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Bystander effects and the structure of dominance hierarchies

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Prior modeling work has found that pure winner and loser effects (i.e., changing the estimation of your own fighting ability as a function of direct prior experience) can have important consequences for hierarchy formation. Here these models are extended to incorporate ''bystander effects.'' When bystander effects are in operation, observers (i.e., bystanders) of aggressive interactions change their assessment of the protagonists' fighting abilities (depending on who wins and who loses). Computer simulations demonstrate that when bystander winner effects alone are at play, groups have a clear omega (bottom-ranking individual), while the relative position of other group members remains difficult to determine. When only bystander loser effects are in operation, wins and losses are randomly distributed throughout a group (i.e., no discernible hierarchy). When pure and bystander winner effects are jointly in place, a linear hierarchy, in which all positions (i.e., α to δ when $N = 4$) are clearly defined, emerges. Joint pure and bystander loser effects produce the same result. In principle one could test the predictions from the models developed here in a straightforward comparative study. Hopefully, the results of this model will spur on such studies in the future. *Key words:* aggression, bystander, observer, hierarchy, dominance. *[Behav Ecol 12:348–352 (2001)]*

Given the ubiquity of aggression in even the most cooperative of animal societies (Archer, 1988; Dugatkin, 1997a; Gadagkar, 1997; Huntingford and Turner, 1987) it should come as no surprise that theoreticians and empiricists have a long-standing interest in understanding both proximate and ultimate factors influencing aggression and dominance hierarchies. Behavioral ecology models of aggression partition the effects that influence fighting into two compartments—intrinsic and extrinsic factors (Landau, 1951a,b). Intrinsic factors, as the label implies, typically refer to traits that correlate with an animal's fighting ability in terms of physical prowess—that is, its resource holding power or RHP (Parker, 1974). The most common of these factors is some measure of size (Archer, 1988; Huntingford and Turner, 1987).

Extrinsic factors are encapsulated by what have come to be known as winner and loser effects (Landau, 1951a,b; 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 *T*-1, *T*-2, and so on, respectively. I shall refer to these as ''pure'' winner and loser effects to contrast them clearly with terminology I introduce below. Exactly how winner and loser effects influence fighting behavior is not well understood for many systems, but endocrinological changes after victory or defeat are the likely proximate mechanisms (Nelson, 1995). For example, in copperheads, when compared to winners, losers have elevated levels of plasma corticosterone, but decreased levels of plasma testosterone (Schuett, 1997).

Much of the theoretical work on aggression focuses on intrinsic factors. Extrinsic effects have been the subject of less attention, and studies to date tend to examine winner and loser effects in terms of their impact on pairwise interaction, rather than on dominance hierarchies. I have recently modeled the effect of pure winner and loser effects on hierarchy structure per se (Dugatkin, 1997b). When winner effects alone were important, a hierarchy in which all individuals held an unambiguous rank was found. When only loser effects were important, a clear alpha individual always emerged, but the rank of others in the group was unclear because of the scarcity of aggressive interactions. Increasing winner effects for a given value of the loser effect increases the number of individuals with unambiguous positions in a hierarchy and the converse is true for increasing the value of the loser effect for a given winner effect. In addition, pure winner and loser effects have ramifications for intervention behavior and coalition formation (Dugatkin, 1998a,b; Johntsone and Dugatkin, 2000).

While pure winner and loser effects examine how the actual experience of contest outcome can affect fighting abilities, there two related types of extrinsic factors—audience and bystander effects—that have not been the subject of any formal mathematical modeling. Audience effects occur when individuals change their fighting behavior as a result of being watched by others (Doutrelant et al., 2001; Evans and Marler, 1984; McGregor and Peake, 2000). The bystander effect, which we shall be focusing on here, refers to the case in which an individual changes its estimation of the fighting abilities of others based on what it observes. Given that fighting costs can often be significant during animal contests (Archer, 1988; Abbott and Dill, 1985; Enquist et al., 1990; Huntingford and Turner, 1987) selection should, whenever possible, favor any assessment that curtails such costs. Despite their potential importance, bystander effects have not been the subject of a great deal of empirical work, although they have been demonstrated in chickens (Chase, 1982a,b, 1985; Coultier et al., 1996), rainbow trout (*Oncorhynchus mykiss*; Johnsson and Akerman, 1998) and fighting fish (*Betta splendens*; Oliveira et al., 1998).

