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# Group fusion: the impact of winner, loser, and bystander effects on hierarchy formation in large groups

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We present the results of a series of computer simulations that examined the impact of winner, loser, and bystander effects on hierarchy formation in fused groups. These effects and their implications for hierarchy structure and aggressive interactions were first examined in small four-member groups. Subsequent to this, the two small groups were fused into a single larger group. Further interactions took place in this fused group, generating a new hierarchy. Our models demonstrate clearly that winner, loser, and bystander effects strongly influence both the structure and types of interactions that emerge from the fusion of smaller groups. Four conditions produced results in which the same general patterns were uncovered in pre- and postfusion groups: (1) winner effects alone, (2) bystander loser effects alone, (3) winner and bystander winner effects operating simultaneously, and (4) all four effects in play simultaneously. Outside this parameter space, hierarchy structure and the nature of aggressive interactions differed in pre- and postfusion groups. When only loser effects were in play, one of the two clear alphas from the prefused groups dropped in rank in the eight-member fused group. When bystander winner effects were in play, it was difficult to rank any of the eight individuals in the fused group, and players interacted almost exclusively with those that were not in their original four-member group. When loser and bystander loser effects operated simultaneously, two top-ranking individuals emerged in the fused groups, but the relative rank of the other players was difficult to assign. *Key words:* bystander effect, group fusion, loser effect, mathematical model, winner effect. *[Behav Ecol 14:367–373 (2003)]*

Recently, behavioral ecologists interested in aggression and dominance hierarchies have focused more attention on extrinsic factors. Intrinsic factors typically refer to traits that correlate with an animal's fighting ability in terms of physical prowess, such as its resource holding power or RHP (Parker, 1974), whereas extrinsic factors are encapsulated by what have come to be known as winner, loser, and bystander effects (Landau, 1951a,b; McGregor and Peake, 2000; Mesterton-Gibbons, 1999; Slater, 1985; see Chase et al., 1994, for a review of empirical work on winner and loser effects). Winner and loser effects are usually defined as an increased probability of winning at time *T*, based on victories at time *T*-1, *T*-2, and so on, and an increased probability of losing at time *T*, based on losing at time *T*-1, *T*-2, and so on. In a pair of influential papers, Landau (1951a,b) examined how extrinsic and intrinsic factors might explain the presence of the linear hierarchies that he believed were so common in nature. Landau (1951a,b) created an index of linearity ($H$; $0 \leq H \leq 1$) and found that, except under extreme conditions, intrinsic factors alone did not produce linear hierarchies. However, once extrinsic factors were added, Landau's models produced more strongly linear hierarchies.

Despite the importance and impact of Landau's (1951a,b) work on research in the area of dominance hierarchies, a number of critical questions surrounding winner and loser effects, and how they interact, remained unanswered some 40 or more years after the original papers were published. For example, Landau (1951a,b) did not examine winner and loser effects independently, but rather considered their joint effect on hierarchy formation. Furthermore, animals did not assess each other's RHP in Landau's model. Dugatkin (1997) built a simulation model to address just these issues.

Separating winner and loser effects had a stark impact on the distribution and type of encounters among members in a hierarchy (Dugatkin, 1997). When winner effects alone were examined, a hierarchy in which all individuals held an unambiguous rank was found. In these hierarchies the majority of the interactions were true fights, where both individuals choose to be aggressive, as opposed to attack–retreat sequences, where only one individual chooses to be aggressive. This situation mimics the large number of studies that have found strict linear hierarchies in a wide variety of animals (Archer, 1988; Chase, 1982b; Huntingford and Turner, 1987; Landau, 1951a,b). When examining loser effects in the absence of winner effects, however, a clear alpha individual always emerged, but the rank of others in the group was unclear. In these hierarchies the majority of the interactions were of the attack–retreat form (as opposed to fights). This type of hierarchy resembles despotic animal societies in which a single individual is clearly dominant to all others, but the relative position of all other group members in relation to one another is sometimes difficult to determine (Hand, 1986; Vehrencamp, 1983).

