THE ROYAL SOCIETY

A model of coalition formation in animals

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A simple three-player model is presented for the evolution of coalitions. The model demonstrates that, under certain conditions, 'winner' and 'loser' effects both favour coalition formation. Winner effects are defined as an increased probability of winning at time $T+1$, given a victory at time T, whereas loser effects entail an increased probability of losing at time $T+1$, given a loss at time T. Increasing the strength of loser effects or winner effects, or the strength of an individual's position in the hierarchy, makes coalition formation in general more likely, whereas increasing the costs of giving aid does the opposite.

The model does not assume any form of reciprocity, but rather examines whether some form of reciprocity or pseudoreciprocity emerges from the model itself. When either winner or loser effects exist, reciprocal coalition formation (e.g. i helps j against k, and j helps i against k) between β (second-ranked individual) and α (highest-ranked individual) or between α and γ (lowest-ranked individual) was possible, but reciprocal aid-giving between γ and β was never favoured. Thus, we have the counter-intuitive result that although a coalition between the two lowest members of a hierarchy against the dominant individual is possible (as selection may favour γ aiding β against α), such a coalition is not predicted to be reciprocal in kind.

Interpopulational comparisons examining winner–loser effects and coalition formation would allow for a test of many of the model's most basic predictions. Unfortunately, most work on coalitions has been undertaken in primates, whereas work on winner and loser effects has focused on rodents, and more recently, in fish and birds. Hopefully, the model presented here will spur future work that will look at all of these factors simultaneously in many taxa.

Keywords: coalitions; intervention; aid-giving; hierarchy; aggression; dominance

1. INTRODUCTION

Behavioural ecologists and ethologists often define a coalition as two individuals, acting cooperatively against a third party, in an aggressive or competitive context (Harcourt & de Waal 1992). Should coalitions be temporally stable, they are referred to as alliances. One interesting feature of coalitions and alliances is that they bring together cooperation and conflict—two areas often, but not exclusively, modelled as separate traits—into a single domain, and as such are potentially critical to developing a comprehensive understanding of the evolution of social behaviour.

Coalitions and alliance formation have been examined most extensively in primate species (Harcourt & de Waal 1992; Chapais 1995). Given the cognitive abilities of many primates, they are a logical starting point for studying potentially complex social interactions such as alliances and coalitions. Work in this area, however, is not limited to primate studies. For example, hyenas (*Crocuta crocuta*; Zabel *et al*. 1992), wolves (*Canis lupus*; Fentress *et al*. 1986), lions (*Panthera leo*; Packer & Pusey 1982), cheetahs (*Acinonyx jubatus*; Caro 1994), coatis (*Nasura narica*; Russell 1983), and dolphins (*Tursiops trucatus*; Connor 1992; Connor *et al*. 1992), are also known to form coalitions under certain conditions.

Polyadic aggressive interactions such as coalitions usually involve an animal intervening in a dyadic interaction between other group members (Harcourt & de Waal 1992). In principle, intervening animals may break up an interaction between two others without siding with either putative combatant. This type of intervention has been found in various primate species (Harcourt & de Waal 1992), and in the cichlid fish *Melanochromatis auratus* (Nelissen 1985). A recent model (Dugatkin 1998) has looked at the evolution of this particular type of intervention behaviour (i.e. the intervener does not side with either party) and found that it is favoured when 'winner' effects exist (winner effects are defined as an increased probability of winning at time $T+1$, given a victory at time T). Intervention is favoured in these circumstances because, in essence, it stops others from 'getting on a roll' and climbing up any hierarchy that exists. When loser effects alone are operating (losers of fights at time T are more likely to lose again at time $T+1$), intervention is not favoured (see Chase *et al*. (1994) for a review of studies on winner and loser effects, and Landau (1951*a*,*b*) and Dugatkin (1997*a*) for theoretical treatments).

The most common type of intervention takes the form of the intervener coming to the aid of one of the two other individuals involved in an interaction (Harcourt & de Waal 1992). Many functions have been put forth in an attempt to understand this type of 'coalition forming' intervention behaviour, e.g. supporting kin, reducing 'social disruption', formation of alliances, promotion of group cohesion, and 'tension reduction' (see Ehardt & Bernstein (1992) for a review). To my knowledge, however, to date no theoretical work (i.e. mathematical

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Received 20 July 1998 *Accepted* 27 July 1998

model) has examined the evolution of coalition behaviour in animals. Below, I present such a model.