Chase's ''jigsaw model'' (Chase, 1980, 1982a) was the first serious attempt to place bystander effects into a theoretical framework. Chase developed a three-player scenario, wherein a bystander (C) observes an interaction between the two other group members (A and B). Subsequent to this C interacts with either A or B. In such scenarios, there are four possible dyadic outcomes: (1) double dominance where A defeats C, (2) double subordinance in which C defeats B, (3) bystander domi-

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nates initial dominant, wherein C defeats A; and (4) initial subordinate dominates bystander, wherein B defeats C.

Chase's models found that regardless of the direction of the third relationship, *double dominance* and *double subordinance* led to transitive, linear hierarchies (A→B, B→C, A→C, or A→B, C→B, A→B) while *bystander dominates initial dominant* and *initial subordinate dominates bystander* always lead to intransitive, relatively nonlinear hierarchies. Chase's experimental work with chickens demonstrated that double dominance and double subordinance were indeed the most likely outcomes, suggesting that bystander effects tend to stabilize dominance hierarchies (Chase, 1982a,b; this also held true when examining triadic interactions in four-person hierarchies; see Chase, 1985).

Chase's jigsaw model, though suggestive, leaves many questions about bystander effects and dominance hierarchies unanswered. This is in part due to the fact that these verbal models contain no explicit parameters that can be manipulated. In particular, Chase did not examine ''bystander winner'' and ''bystander loser'' effects independently (see more below), but only considered the effects on hierarchy formation when both are present. Furthermore animals did not assess each other's RHP in Chase's model work, nor were bystander effects combined with pure winner and loser effects to examine their joint effects. Here, spurred by Chase's seminal work on bystander effects, I develop models that explicitly address the issues raised. It is important, however, to note that the models presented here do *not* examine the *evolution* of bystander effects. Rather, given that the literature suggests that winner, loser, and bystander effects may play a role in animal social behavior, the models ask what impact these effects have on hierarchy formation.

MODELS

General rules and parameters

As in Dugatkin (1997b), individuals in a group of size N are randomly paired in potentially aggressive contests. For simplicity, I will examine groups in which N is even. The simulation proceeds through time intervals, $T = 1,2,\ldots T_{max}$, and during each interval $N/2$ interactions occur. At the start of a simulation, each player is assigned a number that measures the individual's assessment of its own fighting ability. This value can be thought of as a player's estimate of its own RHP. A player's assessment of itself at time T is labeled $RHP_{player\ i,\ self,\ T}$.

Aggression in these simulations encompasses both chases (where one player opts to fight, while its opponent does not) and actual fighting. In an encounter, players are aggressive if:

$$RHP_{player\ i,\ self,\ T}/RHP_{opponent} \geq \Phi \quad (1)$$

where $RHP_{player\ i,\ self,\ T}/RHP_{opponent}$ will be referred to as ''relative RHP'' and Φ (where $\Phi \leq 0$) will be called the ''aggression threshold'' (Mesterton-Gibbons and Dugatkin, 1995). 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 that they assess to be smaller than or equal to 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 fight. In such cases, one individual wins and one loses. (2) Player i meets the aggression threshold, while player j does not, or vice versa. In this case, we will say that one player ''attacked,'' while the other player ''retreated.'' Attackers are considered to have won such interactions. (3) Neither player i nor player j meets the aggression threshold, and hence neither opts to fight. This will be referred as a ''double kowtow.''

