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Longevity suppresses conflict in animal societies

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Models of social conflict in animal societies generally assume that within-group conflict reduces the value of a communal resource. For many animals, however, the primary cost of conflict is increased mortality. We develop a simple inclusive fitness model of social conflict that takes this cost into account. We show that longevity substantially reduces the level of within-group conflict, which can lead to the evolution of peaceful animal societies if relatedness among group members is high. By contrast, peaceful outcomes are never possible in models where the primary cost of social conflict is resource depletion. Incorporating mortality costs into models of social conflict can explain why many animal societies are so remarkably peaceful despite great potential for conflict.

1. Introduction

Competition is ubiquitous among animals. Animals compete over territories, and individuals within animal societies compete over resources and/or breeding opportunities. Such competition often takes the form of aggressive conflict (fighting), which is energetically costly, bears a substantial risk of injury and is sometimes even fatal (reviewed by [1]). While theoretical models of territorial conflict have generally appreciated these costs [1,2], models of social conflict (i.e. models focusing on conflict among individuals within groups) have largely focused on a different form of costs. They have assumed that effort invested in social conflict reduces the value of the communal resource, e.g. because energy wasted in conflict is lost for offspring production or parental care (reviewed by [3]). However, if conflict takes the form of physical fighting or agonistic interaction, the costs may be in terms of increased mortality rather than reduced fecundity.

We develop a simple, inclusive fitness model of social conflict which takes these costs into account, i.e. in which the players' conflict efforts reduce their survival prospects. We have two aims: first, we compare predictions of this model to predictions of models assuming that conflict effort reduces the value of the communal resource (hereafter: resource depletion models, RDMs). Second, we examine the effects of baseline survival (longevity) and relatedness among group members on the evolution of within-group conflict. We are interested, specifically, in the circumstances under which peaceful associations with complete resource monopolization by dominant group members can evolve, a situation realized in many cooperatively breeding animal societies.

2. The model

We consider an association of two individuals, a dominant and a subordinate, that are symmetrically related by coefficient of relatedness r, and that compete over a resource of value V ($V > 0$). According to most models of social conflict, the dominant's share, p_D, of the contested resource is given by the following function, the contest success function (CSF, [3]):

$$p_D(x, y) = \frac{x}{x + by}, \tag{2.1a}$$

where x ($x \geq 0$) is the effort invested by the dominant in the conflict over the resource, y ($y \geq 0$) is the effort invested by the subordinate and b ($0 \leq b \leq 1$) is the power asymmetry between dominant and subordinate. The subordinate's share, p_S, of the resource is simply given by $p_S = 1 - p_D$, or

$$p_S(x, y) = \frac{by}{x + by}. \tag{2.1b}$$

As discussed in detail by Cant [3], CSFs of the form of expressions (2.1*a*,*b*) cannot yield unilaterally or mutually peaceful outcomes (in which either x, or y, or both are zero). This is because, if both players had reduced their conflict efforts to zero, any player would gain by investing an infinitesimally small amount of effort, as this would increase its share of the resource from 0.5 to 1. The marginal gains of investment at $x = y = 0$ are thus infinite [3]. To avoid this problem, and to investigate the circumstances under which peaceful associations with complete resource monopolization by dominants can evolve, we insert an arbitrarily small constant k (in the present analyses, $k = 10^{-10}$) into expressions (2.1*a*,*b*), such that the individuals' shares of the contested resource are given by the following expressions:

$$p_D(x, y) = \frac{k + x}{k + x + by} \tag{2.2a}$$

and

$$p_S(x, y) = \frac{by}{k + x + by}. \tag{2.2b}$$

With this simple modification, if no individual invests in conflict, the dominant claims the whole resource for itself. This is perhaps a more realistic assumption in dominance structured societies than the assumption of even sharing, and it allows peaceful outcomes to be stable, provided that the subordinate is favoured to refrain completely from fighting and to leave the whole resource to the dominant. If this outcome is not favoured by the subordinate, such that it is better off engaging in conflict over a share of the resource, x and y will coevolve. In this case, because k is small, it has no significant effect on the evolutionarily stable levels of x and y. We use expressions (2.2*a*,*b*) instead of (2.1*a*,*b*) in all our analyses.

RDMs of social conflict generally assume that the value of the contested resource declines with the sum of the players' efforts, such that the fitness of the dominant is proportional to

$$W_D(x, y) = p_D(x, y)V(1 - x - y) \tag{2.3a}$$

and the fitness of the subordinate is proportional to

$$W_S(x, y) = p_S(x, y)V(1 - x - y), \tag{2.3b}$$

subject to the condition $(x + y) \leq 1$ (since the value of the resource cannot be negative).

We change this assumption by assuming instead that conflict takes place in several discrete bouts (e.g. breeding seasons, litters or clutches), and that the intensity of aggression in a given conflict bout reduces the survival prospects of both players. Specifically, we assume that both players have a baseline, species-specific probability S_B of surviving from one bout to the next, which declines with the sum of their investment in conflict. We can thus derive the following function for the survival probabilities of dominants (S_D) and subordinates (S_S):

$$S_D(x, y) = S_S(x, y) = S_B(1 - x - y), \tag{2.4}$$

subject, again, to the condition $(x + y) \leq 1$ (since survival cannot be negative).

