Reproductive skew, concessions and limited control

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Models of reproductive skew in cooperative and eusocial societies suggest that dominants allow subordinates to breed to induce them to remain peaceably in the group. However, it is not yet clear how widely the assumptions of these models apply to animal societies, and many of the trends that they predict are consistent with the simpler suggestion that there is a struggle for reproduction between dominants and subordinates, whose outcome depends on the potential costs and benefits of the contest to both parties. Models of reproductive skew that incorporate contests of this kind and empirical studies that can discriminate clearly between reproductive concessions and failures of control are now needed.

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In some social animals, a single female in each group produces most or all of the young, and subordinate females rarely breed until they attain a dominant position. In others, reproduction is more equally distributed among adult females, and most, or all, adult females breed. Groups where a small proportion of females breed at any one time are said to show high reproductive skew, whereas those where breeding is more equally distributed show low reproductive skew[1]. Similar contrasts in skew occur in the distribution of male mating success in groups that include multiple males.

Reproductive concessions

Understanding the reasons for differences in reproductive skew has become one of the principal focuses of research on cooperative breeding[1–3]. Research on the control of reproductive skew was stimulated by models produced more than a decade ago[4–9], which investigate the reproductive strategies of dominants and subordinates under a range of ecological and social conditions and make the assumption that dominants can control the incidence of subordinate reproduction. In particular, they argue that subordinates should be reluctant to disperse from their natal group if the chances that they will survive and breed are low and suggest that, under these conditions, subordinates might remain for protracted periods in their natal groups, even if they are prevented from breeding by the dominant. Subsequent empirical studies have provided extensive support for these predictions[1–3].

One important component of most models of reproductive skew is the suggestion that, where the presence of subordinates increases the fitness of dominant breeders, dominants may allow subordinates to breed in order to retain them in the group. Recent models of reproductive skew in insect societies[1,10] have attempted to predict the level of reproduction necessary to induce subordinates to stay in the group ('staying incentives') or to forego challenging the dominant ('peace incentives'). I refer to this component of reproductive skew theory as 'concession' theory to emphasize its reliance on the suggestion that dominants make reproductive concessions to subordinates and to distinguish it from other predictions about reproductive skew.

Concession theory suggests that where (1) the presence of subordinates increases the fitness of dominants, (2) subordinates are less likely to emigrate or to challenge the dominant if they are allowed a measure of reproduction, and (3) dominants can control the breeding attempts of subordinates without suffering a cost, the frequency of subordinate breeding and the degree of skew will be affected by four principal parameters: the relative fitness of subordinates that disperse to form new breeding units versus those that remain in the group; the subordinate's contribution to reproductive success in the group; genetic relatedness between group members; and the probability that a subordinate will win a lethal fight with a dominant without being severely injured[1]. Predictions derived from these ideas are that skew should be high where:

- The chance that subordinates will disperse and breed successfully is low (because only a small incentive is required to induce subordinates not to emigrate if the net benefits of other options are low).
- Subordinates are unlikely to challenge the dominant successfully.
- Subordinates are closely related to dominants (because related subordinates will gain larger indirect benefits from cooperating with the dominant than unrelated individuals and will consequently require smaller incentives to stay and cooperate).
- The subordinate's contribution to the productivity of the colony is high (because the larger this contribution is, the less the subordinate needs to be compensated for remaining in the group).

It is suggested that models of reproductive skew incorporating concession theory provide a general framework for predicting the distribution of reproduction in cooperative and eusocial species of vertebrates, as well as invertebrates[1], and a range of empirical studies have produced results consistent with their predictions. For example, across different species of social and eusocial insects, high relatedness between foundresses is commonly associated with high skew[10,11]. Similarly, among cooperative vertebrates, high levels of skew are typical of species (e.g. the naked mole-rat, *Heterocephalus glaber*) for which the chances of subordinates dispersing and establishing novel breeding groups are low[1,12]. Several intraspecific trends are also consistent with the predictions. In dwarf mongooses (*Helogale parvula*), for example, older subordinate females are more likely to disperse or to challenge the dominant female than younger ones and are also more likely to breed[13], and subordinate males that breed are less closely related to the dominant male than those that do not[14]. In African lions (*Panthera leo*), large coalitions of males show both a higher coefficient of relatedness and higher reproductive skew than smaller coalitions[15].

Recent reviews have emphasized the success of concession theory in predicting the distribution of subordinate breeding and reproductive skew[1–3,16]. But how widely do the assumptions of concession theory apply to vertebrates? Are there other evolutionary frameworks that make similar predictions or are consistent with the same trends? In particular, is it possible that the frequency of subordinate breeding (and the degree of skew) depends principally on the dominant's capacity to control reproduction in subordinates[17]?