If both players opt to be aggressive (i.e., a fight occurs), the probability that player i will defeat player j is given as:

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

Embodied in (1) and (2) is the assumption that an animal's decision about being aggressive is determined by its assessment of its own RHP (Jackson, 1991) and that of its potential opponent, but the probability of winning an aggressive interaction, given that one occurs, is dependent only on each individual's assessment of its *own* RHP (i.e., player i's *assessment* of j does not affect player i's probability of victory).

T_{max} was set to 250, group size (N) was either four or eight, Φ was set at either 0.25, 0.5, 0.75, or 0.9, the initial RHP value for each group member was set at 100 (i.e., all group members started out with the same RHP value) and each combination of parameters was run 10 times.

Model I: bystander effects only

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 one of its group mates because it has just seen that group mate emerge victorious in an aggressive interaction, bystander winner effects are in play. Conversely, should a bystander see another individual lose a fight and then subsequently devalue the fighting ability of such a loser, bystander loser effects are at work. Both effects can be in operation simultaneously.

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

$$RHP_{bystander,\ j,\ T+1} = (1 + BW)\ RHP_{bystander,\ j,\ T} \quad (3)$$

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 pure winner or loser effects).

Now imagine the same interaction when only BL effects are modeled. *Each bystander* should now change its estimate of k's RHP as follows:

$$RHP_{bystander,\ k,\ T+1} = (1 - BL)\ RHP_{bystander,\ k,\ T} \quad (4)$$

In Model I, BW and BL were incremented from 0 to 0.5 independently (for a total of 36 BW/Bl combinations).

Model II: bystander and pure winner/loser effects

Model II considers the case in which, in addition to bystander effects, pure winner (W) and loser (L) effects are also at work. I shall examine this 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 (pure winner and loser effects alone were examined in Dugatkin, 1997b).

Again, consider the situation raised above. If BW and W are both in play, not only do bystanders change their assessment (as in Equation 3), but now:

$$RHP_{j,\ self,\ T+1} = (1 + W)\ RHP_{j,\ self,\ T} \quad (5)$$

Conversely, if BL and L are both at work, not only do bystanders change their estimates as in Equation 4, but:

$$RHP_{k,\ self,\ T+1} = (1 - L)\ RHP_{k,\ self,\ T} \quad (6)$$

Last, if BW, BL, W, and L are all in play at once, then Equations 3–6 are all employed in the model.

BW/W and BL/L were each increased from 0 to 0.5 (in increments of 0.1). In all simulations, an animal was consid-

Table 1

Bystander winner effects. N = 4, BW = 0.3, ϕ = 0.5, 250 interactions (including double kowtows which score zero for each player involved in such an interaction)

	A	B	C	D
A	—	1	1	41
B	1	—	6	43
C	2	0	—	30
D	0	1	1	—

Entries in rows represent the sum of the number of times the row player defeated the column player in fights and attacked the column player. Only the omega ranked individual in this group (D) is clearly discernible.

Table 2

Bystander loser effects. N = 4, BL = 0.3, ϕ = 0.5, 250 interactions (including double kowtows which score zero for each player involved in such an interaction)

	A	B	C	D
A	—	15	8	25
B	25	—	17	25
C	17	28	—	25
D	19	21	25	—

Entries in rows represent the sum of the number of times the row player defeated the column player in fights and attacked the column player.

ered dominant to another if it defeated that individual in greater than 50% of the encounters between the pair. All computer simulations were constructed using TrueBasic™.

RESULTS

As in prior work on winning and losing, (Dugatkin, 1997b) varying either Φ (the aggression threshold) or N (group size) does not qualitatively affect the results presented below (i.e., the same general patterns were uncovered regardless of Φ or N), and so I shall focus on $\Phi = 0.5$ and $N = 4$. In addition, repeated simulations with the same set of parameter values were very consistent in their outcomes.

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 (Table 1). To understand this pattern, recall that all individuals begin with an $RHP_{i,\, self,\, 1}$ of 100. During early interactions, one individual (let's call him D in accordance with Table 1), by chance, loses a majority of its early interactions. Others in the group observe this and now act as if D has the same (or close to the same) RHP it began with (i.e., 100), while they all view each other's RHP as larger than 100 (because most group members will have won some early fights). This quickly devolves into a situation in which upon encounter everyone attacks D (who always retreats), but never attack each other. In this scenario, most aggressive interactions are of the "attack-retreat" rather "both individuals opt to fight" variety.

