

Group sex in the acorn woodpecker:

who comes out on top, and why

Walter Koenig and Joey Haydock

University of California, Berkeley and Gonzaga University, USA

Family-based societies are frequently faced with the conundrum of balancing the competing reproductive interests of closely related group members. How this is accomplished is the subject of considerable current research, and is epitomised in the complexities of a bizarre species of woodpecker, common in California's oak woodlands.

Although many aspects of animal behaviour are foreign to us as humans, one that is not is the propensity for most social species to live together in kin (family) groups. Families may be small and include only a pair of breeders and a small number of their offspring, or large and include individuals from more than two generations. In the latter, some individuals may compete among themselves for reproductive opportunities within, and in some cases outside of, the group, often with the single (but surprisingly important) proviso of avoiding incest (Pusey and Wolf, 1996). Such complexities make delineating 'an evolutionary theory of the family' a particularly engaging exercise (Emlen, 1995).

One of the more intriguing aspects of families is how they resolve the two inherently contradictory selective forces of close kinship fostering cooperation and altruism, and limiting reproductive opportunities that can lead to competition and conflict. Over 20 years ago, Vehrencamp (1979) first explored this problem from the viewpoint of two (or more) individuals of the same sex acting to (selfishly) maximise their own fitness. Under what conditions should they work together rather than split up? If they stay together, should they divide up the group's reproduction equally (an egalitarian, low-skew society) or should one individual monopolise all the reproduction (a dominance-based, high-skew society)? And finally, how are these decisions affected by the ecological and social factors that vary from year to year or from society to society?

Not all of the answers to these questions are intuitively obvious. Unfortunately, most turned out to be virtually impossible to test, at least at the time, primarily because the techniques available to determine parentage were relatively primitive. Now, with advances in molecular techniques, particularly DNA 'fingerprinting' (Schmidtke and Krawczak, 1999), it's finally possible to obtain good data on reproductive partitioning within social groups and to test the assumptions and predictions of 'optimal skew' theory with the goal of understanding this basic dilemma of family life.

Dividing up the kids

Optimal skew theory starts with the assumption that one individual, the dominant, controls all the reproduction of his or her sex within the group. Assuming this to be true, the question then becomes, 'Are there conditions by which it would not be in the dominant's best interest to monopolise reproduction and parent all the group's offspring?'

The answer appears to be yes, primarily because optimal skew theory also assumes that the subordinate can leave the group if it is in his or her best interest to do so. If there are fitness advantages to living in a group, it is likely to be advantageous to the dominant to make it worthwhile for the subordinate to stay. In order to do this, the dominant may have to offer a 'staying incentive' to the subordinate in the form of reproduction. Expanding on kin selection and



Caption to come

inclusive fitness theory (Hamilton, 1964), optimal skew theory goes on to quantitatively predict the degree to which the dominant should concede reproduction to a subordinate and the ecological conditions under which such concessions should be big (low skew) or small (high skew). Because of the nature of this potential interaction between cobreeders, optimal skew theory is also known as 'concessions' theory. Due to its analogy to a business deal between two individuals, it is also known as a 'transactional' model of reproductive partitioning.

The kinds of ecological factors that influence reproductive sharing under the assumptions of optimal skew theory include the relative benefits of living in groups compared to being on one's own, the difficulty of securing a breeding position on one's own, and the genetic relatedness between cobreeders. In general, the greater the relative fitness benefits of being in a group, the more the dominant can monopolise reproduction (and thus the greater the expected reproductive skew) before the subordinate should 'throw in the towel' and leave the group. This means that we should expect increased skew when the benefits of group living are greater or when the difficulties of obtaining an independent breeding position are greater, since the latter would enhance the relative benefit of remaining in a group. We would also expect greater skew in societies consisting of closely related cobreeders than in societies in which cobreeders are unrelated (Keller and Reeve, 1994). This somewhat counterintuitive prediction stems from the fact that a nonbreeding subordinate gains inclusive fitness benefits only if related to the dominant breeder, and thus an unrelated cobreeder must be offered greater concessions, in the form of reproduction, in order to remain in the group than a related cobreeder.