Winner and loser effects occur as a consequence of an individual's direct involvement in aggressive contests and are manifest as changes in the contestants' assessment of their own RHP. In addition to winner and loser effects, there is a related type of extrinsic factor called the bystander effect (Chase, 1980, 1982a,b; Slater, 1985). When bystander effects are in operation, an individual changes its estimation of the fighting abilities of others based on what it observes. The bystander effect comes in two flavors: bystander winner (BW) and bystander loser (BL). If a bystander raises its estimation of the fighting ability of an individual it has just observed win, then bystander winner effects are in play. Conversely, should a bystander see another individual lose a fight and subsequently devalue its estimation of the loser's fighting ability, then bystander loser effects are at

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work. Despite their potential importance, bystander effects have not been the subject of a great deal of empirical work, although they have been demonstrated in songbirds (*Parus major*; McGregor, 1993; Peake et al., 2001; *Luscinia megarhynchos*; Naguib and Todt, 1997; Naguib et al., 1999), fighting fish (*Betta splendens*: Oliveira et al., 1998) and swordtails (*Xiphophorus helleri*; Earley and Dugatkin, 2002).

Dugatkin (2001) built a simulation model similar to the winner/loser model described above to examine the impact of bystander effects on hierarchy formation. This model allowed for bystander winner (BW) and bystander loser (BL) effects alone or in conjunction with standard winner and loser effects. When bystander winner effects alone are at play, each group has a clear omega (bottom-ranking individual), but the ranking of other group members is difficult to determine. In this scenario, most aggressive interactions are of the attack–retreat rather than the fight variety. The situation is dramatically different when only bystander loser effects are in operation. Now, wins and losses are randomly distributed throughout a group, and no discernable hierarchy exists. In contrast to the bystander winner case in which attack–retreat interactions prevail, now individuals always fight when they meet. Joint winner and bystander winner effects, joint loser and bystander loser effects, and all four effects in play simultaneously all produced a linear hierarchy in which all positions were clearly defined and most interactions were of the attack–retreat variety (Dugatkin, 2001).

Here we extend the winner/loser and bystander winner/bystander loser models in a new direction—namely, by examining how these effects impact dominance hierarchy formation when two previously independent groups fuse to form a larger unit. Experimental group fusion protocols are often used to detect how residency (e.g., when one flock is introduced into the home aviary of another) or individual familiarity influence flock dynamics in birds (e.g., Balph, 1979; Cristol, 1995; Cristol et al., 1990; Wiley, 1990; Wiley et al., 1999; Yasukawa and Bick, 1983). Often, however, added asymmetries such as residency may confound interpretations about the role of extrinsic factors (e.g., winner, loser, bystander winner, and bystander loser effects) in mediating postfusion hierarchy establishment. Earley and Dugatkin (in review) isolated the relative effects of prefusion rank and early postfusion dynamics on the ensuing hierarchy structure in green swordtail fish (*Xiphoporus helleri*). They found that extrinsic factors above and beyond prefusion status asymmetries may play an important role in shaping the postfusion hierarchy. At the empirical level, it is difficult, but not impossible, to simultaneously examine the influence of winner, loser, bystander winner, and bystander loser effects (or any combination thereof) and to tease apart the exact contribution of each of these to postfusion hierarchy dynamics.

To overcome this difficulty, we introduce a model designed to partition the relative influence of each of these extrinsic factors on the establishment of postfusion hierarchies. Our simulation model begins with the formation of hierarchies in two groups of four, initially identical, individuals. In these groups, winner, loser, bystander winner, and bystander loser effects then influence the RHP, and eventual rank-order, of the group members. These small groups, now characterized by some level of differentiation in individual RHP, are merged into one larger assemblage. Hierarchy formation in this larger group then occurs and can be influenced by the same suite of extrinsic factors, as well as any preexisting status asymmetries generated by interactions in the small groups. The models detailed below are capable of separating the effects of previous status from the influences of winning, losing, and watching fights at the postfusion level and, as such, generate predictions that are otherwise unavailable in the current literature.

## The models

We present our models for the case when smaller groups are composed of four individuals, and the group that forms as a result of their fusion possesses eight individuals. Similar patterns occur for smaller and larger pre- and postfusion group sizes.

### Four-member groups

*General rules and parameters*

Unless otherwise noted, in each of the four-member (smaller) groups, the following rules and parameters apply.

Consider a group of $N = 4$ animals. In each group, randomly chosen pairs of individuals are pitted against one another in potentially aggressive contests. Discrete time intervals, $T = 1, 2, \ldots T_{max}$, are simulated, and at each interval, two interactions occur (i.e., all four group members are involved in contests). For example, at the start of a time interval, imagine that individual 1 is randomly chosen. Then from the remaining three members of a group, a second randomly chosen individual—let's say individual 2—is selected and pitted against individual 1. By default, individuals 3 and 4 would also pair off against one another.

