
Social queuing in animal societies: a dynamic model of reproductive skew

Hanna Kokko and Rufus A. Johnstone

Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK (h.kokko@zoo.cam.ac.uk)

Previously developed models of reproductive skew have overlooked one of the main reasons why subordinates might remain in a group despite restricted opportunities to breed: the possibility of social queuing, i.e. acquiring dominant status in the future. Here, we present a dynamic ESS model of skew in animal societies that incorporates both immediate and future fitness consequences of the decisions taken by group members, based on their probability of surviving from one season to the next (when post-breeding survival probabilities drop to zero, our analysis reduces to the model produced by Reeve and Ratnieks in 1993, which considered only a single breeding season). This allows us to compare the delayed benefits of philopatry and the immediate opportunities for independent breeding. We show that delayed benefits greatly reduce the need for dominants to offer reproductive concessions to retain subordinates peacefully in the group. Moreover, this effect is strong enough that differences in survival have a much greater impact on the group structure than differences in other parameters, such as relatedness. When the possibility of acceding to dominant status is taken into account, groups where the dominant completely monopolizes reproduction can be stable, even if they consist of unrelated individuals, and even if subordinates have a reasonably high probability of winning a fight for dominance. Finally, we show that stable groups are possible even if association leads to a decrease in current productivity. Subordinates may still stand to gain from group membership under these circumstances, as acquiring breeding positions by queuing may be more efficient than the attempt to establish a new territory. At the same time, the dominant may be unable to exclude unwelcome subordinates, may enjoy increased survival when they are present, or may gain indirect benefits from allowing relatives to stay and queue for dominance. We conclude that reproductive skew in animal groups, ranging from eusocial insect colonies to mating aggregations (leks), will be strongly influenced by the future prospects of group members.

Keywords: benefits of philopatry; cooperative breeding; delayed dispersal; queuing; reproductive skew theory; resource inheritance

1. INTRODUCTION

In most types of animal group, the benefits of association are unevenly shared among group members. In cooperatively breeding groups (families; reviewed in Emlen (1995, 1997)), foraging groups (Ranta *et al.* 1993) and leks (Mackenzie *et al.* 1995; Widemo & Owens 1995), for example, dominant individuals often enjoy a disproportionately large share of reproduction, food or mates. However, a group will only prove stable if subordinate members receive a large enough share of such benefits to make staying worthwhile, since they will otherwise depart. Models of reproductive skew (e.g. Vehrencamp 1979, 1983*a,b*; Reeve & Ratnieks 1993; Reeve 1998; Johnstone *et al.* 1999) have therefore suggested that in breeding groups, dominants may have to concede a share of reproduction which they might otherwise have claimed for themselves, in order to retain subordinates in the group (though see Cant 1998; Clutton-Brock 1998; Reeve *et al.* 1998; Cant & Johnstone (1999), for alternative explanations for incomplete skew). Such concessions can prove worthwhile, from a dominant's perspective, when the contribution of subordinates to group productivity outweighs the share the dominant must yield.

In emphasizing the need for reproductive concessions, however, models of reproductive skew have overlooked one of the main reasons why subordinates might remain in the group: the possibility of inheriting dominant status (and hence control over local resources) in the future (Wiley & Rabenold 1984; Koenig *et al.* 1992; Zack & Stutchbury 1992; Lucas *et al.* 1997; Ragsdale 1999). In temporally stable groups, a reassessment of membership needs to be made each time a member dies or leaves, and individuals often take over superior positions according to age (although precedence may be reassessed in fights and challenges). When some degree of hierarchy is preserved over time, one can speak of a queue towards dominant status. Social queues of this kind are widely recognized in animal societies (e.g. Kuester & Paul 1988; Blanckenhorn & Caraco 1992; Zabel *et al.* 1992; Herrera & MacDonald 1993; Holekamp & Smale 1993; Creel & Waser 1994; Poston 1997; Field *et al.* 1999) and provide a compelling reason for subordinates to remain (Wiley & Rabenold 1984), even in the absence of reproductive concessions.