How widely do the assumptions of concession theory apply?

Although all three assumptions of concession theory probably hold in some cases, none of them applies to all eusocial or cooperative animals. In some cases, retention of individual helpers is unlikely to provide sufficient benefits to the dominant to offset the disadvantages associated with an additional breeder. The presence of nonbreeding subordinates can have little effect on the fitness of dominants[18–21],

  0169-5347/98/$19.00 PII: S0169-5347(98)01402-5

whereas breeding subordinates commonly (although not invariably) lower the success of dominants[14,22–24]. There is also little firm evidence that reproductive concessions reduce either the probability that subordinate females will emigrate or the risk that they will challenge the dominant. It would not be surprising if subordinate females that managed to breed were more likely to challenge dominants, or if those that failed to displace dominants were more likely to emigrate than nonbreeders. Finally, although dominants entirely control the reproduction of subordinate females in some social insects[25] and can induce hormonal changes and infertility of females in some social mammals[26,27], reproduction by subordinate females still occurs and this often appears to happen where dominants fail to control subordinates[28,29]. For example, in colonies of naked mole-rats, dominant females are sometimes unable to suppress the reproductive activity of subordinates, some of which develop perforated vaginas and enlarged nipples and sometimes breed as secondary females[27,30]. This can occur during late pregnancy when the dominant females are relatively immobile. Similarly, although dominant female wild dogs (*Lycaeon pictus*) may persistently attack subordinates that attempt to breed, the subordinates can sometimes avoid the dominant's control by giving birth in a separate den and only moving their pups back at an age when the dominant female is unlikely to kill them[31,32]. Hormonally mediated reproductive suppression of subordinates is less common in males (although in naked mole-rats and African wild dogs, subordinate males do show lower testosterone levels than dominants) and dominant males typically attempt to prevent subordinates from breeding by restricting their opportunities to mate[28,33].

The presence of overt conflict suggests that subordinate reproduction might occur where dominants are unable to prevent subordinates breeding or where the costs of suppressing subordinates outweigh the benefits[8,9] (although this need not necessarily be the case because dominants could use the responses of subordinates to assess the necessary magnitude of incentives required to make them stay or to prevent competition). Where dominants do not have full control of subordinates, the level of subordinate breeding probably represents the outcome of a struggle between dominants and subordinates. If so, predictions about the degree of skew will need to consider the costs and benefits of winning to subordinates as well as to dominants[2,3,8,9]. High costs of competing or low benefits of breeding to subordinates are likely to lead to high skew (Box 1), whereas high costs or low benefits of suppression to dominants will lead to subordinate breeding and low skew (Box 2)[17,19,34].

Box 1. Constraints on subordinate breeding

The costs to subordinates of attempting to breed could include:

- The costs of losing a contest (which may include ejection from the group or death as a result of subsequent persecution by the dominant).
- The costs of successful breeding to the subordinates' survival or subsequent breeding success (which may often be greater than for dominants if subordinates are younger, smaller or thinner or if other group members are less likely to assist them).
- Any effects of subordinate reproduction on the fitness of related dominants (and hence on the inclusive fitness of the subordinate breeders themselves), such as the consequences of raising brood size above the optimum[35] or the costs of inbreeding to relatives.

The benefits of breeding to subordinates will vary, affecting their optimal expenditure on contests with dominants and, in extreme cases, favouring a delay in breeding. The benefits of breeding to subordinates may be low where:

- Subordinates are younger, smaller or thinner than dominants and their offspring are consequently less likely to survive.
- Subordinate breeding raises combined brood size above the optimal level to the detriment of the subordinate's offspring[35].
- Other group members give subordinates less assistance than dominants and this reduces the survival or breeding success of offspring born to subordinates.
- Dominants are able to eject their eggs, destroy their nests or kill their offspring.
- Confidence of parentage is lower for subordinates than dominants.
- Only related adults of the opposite sex are available for mating and progeny born to inbred matings show low fitness[3,34].