Work on social insects has provided impressive support

for several of these predictions (Reeve *et al.*, 2000; Reeve and Kelller, 2001). However, results from vertebrate societies have been mixed, leading to questions as to the generality of optimal skew theory and the degree to which more complex models incorporating interactions between males and females are needed (Clutton-Brock *et al.*, 2001; Haydock and Koenig, 2002).

A model system: the acorn woodpecker *Melanerpes formicivorus*

Acorn woodpeckers are common inhabitants of oak forests throughout southwestern United States, Mexico, and Central America. However, they are particularly common and conspicuous in California, where ten species of acorn-producing tree (all but one are oaks of the genus *Quercus*) and a panoply of shrub oaks dominate millions of hectares. Throughout these regions, acorn woodpeckers are noisy and conspicuous inhabitants, well known for their habit of storing acorns, often by the thousands, in individually drilled holes placed in special storage trees or granaries (Title Figure). These granaries, as much as the acorns the birds store in them and the oaks that produce the acorns, are critical resources essential to the life style of the birds. First, granaries containing stored acorns are needed in order to allow the birds to remain resident throughout the cool, wet California winters; and, second, access to stored acorns is important, both to survival during the winter and to successful reproduction the following spring. At least for the woodpeckers, granaries are high-priced real estate, basic to the success and maintenance of their families.

Granaries are accumulated by generations of birds, each drilling a few holes every year, and are so critically important to survival and reproduction that they have led to the evolution of one of the most complicated social systems of any vertebrate. Offspring, often unable to find an unused granary, and thus obtain a breeding position elsewhere in the population, frequently delay dispersal and remain as 'helpers' in their natal group for many years. Meanwhile, sets of siblings compete as unisexual sibling units in chaotic 'power struggles' for the right to fill reproductive openings, or vacancies, outside their natal group, with the winning birds then forming a coalition of cobreeders who vie for parentage among themselves. Offspring do not breed within their natal groups unless their parent and closely-related cobreeders of the opposite sex have died and been replaced by unrelated birds from outside of the group, and thus incest is avoided – despite groups being composed of close relatives (Koenig *et al.*, 1998).

Nonetheless, groups frequently contain multiple cobreeders of both sexes and thus exhibit the rare mating system known as 'polygynandry'. Within polygynandrous groups, cobreeder males (usually brothers or a father and son) compete for mating opportunities and cobreeder females (usually sisters of a mother and daughter) lay their eggs communally in the same nest cavity (Koenig *et al.*, 1995).

Testing optimal skew theory

At Hastings Reservation in central coastal California, where we have been studying a colour-banded population of acorn woodpeckers since 1971, 20% of groups contain two (rarely three) joint-nesting females and nearly half of groups contain two and sometimes as many as six cobreeder males (Haydock *et al.*, 2001). This sets the stage for testing optimal skew theory in a species where more than a single male and female frequently cobreed within

the same social unit. And, in a few cases, the theory appears to be successful.

For example, the advantages of living in groups are greater for males, primarily due to higher survival rates in males than females, and the constraints on independent reproduction appear to be greater for males than females based on the lower proportion of males that achieve independent breeding positions. Both these facts imply that dominant males should be able to monopolise reproduction more completely than dominant females before subordinates will leave, and thus lead to the prediction of greater skew among cobreeder males than joint-nesting females.

And this turns out to be true: 68% of broods produced by groups with cobreeder males are sired by a single male and, on average, the most-successful male fathers over three times as many offspring as the next most successful male. In contrast, joint-nesting females share maternity of offspring evenly; in fact, the split is more even than one would expect by chance, assuming that maternity of each egg is determined by the flip of a coin.

A second prediction of optimal skew theory is that skew should be greater during times when it's more difficult to obtain an independent breeding position. We were able to test this prediction in males, where skew is relatively great, by examining cobreeder males in years when the number of reproductive vacancies in the population during the three months prior to breeding was relatively small, compared to years when vacancies were common. Divided in this way, skew was significantly greater in years when vacancies were rare, suggesting that the dominant male is indeed able to monopolise more of the group's reproduction when constraints to dispersal and independent breeding are high. Unfortunately, this relationship fails to hold up when the number of vacancies was standardised by considering the number of birds in the population potentially competing for the vacant slots. Since this should yield a more accurate measure of competition for vacancies, and thus ecological constraints, than the absolute number of vacancies, it casts the first seed of doubt regarding the ability of optimal skew theory to satisfactorily explain patterns of reproductive partitioning in this species.