2. THE MODEL

Consider the simplest possible group structure that allows for coalition formation behaviour: a group of $N=3$. The group is composed of an α (highest-ranked) individual, a β (second-ranked) individual and a γ (lowest-ranked) individual. Within such groups I will assume that: (i) dyadic interactions are formed at random, (ii) interventions take place only after an initial round of fights that determine the rank of the three group members (α, β and γ), (iii) interventions are always successful (that is, aid is given to the intended recipient and the recipient of such aid also emerges victorious in its current encounter), and (iv) winner and loser effects have a memory window of one move (that is, a victory during aggressive encounter T would make winning more likely in the next encounter a player had (encounter $T+1$), but not in encounters $T+2$, $T+3$, etc.).

Here, I define a coalition as follows: when individual i intervenes on behalf of individual j, while j is engaged in an aggressive interaction against k, and such intervention leads to j being more likely to defeat k, then i and j have formed a coalition. Note that this definition involves no components of reciprocity. Rather, I will examine whether or not reciprocity emerges from the model. Furthermore, as mentioned earlier, coalitions can be short in duration (as opposed to alliances).

As in Dugatkin (1998), let:

p_{ij} = the probability that individual i defeats individual j, given that no winner or loser effects are in operation. i and j can assume any of the three possible positions in a hierarchy: α, β or γ.

B_i = the net benefits to individual i for holding its position in the hierarchy (see Pusey & Packer (1995) for a review of such benefits).

C_i = the cost to individual i for intervening in a fight between others. These costs might include risk of injury, energy expenditure, etc. (Silk 1992).

W = 'winner effect'. This measures an individual's increased probability of victory at time $T+1$, given a previous victory at time T. W is represented as the reduced probability of defeating an individual with previous winning experience ($0 \leqslant W \leqslant 1$). It is worth noting that the models presented here assume the prior existence of winner and loser effects. That is, no attempt is made here to model the evolution of winner and loser effects (see §§ 1 and 3 for more on the nature of such effects).

L = 'loser effect'. The increased probability of losing at time $T+1$, given previous defeats at time T. L is modelled as the increased probability of defeating an individual with previous losing experience ($0 \leqslant L \leqslant 1$).

(a) *Model I: winner effects only*

(i) *Case I: α intervention in fights between β and γ*

When an aggressive interaction is on-going between individuals β and γ, α has three options: aid β (form a coalition with β), aid γ (form a coalition with γ), or do not aid either β or γ (form no coalitions).

When α helps β defeat γ, its incremental change in fitness after such an act is defined as

$$\frac{p_{\alpha\beta}B_\alpha - Wp_{\alpha\beta}B_\alpha}{2} + \frac{p_{\alpha\gamma}B_\alpha}{2} - C_\alpha. \qquad (1)$$

The left-hand term in expression (1) is the probability of α defeating β times the pay-off for such a victory, weighted by the probability of such an interaction (i.e. the probability that the next interaction will be with β). The second term is the probability of α defeating γ times the pay-off for such a victory (again, weighted by the probability of such an interaction), and the last term is the cost of intervening.

Expression (1) can be rewritten as

$$\frac{B_\alpha(p_{\alpha\beta}(1-W) + p_{\alpha\gamma})}{2} - C_\alpha. \qquad (2)$$

Should α aid γ, its fitness increment would be

$$\frac{B_\alpha(p_{\alpha\beta} + p_{\alpha\gamma}(1-W))}{2} - C_\alpha. \qquad (3)$$

The fitness of α, should it not intervene, can be defined as follows:

$$\frac{[p_{\beta\gamma}(p_{\alpha\beta}B_\alpha - Wp_{\alpha\beta}B_\alpha) + p_{\gamma\beta}(p_{\alpha\beta}B_\alpha)]}{2} + \frac{[p_{\gamma\beta}(p_{\alpha\gamma}B_\alpha - Wp_{\alpha\gamma}B_\alpha) + p_{\beta\gamma}(p_{\alpha\gamma}B_\alpha)]}{2}. \qquad (4)$$

The term in the first set of squared brackets represents α's interactions with β. The left-hand term in the numerator is the probability of defeating β, weighted by the appropriate pay-off, given that α did not aid β (in a fight between β and γ) and β went on to win such a fight. The right-hand side of the numerator is the same case, given that γ went on to win such a fight. The term in the second set of squared brackets represents α's interactions with γ and should be interpreted in a manner similar to that just described.