Box 2. Constraints on the suppression of subordinate breeding by dominants

Where dominant animals do not have full control of subordinate reproduction, the following intuitive predictions are plausible on the basis of our current understanding of social relationships:

- Effective suppression is more likely where there is a substantial difference in the Resource Holding Potential (RHP) between dominants and subordinates[2]. Suppression is most likely to break down at times when the dominant's RHP advantage is reduced (e.g. when resources are super-abundant and relative RHP has little effect on condition).
- Suppression is likely to be achieved more easily where there is a well-established dominance relationship between subordinates and dominants. In addition, daughters should be more likely to allow themselves to be suppressed by mothers (who will produce full sibs) than by sisters (whose progeny will be less closely related to them) unless the mother has re-mated[34,36].
- Suppression is likely to be more complete where breeding subordinates and their offspring cannot evade close interactions with dominants. Thus, effective suppression might be more common in species where group members have a sleeping chamber (as in many cooperative rodents and some carnivores) than in species where females feed and sleep at some distance from each other (as in many social primates).
- Subordinate reproduction might occur more often where the costs of suppression to dominants are relatively high; for example, the risks of suppression to the dominant could rise where subordinates carry potentially lethal weapons, such as large canines, so that aggressive interactions can have high and unpredictable costs.
- Failures of suppression are more likely to occur where subordinates have access to unrelated breeding partners (Box 1). Conversely, subordinates should be most likely to allow themselves to be suppressed where only close relatives are available as potential partners.
- Failures of suppression are more likely to occur where it is in the interests of other members of the group to encourage them to breed; for example where females court subordinate males to enlist their assistance or support[19].

Tests of concession theory

If we assume that dominants do not always have total control of reproduction among subordinates, many of the results cited as examples of reproductive concessions can be interpreted in other ways[34,37]. To take a general example, relatives that have been born into the same group as the dominant may often be more completely suppressed than unrelated individuals simply because they are younger, smaller, less developed and more closely related to the opposite sex breeder than are unrelated immigrants. Among marmosets and tamarins, for example, suppression of fertility fails with greater frequency when subordinate females have the opportunity to interact and potentially mate with an unrelated male[29]. Similarly, animals that have a higher chance of emigrating and breeding successfully may be more likely to breed before dispersing because they are larger, older, stronger, less closely related to the opposite sex breeder and, consequently, are harder to suppress, rather than because they require larger incentives to remain in the group.

Few, if any, of the vertebrate studies cited as examples of reproductive concession can rule out alternative interpretations of this kind. For example, Creel's remarkable studies of dwarf mongooses are commonly cited as evidence supporting the predictions of reproductive concession models[1,3]. Here, most subordinate females do not become pregnant but 15% of pups have subordinate mothers[28]. The probability that subordinate females will disperse and breed successfully in other groups increases with their age so that the 'staying incentive' required by subordinates rises as animals become older[13,28]. Creel and Waser[13] show that the distribution of breeding by subordinate females increases with age at approximately the rate predicted by concession theory, indicating that dominant females allow them enough reproduction to retain them in the group[13,28]. But other models could predict the same trend. Perhaps older subordinates breed because they are more able to resist attempts by animals to suppress them, or perhaps they are less closely related to breeders of the opposite sex. The observed correlation (0.67, explaining 45% of the variance) between predicted staying incentives and observed levels of reproduction could occur because the dominant female's ability to control subordinates declines as their age increases. Alternatively, the correlation may arise because older subordinates that do not manage to breed in their natal group are progressively more likely to disperse, thus removing themselves from the sample of resident subordinates.

Packer's outstanding study of lions is also commonly cited as evidence of reproductive concessions[1]. In African lions, coalitions of 2–7 males defend access to groups of 2–18 females that often breed synchronously[15,38]. Male breeding success increases with coalition size because larger coalitions are better able to win access to female groups and to maintain residence in them for longer periods. In larger coalitions, a proportion of males usually fail to breed and the (standardized) variance in male success increases with coalition size. Packer's results show that coalitions involving unrelated males show lower skew than those involving relatives and are commonly cited in support of reproductive concession theory. However, as Packer and his co-workers note[15], unrelated males usually form coalitions with one other male, and the reduced skew typical of coalitions involving unrelated animals may be attributable to their small size. The lower skew found in small coalitions could also be a by-product of the breeding system. Females within a pride commonly enter oestrous synchronously. Consequently, individual males may be unable to monopolize more than one mating partner effectively. In small coalitions, breeding success will commonly be divided between partners but, in larger coalitions, two males can monopolize most oestrous females so that additional members of the coalition will fail to breed, causing skew to increase.

I have focused on these two studies because more is known of the breeding system and of the origin of group members than in many other studies. As examples of reproductive concessions, other intraspecific comparisons of skew in vertebrates[24,39–42] suffer from similar problems to a greater or lesser degree. Interspecific comparisons have similar limitations. For example, the tendency for subordinate reproduction to be relatively uncommon where successful dispersal is rare might occur because a high proportion of adult subordinates have been born in the group and, therefore, lack access to unrelated mating partners. As a result, the tendency for reproductive skew to increase where groups consist of close relatives[17] does not necessarily provide support for concession theory.