In this paper, we present an ESS model of reproductive skew that takes into account the delayed benefits of staying in the local group, i.e. the possibility of

subordinates acceding to breeding status following the death of the current dominant. Our model is based on the framework of Reeve & Ratnieks's (1993) concession model. However, while they focus on only a single breeding season, we assess the lifetime fitness consequences of the actions that group members may take, based on their probability of surviving from one season to the next. The resulting dynamic skew model enables us to compare both immediate and delayed advantages of staying versus dispersing using a common currency of lifetime inclusive fitness. In this way, we aim to determine how group formation and reproductive skew are influenced by the future prospects of group members (see Ragsdale (1999), for an alternative analysis of this problem, which was developed independently of our own). While our model is phrased in terms of reproductive skew theory in cooperatively breeding societies, it is applicable to many kinds of group in which the benefits of association are unequally shared among members.

2. THE MODEL

We consider the smallest possible group (and thus the shortest possible queue), which comprises two individuals: a dominant and a subordinate. We assume that dominance is determined by priority, so that the most recent arrival is subordinate. The two-person game we present can be considered an extension of the skew model of Reeve & Ratnieks (1993), as it reduces to their analysis if the number of breeding cycles is restricted to one. Other models of reproductive skew, such as those assuming incomplete control (Cant 1998; Reeve *et al.* 1998), multiple group members (Johnstone *et al.* 1999) or dominant bidding (Reeve 1998), could be similarly extended to encompass future benefits.

Many of the model parameters are retained from earlier skew models (a complete list of symbols is given in table 1). The productivity of the group, k , is now measured during one breeding cycle, whereas the fitness of an individual accumulates throughout her lifetime. As in the Reeve & Ratnieks's (1993) model, we assume that the productivity (per time unit) of a lone breeder equals one. However, we do not make their assumption that $k > 1$, as the presence of a queuer waiting for future benefits does not necessarily improve the current productivity of the group. The variable x is defined as the probability that an individual who departs becomes established as a lone breeder. Low values of x have thus been described as indicating strong 'ecological constraints' (Reeve & Ratnieks 1993). While we continue using this terminology here, we emphasize that the establishment probability is also influenced by the life history of the species (see § 3). Finally, the probability that a subordinate wins a lethal fight against the dominant is f , and the fraction of group productivity that the dominant yields to the subordinate is denoted p .

We proceed with the development of the dynamic skew model in three steps. First, we introduce survival probabilities from one breeding season to the next, investigate how survival affects the probability that a subordinate eventually inherits the dominant position, and derive expressions for lifetime inclusive fitness for dominants, subordinates and lone breeders. Second, using these expressions, we consider whether staying incentives

Table 1. *Symbols used in the model, and their explanation*

a	probability of a lone breeder being joined by a subordinate before the next breeding season
f	subordinate's fighting ability, expressed as the probability of a subordinate winning a lethal fight against a dominant
k	productivity of a dominant–subordinate group, relative to that of a lone breeder
p	reproductive concession, i.e. fraction of reproduction that a dominant gives to a subordinate
p_s	staying incentive, the value of p needed to prevent dispersal of a subordinate
p_p	peace incentive, the value of p needed to prevent a subordinate from starting a lethal fight
r	relatedness between the dominant and the subordinate
s_D	survival (from one breeding season to the next) of a dominant
s_S	survival of a subordinate
s_L	survival of a lone breeder
$w_D(p)$	expected lifetime direct fitness of a dominant aided by one subordinate
$w_S(p)$	expected lifetime direct fitness of a subordinate that may become a dominant in the future
$w_L(p)$	expected lifetime direct fitness of a lone breeder that may be joined by a subordinate in the future
x	probability of a dispersing individual becoming established as a lone independent breeder

(concessions of reproduction given by a dominant to make the subordinate stay) are needed for group stability. Third, we similarly investigate the need for peace incentives (concessions given to make the subordinate refrain from fighting for dominance).

(a) *Fitness in a dynamic setting*

We denote survival probabilities from one breeding cycle to another by s_D , s_S and s_L for a dominant (with a subordinate present in the group), a subordinate and a lone breeder, respectively. It follows that a subordinate who stays in the group will eventually inherit the local resource and become (initially) a lone breeder at that site with probability

$$q = s_S(1 - s_D) + s_S^2 s_D(1 - s_D) + s_S^3 s_D^2(1 - s_D) + \dots$$

$$= s_S(1 - s_D) \sum_{i=0}^{\infty} (s_D s_S)^i = \frac{s_S(1 - s_D)}{1 - s_S s_D}. \quad (1)$$

The value of q and hence the importance of queuing generally increases with survival, although queuing becomes less successful in cases where dominants are very long-lived while subordinates lag behind in their survival prospects (figure 1).

