

Reproductive skew in birds: models, problems and prospects

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In recent years there has been a resurgence of interest in models to explain the partitioning of direct reproduction ('reproductive skew') among members of one sex within social groups. We review models of skew, identify problems of testing models, and consider how to make progress. One series of models assumes that dominants have complete control of subordinate reproduction, but may allow subordinates some reproduction as a way of enticing them to help or getting them to share the cost of reproduction. Another series of models assume that dominants have limited control of subordinate reproduction. Reproductive skew may also be affected by incest avoidance or control by the opposite sex. Models are largely untested because no study of birds has quantified all relevant parameters, and we see no prospect of this happening soon. A common simplifying approach is to test qualitative predictions about the effect on skew of relatedness among group members. However, these data alone cannot distinguish among models because models do not make unique predictions, partly because skew is also affected by other factors. A major problem in cooperatively-breeding birds is that any effect of relatedness will often be confounded by covariation with relatedness asymmetry and subordinate competitiveness. Progress can be made with the development of theory, controlling confounding variables through the choice of study species or types of social group, and, most importantly, testing assumptions underlying hypotheses.

Cooperatively-breeding groups of birds can range from 'despotic', in which a single individual monopolizes reproduction despite others of the same sex being present, to 'egalitarian', where individuals share reproduction equally. Such variation can be quantified as 'reproductive skew', ranging from 1 (monopolization) to 0 (egalitarian). Vehrencamp (1980) first addressed the question of why such variation occurs in a model of optimal reproductive skew presented at the International Ornithological Congress in 1978. A key feature of the model is that dominant individuals control the reproduction of subordinates, and therefore reproductive skew, but that they can be selected to allow subordinates to share reproduction as a way of enlisting their cooperation. In other words, dominants can 'forfeit' reproduction (Emlen 1982) or offer 'concessions' (Clutton-Brock 1998) in return for the benefits of subordinate cooperation. Early development of optimal skew theory was based around this principle (Vehrencamp 1979, 1980, 1983a, b, Emlen 1982).

In the last few years there has been a resurgence of interest in reproductive skew, perhaps stimulated by molecular methods to determine parentage. The renewed interest is revealed in the development of new and insightful models of optimal skew (Reeve and Ratnieks 1993, Keller and Reeve 1994, Reeve and Keller 1995, 1996, 1997, Cant 1998, Reeve 1998, Reeve et al. 1998, Cant and Johnstone 1999, Johnstone and Cant 1999a, b, Johnstone et al. 1999, Kokko and Johnstone 1999, Ragsdale 1999, Johnstone in press, Reeve in press), as well as reviews and critiques (Emlen 1996, 1997, 1999, Clutton-Brock 1998, Heinsohn et al. 1999, Keller and Chapuisat 1999, Magrath 1999, Johnstone in press, Reeve in press), and applications of skew theory to empirical data (McRae 1996, Jamieson 1997, Whittingham et al. 1997, Lundy et al. 1998).

Reproductive skew models were applied from the start to both cooperatively-breeding birds and insects (Vehrencamp 1980), and the primary aim was to explain variation in reproductive skew across species. Recent work on the subject continues to seek models of reproductive sharing that are applicable to diverse taxa, as well as within species and even within single populations (Keller and Reeve 1994, Reeve et al. 1998).

In this paper we briefly review models of skew, and then consider the problems and prospects of using these models to understand reproductive sharing in birds. We focus specifically on the predictions that models make about the effect of relatedness on reproductive skew, because relatedness is the easiest parameter to quantify and often the only one for which precise data are available. We conclude that skew theory is potentially central in understanding reproductive sharing, but that it is currently difficult to test specific models. This is not because the models are flawed, but because the sophistication of models has outstripped the availability of data to test them; we are left trying to distinguish among models using only partial information.

We find that the major problems in testing models of skew are that: (1) almost any pattern of reproductive skew can be 'explained' by at least one optimality model; yet (2) different models can make similar predic-

tions; (3) it is difficult to measure all factors that could influence reproductive skew and yet confounding factors may be common; and (4) quantitative modelling has not considered the potentially critical influence of the opposite sex on reproductive sharing, and has only begun to examine the effect of concessions and benefits other than current reproduction.

We argue that progress in understanding reproductive skew requires: (1) considering multiple hypotheses and confounding variables when assessing models of skew; (2) emphasis on testing assumptions rather than exclusively predictions; (3) further modelling incorporating inter-sex effects and benefits of cooperation unrelated to current reproduction. With the ever-expanding range of models of skew, future studies of variation in reproductive skew should collect data on all parameters of models to be tested, or choose species for which unmeasured parameters are unlikely to confound results.

Models of reproductive skew

We will not use the terms 'reproductive skew' or 'optimal reproductive skew' to refer to a particular type of model, since the degree of reproductive sharing is what all models try to explain, and all hypotheses could be cast in an optimality framework. Instead, we use names that reflect distinguishing features of models.

It is difficult to draw up a simple conceptual framework. There are many models, assessing different parameters and making different assumptions, and there is scope for unification (e.g. Johnstone in press, Reeve in press). For example, incest avoidance is sometimes identified as a distinct hypothesis, but it would be more usefully incorporated as a constraint or parameter in other models (Emlen 1999). Here we separate hypotheses because we aim to highlight processes that could influence reproductive skew but have not necessarily been included in optimality models. We focus specifically on the predicted effects of relatedness on skew, as this has been the most common approach to date. Keller and Chapuisat (1999), Johnstone (in press), and Reeve (in press) also provide brief reviews of skew theory, and Johnstone and Cant (1999a), Reeve 1998 and Reeve and Keller 1997 deal with issues not included here.