Rearranging and simplifying, expression (4) can be rewritten as

$$\frac{B_\alpha[p_{\alpha\beta}(1-Wp_{\beta\gamma}) + p_{\alpha\gamma}(1-Wp_{\gamma\beta})]}{2}. \qquad (5)$$

I can now address the following question: when is intervention on behalf of either party (β or γ) favoured over non-intervention? α individuals should intervene on behalf of β whenever expression (2) > expression (5). This occurs when

$$\frac{W(p_{\alpha\beta}(p_{\beta\gamma}-1) + p_{\alpha\gamma}p_{\gamma\beta})}{2} > \frac{C_\alpha}{B_\alpha}. \qquad (6)$$

α individuals should then intervene on behalf of γ whenever expression (3) > expression (5). Namely, when

$$\frac{W(p_{\alpha\beta}p_{\beta\gamma} + p_{\alpha\gamma}(p_{\gamma\beta}-1))}{2} > \frac{C_\alpha}{B_\alpha}. \qquad (7)$$

Hence, whenever the condition in inequalities (6) or (7) is met, intervention is favoured over non-intervention. This amounts to intervention being favoured whenever

Table 1. *Winner effects (model I): conditions under which column player should aid row player*

	α	β	γ
α	—	$\frac{W(p_{\beta\alpha}(p_{\alpha\gamma}-1)+p_{\beta\gamma}p_{\gamma\alpha})}{2} > \frac{C_\beta}{B_\beta}$	$\frac{W(p_{\gamma\alpha}(p_{\alpha\beta}-1)+p_{\gamma\beta}p_{\beta\alpha})}{2} > \frac{C_\gamma}{B_\gamma}$
β	see inequality (6)	—	$\frac{W(p_{\gamma\alpha}p_{\alpha\beta}+p_{\gamma\beta}(p_{\beta\alpha}-1))}{2} > \frac{C_\gamma}{B_\gamma}$
γ	see inequality (7)	$\frac{W(p_{\beta\alpha}p_{\alpha\gamma}+p_{\beta\gamma}(p_{\gamma\alpha}-1))}{2} > \frac{C_\beta}{B_\beta}$	—

$$\mathrm{Min}\left\{\frac{W(p_{\alpha\beta}(p_{\beta\gamma}-1)+p_{\alpha\gamma}p_{\gamma\beta})}{2},\frac{W(p_{\alpha\beta}p_{\beta\gamma}+p_{\alpha\gamma}(p_{\gamma\beta}-1))}{2}\right\}>\frac{C_\alpha}{B_\alpha}. \quad (8)$$

In terms of whether α should aid β or γ, a comparison of inequalities (6) and (7) shows that when $p_{\alpha\gamma}>p_{\alpha\beta}$, the left-hand side of inequality (6) is greater than the corresponding part of inequality (7). Hence, if α aids anyone (i.e. inequality (8) is met), then it should help β rather than γ, whereas when $p_{\alpha\beta}>p_{\alpha\gamma}$, α should aid γ. In either case, inequalities (6) and (7) both show that increasing winner effects or the strength of α's position in the hierarchy (reflected by $p_{\alpha\beta}$ and $p_{\alpha\gamma}$) makes aid-giving by α likely, whereas increasing the costs of aid-giving does the opposite.

(ii) *Case II: β intervention in fights between α and γ*

β has three options with respect to aggressive interactions occurring between α and γ: aid α, aid γ, or aid neither α nor γ. The same procedure used for case I can be used to examine β's behaviour. Conditions for β to help α or γ are shown in table 1. Intervention *per se* is favoured whenever the minimum value of the left-hand side of the equations in the β (middle) column in table 1 is met.

A further examination of the β column in table 1 shows that as $p_{\beta\gamma}>p_{\beta\alpha}$, β should always favour aiding α over γ. Table 1 also demonstrates that an increase in the magnitude of winner effects or the strength of β's position in the hierarchy makes aid-giving by β more likely.

(iii) *Case III: γ intervention in fights between α and β*

With respect to aggressive interactions occurring between β and α, γ has three options: aid α, aid β, or aid neither. The same procedure used for cases I and II can be used to examine γ's behaviour. Table 1 illustrates the condition for γ aiding β or α. Intervention *per se* is favoured whenever the minimum value of the left-hand side of the inequalities of the γ (third) column in table 1 is met.

The γ column in table 1 shows that when $p_{\gamma\alpha}>p_{\gamma\beta}$, γ is more likely to help β than α, whereas when $p_{\gamma\beta}>p_{\gamma\alpha}$, γ is more likely to aid α than β. Table 1 further demonstrates that an increase in the magnitude of winner effects or the strength of γ's position in the hierarchy makes aid-giving by γ more likely.