If either individual dies, the remaining individual becomes a lone breeder [4]. Lone breeders gain the whole resource for themselves, yet the value of the resource is reduced by a factor λ (less than or equal to 1, e.g. because lone breeders can only defend a smaller territory or raise fewer offspring). Because lone breeders do not need to engage in social conflict, their survival probability is simply given by the baseline survival probability S_B. In electronic supplementary material, appendix A, we show how the above assumptions can be altered to address asymmetries in baseline survival of dominants, subordinates and lone breeders.

With probability a lone breeders are joined by a new group member before the next bout, in which case they become a dominant, whereas the new group member becomes the new subordinate [4]. For simplicity, we assume that group members in this new association are related by the same coefficient of relatedness r as were group members in the old association.

We denote the (direct) fitness of individuals in the three behavioural states by $W_D(x,y)$, $W_S(x,y)$, W_L for dominants, subordinates and lone breeders, respectively. The fitness of individuals in each state is given by their reproductive success while in that state (which, for dominants and subordinates, is a function of their investment in conflict, x, y), plus their future fitness pay-offs. The future fitness pay-offs are determined by the survival probabilities of individuals in a given state as well as their transition probabilities to different states, the latter being determined by the survival probabilities of co-breeders and/or the recruitment probability a (see [4] for details). We can thus write for the fitness of dominants, subordinates and lone breeders, respectively:

$$\begin{aligned} W_D(x, y) = {} & p_D(x, y)V \\ & + S_D[(S_S + (1 - S_S)a)W_D(x, y) + (1 - S_S)(1 - a)W_L], \end{aligned} \tag{2.5a}$$

$$\begin{aligned} W_S(x, y) = {} & p_S(x, y)V \\ & + S_S[S_D W_S(x, y) + (1 - S_D)(aW_D(x, y) + (1 - a)W_L)] \end{aligned} \tag{2.5b}$$

and $$W_L = \lambda V + S_B[aW_D + (1 - a)W_L]. \tag{2.5c}$$

For reasons of clarity, we omitted the arguments (x) and (y) in the survival functions above.

(a) Solving the model

To solve our model, we first solve recursions (2.5*a*–*c*) simultaneously to obtain expressions for $W_D(x,y)$, $W_S(x,y)$ and W_L, which do not themselves depend on $W_D(x,y)$, $W_S(x,y)$ and W_L. Next, we need to find the evolutionarily stable effort levels x^* and y^* by finding the non-negative values x^* and y^* simultaneously satisfying $\partial W_D/\partial x + r(\partial W_S/\partial x) = 0$ at $x = x^*$ and $\partial W_S/\partial y + r(\partial W_D/\partial y) = 0$ at $y = y^*$. Because we cannot solve the above inclusive fitness problem analytically, we use an iterative, numerical solution procedure, which is detailed in electronic supplementary material, appendix B.

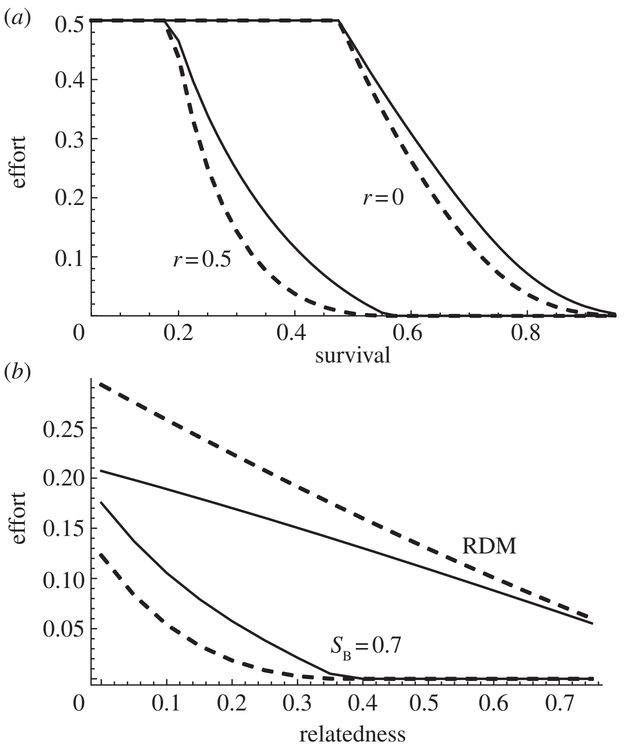

Figure 1. (*a*) Depicts stable conflict effort of dominants (x, solid line) and subordinates (y, dotted line) as a function of baseline survival (S_B) for two different levels of relatedness (as indicated). (*b*) Depicts stable conflict efforts of dominants (x, solid line) and subordinates (y, dotted line) as a function of relatedness in RDMs, compared to our model (for $S_B = 0.7$). In (*a*,*b*), $a = 0.5$, $b = 0.5$, $\lambda = 0.75$.