Ignoring relatedness and all details of the dynamic fitness prospects when establishing a breeding site, equation (1) already suggests that queuing can dramatically increase the stability of groups. An individual will benefit from staying within the group if the probability of inheriting the local resource is greater than the probability of breeding elsewhere (i.e. $q > x$), even if it is completely unrelated to the dominant, has no chances of challenging the dominant's status and never gains any reproductive concessions from the dominant. The simple probability

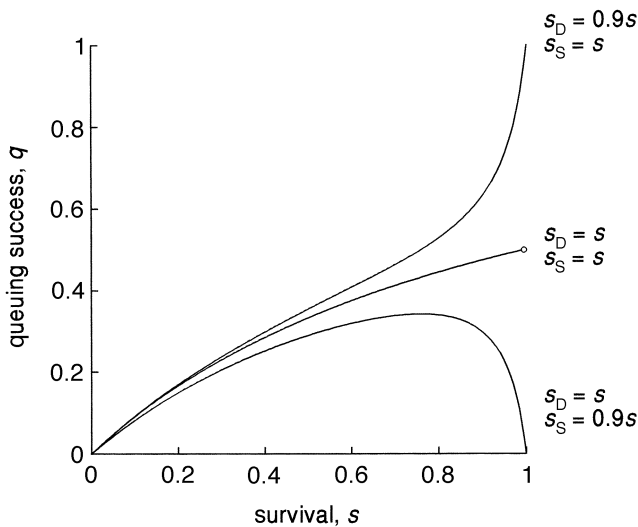


Figure 1. Queuing success q (the probability that the waiting subordinate outlives the dominant) as a function of survival. Curves from top to bottom give cases where subordinate survival exceeds dominant survival, the two survival values are equal (excluding the point $s_D = s_S = 1$, which assumes immortality and produces a singularity in equation 1), and where the subordinate has a survival disadvantage. An unrelated individual who does not gain reproductive concessions will attempt to stay in the group whenever queuing success exceeds its chances of independent reproduction, i.e. $q > x$. Queuing success q increases with increasing survival, except in the case where survival of dominants is very high and exceeds subordinate survival.

that the subordinate will outlive the dominant is enough to form the benefit.

In a more complete model, we need to take into account relatedness r , as well as possible time-lags in acquiring a new subordinate if there is currently none. The latter is incorporated as the probability a of a solitary breeder being joined by a subordinate during the time span of one breeding cycle. We start by defining $w_D(p)$, $w_S(p)$ and $w_L(p)$, the expected direct lifetime fitness of a dominant, a subordinate and a lone breeder, respectively, when the reproductive share for the subordinate equals p . By adding current breeding success to the future component of fitness, which is scaled by the transition probabilities to each stage, we get

$$\begin{aligned} w_D(p) &= k(1-p) + s_D\{[s_S + (1-s_S)a]w_D(p) \\ &\quad + (1-s_S)(1-a)w_L(p)\}, \\ w_S(p) &= kp + s_S\{s_D w_S(p) + (1-s_D)[aw_D(p) \\ &\quad + (1-a)w_L(p)]\}, \end{aligned} \quad (2)$$

$$w_L(p) = 1 + s_L[aw_D(p) + (1-a)w_L(p)].$$

Solving for $w_D(p)$, $w_S(p)$ and $w_L(p)$ gives the solutions

$$w_D(p) = \frac{k(1-p)[1 - (1-a)s_L] + s_D(1-s_S)(1-a)}{[1 - (1-a)s_L](1-s_D s_S) - a s_D(1-s_S)},$$

$$w_S(p) = \frac{(1-a)s_S(1-s_D)(1-s_S) - k\{p(a(s_D+s_S-s_L) + s_D s_S[1-2a-(1-a)s_L] + s_L-1) - a(1-s_D)s_S\}}{(1-s_D s_S)\{[1 - (1-a)s_L](1-s_D s_S) - a s_D(1-s_S)\}}$$

$$w_L(p) = \frac{(1-s_D s_S) - a[s_D(1-s_S) - k(1-p)s_L]}{[1 - (1-a)s_L](1-s_D s_S) - a s_D(1-s_S)}. \quad (3)$$

(b) Staying incentives

A staying incentive p_s is intended to make staying a better option for the subordinate than leaving. To solve p_s , the following questions must be asked (see Reeve & Ratnieks 1993):

- (Si) Does the subordinate stay if $p_s = 0$?
- (Sii) If not, is there a minimum value $0 < p_s \leq 1$ that makes the subordinate stay?
- (Siii) Does the dominant do best to offer this value of p_s ?