(b) *Model II: loser effects only*

(i) *Case I: α intervention in fights between β and γ*

Should α aid β over γ, its fitness increment would equal

$$\frac{B_\alpha(p_{\alpha\beta}+p_{\alpha\gamma}(1+L))}{2}-C_\alpha. \quad (9)$$

Should α aid γ, its fitness increment would be

$$\frac{B_\alpha(p_{\alpha\beta}(1+L)+p_{\alpha\gamma})}{2}-C_\alpha. \quad (10)$$

The fitness increment for α, should it aid neither β nor γ, is

$$\frac{[p_{\beta\gamma}(p_{\alpha\beta}B_\alpha)+p_{\gamma\beta}(p_{\alpha\beta}B_\alpha+Lp_{\alpha\beta}B_\alpha)]}{2}+\frac{[p_{\gamma\beta}(p_{\alpha\gamma}B_\alpha)+p_{\beta\gamma}(p_{\alpha\gamma}B_\alpha+Lp_{\alpha\gamma}B_\alpha)]}{2}. \quad (11)$$

Rearranging and simplifying, expression (11) can be rewritten as

$$\frac{B_\alpha[p_{\alpha\beta}(1+Lp_{\gamma\beta})+p_{\alpha\gamma}(1+Lp_{\beta\gamma})]}{2}. \quad (12)$$

α individuals should aid β whenever expression (9) > expression (12). This occurs when

$$\frac{L(p_{\alpha\gamma}(1-p_{\beta\gamma})-p_{\alpha\beta}p_{\gamma\beta})}{2}>\frac{C_\alpha}{B_\alpha}. \quad (13)$$

α individuals should aid γ whenever expression (10) > expression (12). This occurs when

$$\frac{L(p_{\alpha\beta}(1-p_{\gamma\beta})-p_{\alpha\gamma}p_{\beta\gamma})}{2}>\frac{C_\alpha}{B_\alpha}. \quad (14)$$

Whenever inequalities (13) or (14) are met, intervention is favoured over non-intervention. Intervention is then favoured over non-intervention when

$$\mathrm{Min}\left\{\frac{L(p_{\alpha\gamma}(1-p_{\beta\gamma})-p_{\alpha\beta}p_{\gamma\beta})}{2},\frac{L(p_{\alpha\beta}(1-p_{\gamma\beta})-p_{\alpha\gamma}p_{\beta\gamma})}{2}\right\}>\frac{C_\alpha}{B_\alpha}. \quad (15)$$

A comparison of inequalities (13) and (14) shows that when $p_{\alpha\gamma}>p_{\alpha\beta}$, α should help β over γ, whereas when $p_{\alpha\beta}>p_{\alpha\gamma}$, α is more likely to aid γ than β. Inequalities (13) and (14) also show that increasing loser effects or the strength of α's position in the hierarchy makes aid-giving

Table 2. *Loser effects (model II): conditions under which column player should aid row player*

	α	β	γ
α	—	$\frac{L(p_{\beta\gamma}(1-p_{\alpha\gamma})-p_{\beta\alpha}p_{\gamma\alpha})}{2}>\frac{C_\beta}{B_\beta}$	$\frac{L(p_{\gamma\beta}(1-p_{\alpha\beta})-p_{\gamma\alpha}p_{\beta\alpha})}{2}>\frac{C_\gamma}{B_\gamma}$
β	see inequality (13)	—	$\frac{L(p_{\gamma\alpha}(1-p_{\beta\alpha})-p_{\gamma\beta}p_{\alpha\beta})}{2}>\frac{C_\gamma}{B_\gamma}$
γ	see inequality (14)	$\frac{L(p_{\beta\alpha}(1-p_{\gamma\alpha})-p_{\beta\gamma}p_{\alpha\gamma})}{2}>\frac{C_\beta}{B_\beta}$	—

by α likely, whereas increasing the costs of aid-giving does the opposite.

(ii) *Case II: β intervention in fights between α and γ*

Conditions for β helping α or γ are shown in table 2. Intervention *per se* is favoured when the minimum value of the left-hand side of the inequalities in the β column of table 2 is met.

Further examination of the β column in table 2 demonstrates that as $p_{\beta\gamma}>p_{\beta\alpha}$, β should always favour aiding α over γ. Table 2 also shows that increasing loser effects or the strength of β's position in the hierarchy makes aid-giving by β likely, whereas increasing the costs of aid-giving does the opposite.