3. Results

The level of within-group conflict decreases substantially as baseline survival increases (figure 1*a*). If survival is reasonably high, conflict is much lower than in RDMs (figure 1*b*), and can go to zero (i.e. $x = 0$, $y = 0$) if relatedness is sufficiently high (figure 1*a*,*b*). Thus, if both survival and within-group relatedness are sufficiently high, peaceful animal societies can evolve (figure 2). By contrast, peaceful associations can never evolve according to RDMs, not even with our modification of the CSF. The reason is that in RDMs subordinates virtually always gain from increasing their (current) direct fitness. In our model, by contrast, subordinates can gain substantial future fitness by inheriting the resource upon the dominant's death, but they are less likely to do so if they invest too heavily in current conflict. Future fitness gains, therefore, select against conflict, and this effect is strongest if survival is high (i.e. as future fitness becomes more valuable).

Unlike in RDMs, in our model, it is always the dominant (rather than the subordinate) that invests more strongly in the conflict (figure 1). In RDMs, the dominant invests less than the subordinate because it gets a greater share of the contested resource, and suffers more from reducing the value of this resource [5]. This is not the case in our model. Rather, it is precisely *because* dominants gain a larger share that they invest more strongly than subordinates in their current rather than their more insecure future fitness gains. Note, however, that this relationship can become reversed if survival is asymmetric (see electronic supplementary material, appendix A).

Investment in conflict by both parties increases as λ decreases (i.e. as the future fitness associated with becoming a lone breeder decreases; see electronic supplementary material, appendix C). This result suggests that if group breeding yields higher productivity benefits, within-group conflict is more pronounced (but note that this effect is often low, e.g. if relatedness and/or survival is high, electronic supplementary material, appendix C). As in RDMs, the level of conflict increases, as the power asymmetry between dominant and subordinate decreases (as b increases; results not shown).

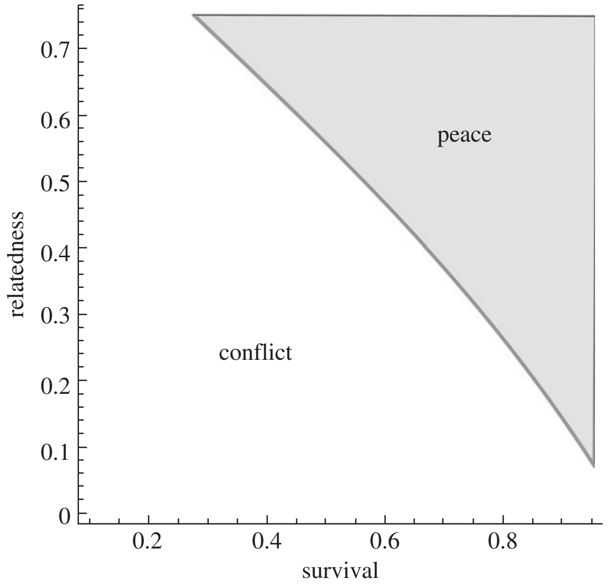

Figure 2. Zone of the parameter space for which peaceful outcomes are stable (denoted 'peace'; $x^* = 0$, $y^* = 0$), as a function of baseline survival and relatedness, at $a = 0.5$, $b = 0.5$, $\lambda = 0.75$. In the zone denoted 'conflict', $x^* > 0$, $y^* > 0$.

4. Discussion

Our model shows that when conflict involves mortality costs, longevity substantially reduces the level of within-group conflict. Together with high relatedness among group members, this can lead to the evolution of peaceful associations with complete resource monopolization by dominants, such as in many cooperatively breeding birds and mammals, in which breeding is (largely) restricted to the dominant breeding pair [6,7]. By contrast, peaceful associations are never predicted to evolve according to RDMs.

RDMs do also not correctly predict patterns of aggression in co-foundress associations of polistine wasps. First, in the species studied so far, dominants were found to be more aggressive than subordinates [8–10]. This is exactly opposite to the predictions of RDMs, but can readily be explained if conflict imposes mortality rather than fecundity costs. Our model even predicts that subordinates can be less aggressive than dominants if they suffer higher mortality, provided relatedness is sufficiently high (as in polistine wasps [8], see electronic supplementary material, appendix A). Second, aggression between co-foundresses generally increases towards the end of the season [8–10], a pattern which cannot easily be reconciled with RDMs [8,9], but which can be explained by our model, on the grounds that survival and future fitness gains decline towards the end of the season (see also [10]).

It is important to note that our model is concerned with social conflict within animal societies, but does not address the question of why groups form in the first place and/or remain stable over time. Specifically, we do not consider alternative options available to individuals outside their group, i.e. individuals cannot 'choose' to become a lone breeder (e.g. by leaving the group or evicting their partner). The availability of such outside options should affect the settlement of conflict within groups [11] and may allow individuals to negotiate their optimal investment in conflict [12]. However, outside options do not usually eliminate the potential for conflict completely [11], and where conflict occurs our results should still hold. These results indicate that the outcome of conflict is highly sensitive to the assumed nature of costs. If conflict causes mortality costs, longevity and the associated future fitness gains can substantially reduce the level of conflict in animal societies. The shadow of the future can thus suppress within-group conflict in the present.

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