RELATEDNESS ASYMMETRY AND REPRODUCTIVE SHARING IN ANIMAL SOCIETIES

We have shown (Reeve and Keller 1995) that reproduction in social groups is generally shared more equally in sister-sister groups than in mother-daughter associations, and we proposed a model based on the relatedness asymmetry between group members to account for this pattern. Emlen (1996) endorses our model but raises the possibilities that the model might not apply to several types of vertebrate familial societies, that the well-documented dominance of parents over offspring confounds the prediction of our model, and that greater skews in mother-daughter associations may reflect greater avoidance of incestuous mating in these associations. Below we consider these points in turn.

Our model examines the consequences of females having asymmetric relatedness to each other's offspring (as will arise in mother-daughter associations) in the simple case in which females have a single mate. However, as Emlen points out, extrapair fertilization is common in vertebrates, with the effect of decreasing the relatedness among siblings. If a fraction f of the brood is sired by another male (unrelated to the parental male or female), the average relatedness between siblings is

$$(f^2)(\tfrac{1}{2}) + (1 - f)^2(\tfrac{1}{2}) + 2\,(f)\,(1 - f)(\tfrac{1}{4}) = \frac{1 - f + f^2}{2}.$$

Thus, extrapair copulations will affect an important component of our model, r_{sd}, which is defined as the mean relatedness of the daughter to the mother's offspring, divided by the daughter's relatedness to its own offspring. The daughter's relatedness to its own offspring ($r = 0.5$) remains unaffected by extrapair fertilizations so that r_{sd} equals $1 - f + f^2$. Hence, r_{sd} decreases as the fraction of the brood sired by another male increases, the minimal value (0.75) being attained when f is equal to 0.50 (i.e., half of the brood is sired by an extrapair male). The mother's relatedness to the daughter's offspring, divided by her relatedness to her own offspring (i.e., r_{ds}) will equal 0.50, regardless of f. Since r_{sd} will always exceed r_{ds}, it follows that a relatedness asymmetry will persist in matrifilial associations and be absent in sibling associations, regardless of f. Indeed, this will be the case regardless of the number of males that fertilize the female, except in the extreme situation in which each individual offspring is sired by a different male, in which case the relatedness asymmetry in matrifilial associations disappears. The relatedness asymmetry will increase as the relatedness between males fertilizing a female increases (e.g., if the extrapair male is a brother to the paired male) because this would increase r_{sd} but not r_{ds}. It is important to note that reductions in relatedness asymmetry do not necessarily lead to continu-
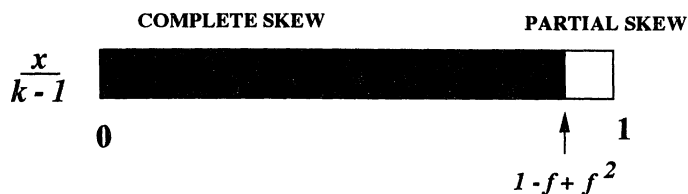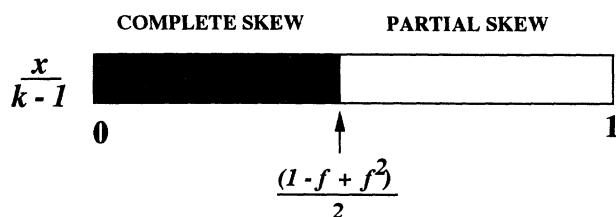
MATRIFILIAL ASSOCIATION

COMPLETE SKEW **PARTIAL SKEW**

$$\frac{x}{k-1}$$

0   ↑   1

$$1-f+f^2$$

SIBLING ASSOCIATION

COMPLETE SKEW **PARTIAL SKEW**

$$\frac{x}{k-1}$$

0   ↑   1

$$\frac{(1-f+f^2)}{2}$$

FIG. 1.—Reproductive skew as a function of x, the reproductive success of a potential helper if it breeds independently (relative to 1.0 for a solitary breeder in an already established nest); k, the total reproductive output of the group (also relative to 1.0); f, the frequency of extrapair copulation; and the type of group (matrifilial or sibling). The threshold value of $x/(k - 1)$ above which partial skew is favored and below which complete skew is favored will always be higher for matrifilial associations than for sibling associations. (This threshold is obtained by setting the staying incentive given by eq. [3] in Reeve and Keller 1995 equal to zero.) Arrows indicate the threshold for complete skew if $f = 0.13$, the overall mean proportion of the brood sired by extrapair matings as estimated by Birkhead and Møller (1993) for 11 species. (This threshold is 0.89 for matrifilial associations and 0.45 for sibling associations.)

ous reductions in skew; maximum skew may be favored even when relatedness asymmetries are slight, depending on ecological conditions (fig. 1).