We note that question (Siii) needs to be asked even if $p_s = 0$ is acceptable to the subordinate, since individuals waiting for future success do not necessarily increase the productivity of the group (i.e. k need not be greater than 1). The outcome of a case where waiting without reproduction ($p_s = 0$) is accepted by the subordinate, but not by the dominant, depends on whether forceful ejection from the group is possible (see § 3).

The questions (Si)–(Siii) translate to the following conditions:

- (Si) Subordinate stays with $p_s = 0$ if $w_S(0) + r w_D(0) \geq (x+r)w_L(0)$.
- (Sii) If not, subordinate requires staying incentive p_s defined by $w_S(p_s) + r w_D(p_s) = (x+r)w_L(p_s)$.
- (Siii) Dominant does best to yield staying incentive if $w_D(p_s) + r w_S(p_s) \geq (1+rx)w_L(p_s)$.

Substituting equation (3) into conditions (Si)–(Siii) yields solutions (not shown because of their length) that confirm the queuing advantage: stable, cooperative associations can form even between completely unrelated individuals because of the interest of subordinates in inheriting the resource. The need for reproductive concessions is reduced when survival increases (figure 2*a,b*), although an exception is again found in cases where dominant survival is very high and subordinates suffer a survival disadvantage (figure 2*c*). Although high relatedness reduces the concessions needed (as in the classical skew model), changes in survival have a much stronger effect than relatedness. Concessions are not needed at all in almost all cases where reasonably high survival (say, $s > 0.5$) combines with a reasonable degree of ecological constraints (say, $x < 0.5$) (figure 2; note also that positive survival from one season to the next, $s_S > 0$, and not positive relatedness $r > 0$, is the key factor that determines whether stable groups can exist without concessions). It should be noted that ecological constraints x , which also strongly influence the stability of groups, are also partly determined by survival: x equals the probability that a leaving individual will end up establishing a new breeding site and has thus a direct relationship to dispersal mortality. By contrast, the parameter a , which scales the time that a lone breeder is expected to spend alone, has very little influence on the solutions.

Not surprisingly, increasing group productivity k improves the stability of groups. When dominants can control group membership, helping, i.e. $k > 1$, is required for group stability if subordinates are unrelated and survival values are independent of group size (figure 3*a*).