At the start of a computer simulation, each player in each group is assigned a score that denotes the individual's assessment of its own fighting ability. This score is analogous to a player's estimate of its own RHP and is denoted as $RHP_{player\ i,self,T}$ (assessment of one's own RHP at time $T$, where, as noted above, $T$ is a counter that is initialized at 1 and increases by a single unit *after* each pairwise encounter). Individuals are aware not only of their own initial RHP value but of the initial RHP of all other group members as well ($RHP_{other}$).

In each contest an animal can choose either to "be aggressive" or "leave." Players use a simple rule to determine which option to employ. Individuals assess their own RHP and that of their opponent and choose to be aggressive if:

$$RHP_{player\ i,self,T}/RHP_{other} \geq \phi, \qquad (1)$$

where $RHP_{player\ i,self,T}/RHP_{other}$ is referred to as "relative RHP" and $\phi$ (where $\phi \geq 0$) is called the "aggression threshold" (see Mesterton-Gibbons and Dugatkin, 1995, for more on this idea). For example, if $\phi = 0$, animals will always fight, regardless of who their opponent is, if $\phi = 0.5$, they will fight another individual whose RHP they assess to be up to twice as great as their own, and if $\phi = 1$, they will fight anyone with an RHP they assess to be smaller than their own. Given this, three outcomes are possible when player $i$ meets player $j$:

1. Both player $i$ and $j$ meet the aggression threshold, and both decide to be aggressive. This is referred to as a fight.
2. Player $i$ meets the aggression threshold, but player $j$ does not, or vice versa. In this case, we say that one player attacked and that the other player retreated.
3. Neither player $i$ nor player $j$ meets the aggression threshold, and hence neither opts to be aggressive. This is referred to as a "double kowtow."

If both players opt to be aggressive, the probability that player $i$ will defeat player $j$ is given as:

$$RHP_{player\ i,self,T}/(RHP_{player\ i,self,T} + RHP_{player\ j,self,T}). \qquad (2)$$

*Winner and loser effects*

In the basic winner and loser model, an individual's assessment of the RHP of others ($RHP_{other}$) does not change through time. An individual's assessment of its own RHP, however, does change through time as a result of whether it wins or loses a fight, and/or whether it retreats from an opponent, or whether its opponent retreats. In other words, winner and loser effects are a result of either actually winning or losing a fight or retreating or having someone retreat from your attack.

When player $i$ wins a fight or has its opponent retreat from its aggressive approach, it increases its own RHP by a factor of $W$, and so

$$\mathrm{RHP}_{\text{player } i,\text{self},T+1} = (1 + W)\mathrm{RHP}_{\text{player } i,\text{self},T}. \quad (3)$$

This will be referred to as the winner effect. Conversely, when a player loses a fight or retreats from an aggressive act by an opponent, its RHP is lowered by a factor $L$, and

$$\mathrm{RHP}_{\text{player } i,\text{self},T+1} = (1 - L)\mathrm{RHP}_{\text{player } i,\text{self},T}. \quad (4)$$

As such, $L$ measures loser effects. It is important to note that in this winner and loser effect model, individuals do not keep track of who they defeated or who has defeated them, only that they have won or lost. As such, the model does not require individual recognition or familiarity with past opponents, per se. Rather, an individual simply recognizes the RHP of others and itself. $\mathrm{RHP}_{\text{player } i,\text{ self, } T}$ changes based on all relevant prior interactions, but memory of interactions with specific other group members is not a part of the model.

In all simulations, winner effects and loser effects are independent of one another in the sense that individuals in a given run of a simulation may be affected by winner effects alone, loser effects alone, both winner and loser effects, or neither. We assume that winning a fight and having one's opponent retreat before a fight have the same effect on $W$ and that losing a fight or retreating have the same effect on $L$. This assumption could, of course, be relaxed if one $W$ value is used for winning a fight and another for having your opponent retreat before any aggressive interactions take place (and similarly for $L$). In fact, we relaxed this assumption in numerous computer simulations but it did not qualitatively change the results presented below.