The seed sprouts and takes firm root upon additional analyses and closer scrutiny. Problems with optimal skew theory arise on several increasingly problematical fronts. First, two additional predictions are not supported by our data. The first has to do with the size of male cobreeder coalitions, which vary commonly from two to four and are, rarely, even larger. Prior work has shown that larger coalitions of birds are more competitive in power struggles over reproductive vacancies (Hannon *et al.*, 1985). Thus, the three subordinates in a quartet of male cobreeders should be less constrained and more able to strike off on their own than the single subordinate in a cobreeding duo, and it follows that skew should be greater in smaller cobreeding groups. Instead, skew is significantly greater in larger coalitions, when compared using a standard skew index (Table 1), and, at best, exhibits no consistent relationship with coalition size when using an index that controls for variable offspring production.

Although completely unrelated coalitions are extremely rare, we are able to test the relationship between relatedness and skew by comparing cobreeding groups of males that are known to be close relatives (brothers or fathers and sons), with males that are related to a lesser degree. Again, in contrast to the prediction of optimal skew theory, skew was significantly lower, instead of higher, among close relatives (Table 1).

Table 1

Reproductive skew among male cobreeder coalitions of acorn woodpeckers as a function of coalition size and relatedness. All nests for the same coalition of birds were combined. Skew was calculated on a scale of 0 (each cobreeder obtained exactly the same amount of paternity) to 1 (complete monopolisation of paternity by a single individual) according to an index devised by Reeve and Keller (1995). Thus, skew increases with larger coalition size and is greater among less closely related cobreeders. From Haydock and Koenig (unpublished data)

N cobreeder males	N groups	Observed mean skew*
<i>Coalition size</i>		
2	25	0.42
3	9	0.57
4 or more	6	0.63
<i>Coalition relatedness</i>		
Close relatives ($r = 0.5$)	31	0.44
Less closely related birds ($r < 0.5$)	9	0.67

Support for concessions theory further degenerates when we start considering the actual behaviour of the birds rather than reducing everything to estimates of reproductive skew. First, consider joint-nesting females. We know that females are unable to protect their nests from their cobreeders and that either (or, in some cases, both) females will destroy their cobreeder's eggs in a nest (Koenig *et al.*, 1995). Since egg destruction typically occurs up to the day when both birds lay together in the same nest cavity, this explains why females are so strikingly egalitarian in terms of dividing maternity within joint nests. It also implies that neither female is able to control reproduction and, thus, that this basic assumption of optimal skew theory is violated. Indeed, dominance interactions are rarely observed among cobreeders of either sex and, if a female happens to gain maternity of slightly more than half the eggs in one nest, it's quite likely that she'll parent slightly less than half the eggs in the next. Joint-nesting females share maternity equally – not because the dominant offers unusually large reproductive concessions to the subordinate, but because neither bird is able to control breeding and the result is a dead-on draw.

The situation among cobreeder male coalitions is more complex; but the behaviour of the birds again raises questions about the ability of optimal skew theory to explain the observed patterns. Two observations stand out. First, the kind of 'switching' seen between joint-nesting females, with the more successful bird in one nest often being the less successful in the next, reoccurs with a vengeance. Among cobreeder males that produced at least two nests together, the same male obtained the dominant share of reproduction in only eight of 25 cases (32%), a situation that fails to improve even when considering only cobreeder males known to be of different ages. As a consequence, skew among cobreeder males, which starts off very high when considering individual nests, decreases considerably as our sample of nests from the same set of individuals increases (Table 2). This leads to the second observation, which is that we are unable to determine, *a priori*, which male in a cobreeding coalition will be 'dominant' and obtain the majority of paternity within a brood by standard char-



Caption to come

acters such as age, body size, or condition (Haydock and Koenig, 2002).

Reconciling the strong dominance, which is implied by high reproductive skew among cobreeder males, with the observations of frequent and regular switching is a challenge. Are we making any assumptions that, if looked at differently, might resolve these conflicting results?