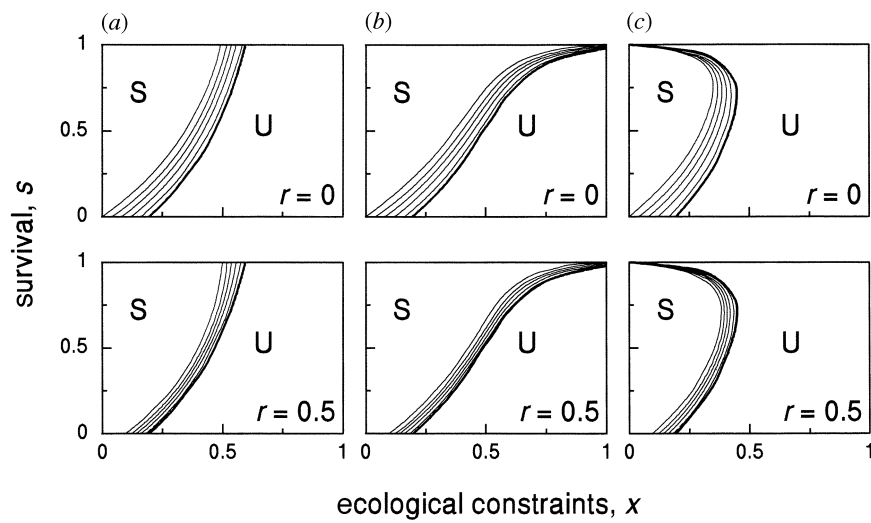


Figure 2. Stability of the group according to the strength of ecological constraints and survival, with $k = 1.2$ and $a = 0.5$. The area marked with ‘S’ describes the stable region where no concessions are needed (simple families in terms of Emlen (1995)). ‘U’ gives the region where groups are unstable. Contour lines separating these two regions indicate staying incentives (i.e. extended families, Emlen (1997)), increasing from left to right in steps of 0.05. (a) Survival is equal for all individuals, $s_D = s_S = s_L = s$. (b) Dominants have a 10% survival disadvantage, $s_D = 0.9s$, $s_S = s_L = s$. (c) Subordinates have a 10% survival disadvantage, $s_S = 0.9s$, $s_D = s_L = s$.

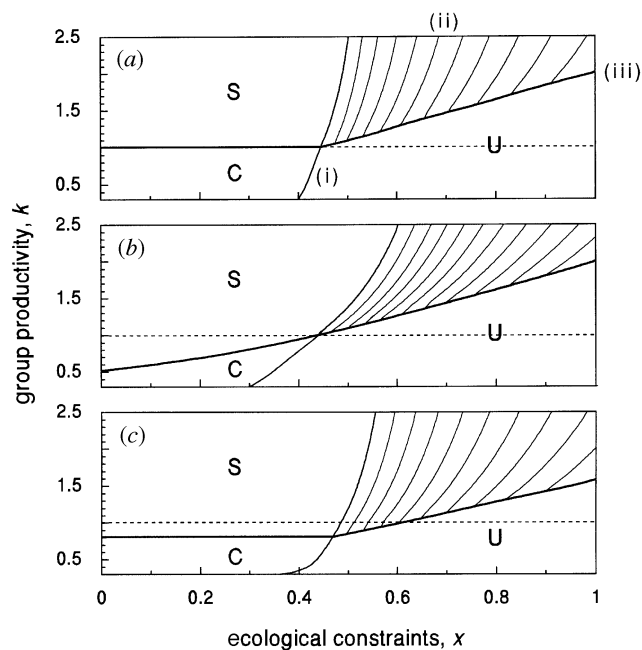


Figure 3. Stability of the queue according to x and k , with $a = 0.5$. Area descriptions as in figure 2, with the addition that ‘C’ indicates a conflict where the subordinate would benefit from staying, but the dominant wants it to leave. The dashed line marks $k = 1$. (a) Survival $s_D = s_S = s_L = 0.8$, relatedness $r = 0$. Stable groups occur only if $k > 1$, but concessions are not needed with low x . Curves stem from conditions (Si), (Sii) and (Siii) as indicated. (b) Survival $s_D = s_S = s_L = 0.8$, relatedness $r = 0.5$. Stable groups can occur at $k < 1$, if ecological constraints are strict (small x). (c) Case with unrelated individuals, and a slight survival disadvantage of a lone individual: $r = 0$, $s_D = s_S = 0.8$, $s_L = 0.75$. With small x , groups are stable with up to 20% reduction in the group productivity ($k = 0.8$).

With strict ecological constraints (small x), any increase in productivity ($k > 1$) gives stability without the need for concessions, while weaker constraints (larger x) mean that a greater value of group productivity k is required, but also that the subordinate can claim a share in reproduction. In the case of related individuals, dominants may accept the presence of subordinates that harm

current reproduction ($k < 1$) provided that ecological constraints are strict (figure 3b). This region illustrates the possibility of parental facilitation through prolonged brood care (Brown & Brown 1984; Brown 1987; Ekman *et al.* 1994), where parents allow the young of previous years to stay using their resources, even if none of them help to rear new offspring.

There also exists an alternative way of finding stable groups with decreased group productivity $k < 1$. If the presence of the subordinate improves the survival of the dominant, the dominant will trade off current productivity k against its own survival s_D and tolerate $k < 1$ even from unrelated individuals (figure 3c). Improvements in the dominant’s survival need be neither large nor ‘intentional’ to generate the tolerance; for example, a passive predation dilution effect could suffice. However, dominants are not expected to accept arbitrarily large reductions in current productivity. There hence exists a region with low k and low x where the subordinate would benefit from queuing (especially if subordinates also gain the survival advantage as in figure 3c), but as its presence harms current productivity, the dominant is likely to attempt eviction. How such a conflict is resolved depends on how membership in a group is determined (Johnstone & Cant 1999; see § 3).