1. Complete control by dominants

One series of models, including the original 'optimal skew model' of Vehrencamp (1979, 1980), assume that the dominant has complete control over subordinate reproduction, but may maximize inclusive fitness by permitting a subordinate to have a specific share of reproduction.

Concession model ('optimal skew model')

In both Vehrencamp's original models and Emlen's (1982) concept of 'fitness forfeiting', dominant individuals may attempt to maximise their inclusive fitness by bribing subordinates to stay in social groups. Dominants have total control over the reproduction of subordinates, but adjust the size of the bribe to entice the subordinate to stay and cooperate peacefully. The minimum size of the bribe they need to offer, to make it in the interests of the subordinate to stay, depends on their relatedness to the subordinate, the subordinate's effect on the group's reproductive productivity, and the subordinate's other options and competitive ability (Vehrencamp 1979, 1980, Emlen 1982, Reeve and Ratnieks 1993). The bribe is modelled as the amount of direct reproduction the dominant permits the subordinate. Thus the size of the bribe determines the amount of skew. This is often called the 'optimal skew model', but we think Clutton-Brock's (1998) term 'concession model' nicely encapsulates the principle of the dominant making concessions to entice the subordinate to stay in the group and to cooperate.

Under this model, a dominant is most despotic when the subordinate is: (a) closely related, (b) has little chance of reproducing independently, (c) is a poor competitor compared with the dominant, and (d) has a large effect on the group's productivity. At the other extreme, the dominant may have to allow the greatest sharing of reproduction when the subordinate is unrelated, has a good chance of reproducing elsewhere, is a strong competitor, and has a limited effect on group productivity. This last effect is counter-intuitive and arises because the lower the subordinate's effect on group productivity, the lower the indirect fitness that can be obtained by helping relatives and therefore the greater the share of direct reproduction the dominant must offer to get the subordinate to stay. Nonetheless, if the dominant has very little to gain from the subordinate's presence, it might offer no concessions and the subordinate will depart. Intermediate levels of relatedness, constraint, competitive ability or contribution to group success can lead to intermediate levels of skew.

Asymmetrical relatedness

An important complication to the original 'concession' model comes from asymmetrical relatedness (Reeve and Keller 1995, 1996). We explain by example. In a trio consisting of a father and son (or two brothers) with an unrelated female, each male is related to the offspring of the other by the same amount ($r = 0.25$); relatedness is symmetrical. However, in a nuclear family consisting of a father and son with the son's mother, the father is less closely related to offspring sired by the son ($r = 0.25$) than the son is to offspring sired by his father ($r = 0.5$). Hence, other things being equal, the father will offer fewer concessions when his son's mother is present, because of asymmetrical relatedness.

Concessions and the cost of reproduction for females

It can be optimal for a dominant female to allow a related subordinate to lay eggs in her nest if the cost of laying eggs is an accelerating function of clutch size (Cant and Johnstone 1999). Because it is more costly to lay each successive egg, there comes a point when the net benefit to a dominant of laying another egg is less than allowing a relative to lay eggs at a lower cost.

The basic model assumes that the subordinate is constrained to remain in the group and contributes nothing to parental care. In this situation, dominants will grant subordinates that are closer relatives a greater share of reproduction. Thus reproductive skew will decline with relatedness, the opposite prediction to that of 'concession' models. However, a second model incorporated the possibility of both subordinate dispersal and an increase in brood productivity when there are two females in the group. In other words, the second model included a cost of reproduction in a concession model framework.

The extended model predicts that reproductive skew will initially increase with relatedness because, as in the concession model, the dominant can offer a lower reproductive concession when subordinates are closer relatives (Cant and Johnstone call this the 'incentive effect'). However, above a threshold relatedness, reproductive skew declines with relatedness. This is because of the effect predicted in the basic model: dominants offer more reproduction to closer relatives as their own cost of laying increases (the 'beneficial sharing' effect).

The model also predicts that the 'incentive effect' will predominate over most values of relatedness when the cost of laying is low, but that the 'beneficial sharing' effect will predominate when costs are high. In other words, the predominant relationship between relatedness and skew depends on the cost of reproduction, yet in all cases the pattern differs above and below a (variable) threshold relatedness.

The model is important because it highlights the fact the differences in breeding biology and life-history between species can have profound effects on the predicted patterns of reproductive skew. Whereas the original concession models may be applicable to social insects, the costs of reproduction for birds and mammals mean that there may be no association between relatedness and skew, or even reduced skew with closer relatedness (Cant and Johnstone 1999). Furthermore, there could be fundamental differences between males and females, because only the latter are likely to suffer an accelerating cost of producing successive young (Cant and Johnstone 1999).

Multi-member groups

Most models of reproductive skew make the simplifying assumption that only two individuals of one sex compete to share reproduction, or that subordinates are

identical in relatedness and prospects of successful dispersal. However, avian groups often contain more than two members of one sex, and there can be differences between them. Johnstone et al. (1999) model reproductive sharing among three individuals of the same sex, assuming that dominants have complete control of reproduction of all subordinates, who are themselves equally subordinate but may differ in their relatedness to the dominant and to each other. The model makes the additional simplifying assumption, in common with most other models, that the group's reproductive productivity increases with group size, although in this model the increase is allowed to be a decelerating or accelerating function (the second subordinate may have a smaller or larger effect than the first).