We believe the answer is yes. So far, we have made the assumption, standard in most studies, that paternity is determined independently for each egg. But what if this is not the case? To understand how this changes things, consider that skew, which measures the disparity between the reproductive success of cobreeders, can potentially arise by chance alone. Furthermore, the magnitude of skew expected by chance increases as the sample size decreases. Assuming that paternity of eggs is determined independently means that the sample sizes we are dealing with are modest, since brood sizes are usually on the order of only two to five offspring. Given this assumption, the degree of skew expected by chance alone (the 'null' expectation) can be determined by flipping a virtual coin (which has the

same number of sides as the number of cobreeders in the group) for each offspring and assigning paternity randomly depending on the outcome.

The results that we have presented thus far are based on the finding that the observed degree of skew among cobreeder males is significantly greater than the amount expected by chance following this procedure. Consider, however, that two-thirds of broods in multi-male groups are sired by a single male. The paternity of such broods is largely a 'winner-takes-all' affair, as could very well be true if females, either by design or as a consequence of sperm competition within the female reproductive tract, generally fertilise their eggs with sperm from the same male. Then, paternity within individual nests would usually be strongly biased toward the single successful male, but which male that is might be random; *i.e.*, each cobreeding male might have an equal probability of being the winning sire at any particular nest. The appropriate null expectation would then be obtained by flipping the virtual coin only once for each brood and assigning paternity of all offspring based on the result.

As it happens, our results provide a striking match to the null expectation obtained by doing exactly this (Table 2). Furthermore, the 'switching' of paternity between nests and our inability to predict which male is reproductively dominant based on age or physical characters suddenly cease to be a problem. As with joint-nesting females, the implication is that no male is in permanent control of reproduction and that the observed pattern of reproductive partitioning is a consequence of either chance or female control, rather than reproductive concessions on the part of a dominant individual.

Where to next?

These results serve to highlight some of the difficulties that we and others have had applying reproductive skew theory to vertebrates. The biggest problem may stem from a fundamental difference between insect societies (a large proportion of which are unisexual and composed entirely of females except for a short period when male reproductives are produced) and vertebrate societies (which involve both males and females in what are often complex social interrelationships). In the absence of the potential complications of incest or mate choice in settled colonies, it's not

surprising that the limited number of factors considered by optimal skew theory enjoy considerable success at explaining patterns of reproductive partitioning among social insects.

Other, less dramatic issues are probably involved as well. Insect societies are frequently focused in a confined space where olfactory and other mechanisms of social dominance can be remarkably effective. Indeed, the highly structured

Table 2

Observed and expected reproductive skew (using the same Reeve and Keller index as in Table 1) in male coalitions depending on the number of nests for which paternity was determined. Expected values were determined under the assumption that paternity of each nestling is determined independently ('by nestling') and under the alternative assumption that paternity of each clutch is all or none ('by clutch'). Observed skew is always greater than expected skew assuming equal probability of parentage and that paternity is independently determined for each egg. However, if paternity is all or none within broods, observed skew closely matches predicted skew once two or more nests are available for each coalition. Modified from Haydock and Koenig (2002).

	<i>N</i> groups or nests	Mean <i>N</i> offspring	Observed mean skew	Skew expected assuming equal probability of parentage	
				By nestling	By clutch
Single nests	99	3.0	0.76	0.42**	1.0**
2 nests	35	5.9	0.54	0.19**	0.56 (ns)
3 nests	18	9.5	0.33	0.11**	0.36 (ns)

** Using randomization tests, observed skew was significantly different from the expected value. Values marked with (ns) are not significantly different from observed

caste system of many social insects, in which only one or a small number of individuals (the queens) are physiologically capable of laying eggs, lends itself well to the complete control by a single individual assumed by optimal skew theory. Haplodiploidy, whereby females are diploid and males haploid, is a common feature of many highly social insects and helps to accentuate the potential fitness consequences of kin-based behaviours (Hamilton, 1964), as well as providing intriguing asymmetries in relatedness that affect the predictions of reproductive skew (Reeve and Keller, 1995). Finally, the reproductive system of most social insect societies, where reproduction occurs repeatedly throughout a relatively long breeding season, is far more amenable to the concept of transactions among individuals leading to an optimal degree of reproductive partitioning than the typical vertebrate system, in which it is literally not unusual for all eggs to be laid in a single basket.