(c) **Peace incentives**

Assuming that the subordinate stays, a peace incentive p_p may be necessary to ensure that it does not pay for the subordinate to try to kill the dominant (Reeve & Ratnieks 1993). In the current setting, the peace incentive is derived by a three-step process analogous to the staying incentives:

- (Pi) Accept peace with $p_p = 0$ if $w_S(0) + rw_D(0) \geq [f + r(1 - f)]w_L(0)$.
- (Pii) If not, require peace incentive p_p defined by $w_S(p_p) + rw_D(p_p) = [f + r(1 - f)]w_L(p_p)$.
- (Piii) Dominant accepts giving peace incentive if $w_D(p_p) + rw_S(p_p) \geq [fr + (1 - f)]w_L(p_p)$.

As in the case of staying incentives, there exists a large region where peace incentives are not needed even if the subordinate has a chance of winning a lethal fight ($f > 0$) and individuals are completely unrelated ($r = 0$)—a possibility not permitted in Reeve & Ratnieks’s (1993)

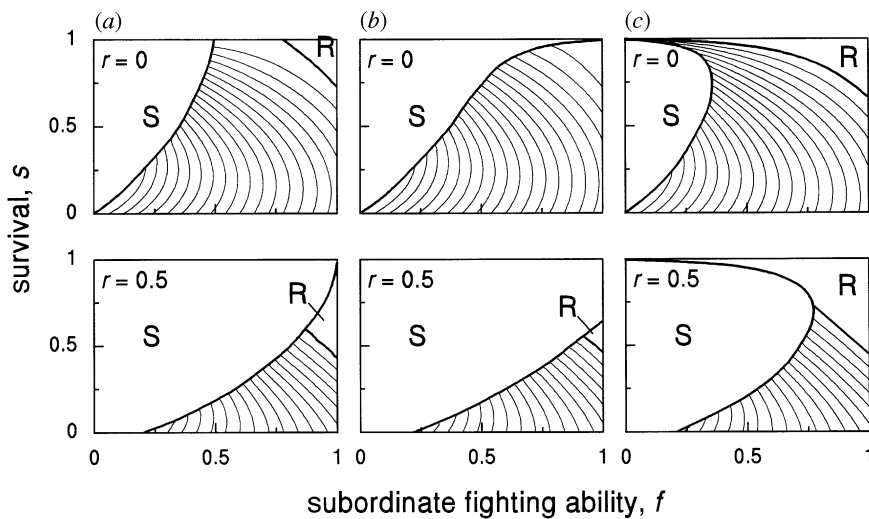


Figure 4. Peace incentives p_p when $k=1.2$, $a=0.5$, and with varying survival and subordinate fighting ability. (a), (b) and (c) assume equal survival, subordinate advantage, and subordinate disadvantage as described in figure 2. 'S' indicates a stable queue with $p_p=0$, contours give values of p_p increasing from left to right with steps 0.05, and 'R' relates to a case where the roles of the dominant and the subordinate are reversed (stable queue with $p_p=1$; see text for further discussion). Note that 'R' does not exist in (b) with $r=0$, and the top right corner describes $0.95 < p_p < 1.00$ instead.

skew model (figure 4). When dominance status increases mortality, fighting may not occur, even if peace incentives are not offered and subordinates are unrelated and have a high probability of winning a fight (figure 4b); queuing may be a more efficient way than fighting to inherit the resource.

Where needed, peace incentives are usually smaller if individuals are related, but not always: as an example, survival ≈ 0.5 and very high fighting ability of the subordinate in figure 4a leads to a case where $p_p \approx 0.9$ if $r=0$, but $p_p=1$ if $r=0.5$. With such a high probability of the subordinate winning a fight, the dominant does best by effectively accepting a change in the dominant hierarchy, which reverses the roles of the dominant and the subordinate (region 'R' in figure 4). (To prevent endless reversals we must assume that fighting abilities are individual properties and are not 'inherited' by status.) A role reversal may happen more easily if individuals are related, as the former dominant has some interest in the former subordinate's reproduction as well. But even among unrelated individuals and with a complete skew in the new dominance order, the dominant may accept a role reversal and completely abandon all immediate reproductive rights given enough threat f combined with a high survival probability (figure 4a). Again, the prospects of eventually outliving the new dominant suffice to make the fitness gain from staying in the group positive (equation (1)).