Importantly, increased frequency of extrapair copulations will tend to decrease skew in both matrifilial and sibling associations, such that reproductive skews in the former will always tend to exceed skews in the latter. As shown by equation (3) in our earlier article (Reeve and Keller 1995), the skew will tend to decrease as r_{sd} decreases. In matrifilial associations with extrapair fertilizations (by a male unrelated to the parental male), r_{sd} will have the value $1 - f + f^2$, whereas in sibling associations it will have the always lower value $(1 - f + f^2)/2$. Thus, reproductive skews should always tend to be higher in matrifilial associations than in sibling associations, regardless of the frequency of extrapair fertilizations, as we argued in our original article (Reeve and Keller 1995, p. 124); that is, the occurrence of extrapair fertilizations does not alter the basic prediction of our original model.

Emlen correctly predicts that skews will tend to be higher in matrifilial associations with mate fidelity than in matrifilial associations with mixed paternity, but we emphasize that this will be true only for a very narrow range of parameter values for constraints on independent reproduction and benefits of grouping; under most ecological conditions, complete skew will be expected in both kinds of associations (fig. 1; Reeve and Keller 1995).

When daughters in a matrifilial group are all full sisters and the mother changes its mate, the reproductive skew is expected to be identical to a sibling association in which all females are full sisters, as predicted by Emlen. In the latter case subordinates will help rear nieces ($r = 0.25$), and so r_{sd} is 0.5, as in the matrifilial group. Thus, since r_{sd} is identical in both types of societies, the reproductive skew should be identical if the differences in fighting abilities of the mother and daughters are similar to those between dominant and subordinate siblings, and the dominant female (the mother when present) controls the amount of reproduction allocated to the subordinates. However, the aforementioned situation of a group composed of full sisters, their mother, and a replacement male is probably not common. If mate replacement frequently occurs, the daughters generally will not be full sisters (leading to lower skews in sibling associations). On the other hand, if mate replacement is rare, most associations will still be composed of the offspring and their parents, a situation always leading to a greater relatedness asymmetry and greater reproductive skew in mother-daughter associations than in sibling associations. Thus, mate switching is unlikely to eliminate a difference in the mean skews of matrifilial and sibling associations. If helpers can assess when mate replacement occurs, we agree with Emlen that skews in matrifilial associations with replacement males should be less than in matrifilial associations in which the fathers are still present. Such a result would provide especially strong support for the relatedness asymmetry subhypothesis of optimal skew theory because differences in fighting ability between mothers and helping daughters would be similar in the two groups.

Emlen suggests that dominance asymmetry confounds the prediction based on relatedness asymmetry. However, dominance by itself (i.e., simply the observation that principal breeders have priority of access to resources over helpers) is not confounding, regardless of whether it is based on age or fighting ability (or both). Indeed, our matrifilial model assumes that the mother is dominant to the daughter—a dominant individual controlling reproduction is assumed in all skew models. What would be confounding is if subordinate daughters received smaller peace or staying incentives in matrifilial associations than did subordinate sisters in sibling associations for reasons unrelated to relatedness asymmetry. Such a situation theoretically could occur only if daughter subordinates had lower fighting ability (relative to dominants) or worse prospects for independent breeding than did sister subordinates. Emlen provides evidence only that parents are behaviorally dominant over helper offspring, not that subordinates in matrifilial associations have lesser relative fighting ability or potential for independent reproduction than do subordinates in sibling associations (although this may be true). Thus, evidence of dominance asymmetry by itself is insufficient to undermine

our point that differential fighting ability is much less of a confounding factor in vertebrate than in insect societies.

Emlen suggests that active incest avoidance between parents and their offspring provides an alternative explanation for the rarity of reproductive sharing between mothers and daughters in many vertebrate species. Inbreeding avoidance probably prevents matings between the male offspring and their mother (although evidence of inbreeding having strong detrimental consequences in birds is still scarce; Rowley et al. 1993; Keller et al. 1994). However, females of most vertebrates would seem to have easy access to unrelated males outside the family (e.g., males in "bachelor herds" or parental males engaging in extrapair copulations away from the group) and thus conceivably could raise noninbred offspring within the group. Thus, inbreeding avoidance by itself does not explain the higher skew in matrifilial associations in the case of female subordinates.

Emlen points out that if subordinates initiate reproduction after having been fertilized by a male from outside the group, their brood is frequently destroyed, they are harassed to the point that their pregnancy is terminated, or they simply are driven out of the group. These observations do not challenge the conclusion that the greater relatedness asymmetry is responsible for the greater reproductive skew in mother-daughter associations. On the contrary, these data demonstrate that, as predicted by the skew model, parents will prefer to have subordinates raise the parents' own offspring over the parents' grand-offspring (or less related offspring). However, our model also predicts that, in the absence of extrapair fertilizations, only minimal harassment will be necessary to cause daughters to cease reproduction and help raise siblings, because they should be neutral over whether their own offspring or full siblings are raised in the group. (Indeed, Emlen and Wrege [1992] have shown that sons do not strongly resist reproductive harassment by their parents.) Thus, Emlen's observation generates a new prediction, in light of the extended model incorporating extrapair fertilizations: the cases of intense reproductive harassment that Emlen describes either should be directed primarily at female subordinates of relatively low relatedness to the dominant or, if the subordinates are daughters, should be more common when broods have mixed paternity.