The specific predictions of the model cannot be summarized simply, because both quantitative and qualitative effects of relatedness on skew depend on other variables. For example, skew can increase or decrease with the relatedness between subordinates and the effect is stronger when the subordinates are more closely related to the dominant. Whether skew increases or decreases depends on whether reproductive productivity is, respectively, a decelerating or accelerating function of group size. An important conclusion is that the reproductive share granted to one subordinate can be affected by characteristics of the other subordinate and the specific effect of group size on reproductive productivity.

The model for three-member groups highlights a limitation of skew theory when applied to cooperatively-breeding birds. Reproductive skew in large groups is not easily predicted on the basis of two-member models, yet these have predominated due to their greater tractability. This is analogous to the difficulties of applying other two-player models to the complex dynamics of larger groups (e.g. the prisoner's dilemma, Boyd and Richerson 1988). Johnstone et al. (1999) themselves state that, although some attributes of their model can be generalised, the number of parameters required for a full analysis of all possible outcomes becomes unfeasible for larger groups. Thus the present scope of skew theory is most easily applied to species that live in small groups.

Delayed benefits and adult survival

Previous models of reproductive skew have considered only current reproduction within a group, but many cooperatively-breeding birds are long-lived and subordinates may gain the delayed benefit of inheriting dominance within the group (Wiley and Rabenold 1984, Emlen 1999). Thus the benefits of group membership may include future reproduction, not just current direct and indirect fitness. Kokko and Johnstone (1999) put skew theory into a life-history framework in a dynamic model looking at the probability of inheriting domi-

nance status with the death of the current dominant. In addition to the parameters of a basic concession model, they consider the probability of survival of the dominant and subordinate from one breeding season to the next.

Kokko and Johnstone found that dominants need offer fewer concessions when subordinates can inherit the dominant's position; reproductive skew was usually much higher when future benefits were taken into account. In general, an increase in adult survival led to a greater chance of inheritance and hence a reduced need for concessions (this was true if the subordinate had similar or higher survival than the dominant, but not always true if subordinates had lower survival). Subordinate survival usually had a much greater effect on skew than relatedness, and despotic groups were often stable, even when the dominant and subordinate were unrelated. If there was an effect of relatedness, it was towards greater skew with higher relatedness, as in the concession model. Dominants would even tolerate a small reduction in group productivity if the subordinate was a relative, as long as the subordinate's probability of independent reproduction was low enough (illustrating the idea of parental facilitation proposed by Brown and Brown 1984). Similarly, the dominant tolerated some reduction in group productivity if it had increased survival when a subordinate was present (even if unrelated).

Ragsdale (1999) also modelled delayed benefits, using a different approach, and similarly found that future benefits permitted higher skew and group stability in a greater range on conditions.

2. Incomplete control

Recent models by Cant (1998), Reeve et al. (1998) and Johnstone and Cant (1999a, b) have explored the consequences of dominants lacking the ability to completely control subordinate reproduction. Thus these models change a major assumption of 'complete control' models.

Females contributing to the same clutch

Cant (1998) models the optimal number of eggs that dominant and subordinate females should contribute to the same clutch, assuming that the dominant has no direct control over subordinate reproduction. However, the dominant is the first to decide her optimal clutch, and the subordinate responds with hers. In the basic model the dominant lays her 'personal' optimum, while in the extended model the dominant takes into account how many eggs the subordinate will lay when deciding her own clutch size. A dominant's personal optimum takes into account the per capita survival of young (assumed to be a linear decline with clutch size) and the

cost of reproduction (assumed to be a linear increase with clutch size). In the extended model, the dominant takes into account the total clutch size resulting from her and the subordinate's contributions, and the relatedness to the subordinate. In each model, the subordinate takes into account the total clutch size and relatedness to the dominant, and lays the number of eggs that maximizes inclusive fitness.

In both models reproductive skew increases with closer relatedness between the females. This is for two reasons. In the basic model, subordinates should lay fewer eggs when the dominant is a closer relative because of the indirect cost of reducing the fitness of the dominant's offspring as the clutch size exceeds the most productive. In the extended model, there is the additional effect that the dominant is selected to lay a clutch which is larger than her personal optimum if the other female is a relative. This increases the dominant's inclusive fitness because it raises the indirect fitness cost to the subordinate of contributing to the clutch, and means that skew increases more rapidly with relatedness. The model assumes no increased productivity of the group following from subordinate reproduction, but it is claimed that such an effect would not change the qualitative predictions.

The risk of eviction

In species in which dominants cannot directly control reproduction by subordinates, they may nonetheless exert indirect control through the threat of eviction (Johnstone and Cant 1999b). This model examines the partition of reproduction between a dominant and subordinate without making assumptions about whether subordinate reproduction increases or decreases group productivity. The subordinate is not prevented from reproducing by the dominant, but the dominant can evict a subordinate which then may suffer a reduction in fitness. Thus the subordinate is selected to take the largest share of reproduction that will not evoke eviction from the group.

The predictions about reproductive skew from this model are mostly opposite those of the concession model: (1) subordinates can take a *greater* share of reproduction when they are more closely-related to the dominant, and (2) related subordinates can afford to take a *greater* share of reproduction when ecological constraints are stronger. These trends occur because the indirect cost to the dominant of evicting the subordinate is larger when a subordinate is closely related or when a related subordinate faces poor chances of breeding if evicted. It will therefore tolerate more reproduction by the subordinate.