As a major difference to the staying incentives, relatedness r has a very strong effect on the region where peace incentives are needed (figure 4)—relatives clearly need them less often. In the context of queuing, lethal fighting can be considered an extreme form of 'queue-jumping'. For non-relatives, the only purpose of staying in the queue is to end up in the top position (if concessions are not given). Relatives, on the other hand, can gain indirect fitness already while in the queue, and they also value the future success of their kin. Non-relatives are therefore less likely to obey orderly 'queuing rules' than relatives and can claim peace incentives at lower relative fighting abilities.

3. DISCUSSION

Our model reduces to Reeve & Ratnieks's (1993) concession-based skew model when post-breeding survival is set to zero. Therefore, it too allows group

formation based on concessions, and we find that most of the predictions of their model are retained in our dynamic version: concessions generally decrease with relatedness r (although exceptions are now possible), and increase when prospects of independent breeding, x , or fighting ability of subordinates, f , improve.

At the same time, however, our model reveals that survival probabilities greater than zero greatly reduce the need for concessions. This effect is strong enough that differences in survival can have a much greater impact on the results than differences in other parameters, such as relatedness. When the possibility of acceding to dominant status is taken into account, groups where the dominant completely monopolizes reproduction can be stable, even if they consist of unrelated individuals, and even if subordinates have a reasonably high probability of winning a fight for dominance. Such cases are not permitted in existing concession models (e.g. Reeve & Ratnieks 1993; Reeve 1998), which ignore the potential future benefits of acceding to dominance, yet examples are abundantly found in nature: many long-term bird studies suggest that some helpers are unrelated to the young they care for (reviewed in Stacey & Koenig 1990), and recent evidence from birds (superb fairy-wrens *Malurus cyaneus*, Dunn *et al.* 1995) and mammals (suricates *Suricata suricatta*, Clutton-Brock *et al.* 1999) shows that helping behaviour can be completely independent of relatedness.

The suggestion that subordinates may accept a non-breeding position in a group because of the possible future benefits to be gained has been referred to as the 'benefits of philopatry' hypothesis (Stacey & Ligon 1987). It was originally contrasted with the 'ecological constraint' hypothesis, which emphasizes the opportunity for independent breeding, or lack thereof (Zack 1990; Stacey & Ligon 1991; Macedo & Bianchi 1997). The recognition that these hypotheses are merely the two sides of the same coin (Koenig *et al.* 1992; Emlen 1994) has so far not been fully incorporated in skew models of cooperative breeding, as the essential future component of the benefits of philopatry has been lacking from these models. Our dynamic model formally integrates both factors in a single model of cooperative breeding and skew, by comparing both immediate and delayed advantages of staying versus dispersing using a common currency of lifetime inclusive fitness.

Since greater survival probabilities enhance the expected benefits of queuing, and thus reduce the need for reproductive concessions, our model predicts that cooperatively breeding groups are more likely to prove stable in long-lived species. In support of this prediction, a phylogenetic analysis of birds shows that switches to cooperative breeding are associated with decreases in annual adult mortality, and that low mortality predisposes cooperative breeding rather than vice versa (Arnold & Owens 1998). Although it has been pointed out that low mortality leads to low population turnover, restricting opportunities for dispersal and independent breeding in long-lived species (Russell 1989; Rowley & Russell 1990), our model shows that low mortality also has an inevitable direct effect on group stability via increased importance of future versus current benefits (as predicted by general life-history theory, Roff (1992); this is also implicitly present in Rowley & Russell's (1990) argument that long-lived birds can 'afford to wait' longer). Moreover, this effect does not require that survival in groups is higher than that of solitary individuals, as queuing benefits increase with overall survival even without any group size dependence in survival (figure 1).