(iii) *Case III: γ intervention in fights between α and β*

Table 2 illustrates the condition for γ aiding β or α. Intervention *per se* is favoured whenever the minimum value of inequalities on the left-hand side of the γ column in table 2 is met.

The γ column in table 2 shows that when $p_{\gamma\beta}>p_{\gamma\alpha}$, γ should aid α over β, and when the converse is true, γ should help β defeat α. Increasing loser effects or the strength of γ's position in the hierarchy makes aid-giving by γ likely, whereas increasing the costs of aid-giving does the opposite.

3. DISCUSSION

The family of simple models presented here examines coalition formation when winner or loser effects are operating. All 12 possible coalition scenarios (α aids β against γ when winner effects are in place, etc.) were examined. Under certain conditions, winner effects and loser effects can both allow for coalition formation.

Increasing the strength of loser effects or winner effects or the strength of an individual's position in the hierarchy makes coalition formation in general more likely, whereas increasing the costs of giving aid does the opposite. Interpopulational comparisons examining winner–loser effects and coalition formation would allow a test of this basic prediction. Unfortunately, most work on coalitions has been undertaken in primates (Harcourt & de Waal 1992), whereas work on winner and loser effects has focused on rodents (Ginsburg & Allee 1942; Seward 1946) and more recently on fish (see Chase *et al.* (1994) for a review) and birds (Drummond & Canales 1998). Hopefully, the model presented here will spur on future work to look at all these factors simultaneously in primates, fish, birds, and many other taxa.

The models described here did not include reciprocity in the definition of a coalition. Instead, I can examine whether reciprocity emerges from the cases studied. For example, under what conditions is it true that individual *i* aids *j* against *k*, and that *j* aids *i* against *k* as well? I demonstrate here that both winner and loser effects allow reciprocal coalition formation under two conditions. First, when $p_{\alpha\gamma}>p_{\alpha\beta}$, then β aids α and α aids β. Second, if $p_{\gamma\beta}>p_{\gamma\alpha}$ and $p_{\alpha\beta}>p_{\alpha\gamma}$, then α aids γ and γ aids α. Neither loser or winner effects favour reciprocal aid-giving between γ and β. Thus, although reciprocity may emerge in coalitions, it is not a prerequisite for their evolution. It is also worth noting a counterintuitive prediction emerging from this model. Namely, that although coalitions between the two lowest members of a hierarchy against the dominant individual are possible (as selection may favour γ aiding β against α), such coalitions are not predicted to be reciprocal in kind.

It is important to note that the reciprocal aid-giving mentioned above is different in nature from conditionally reciprocal strategies, the most famous of these being tit-for-tat (see Dugatkin (1997*b*) for a review of conditionally cooperative strategies). For example, tit-for-tat would predict that whether player *i* aided player *j* would be dependent on whether *j* had aided *i* in the past. No such dependence exists in the reciprocal aid-giving found in the current model. Rather, the reciprocal aid-giving described here might be thought of as 'accidental' in the sense that it is a consequence of the direct 'selfish' benefits received by each of the players. When it pays to aid another, such aid is dispensed. When player *i* finds it profitable to help player *j* and vice versa, reciprocal aid-giving is possible, otherwise it is not. Neither players' action is dependent on previous experience with the other. As such, one might use the framework of by-product mutualism to understand the swapping of aid-giving described in models I and II (Connor 1986, 1995, 1996; Dugatkin 1997*b*). Of course, the reciprocity described in my model does not preclude 'true conditional reciprocity' (such as tit-for-tat) from playing a role in coalition formation as well.

The predictions of the model developed here differ in one important manner from an earlier model that examined intervention behaviour which stopped an aggressive interaction between two individuals, but did not favour either party (Dugatkin 1998). In the latter model, intervention was favoured only when winner effects were operating, while the type of intervention modelled here can be favoured both under winner and loser effects. Why the difference?

In Dugatkin (1998), winner effects favoured intervention because they allowed the intervener to stop others in their group from getting on a 'winning streak', and potentially threatening a change of positions within a hierarchy. Loser effects, however, did not favour intervention, because a potential intervener was better off letting one of the two interacting individuals suffer a loss, and thereby decrease its (the individual who lost) chances of winning in future bouts.

In the current model, winner effects favour intervention for reasons similar to Dugatkin (1998). Loser effects, however, can favour intervention because, unlike the model in Dugatkin (1998), an intervening individual may now secure its position in the hierarchy in a more effective manner by insuring that a particular other group member suffers a loss (and thereby increases its chances of losing in the future). If the benefit of ensuring that a particular other individual loses outweighs the cost of intervention, coalition formation may be favoured.

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