The effect of competitive ability of the subordinate is, nonetheless, similar to other models. The more costly it is for a dominant to evict a subordinate (measured as a direct fitness cost), the more sharing it will tolerate.

Thus skew will be lower when the subordinate is a relatively good competitor who can cause injury or substantive energetic costs.

Although we have classified this model as one of 'incomplete control', it shares with the concession model a 'transactional' view of social interactions (Reeve et al. 1998, Reeve in press, Emlen pers. comm., Vehrencamp pers. comm.). In this case, the subordinate 'gives' the dominant a specific share of reproduction in return for not being evicted from the group. Nonetheless, it is a model of 'incomplete control' in the sense that although dominants can evict subordinates, they have no control over the reproduction of a subordinate member of the group. The model therefore raises the issue of who is truly 'dominant', and what mechanisms of control are available to each member of the group.

Costly control of subordinate reproduction

Reeve and colleagues' (1998) model predicted skew in a group in which control by dominants of subordinates comes at a price. They assume that a given productivity is divided between competing reproductives, and that there is a cost, in terms of reduced group productivity, following from resources channelled into competition rather than reproduction. Dominant individuals have access to greater resources, or are more efficient at using resources, so have some advantage in competition with subordinates. Group productivity is assumed to increase linearly with the amount of resources that are not devoted to competition.

In any one model, skew is either not affected by relatedness or declines with relatedness; the opposite prediction to the concession model. The specific predictions about the effect of relatedness are sensitive to the detail of the model and qualitative effects can vary over values of parameters. For example, if one assumes symmetrical relatedness, small group sizes and less efficient resource use by subordinates, kinship is predicted to have little or no effect on reproductive skew. On the other hand, if competing males have stored resources, yet equal efficiency of using them, reproductive skew initially declines with increasing relatedness but then becomes constant.

In common with concession models, skew is higher when relatedness is asymmetrical than when it is symmetrical; as with other models, skew will increase as the competitive differences between dominants and subordinates increase.

Concessions, risk of eviction and incomplete control

Johnstone (in press) and Reeve (in press) develop models containing features of both transactional models (concessions and eviction) and costly control models. The principle of these synthetic models is similar. The concession model identifies the minimum share of reproduction that a subordinate will tolerate without

leaving the group, while the eviction model identifies the maximum share of reproduction by a subordinate that the dominant will tolerate before evicting the subordinate. However, between these 'transactional' thresholds for group stability there is a 'window of selfishness' (sensu Reeve in press), in which there is room for a 'tug-of-war' or 'compromise' over reproductive share. The relationship between relatedness and reproductive skew is therefore variable and depends on the mechanism of control and other parameters, as is clear from the discussion of antecedent models (above).

3. Incest avoidance

A subordinate may avoid reproduction if this would entail incest (Emlen 1995, 1996). In this case, there is no need for the dominant to bribe or constrain the subordinate, and there should be neither risk of eviction nor competition with the dominant. A constraint on incest might result in complete skew or no skew depending on whether direct reproduction would involve incest or not.

Given that most species will have groups of variable composition, it seems likely that dominants will monitor reproduction by subordinates at least in groups in which the subordinate is unrelated to the breeder of the opposite sex. Thus any avoidance of incest, or effects of incest, should be incorporated in models making assumptions about the control that dominants exercise over subordinates (Vehrencamp 1983a, Emlen 1999). For example, dominants may ignore sons when still with their mother, but attempt to control or evict sons that copulate with stepmothers. Although we have highlighted incest avoidance, and implied a cost of incest, this may not be true for all species.

4. Female control of reproductive skew among males

Reproductive skew amongst males can be affected by conflicts of interest with breeding females and may therefore at least partly reflect female control. Females can have a vested interest in reproduction by subordinates in species with male care of young. This is particularly clear in Dunnocks *Prunella modularis*, in which groups are composed of adults that are unrelated to each other. In a polyandrous trio of this species, whether a beta male helps feed nestlings is influenced by whether he copulates with the female, so it is in the female's interest to copulate with both males and she appears to take active steps to achieve that goal (Davies 1992). On the other hand, it is in the alpha male's interest to try to stop the beta male copulating with the female. Thus there is conflict between the sexes and low reproductive skew is partly the result of female control. This is quite different from preceding models, all of

which assume that reproductive skew results entirely from conflict, 'negotiation', or choices about reproduction within a sex.

A female's perspective on reproductive skew among males might also involve genetic costs and benefits. For example, a subordinate male may gain some net benefit from offspring of an incestuous mating with his mother even if those offspring are of lower fitness than offspring of the dominant; however, it seems less likely to be in the interests of the female to raise her son's inbred offspring in comparison with the dominant's outbred offspring. Females would then attempt to maximize skew when related to one of the males. Similarly, females may benefit from genetic diversity among their offspring and so mate with more than one male when the males are unrelated to each other; or females might only mate with older subordinates, if age correlates with genetic quality.

In contrast to the predictions above, females might avoid mating with unrelated males because this will reduce relatedness among siblings and this in turn could increase the reproductive concessions they require to become helpers in future (Johnstone et al. 1999). A reduced relatedness among siblings might therefore mean that the female has to share more reproduction in future or have fewer helpers.

As far as we know, there has been no formal modelling of the effects on reproductive skew of the opposite sex, despite the fact that the problem was identified in early discussions of reproductive skew by both Vehrencamp (1979, 1980) and Emlen (1982). As implied above, we expect that in birds this will mostly take the form of female control over male reproduction because joint-nesting by females is relatively uncommon.