Even if optimal skew theory is ultimately deemed less than satisfactory in explaining reproductive partitioning in vertebrates, it will hardly have been a failure. This is both because of its success in insect societies and because it will have served the valuable function of focusing attention on the causes and consequences of this most important property of societies. Quite possibly, it will be expanded to include a wider range of social situations, a process that is already taking place but has yet to include the complications of bisexual societies discussed above. In any case, as a comprehensive theory for reproductive partitioning evolves, it will be a continuing challenge for field studies such as ours to generate enough data to provide satisfying tests.

Acknowledgement

This research was funded by the National Science Foundation.

References and further reading

- Clutton-Brock T H, Brotherton P N M, Russell A F, O'Riain M J, *et al.* (2001) Cooperation, control, and concession in meerkat groups. *Science*, **291**, 478 – 481.
- Emlen S T (1995) An evolutionary theory of the family. *Proceedings of the National Academy of Sciences (USA)*, **92**, 8092 – 8099.
- Hamilton W D (1964) The genetical evolution of social behavior, I and II. *Journal of Theoretical Biology*, **7**, 1 – 52.
- Hannon S J, Mumme R L, Koenig W D, Pitelka F A (1985) Replacement of breeders and within-group conflict in the cooperatively breeding acorn woodpecker. *Behavioral Ecology & Sociobiology*, **17**, 303 – 312.

- Haydock J, Koenig W D (2002) Reproductive skew in the polygynandrous acorn woodpecker. *Proceedings of the National Academy of Sciences (USA)*, **99**, 7178 – 7183.
- Haydock J, Koenig W D and Stanback M T (2001) Shared parentage and incest avoidance in the cooperatively breeding acorn woodpecker. *Molecular Ecology*, **10**, 1515 – 1525.
- Keller, L, Reeve H K (1994) Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution*, **9**, 98 – 102.
- Koenig W D, Mumme R L, Stanback M T and Pitelka F A (1995) Patterns and consequences of egg destruction among joint-nesting acorn woodpeckers. *Animal Behaviour*, **50**, 607 – 621.
- Koenig W D, Haydock J and Stanback M T (1998) Reproductive roles in the cooperatively breeding acorn woodpecker: incest avoidance versus reproductive competition. *American Naturalist*, **151**, 243 – 255.
- Pusey A, Wolf M (1996) Inbreeding avoidance in animals. *Trends in Ecology and Evolution*, **11**, 201 – 206.
- Reeve H K, Keller L (1995) Partitioning of reproduction in mother-daughter versus sibling associations: a test of optimal skew theory. *American Naturalist*, **145**, 119 – 132.
- Reeve H K, Keller L (2001) Tests of reproductive-skew models in social insects. *Annual Review of Entomology*, **46**, 347 – 385.
- Reeve H K, Starks P T, Peters J M, Nonacs P (2000) Genetic support for the evolutionary theory of reproductive transactions in social wasps. *Proceedings of the Royal Society of London, Series B*, **267**, 75 – 79.
- Schmidtke J, Krawczak M (1999) *DNA fingerprinting*. Berlin: Springer Verlag.
- Vehrencamp S L (1979) The roles of individual, kin, and group selection in the evolution of sociality. In: *Handbook of behavioral neurobiology, volume 3*. Marler P and Vandenberg J G (Eds). New York: Plenum Press.

Websites

www.hastingsreserve.org/AcrnPkr/AcrnPkr.html

A report on the social behavior of the cooperatively breeding Acorn Woodpecker from the Hastings Natural History Reserve homepage.

www.hastingsreserve.org/AWPekrGenes/AWPekrGen.html

A report on parentage in the cooperatively breeding Acorn Woodpecker from the Hastings Natural History Reserve homepage.

Walter Koenig is a Research Zoologist at Hastings Reservation, a field station located in central coastal California run by the Museum of Vertebrate Zoology, University of California Berkeley. Joey Haydock is an Assistant Professor at Gonzaga University in Spokane, Washington.