The problems of distinguishing between reproductive concessions and the effects of limited control emphasize the need to identify contrasting predictions derived from these two frameworks. Predictions concerning the effects of relatedness on skew could offer one of the best possibilities. New models by Reeve, Emlen and Keller[17] consider situations in which subordinate reproduction is decided by a struggle between dominants and subordinates and incorporate many of the factors discussed here (Boxes 1 and 2). In contrast to concession theory, these models predict that reproductive skew should either decline or be unaffected by the degree of relatedness between dominants and subordinates. This is because relatedness between dominants and subordinates generates indirect compensations to the inclusive fitness of losers that are derived from the enhanced breeding success of the related winner. Where these benefits are symmetrical, the degree of relatedness may have no influence on the relative investment of both parties in the struggle and on the degree of skew[17]. However, pronounced differences in breeding potential between dominants and subordinates, or the capacity for dominants and subordinates to make sequential decisions (R. Johnstone, pers. commun.), is likely to complicate these predictions. Moreover, like previous concession models, the 'limited control' models by Reeve *et al.* focus on interactions between pairs of dominants and subordinates. Where multiple subordinates are involved, relationships could be more complex.

In the future, it will be useful to compare the degree of skew in societies where the subordinates' contribution to the care of the young varies. As yet, it is not obvious that there is a close association between the amount of assistance provided by subordinates and the frequency of subordinate reproduction. Subordinate reproduction and low levels of skew occur widely in social species where subordinates give little direct assistance to dominants and may compete with them for food or breeding opportunities[43–45]. In contrast, high levels of skew are found in many cooperative species where subordinates play an important role in caring for the young. Similarly, differences in the extent to which male and female subordinates contribute to the care of the young do not appear to be consistently associated with sex differences in the degree of skew.

Conclusions

What, therefore, should be concluded? First, the assumptions of concession theory are unlikely to apply to all social animals. In vertebrates, there is little evidence that reproductive concessions induce subordinates to remain peaceably in the group, and it is clear that dominants do not always control subordinate reproduction. Second, many of the trends in skew predicted by concession theory are also predicted by models based on limited control[17], whereas the range of circumstances under which concession and limited control models make opposing predictions is not yet clear. Third, there is no unequivocal evidence that dominant female vertebrates make reproductive concessions to subordinates in return for assistance. The vertebrate breeding systems that appear most likely to fit the assumptions of concession models are probably the multimale–multifemale societies in which males form coalitions to gain access to females[46–48]. Here, males are unlikely to maintain alliances unless they benefit from them, individuals can easily change alliances, and males that do not retain their alliance partners run the risk that they will form rival alliances and become competitors. All three characteristics should encourage dominant animals to allow their partners a measure of reproduction.

So what is the way ahead? First, new models of reproductive competition need to be developed that incorporate the costs and benefits to subordinates of attempting to breed and, to dominants, of attempting to suppress subordinate reproduction. In addition, cases where different models make opposed predictions need to be identified. The new model of Reeve *et al.* of reproductive skew for situations of limited control represents an important development[17], although models that consider the interests of more than one subordinate at a time are also needed. Second, better empirical evidence of the extent to which the assumptions of different models apply is required. In particular, we need to know: how commonly the benefits (to the dominant) of the presence of an additional subordinate exceed the costs of plural breeding; whether reproduction by subordinates lowers or raises the chance that they will emigrate or challenge for the dominant position; and to what extent dominants control reproduction among subordinates. Third, there is an urgent need for critical tests to discriminate between cases where dominants make concessions to subordinates and cases where they cannot control them. Experimental studies will probably be necessary to achieve this. One possible approach would be to manipulate the dominant's need for assistance by increasing litter size or reducing the number of helpers while holding the age, size and immigration status of the subordinates constant.

Finally, although it is important to pursue explanations offering the greatest generality, it is unlikely that any single model will account for the distribution of subordinate breeding and reproductive skew in all cooperative and eusocial societies. There are fundamental differences between eusocial invertebrates and cooperative vertebrates that are likely to have profound effects on the selective forces operating on breeders and helpers. In particular, it may seldom be feasible for viviparous animals to develop highly specialized, immobile queens that can absorb the reproductive efforts of large numbers of helpers, and this could strengthen selection favouring reproduction in subordinates. Similarly, differences in mobility between birds and mammals that affect the capacity of individuals to monitor breeding opportunities in adjacent areas might influence both the frequency of extra-group copulations and the capacity of subordinates to escape from damaging attacks by dominants, all of which are likely to affect the costs or benefits of breeding to subordinates and the degree of reproductive skew. To predict reproductive skew, we may need to recognize these contrasts, building different models with different assumptions to fit different situations.