$W$ and $L$ were each increased from 0 to 0.2, in increments of 0.1. $T_{max}$ was set to 300, and the initial RHP value for each group member was set at 10 (i.e., all group members started out with the same RHP value). Repeated simulations with the same set of parameter values were very consistent in their outcomes. All computer simulations were constructed using TrueBasic™.

*Bystander effects*

Following Dugatkin (2001), when bystander effects are in play, we assume that all pairwise interactions in a group are observed by all other group members. Let us consider bystander winner (BW) effects first. Imagine an interaction between players $j$ and $k$ at time $T$. Should $j$ either win a fight or attack $k$ (and have $k$ retreat), *each* bystander (i.e., every individual in the group beside $j$ and $k$) changes its estimation of $j$'s RHP changes as follows:

$$\mathrm{RHP}_{\text{bystander},j,T+1} = (1 + \mathrm{BW})\mathrm{RHP}_{\text{bystander},j,T}. \quad (5)$$

When BW alone is at play, the bystander's estimate of $k$'s (the loser's) RHP does not change, nor does $j$ or $k$'s estimate of their own RHP change (i.e., no winner or loser effects).

Now imagine the same interaction when only bystander loser (BL) effects are modeled. Each bystander now changes its estimate of $k$'s RHP (but not $j$'s) as follows:

$$\mathrm{RHP}_{\text{bystander},k,T+1} = (1 - \mathrm{BL})\mathrm{RHP}_{\text{bystander},k,T}. \quad (6)$$

(BW and BL were incremented from 0 to 0.2 in steps of 0.1.)

We can also examine the case in which, in addition to bystander effects, winner (W) and loser (L) effects are also at work. We entertain this possibility by modeling the case where either BW and W are both in play (and BW = W), BL and L are both in operation (and BL = L), or BW, W, BL, and L are all operating.

Again, consider the situation raised above. If BW and W are both in play, not only do bystanders change their assessment of the winner as in Equation 5, but now the winner changes his assessment of his own RHP as in Equation 3. Conversely, if BL and L are both at work, not only do bystanders change their estimates of the losers as in Equation 6, but now the loser changes his assessment of his own RHP as in Equation 4. Finally, if BW, BL, W, and L are all in play at once, then Equations 3, 4, 5, and 6 are all used in the model.

**Eight-member groups**

Once all 300 interactions have occurred in each of the two four-member groups, the simulation merges these groups into a single unit of 8 individuals, where 300 more interactions take place. In the fused group, interactants are chosen exactly as in the prefused group, and winner, loser, bystander winner, and bystander loser effects all operate exactly as described above. The fusion process works as follows: after all interactions have occurred within the smaller groups, there exists a RHP matrix and a win–loss matrix for each group of four. The RHP matrix stores $\mathrm{RHP}_{self}$ and $\mathrm{RHP}_{other}$ for all group members, while the win–loss matrix keeps track of all fights and attack–retreats. The win–loss matrix is created only for analysis purposes, as individuals do not keep track of their specific interactions, only their RHP and the RHP of others. When groups are fused, the RHP matrix for each of the smaller groups serves as the initial basis for the RHP matrix in the larger group. For example, imagine that winner and bystander winner effects are in play, and at the end of interactions in the four-member group individual 1 has an $\mathrm{RHP}_{self}$ of 18 and judges the $\mathrm{RHP}_{other}$ of its three group mates to be 23. When individual 1 is placed in a fused group, it evaluates its own RHP as 18, the RHP of its three group mates as 23, and the RHP of all members from the unfamiliar group as 10 (the baseline RHP score all individuals are assumed to start with in the absence of any information, as in initiation of the four-member groups).

Though the RHP matrix does carry over from the small to the large group, the win–loss matrix of each four-member group does not. That is, the win–loss matrix in eight-member groups is initialized with zeros in each cell, which will allow us to examine hierarchy formation in the eight-member group itself. Wins and losses at the end of the postfusion simulation then reflect interactions that occurred only in the eight-member group but could be strongly influenced by the initial differences in individual RHPs generated by interactions in the four-member group (since RHP matrices carried over to fused groups).

## RESULTS

Significant differences in hierarchy formation and the form of aggressive interactions individuals adopted were found when different effect(s) were in play, but for a given effect, increasing or decreasing the magnitude of the effects (winner, loser, bystander) or the magnitude of $\phi$ did not produce qualitatively different results. For example, very different results occurred when winner effects were in play versus when loser effects were in play, but changing the winner (or loser) effect from, say, 0.1 to 0.2 or changing $\phi$, for example, from 0.5 to 0.75, did not qualitatively change the results.