Problems of testing models

The fundamental problem in testing models of skew in birds is that there is no species for which all the parameters that could affect reproductive skew have been quantified. To make quantitative predictions from all models, it is necessary to measure constraints on independent reproduction of subordinates, competitive ability of birds vying for reproductive share, relatedness among all individuals potentially involved in reproduction, the precise effect of group size and help on reproductive productivity of the group, and potentially the cost of reproduction and the behaviour of 'third parties', such as members of the opposite sex and additional subordinates. Many of these effects are difficult to quantify; it can be difficult even to show that helpers increase reproductive success in cooperatively-breeding species (Brown et al. 1982, Koenig and Mumme 1990, Mumme 1992, Magrath and Yezerinac 1997, Cockburn 1998), let alone specify the precise shape of the function.

Given the difficulty of quantifying predictions of different models, all tests of models in birds have looked at qualitative predictions, particularly the relationship between relatedness and reproductive skew. The focus on relatedness probably follows from the ease of quantification: molecular genetic data, often in combination with pedigree information, now allows precise measures of relatedness. Relatedness is also the only parameter that can be easily compared across species; it is more difficult, for example, to quantify competitiveness and ecological constraints.

This simplifying approach of examining qualitative predictions of relatedness on skew suffers from two major problems. First, even qualitative predictions can be affected by other variables, so the approach assumes that 'all else is equal' among unmeasured variables; and second, the approach has very limited ability to discriminate among models.

We see three specific problems in relying on an association between relatedness and reproductive skew to distinguishing among models. (1) Any qualitative relationship between relatedness and skew can be predicted from at least one optimality model of skew, so that empirical data should not be used *a posteriori* to support some model of skew. (2) Models using quite different assumptions can make similar qualitative predictions about skew, thus patterns of variation in skew may reveal little about the causes of skew. (3) Factors influencing skew may covary with relatedness, and so explain or obscure any association between relatedness and skew. In particular, relatedness asymmetry and competitive ability seem particularly likely to covary with relatedness not only in social insects (Reeve and Keller 1995), but also in cooperatively-breeding birds (Emlen 1996, 1999). We consider each problem in turn.

1. A multitude of predictions

Different theoretical papers on reproductive skew reach disparate conclusions regarding the likely effect of relatedness on reproductive skew, assuming other variables are held constant. This is true even amongst models which make similar assumptions about the dominant's control of subordinate reproduction. Amongst complete control models, the original models predict that skew will increase with relatedness; the costly reproduction model predicts different trends above and below relatedness thresholds; the multi-member model predicts any pattern depending on other parameters. Amongst models assuming incomplete or no control, Cant's (1998) model of females contributing to a clutch predicts greater skew with increased relatedness; the model of eviction predicts the opposite; and Reeve and colleagues' (1998) models incorporating a cost of competition predict that skew is either not affected by relatedness or declines with relatedness. Assuming fe-

male control, skew seems likely to increase with relatedness but might conceivably decrease.

It can be a good thing that different models make different predictions, otherwise predictions cannot be used to test among models. But the problem here is that any type of association between skew and relatedness could be 'explained' by one or more models. Thus the risk is that empirical data will be used to provide spurious, *a posteriori*, support for particular models of skew. Clearly, it is essential to quantify all relevant variables before claiming to test a model.

2. A convergence of predictions

Models making different assumptions about the causes of reproductive skew can make similar qualitative predictions. For example, an increasing skew with relatedness could result from direct control of subordinate reproduction, or choices by subordinates about how many eggs to contribute to a joint clutch. A decrease in skew with relatedness might imply total control by dominants who incur an accelerating cost of laying, or choices by subordinates about how much reproduction to take based on the risk of eviction.

Convergent predictions are a problem because empirical data on relatedness and skew may shed no light on the mechanisms of reproductive sharing, unless other variables are also measured. The problem of convergence is exacerbated by potentially confounding factors, as is explained in the next section.

3. Confounding variables

An apparent effect of relatedness on reproductive skew could come about because another variable covaries with relatedness (Emlen 1996, 1999). In other words, a tacit assumption that 'all else is equal' may be false. Furthermore, confounding variables can lead to a convergence of predictions by models that make quite different assumptions about dominant control of reproduction. All field data potentially suffer from the problem of confounding variables, but there are serious and pervasive confounding variables particularly with the most common type of cooperatively-breeding society in birds (Emlen 1996, Magrath 1999).

Cooperatively-breeding groups of birds commonly form through natal philopatry of young who become helpers during future breeding attempts by the group. Amongst such societies, male helpers predominate, so we will simplify discussion by considering only males. Natal philopatry will result in a 'nuclear family', consisting of the dominant pair and their son. However, deaths and social re-arrangements over a number of years can lead to groups with variable relatedness. If the female dies or disperses and is replaced by an

immigrant, then a 'stepmother' group is formed. Similarly, replacement of the alpha male leads to a 'stepfather' group. Another single change in the trio can result in an 'unrelated' group in which each adult is unrelated to either of the others. Thus replacement of individuals can result in groups in which beta males are full-siblings or offspring of the dominant pair, to groups in which they are half-siblings and even to groups in which they are unrelated.

The natal-philopatry method of group formation will mean that any effect of relatedness on reproductive skew predicted by complete or incomplete control models can be confounded by relatedness asymmetry, relative competitive ability of subordinates, incest avoidance (Emlen 1996), and probably female choice of mates. This section explains why.