We also predict that non-cooperative groups can form, where association leads to a decrease in current productivity. Subordinates may still stand to gain from group membership under these circumstances, as acquiring breeding positions by queuing may be more efficient than the attempt to establish a new territory (either because dispersing individuals face high mortality risks or because habitat saturation prevents their breeding or forces them to occupy secondary habitats). At the same time, the dominant may benefit from their presence either directly by improved survival (Rood 1990), or if they are related, may gain indirect benefits by tolerating their presence (Brown & Brown 1984; Rowley & Russell 1990; Ekman *et al.* 1994; Johnstone & Cant 1999). Alternatively, the dominant may simply be unable to exclude unwelcome subordinates (Higashi & Yamamura 1993). Studies of oystercatchers *Haematopus ostralegus* provide detailed and compelling evidence for 'unproductive' associations of this kind, in which non-breeding individuals queue for breeding resources, but offer no help to established breeders (Ens *et al.* 1992, 1995). Moreover, populations of many other vertebrate species contain a similarly large fraction of non-breeding 'floaters' (as predicted by ideal habitat selection theory when future benefits are included, Kokko & Sutherland (1998)). The presence of such floaters can be detrimental to the breeding success of territorial individuals (Komdeur 1996; see also Macedo & Bianchi (1997) for an example of reduced breeding success in groups of several breeders).

Many aspects of social queuing are not yet incorporated in our simple model. Most significantly, the present analysis is restricted to an association of only two individuals. Concession-based models have, however, been developed for larger groups (Johnstone *et al.* 1999), and it would be of great interest to introduce dynamic considerations into these analyses; this would lead naturally to the question of how ecological factors affect the maximum lengths of social queues. As an example, Kokko & Sutherland (1998) derive the expected pay-off to remaining in a queue assuming $k=1$, $r=0$, complete

skew, no dominant control over group membership, and either linear progress along the queue or completely random progress among equal subordinates. With these assumptions, the expected pay-off to queuing when there are n subordinates in the group will be proportional both to local habitat quality and to $((1-s_D) + n(1-s_S))^{-1}$, and individuals are expected to disperse as soon as this value drops below x (i.e. from large groups, the threshold being smaller if local resources are meagre).

Apart from considering multi-member groups, there are several other factors which should be included in dynamic skew models to give insight into the rules of social queuing. First, queuing may become more complicated if incest avoidance prevents a subordinate from automatic inheritance of the breeding status when the same-sex dominant dies (Koenig *et al.* 1998), or if individual differences affect queuing success (as assumed, for example, in the hypothesis of 'queuing for status' through competitive helping, Zahavi (1990)). Second, our simple model has assumed status, but not age-dependent survival, even though the latter is likely to have an important influence on quantitative predictions regarding dispersal in long-lived species (Lucas *et al.* 1997). Both the age of the dominant and the age of a subordinate can influence the fitness consequences of remaining in the group or of dispersing. Slight differences in survival prospects have the largest effect on fitness in cases where mean survival is high (figure 1; see also Roff 1992), so cooperative breeders with relatively low mortality are expected to be especially sensitive to such differences.

Although we have formulated our dynamic skew model in terms of social breeding groups, comparison of the current and future benefits of staying versus dispersing is relevant to any temporally stable group in which the benefits of association are unequally shared. For example, there is strong similarity between conflicts over the partitioning of reproduction in cooperative breeders and conflicts over mating shares in lekking males (Widemo & Owens 1995; Kokko 1997). Just like breeding groups, lekking associations can enjoy increased 'group productivity' if females favour large aggregations over small ones (Sutherland 1996). Moreover, queue-like behaviour is often documented in temporally stable lek sites (Wiley 1973; Rippin & Boag 1974; Moyles & Boag 1981; McDonald 1993; Kokko *et al.* 1998), so that stability of lekking groups will be strongly influenced by the possibility of subordinates acceding to dominant status in the future (Wiley 1991). As in breeding groups, these delayed benefits may favour queuing behaviour (in which subordinates accept a negligible share of matings) even when group members are unrelated (McDonald & Potts 1994), and kinship will enhance stability still further (Kokko & Lindström 1996; Höglund *et al.* 1999; Petrie & Burke 1999).

Evolutionarily stable strategy models of reproductive skew have been praised for potentially providing a universal explanation for the organization of animal societies, ranging from colonies of eusocial insects to complicated social organizations in mammals and birds (Keller & Reeve 1994; Sherman *et al.* 1995). While we agree that understanding group formation under conflicting interest requires a fully developed

game-theoretical approach, we emphasize that a truly general model must consider all the consequences of the decisions that group members take: the direct and indirect benefits of both current and future reproduction (Brown 1978). Our analysis represents one step towards this dynamic theory of skew.

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