We focus here on the impact of winner, loser, and bystander

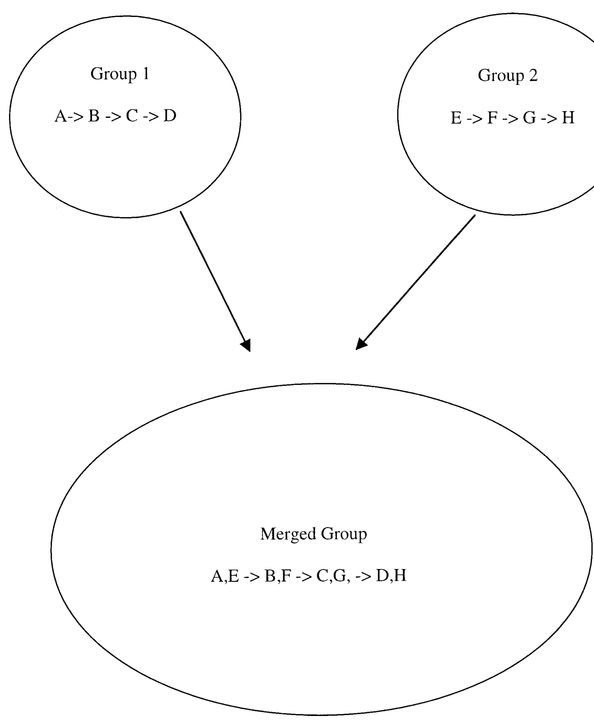


**Figure 1**
A schematic for the case of winner effects alone or the case of winner and bystander winner effects operating together. A→B denotes "A dominates B," while A,E→B, F denotes that A and E are dominant to B and F, but that it is difficult to distinguish rank between A and E or B and F.

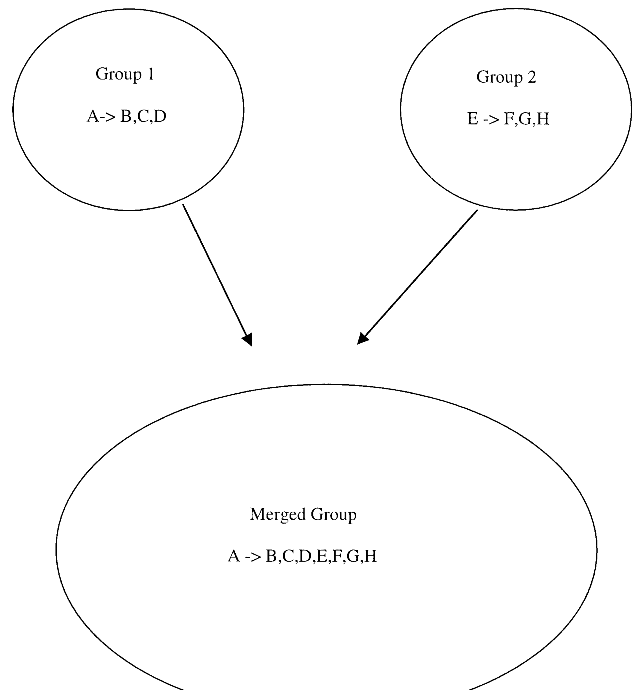


**Figure 2**
A schematic for the case of loser effects alone. Either A or E might be the dominant in the merged group.

effects in fused groups. Within the smaller (four-member, prefusion) groups, winner, loser, and bystander effects produced exactly the sorts of hierarchies found in earlier models (Dugatkin, 1997, 2001), as the same algorithm was used in both the earlier studies and for the four-member groups here. For the fused group, however, the effects of interactions in smaller groups along with behavioral exchanges in the fused group have not heretofore been examined. For each section of the parameter space discussed below, 20 simulations were run. Results were very consistent across simulation runs.

### Winner and loser effects only

When winner effects alone were in play, a clear linear hierarchy with all positions delineated occurred both in the four-member groups (as in Dugatkin, 1997) and in the fused eight-member hierarchy (Figure 1). Rank position in the eight-member group was strongly related to rank position in the four-member group. That is, the two alpha individuals in smaller groups became the two highest ranked members in the eight-member group, the two beta individuals from the smaller groups became the third- and fourth-ranked members of the eight-member group, and so on. Moreover, individuals in the fused group were equally likely to engage in aggressive interactions (fights, attack–retreat) with the three individuals that were in their former four-member smaller group and the four (previously unknown) individuals from the other four-member group. Finally, in both pre- and postfusion groups, the majority of all aggressive interactions were fights, as opposed to attack–retreat and double kowtows.

