunities as a concession to keep subordinates from leaving, this "bribe" is an ineffective means of increasing her fitness through benefits associated with the presence of subordinates.

Importantly, optimal skew theory predicts that dominant females might sometimes force subordinates out of the group. One theoretical reason for this expulsion could be if subordinates attempt to breed more than is optimal for the dominant. Yet Clutton-Brock and colleagues found that expelled meerkats were often nonbreeders that did not breed for long periods even after returning to the group. This indicates that neither reproduction by subordinates nor concessions on the part of the dominant female are likely to be involved in subordinate evictions (*18*). Finally, those subordinates more closely related to the dominant female were more likely to breed, a finding that is contrary to the prediction of optimal skew theory.

These findings are hardly the end of reproductive skew theory. Clutton-Brock *et al.* may reject the optimal skew model, but, perhaps wisely, they avoid any attempt to

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choose among alternative "compromise" and "limited control" models in which reproductive sharing is determined by the competitive abilities of potential cobreeders. Some of these alternatives yield predictions very different from those offered by the optimal skew model. For example, "restraint" models postulate that subordinates grab the biggest share of the reproductive market possible, restrained only by the threat of expulsion from the group. This pattern is in direct contrast to the optimal skew model, which predicts that subordinates are given a minimum share in reproduction, consistent with the interests of the dominant female (*13*).

Deciding which of these models is correct is already difficult and is likely to become more so as the models increase in complexity to accommodate the findings of new field studies. Already, all possible patterns of reproductive partitioning within groups are compatible with one or more existing skew models (*19*). Even more of a challenge will be to go beyond the qualitative results of Clutton-Brock *et al.* and to quantitatively test alternative skew models. Such tests will be necessary if we are to fully grasp the reasons for the evolution of despotic and egalitarian vertebrate societies.

The meerkat study casts doubt on whether the success of optimal skew theory in explaining differing patterns of reproduction in highly skewed societies such as those of ants can be repeated in the more equitable societies of cooperatively breeding vertebrates. This perhaps should not be surprising. After all, it is in vertebrates that intersexual issues such as mate choice, sexual conflict, biparental care, extra-group matings, and incest avoidance are frequent complications. Given the importance of these factors to social evolution in vertebrate societies, a realistic model of the partitioning of reproductive activities in vertebrates will almost certainly have to take into account interactions between, as well as within, the sexes.

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PERSPECTIVES: NANOMATERIALS

Stretching the Mold

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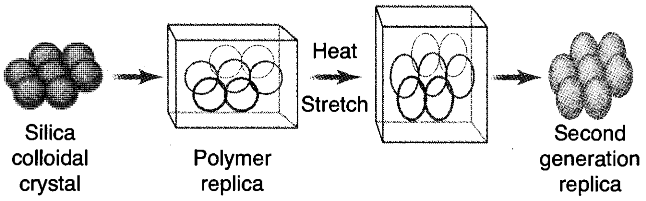
Replica molding has long been used to make macroscopic objects—such as bronze statues, plastic dolls, and compact disks—from a mold or master. In this method, the object is formed by injection or chemical synthesis of one material inside the void spaces of another. With the proper choice of materials, this process can faithfully transfer the shape of the mold to the replica even at length scales of a few nanometers. A recent example of chemical replication that pushes the limits of pattern transfer is the successful synthesis of a carbon replica of zeolite Y, a microporous aluminosilicate. The largest pores in the parent material, just 1.3 nm in diameter, are connected by 0.7-nm-wide necks—about the height of two stacked graphite sheets. The carbon is introduced by impregnating the zeolite with furfuryl alcohol, which is first polymerized and then pyrolized. The remaining void space is filled by chemical vapor deposition of carbon from propylene gas. The pure carbon replica, obtained by etching away the aluminosilicate mold with hydrofluoric acid, shows short-range ordering with the same unit cell as the original zeolite (*1*).



The "lost wax" two-stage replication process. A colloidal crystal of nanoscale silica spheres is converted to a polymer replica, which is then stretched or compressed and filled with a second material. The polymer mold can be removed to give identical free-standing nanoparticles of a wide variety of different materials (*2*).

Recently, replica molding has come into its own as a technique for making nanoparticles in shapes or porous forms that are not accessible by other means. On p. 453 of this issue, Jiang *et al.* describe a two-step process (see the figure) that uses silica (SiO_2) spheres to make a porous plastic replica, which in turn serves as the mold for making solid or hollow particles of a different material—a metal, a metal oxide, a semiconductor, or another polymer (*2*). The plastic mold can be stretched like taffy before it is filled with the second material, resulting in egg-shaped or oblate particles (*3*). Silica is one of the very few materials that allows the facile synthesis of collections of uniform spheres with continuously variable diameters between 30 and 1200 nm. It is thus an ideal master from which to begin the synthesis of spherical and "stretched" nanoparticles of other materials.

The uniform silica spheres used by Jiang *et al.* (*2*) pack into colloidal crystals when a suspension of them is evaporated onto a microscope slide. The spheres are packed tightly just like a stack of cannonballs or a crystal of argon atoms; each sphere has 12 nearest neighbors and together they fill 74% of space. Because the size of the silica spheres is on the order of the wavelength of visible light, these colloidal crystals opalesce; that is, they show diffraction colors in transmitted or reflected light. Colloidal crystals are potentially interesting as photonic band gap materials, which diffract light in much the same way as crystals of atoms diffract electrons (*4*). Given the right crystal structure and a sufficient contrast in refractive index between the nanoparticles and the intervening spaces, light with certain wavelengths cannot propagate in the crystal. Line defects in such crystals should act as low-loss waveguides that can send light around sharp corners, and point defects may be used as laser cavities. The problem is that the two close-packed "cannonball" structures—face-centered cubic and random hexagonal stacking—do not give complete band gaps: Light can leak through the solid along certain crystal directions (*5*). The lowering of symmetry caused by stretching to a lattice of ellipsoids and the increase in contrast afforded by replacing silica with higher index materials could lead to a full photonic band gap in replica colloidal crystals such as those fabricated by Jiang *et al.* (*2*).

There are other compelling reasons for

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