Relatedness asymmetry is associated with mean relatedness of a son to the offspring of the dominant pair. In nuclear families, mean relatedness is 0.5, in stepmother groups it is 0.25 and in unrelated groups it is 0. However, the relatedness of dominant and subordinate to each other's offspring is asymmetrical in nuclear families but symmetrical in the other types of group. The effect of asymmetry is to make the predictions of the concession and costly control models more similar. In the costly control model, relatedness asymmetry leads to a prediction of high skew in nuclear families despite the general prediction that skew will not be affected or will decline with relatedness. This means that both models predict the highest skew in nuclear families.

The competitive ability of subordinate males may covary with their relatedness to the dominant pair (Emlen 1996). Assuming no death or dispersal of group members, a male who remains on his natal territory will join his mother and father. As years pass, it is likely that one or both of the dominants will be replaced. Thus, because of the way groups with different relatedness form, subordinate males will be older, on average, when with an unrelated female and probably dominant male. This correlation has been documented for White-browed Scrubwrens *Sericornis frontalis* (Magrath 1999).

A covariation of competitiveness and relatedness could come about for other reasons. Individuals which force themselves into groups of unrelated individuals may be competitively superior to those that stay on the natal territory. Second, individuals that have been unsuccessful in gaining paternity may eventually leave groups for that reason (Clutton-Brock 1998). This means that, as time goes by, subordinates are on average more competitive and therefore gain a greater share of paternity. In the meantime, the group may have changed composition, so that they are (incidentally) less related to the dominants. It is even conceivable that the opposite effect could occur, at least at some subordinate ages, if better competitors are more likely to leave the group and acquire breeding vacancies.

Almost all models that have examined the effect of competitive ability on skew predict that, as the subordinate becomes more competitive it will either take or be given a greater share of reproduction. The eviction model is an exception if competitive subordinates suffer reduced ecological constraints on breeding independently. In either case an apparent effect of relatedness on skew could be due to a correlated change in competitive ability of the subordinate.

Finally, incest avoidance also predicts the highest skew in nuclear families (Emlen 1995, 1996). Female control could have the same effect if females avoid incest, avoid young males, only mate polyandrously to increase genetic diversity, or preferentially copulate with unrelated males to enlist their help at the nest.

We now illustrate the problem of distinguishing among a subset of models of reproductive skew, given that relatedness asymmetry and competitive ability will often covary with relatedness. We focus on the predicted patterns of relatedness and skew. To simplify the example, we assume that neither ecological constraints nor the relationship between group size and productivity vary with relatedness. We show that it is not possible to use relatedness alone to distinguish among models using a typical cooperative breeder, even assuming that ecological constraints and group size effects are constant.

Table 1 summarizes the convergence of predictions of the effect of relatedness on skew among a subset of models that follow if subordinates of lower relatedness are also better competitors. We do not use

quantitative predictions because they are relevant only to specific situations and depend on factors in addition to relatedness. The table ranks across different types of group the degree of skew expected within each model. A rank of 'A' means that, within that model, that type of social group would have the most extreme skew or equal most extreme skew. The ranking protocol is that rank 'B' is used after rank 'A', even if more than one type of group has the rank 'A'; the same applies for rank 'C'. The rankings within a model do not have absolute meaning, so that they should not be compared across models. For example, a rank of 'B' for one model does not imply greater skew than a rank of 'C' for another model.

Table 1(i) excludes any confounding effect of relatedness asymmetry or competitive ability. We explain the qualitative rankings of reproductive skew across the four types of group. (1) In the concession model, skew is predicted to be higher when offspring of the dominant male and female are closer relatives to the subordinate male. The offspring of dominants are full-sibs of subordinates in nuclear groups, half-sibs in stepfather and stepmother groups, and unrelated in unrelated groups. (2) In the costly control model, skew will remain constant or increase with a decrease in relatedness. If skew is constant with relatedness, all will have a similar skew of 'A', otherwise nuclear families will have the lowest skew ('C'), and unrelated groups will have the highest skew ('A'). (3) Incest avoidance predicts no reproduction by the subordinate (high skew, 'A') when he is with his mother, but

Table 1. Qualitative predictions from some models of reproductive skew amongst males, illustrating similarity of predictions from models especially when potential confounding effects are incorporated. (i) ignores the effects of relatedness asymmetry and competitive ability; (ii) includes both effects. The text gives a full rationale of ranking. The degree of skew is ranked within models from greatest (A) to least (B, C or D depending on the model). Ranks have no absolute values, and so are not comparable between models. Where the model predicts no difference, the same rank is given. The Table is modified from Magrath (1999).

Type of group*	Model of skew			
	Concession**	Costly control**	Incest avoidance	Female control***
(i) All else equal				
Nuclear	A	A or C	A	A
Stepfather	B	A or B	A	A
Stepmother	B	A or B	B	B
Unrelated	C	A	B	C
(ii) Confounds				
Nuclear	A	A	A	A
Stepfather	B	B	A	A
Stepmother	C	C	B	B
Unrelated	D	D	C	C

* Groups are all trios consisting of a female, alpha male and beta male. Groups are defined by the relatedness of the beta male to the female and alpha male. In nuclear groups, a beta male is with his mother and father; in stepmother groups with an unrelated female and his father; in stepfather groups, with his mother and unrelated alpha; and in unrelated groups, with unrelated female and alpha.

** Asymmetrical relatedness should lead to higher skew than would otherwise be the case in both nuclear families and stepfather groups.