When loser effects alone were at play, only the top-ranked member in each of the four-member groups was delineated (as in Dugatkin, 1997). When groups were merged, once again, only a single alpha individual could be identified. That is, for each fusion, one of the alpha individuals from the four-member groups retained its alpha status, and one of the alphas from the four-member group dropped in rank and was part of a group of seven others that spent the majority of their time involved in double kowtows. In both pre- and postfusion groups, the majority of interactions were either attack–retreats or double kowtows (rather than fights; Figure 2).

### Bystander effects only

When bystander loser effects alone are at play, both prefusion and postfusion groups show results similar to prior work on bystander loser effects. Namely, in both pre- and postfusion groups, the majority of interactions are fights, and wins and losses are randomly distributed among group members, producing no discernable hierarchy (Figure 3).

When bystander winner effects alone are in operation, a clear bottom-ranking (omega) individual emerges, but the rank of other individuals is difficult to ascertain in the four-member groups (as in Dugatkin, 2001). In the fused group, most interactions are attack–retreats and double kowtows, but it is difficult to rank any of the eight individuals (Figure 4). Two interesting patterns, however, emerge. First, individuals in the eight-member groups interact almost strictly with those that were not in their original four-member group. Second, within each of the four-member groups that have now fused into a group of eight, one individual clearly ranks lower than the other three. There is, however, no correlation between who this individual is and who the omega individual was in the four-member group before fusion.

### Winner, loser, bystander winner, and bystander loser effects

In the scenario when winner and bystander winner effects operated simultaneously (and W = BW), the results were similar to the case when just winner effects were in play. That

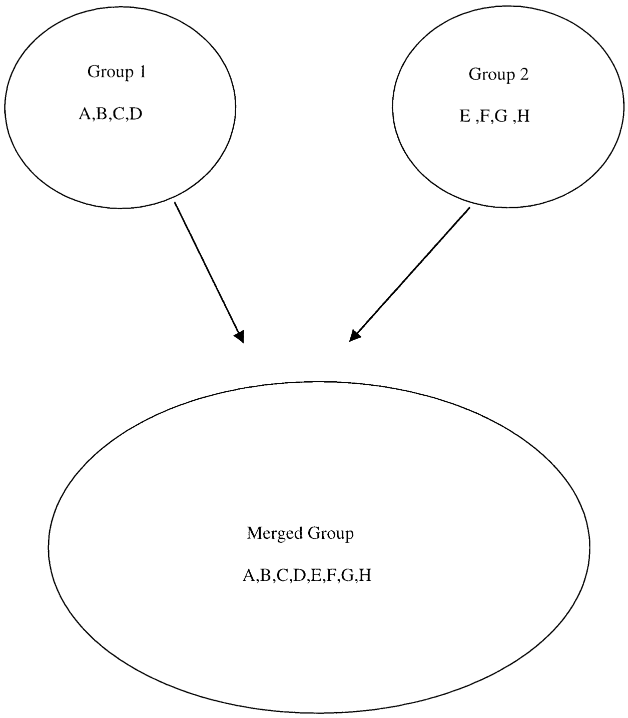


**Figure 3**
A schematic for the case of bystander loser effects alone. No discernable hierarchy occurs in pre- or postfused groups.