Acknowledgements

I am grateful to Peter Brotherton, Paul Sherman, Kern Reeve, Mike Cant, Sue McRae, Laurent Keller, Marthe Hanser, Rosie Cooney, Rosie Woodroffe, Scott Creel, Rufus Johnstone, Berni Crespi, Steve Emlen and Frances Ratnieks for discussion, comments or access to unpublished papers.

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Improving biological control

Nature Wars: People vs. Pests

by Mark L. Winston

Harvard University Press, 1997.
£16.50/$24.95 hbk (x + 210 pages)
ISBN 0 674 60541 1

Thirty six years ago, Rachel Carson's *Silent Spring*[1] dramatically raised public consciousness about the environmental and public health dangers of the unrestricted use of pesticides. Dismissed at the time by sections of the agrochemical industry as 'hogwash', and the author personally abused, the book nevertheless contributed to a sea change in pesticide policy – DDT and other toxic first-generation chemicals went; a huge and complicated regulatory process was imposed on the agrochemical industry; and Western governments invested massive sums in research on biological pest management. Equally significant was that public perceptions of farmers and chemical companies changed for ever. From war-time heroes feeding the country and de-lousing the troops, they became at best just another business sector and at worst, to many people, despoilers of the countryside and pedlars of lethal substances.

In this book, Mark Winston, an applied ecologist from Canada, argues that although there have certainly been improvements since Carson's day, the near-absolute dependence of farming on chemical pest management remains the same (Winston writes almost exclusively about the USA and Canada, but most of what he says also applies to other developed countries). Biological pest management, so dear to Carson's heart, has, with few exceptions, made little impact on farming, is largely confined to specialized niche markets, is ignored by industry and generates an amount of revenue that is dwarfed by that of the chemical pesticide industry. In a series of extended essays on successful and unsuccessful applications of biological pest management, Winston analyses why progress has been so slow and argues for 'a new pest ethic' to reduce pesticide application. This book is not a new *Silent Spring*; virtually all the arguments and ideas it contains have been aired before. However, it is an extremely coherent and concise statement of progressive thinking on how to manage agricultural pests – to me, it positively exudes good sense and rationality. I strongly recommend it to anyone who has thought twice about biting into a shiny apple on a supermarket shelf.

The reasons why farmers are so hooked on chemical pesticides are not hard to fathom. Chemicals both work in the short term and can be seen to work. More environmentally friendly alternatives often don't work as well, are more complex to implement and are more expensive. The public tolerates such a low level of damage that farmers effectively have to eradicate rather than control pests. Regulatory agencies concentrate, inordinately in Winston's view, on pesticide toxicity to humans rather than seeing pesticide reduction as a major part of their brief. To combat this, Winston feels that chemical pesticides ought to be seen as a last, rather than a first, resort, and wants a shift in emphasis from eradicating to managing pests, and an end to prophylactic spraying.

This may just seem an Integrated Pest Management (IPM) retread, but Winston fleshes out the good intentions (arguing, by the way, that the concept of IPM now often just means using several pesticides rather than one). He discusses, quite briefly, how both the consumer and the farmer need to be educated to accept the odd blemish on an orange, and to be weaned off the quick fix of insects lying on their back after a spray. He follows Pimentel in advocating that the indirect environmental and health costs of pesticide damage should be charged to the chemical companies and farmers, even if this leads to higher food prices. But it is on improving alternatives to chemical pesticides that he has most to say, largely through discussing a series of case histories.

Winston is hard on applied entomological research, arguing that much of its concentration on pheromones, semiochemicals, predators and parasitoids, although scientifically fascinating, has only had a modest impact on the farm. The problem is not the basic research *per se*, but that research is poorly coordinated, with the end-use and end-user poorly defined and often with no clear route from the laboratory to the farm. He illustrates successful and unsuccessful applications of biological pest management by bravely wading into North American codling-moth politics. This tortricid moth (*Cydia pomonella*) is the major pest of apple orchards throughout the world. Western consumers won't buy apples damaged by moth larvae ('worms'), and relatively small infestations render crops worthless. In the Okanagan Valley in British Columbia, a very expensive sterile-male release programme looks like failing. In contrast, control measures based on pheromone disruption in the Pacific States of the USA are having modest success, with an increasing (though small) acreage controlled in this way. Winston contrasts the overselling of the sterile-release programme, with its big science facilities and spiralling costs, with the much more pragmatic, low-key and extension-based pheromone disruption programme.

The two areas of biological pest control that have been enthusiastically embraced by industry concern *Bacillus thuringiensis* (Bt)