*** Rankings associated with 'female control' assume a female has more to gain by copulating with a beta male that is unrelated to her or the alpha male.

sharing when the mother has been replaced ('B'). (4) The rankings under female control are speculative, but assume that females avoid incest, and would prefer to mate with subordinates that are older or unrelated to the dominant male. While three models predict the (equal) greatest skew in nuclear families, there are differences in the predicted skew among the other types of group which appear to make it possible to distinguish among models.

Table 1(ii) includes potentially confounding effects of relatedness asymmetry and competitiveness. (1) In the concession model, skew is predicted to be higher when offspring of the dominant male and female are closer relatives to the subordinate male. The offspring are full-sibs and relatedness is asymmetrical in nuclear groups, half-sibs with asymmetrical relatedness for stepfather groups, half-sibs with symmetrical relatedness for stepmother, and unrelated with symmetrical relatedness for unrelated groups. The relative competitiveness of subordinates will be lowest in nuclear families and highest in unrelated groups, reinforcing the pattern. (2) In the costly control model, relatedness asymmetry leads to a prediction of high skew in nuclear families and stepfather groups. The relative competitiveness of subordinates will be lowest in nuclear families and highest in unrelated groups, decreasing skew in the unrelated groups. The combination of effects may mean that qualitative predictions are identical to the concession model. (3) The effect of incest avoidance is similar to (i) except that subordinates gain a greater share in unrelated groups because of greater competitiveness. (4) Predictions about female control are similar to (i).

In a review comparing the concession model with models of incomplete control, which is focused primarily on sharing among female mammals, Clutton-Brock (1998) concludes that 'there is no unequivocal evidence that dominant female vertebrates make concessions to subordinates in return for assistance.' His conclusion is based primarily on the problem of confounding variables (including competitiveness and relatedness), and suggests that the problems identified in our review, which focuses primarily on male birds, apply to both sexes and many vertebrates.

Prospects

Although natural variation in birds often shows an increased skew with increased relatedness (Reeve et al. 1998), our review shows that measuring the effects of relatedness alone does not allow discrimination among models. There are, therefore, major empirical problems with determining the causes of variation in reproductive skew within populations, but we believe that there are many ways in which we can make

progress in the development and testing of different models.

Theory

Despite the rapid development of models of skew in the last two years, further development of the following would be useful: (1) models that include the interests of the opposite sex; (2) further models that examine benefits of group membership other than current reproductive sharing or the kin-selected benefit of increased group productivity (e.g. Kokko and Johnstone 1999, Ragsdale 1999); (3) models that explore the potential differences between the sexes in competition within that sex (e.g. Cant 1998, Cant and Johnstone 1999); (4) models that focus on specific types of animals, given that it is unlikely that single models will apply to all species (Johnstone and Cant 1999a provide an example); (5) models that incorporate potential constraints and effects of incest.

Of the above, the first two – the effect of the opposite sex, and additional benefits of group membership – seem likely to be of general importance and yet have received little attention. It seems anachronistic to us that skew theory still focuses exclusively on within-sex interactions; it is as if the field of evolutionary biology was still debating whether female choice was important in the evolution of secondary sexual characteristics in males!

Similarly, work on cooperatively-breeding birds has identified numerous potential benefits to subordinates of natal philopatry and helping other than direct reproduction or kin-selected benefits of helping relatives (Brown 1987, Heinsohn et al. 1990). In an important recent development, Kokko and Johnstone (1999) and Ragsdale (1999) have broadened the scope of skew theory by examining the effect of delayed reproductive benefits to the subordinate, and shown that subordinates will tolerate reduced reproductive sharing (higher skew) if they may ultimately accede to dominance status within the group. It would be interesting to consider other benefits to subordinates of group living or helping, such as increasing skill (Komdeur 1996) or increasing the chance of local dispersal (Ragsdale 1999). From the dominant's point of view, increasing a relative's skill at breeding, or even just allowing relatives a safe haven while they mature, may also be an indirect fitness benefit, and so a dominant may be prepared to pay a short-term cost (a different type of 'concession') – perhaps accepting some depletion of resources on the territory. Kokko and Johnstone's (1999) and Ragsdale's (1999) models support this argument by showing that a dominant may tolerate subordinates even if they reduce group productivity. This benefit to the dominant is similar to the idea of parental facilitation (Brown and Brown 1984).

Controlling confounding variables

Although using variation in relatedness to test models of skew is necessary, it is also important to take into account potentially confounding variables. It might be possible to quantify and control statistically for competitiveness, select cases in which competitiveness is likely to be similar, or reduce the problem by experiment. For example, it may be possible to control statistically for differences in age between dominants and subordinates, as an indirect measure of differences in competitiveness, when examining the effect of relatedness on reproductive skew.

It is also desirable to select species, or types of group, in which it is possible to avoid the confounding effects of asymmetric relatedness and differences in competitive ability (Emlen 1996, 1999, Magrath 1999). For example, it may be easier to test models of reproductive skew in societies in which individuals form relatively even-aged coalitions than in societies with natal philopatry, asymmetric relatedness and extreme differences in competitive ability (Emlen 1996, 1999). In general, plural breeders with extended families may be helpful (Emlen 1999), although there are potentially problems of examining skew in multi-member groups (Johnstone et al. 1999). In the case of groups formed through natal philopatry, it may be most fruitful to focus on group types (e.g. stepmother and unrelated groups) in which relatedness is symmetrical.

Finally, experiments could be used, for example, to increase the proportion of group types in a population that do not suffer from problems of relatedness asymmetry, or to manipulate parameters of importance in models (Emlen 1999).