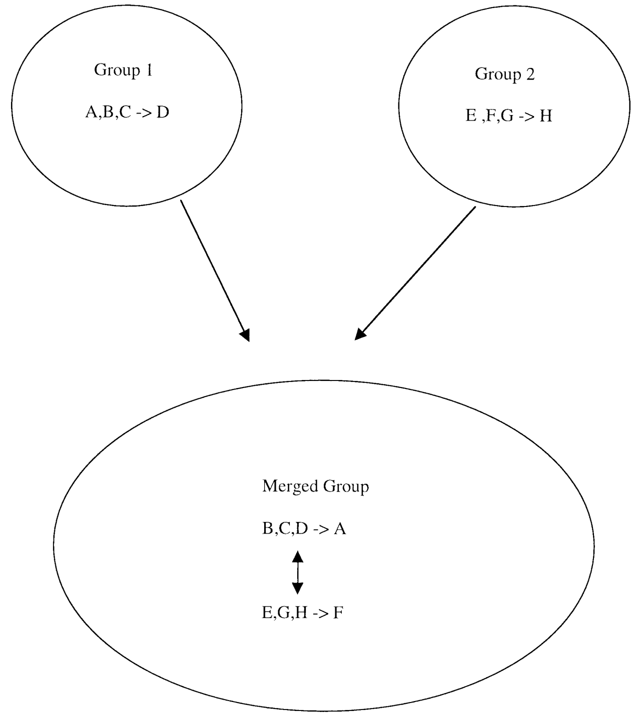


**Figure 4**
A schematic for the case of bystander winner effects alone. Individuals in the fused groups interact almost strictly with those that were not in their pre-fused group (denoted by two-headed arrow). Within each of the prefused groups that have now fused into a group of eight, one individual clearly ranks lower than the other three. There was no correlation between who this individual was and who the omega individual was in the prefused group.

is, a clear linear hierarchy with all positions delineated existed in the pre- and postfusion groups. In addition, rank position in the eight-member group was strongly related to rank position in the four-member group. As was the case when just pure winner effects were operating, individuals in the fused group were equally likely to undertake aggressive interactions with all postfusion group members and all aggressive interactions were fights (as opposed to attack/retreat and double kowtow).

An interesting pattern emerges when loser and bystander loser effects act together (and L = BL). In the prefusion groups, results are similar to the case of loser/bystander loser simulations in Dugatkin (2001). Namely, a clear linear hierarchy emerged with all positions clearly delineated and most interactions being of the attack–retreat form. When smaller groups fuse into a group of eight, most interactions again are of the form attack–retreat, and now two top-ranking individuals emerge, but the relative ranks of the other players is difficult to assign (Figure 5). The reason for this is that only the two top-ranked individuals interact with all other group members. The remaining six individuals interact, but only with those in their former, prefusion group. As such, their rank is only clear with respect to their former group mates, and this rank is consistent with the ranking in the prefusion hierarchy. That is, if A→B→C→D in the prefusion group, then the same ranking exists when examining these four individuals only in the eight-member group.

When winner, loser, bystander winner, and bystander loser effects are all in play, resultant patterns are exactly as in the case just when winner and bystander winner effects are operating together (see above).

## DISCUSSION

Using computer simulations, we have found that winner, loser, and bystander effects have clear implications for hierarchy formation when two groups fuse. The exact nature of these implications depends on which effect (or combination of effects) is operating, but in any case, our models make some clear predictions regarding fused hierarchies.

Part of the parameter space surrounding the eight-member (fused) groups produced results that were similar to those found in four-member groups and in previous models (Dugatkin, 1997, 2001). This was the case when (1) winner effects alone were at play, (2) bystander loser effects alone were operating, (3) winner and bystander winner effects were operating simultaneously, and (4) all effects were in play at once. Fused hierarchies took on new properties outside this parameter space. Here we examine each of these properties in turn.

When loser effects alone were in play, one of the two clear alphas from the prefused groups dropped in rank in the eight-member fused group. In the fused group, only the top-ranked individual's position was clear. Few interactions occurred between the other seven members of the group when loser effects alone were in play. As such, one of the alphas from the prefused group now occupied an unclear position in the new hierarchy. Earlier work (Dugatkin, 1997) not involving fused groups found that when loser effects are in play in eight-member groups that are not formed by the fusion of two smaller groups, the two top-ranked individuals were clearly delineated. This suggests that fusion, and the interactions that followed it, are the cause of the drop in rank of one of the four-member group's alpha individuals. Which of the former alpha individuals retained its rank seemed to be based on early interactions in the fused group, rather than on prior interactions in the smaller groups, as alphas in both smaller