Finally, Emlen states that we mistakenly categorized the white-fronted bee-eater, *Merops bullockoides,* as a matrifilial species showing complete reproductive monopolization. White-fronted bee-eater females may help their parents incubate and feed offspring or breed in their own nests (Emlen 1990). When females stay as helpers, they do not reproduce (Emlen 1990), which is why we classified this species as a matrifilial species showing complete reproductive monopolization.

Emlen's (1996) disagreement with our classification apparently occurs because he defines the group as an entire clan of relatives (which often cooperate in territory defense), regardless of whether there are helper-breeder associations within the clan. His statement that this species "exhibits variable levels of reproductive skew" (p. 761) simply means that helper-breeder associations within the clan form under some conditions and not others, not that the skew varies within

helper-breeder associations. Our tests of the relatedness asymmetry hypothesis focus on the distribution of reproduction only within helper-breeder associations because most of the other cooperative associations we examined are of this kind.

Nevertheless, Emlen's comment raises the interesting point of whether skew models simultaneously apply to higher-level groups such as clans and lower-level groups such as helper-breeder associations. We are inclined to believe that they can; thus, it becomes important to specify explicitly the level of group being considered when applying the skew models. For example, the fact that parents sometimes disrupt the independent breeding attempts of their sons to obtain their help (Emlen and Wrege 1992) can be regarded as a mechanism by which parents ensure reproductive monopolization (high skew) if the clan is considered the group, or, alternatively, it can be viewed as parental manipulation of ecological constraints on independent breeding if the helper-breeder association is considered the group.

CONCLUSION

Emlen's comments are useful in that they point out variations in the structure of vertebrate familial associations that affect relatedness asymmetry. Our analysis reveals that, under most ecological conditions, extrapair copulations will not strongly affect reproductive skew in mother-daughter affiliations. Only when there are only mild ecological constraints on dispersal (high x) and/or small positive effects of additional helpers on group productivity (low k) will extrapair copulations decrease reproductive skew in the latter. However, extrapair copulations will also decrease the relatedness among siblings, which in turn will decrease reproductive skew in sibling associations. Overall, our analysis shows that the reproductive skew will always tend to be higher in mother-daughter associations than in sibling groups, whatever the proportion of offspring fathered by extrapair males. Mate change by females will tend to decrease reproductive skew in mother-daughter associations, but it will also tend to decrease the relatedness among siblings, which in turn will decrease reproductive skew in sibling associations.

The active incest avoidance hypothesis proposed by Emlen may explain higher skews for male subordinates in matrifilial than in sibling associations, but it does not explain (as does the relatedness asymmetry hypothesis) why daughter subordinates do not simply mate with an unrelated mate outside the group, and then attempt to raise these noninbred offspring within the group.

In sum, our theoretical prediction (Keller and Reeve 1995) that reproductive skew should be greater in mother-daughter than in sibling associations seems fairly robust to considerable variation in the details of family structure. However, we enthusiastically agree with Emlen that additional, detailed empirical data on reproductive skews (together with data on inbreeding, relative fighting abilities, and extragroup mating) in different kinds of family groups are needed for rigorous tests of the relatedness asymmetry subhypothesis of optimal skew theory.

LITERATURE CITED

Birkhead, T. R., and A. P. Møller. 1993. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London.

Emlen, S. T. 1990. White fronted bee-eaters: helping in a communally nesting species. Pages 487–526 *in* P. B. Stacey and W. D. Koenig, eds. Cooperative breeding in birds. Cambridge University Press, Cambridge.

———. 1996. Reproductive sharing in different types of kin associations. American Naturalist 148: 756–763.

Emlen, S. T., and P. H. Wrege. 1992. Parent-offspring conflict and the recruitment of helpers among bee-eaters. Nature (London) 356:331–333.

Keller, L., P. Arcese, J. N. M. Smith, W. M. Hochachka, and S. C. Stearns. 1994. Selection against inbred song sparrows during a natural population bottleneck. Nature (London) 372:356–357.

Reeve, H. K., and L. Keller. 1995. Partitioning of reproduction in mother-daughter versus sibling associations: a test of optimal skew theory. American Naturalist 145:119–132.

Rowley, I., E. Russel, and M. Brooker. 1993. Inbreeding in birds. Pages 304–328 *in* N. W. Thornill, ed. Natural history of inbreeding and outbreeding: theoretical and empirical perspectives. University of Chicago Press, Chicago.

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