The best opportunities for controlling confounding variables appear to come from comparisons within populations in which there is a range of group types but other variables can be held constant. Comparisons among populations, and especially species, are likely to be confounded because a difference in one parameter between sites (e.g. habitat constraints) is unlikely to be independent of the other important parameters (e.g. group productivity, demography, competitiveness). At this stage we see little prospect for progress using comparisons among species because of the difficulty in comparing parameters (e.g. habitat constraints).

Testing assumptions

We suspect that the most useful approach in the field will be to focus on testing assumptions and mechanisms, and not (exclusively) predictions of different models. It can be difficult or impossible to distinguish among models on the basis of their predictions, and yet the assumptions of models differ substantially, as do the proximate causes of reproductive skew. For exam-

ple, it may be possible to test the assumption that incest incurs a cost and that subordinates avoid mating with close relatives. In some species of cooperatively-breeding birds, there is evidence for incest avoidance; for example, in Acorn Woodpeckers *Melanerpes formicivorus*, groups may curtail reproduction for years rather than engage in incest (Koenig et al. 1998). In other species, like White-winged Choughs *Corcorax melanorhamphus*, incest is common (Heinsohn et al. 1999). If there is no incest avoidance, it is possible to dismiss one reason for high skew in closely-related groups and avoid one factor confounding the interpretation of other models (Heinsohn et al. 1999).

Similarly, there is little known about proximate mechanisms of reproductive control or control of group membership. There appears to be no direct evidence that subordinate dispersal can be manipulated by reproductive concessions made by dominants (Clutton-Brock 1998), and yet this is a fundamental assumption of concession models. Similarly, it is important to know whether dominants can directly control the reproduction of subordinate members or can just evict them, and whether they have precise control over the magnitude of skew, should they permit subordinate reproduction. What behavioural mechanisms would allow precise control, and how do individuals estimate the actual share of reproduction obtained? One problem of particular importance to vertebrates is that small brood sizes mean that a precise partitioning of reproduction may not be possible or may require keeping track of reproduction over several breeding attempts, which may make assessment of share even more difficult. (Tsuji and Tsuji (1998) and Kokko et al. (1999) consider the more general problem of how to quantify 'reproductive skew' when the number of potential breeders or offspring is variable.)

All models of skew tacitly assume some degree of kin 'recognition' – some behavioural rules which allow differential treatment of individuals of different (average) kinship. This raises the issue of what mechanisms are involved, and what precision of 'recognition' is possible (Keller 1997, Komdeur and Hatchwell 1999). Incest avoidance by males in species with a single female in the breeding group only entails recognising whether the resident female has been replaced or not. By contrast, other models may require very precise kin 'recognition'; for example, distinguishing between older brothers and fathers can be relevant and yet there may be no mechanism by which this could be achieved. Depending on the behavioural constraints on kin 'recognition', models may need to include additional constraints and the predictions may change.

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Process in the evolution of bird migration and pattern in avian ecogeography

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Current ideas about the evolution of bird migration equate its origin with the first appearance of fully migratory populations, and attribute its evolution to a selective advantage generated by increased breeding success, gained through temporary emigration from resident populations to breed in under-exploited seasonal areas. I propose an alternative hypothesis in which migration first appears as a temporary directional shift away from the breeding site outside the reproductive period, in response to seasonal variation in the direction and/or severity of environmental gradients. Fully migratory populations then appear through either extinction of sedentary phenotypes, or colonisation of vacant seasonal areas by migrants. Where colonisation occurs, resident ancestral populations can be driven to extinction by competition from migrants which invade their range outside the breeding season, resulting in fully migratory species. An analogous process drives the evolution of migration between high latitudes and the tropics, since extension of breeding range into higher latitudes may drive low latitude populations to extinction, resulting in an overall shift of breeding range. This process can explain reverse latitudinal gradients in avian diversity in the temperate zone, since the breeding ranges of migratory species concentrate in latitudes where they enjoy the highest breeding success. Near absence of forest-dwelling species among Palaearctic-African migrants is attributable to the lack of forest in northern Africa for much of the Tertiary, which has precluded selection both for southward extension of migration by west Palaearctic forest species, and northward breeding colonisation by African forest species.

(1968, 1985) whose model of the development of the Nearctic/Neotropical migration system is still considered the most plausible scenario for at least some groups of migrants (Lövei 1989, Dingle 1996, Williams and Webb 1996), and has strongly influenced more recent models dealing with the Palaearctic (Safriel 1995), or with Nearctic groups which do not seem to fit Cox's model (Rappole 1995).

A common feature of these models is their identification of the origin of migration with the initial establishment of fully migratory breeding populations, though none has been able to explain how this occurs without an evolutionary 'jump' from sedentary to migratory behaviour. I will propose an alternative model incorporating the idea that partial migration may have formed a critical transition in the evolution of all migratory behaviour (Berthold 1999). The transition from resident to long-distance migrant emerges as a three-stage process, starting with the origin of the migratory habit, followed by the establishment of fully migratory populations, and ending with the disappearance of ancestral resident populations. First I will examine the reasoning behind previous explanations of this transition.

Evolutionary explanations of bird migration must account for the complete transition from a sedentary ancestral state, to long-distance trans-continental and trans-oceanic migration. The approach to this problem has been largely dominated by the thinking of Cox

Current theories

Previous theories recognise only two main stages in the evolution of migration, since the evolution of the migratory habit, and the establishment of fully migratory populations, are thought to occur simultaneously.