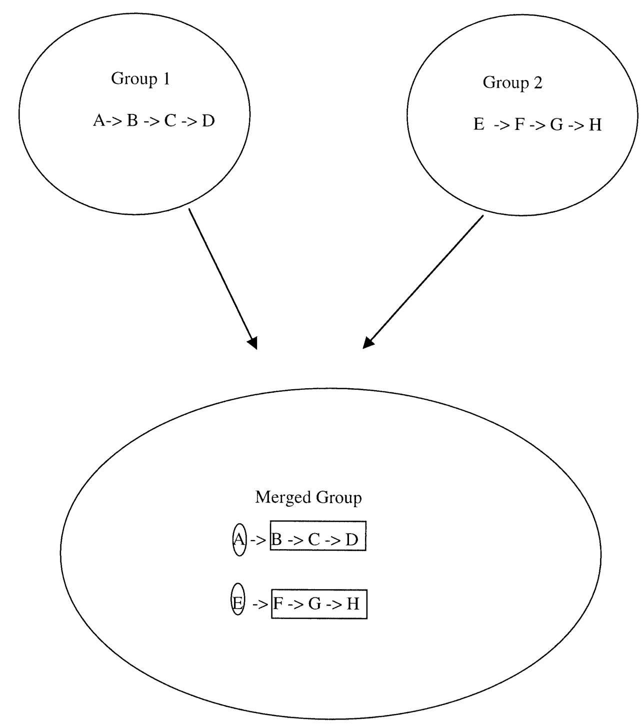


**Figure 5**
A schematic for the case when loser and bystander loser effects operate together. In the fused group, only the two individuals that were top ranked in the prefused groups (circled) interact with all other group members. All other members of the fused group (denoted in rectangles) interact only with those who were in their prefused group.

groups tended to enter the fused group with similar numbers of wins and losses. A few losses early on in the fused group could cause one former alpha to no longer act aggressively when interacting with other individuals and thus become part of a group of seven whose positions in the group are unclear. Earley and Dugatkin's (manuscript submitted) recent work on group fusion in swordtails uncovered this same general pattern for rank shifts in previous alpha individuals.

When bystander winner effects are in play, it is difficult to rank any of the eight individuals. In the eight-member groups, players interact almost strictly with those that were not in their original four-member group. Balph (1979) found a similar dynamic in fused groups of dark-eyed juncos (*Junco hyemalis*) where individuals directed more aggression toward unfamiliar individuals than toward members of their original group. In the model, this occurs because while wins and losses per se from the prefused group are wiped out when the eight-member group is formed, the RHP matrices from these four-member groups carry over to the fused group. When in the four-member groups, bystander winner effects alone create a scenario in which players never change their own RHP (no winner or loser effects are in operation) and only increase their estimation of the RHP of others in their group. As such, when they enter a fused group, players assume a baseline RHP score of 10 for those who were not in their prefusion group, but a higher RHP score than baseline for those that came from their original group (as a result of bystander winner effects in the prefused groups). Individuals then undertake double kowtows with those who were in their four-member group, but interact aggressively with members of the prefusion group to which they did not belong. Within each of the four-member groups that have now fused, one individual clearly ranks lower than the other three, though the identity of this low-ranking individual could not be predicted from rank in the prefusion groups. As such, this configuration is clearly an emergent property of early postfusion dynamics.

When loser and bystander loser effects are in operation simultaneously, two top-ranking individuals emerge in fused groups, but the relative rank of the other players is difficult to assign. The reason for this is different from that used to explain rank-assignment problems when only bystander winner effects are working. Now, aside from the two top-ranked individuals, the remaining six individuals interact, but only with those in their former, prefusion group. Here, individuals in the prefusion hierarchy only lower the estimation of the RHP of their prefusion group mates. Then, when fusion occurs, an individual interacts with its former group members (who have $RHP_{other}$ scores $< 10$), rather than those who were not in its former group (who have $RHP_{other}$ scores $= 10$). It is, however, possible to rank individuals with respect to those in their former group (but not in relation to others). Such rank is consistent with the ranking in the prefusion hierarchy. These findings indicate that the loser–bystander loser effect combination acts to inhibit complete group fusion, as all individuals other than the alphas interact exclusively within their original subgroup.

It is important to recognize two limitations of the models presented here. First, we assume that within groups, individuals interact with others in a random fashion. Although this may be the case for some animal social groups, in others, subordinates avoid interactions with dominant individuals, and hence interactions are not random. Second, while our models can examine different strengths of winner, loser, and bystander effects, the models cannot manipulate how long such effects are in play. In many systems, however, loser effects seems to last longer than winner effects (e.g., Drummond and Cannales, 1998). That being said, the models produced here predict that winner, loser, and bystander effects strongly influence both the structure and types of interactions that emerge from the fusion of smaller groups. Our hope is that these models will spur further work in this area and bring behavioral ecologists closer to a complete understanding of dominance hierarchies in nature.

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