The scenario is dramatically different when only bystander loser effects are in operation. Now, wins and losses are randomly distributed throughout a group (Table 2). In contrast to the bystander winner case in which most aggressive interactions are "attack-retreat," now individuals always fight when they meet. The lack of a clear hierarchy in such groups can be understood as follows: When bystander loser effects are in operation, individuals change the RHP value they assign to others, but only in a negative direction, and they never change the estimation of their own RHP. As a result, when two players meet, each assess the other to have an RHP lower than their own and they both tend to opt for fighting. The results of such fights are random, in the sense that each of the protagonist's RHP always remain at 100 (i.e., $RHP_{j,\, self,\, T} = 100$ for all T), and thus Equation 3 assures such randomness.

While it is not possible to be precise, for values of Φ between 0.1 and 0.5, bystander loser effects appear to be stronger than bystander winner effects. For example, when $N = 4$ and BL = 0.1, BW must be set at 0.5 to produce a typical BW hierarchy (only a clear omega), but when BW = .1, a Bl of 0.2 produces a typical BL set of interactions (wins and losses distributed equally through a hierarchy) (Table 3). This pattern is found for different values of N and Φ and could be interpreted as evidence that bystander loser are more powerful than bystander winner effects. It is worth noting that empirical work on pure winner and loser effects often finds that of the two, pure loser effects tend be more potent (Chase et al., 1994).

Model II examined three cases—joint pure and bystander winner effects, joint and pure bystander loser effects, and all four effects in play simultaneously. All three cases produced a linear hierarchy in which all positions (i.e., α to δ when $N = 4$) were clearly defined, and most interactions were of the attack/retreat variety (Tables 4 and 5). The clearly defined linear hierarchy is due to each individual having the exact same information regarding RHPs. That is, if individual A assesses its own RHP as R, then when joint effects are in play, all other individuals also assess A's RHP as R, hence there is agreement about everyone's RHP. This in turn creates a social environment in which most interactions are of the form "attack-retreat" and individuals fall into rank quickly.

DISCUSSION

In conjunction with prior work (Dugatkin, 1997b), it is now clear that the nature of pure winner, pure loser, bystander

Table 3

The relative strength of BW versus BL

	A	B	C	D
BW = 0.1, BL = 0.2				
A	—	11	11	24
B	21	—	17	25
C	24	19	—	21
D	23	30	14	—
BL = 0.1, BW = 0.2				
A	—	41	5	52
B	0	—	3	17
C	0	47	—	35
D	0	17	25	—
BL = 0.1, BW = 0.5				
A	—	0	0	39
B	0	—	1	42
C	1	0	—	40
D	0	0	0	—

If BW = 0.1, a BL of 0.2 produces a typical BL set of interactions (wins and losses distributed equally through a hierarchy). If BL = 0.1, and BW is set at 0.2, we do not get the typical BW hierarchy, with a single omega, suggesting that bystander loser effects are more powerful than bystander winner effects. When BL = 0.1, BW must be set at 0.5 to produce a typical BW hierarchy.

Table 4

Joint bystander and pure winner effects. $N = 4$, BW = W = 0.3, ϕ = 0.5, 250 interactions (including double kowtows which score zero for each player involved in such an interaction)

	A	B	C	D
A	—	36	47	4
B	1	—	29	4
C	0	3	—	0
D	39	41	45	—

Entries in rows represent the sum of the number of times the row player defeated the column player in fights and attacked the column player.

winner, and bystander loser effects (and their interactions) can have a profound effect on hierarchy formation (or the lack of it). Depending on which effects are in play, a variety of hierarchy forms are possible (Table 6). For example, under the models presented here we have seen that, depending on the parameters, one might expect only a clear bottom-ranking individual, a clearly defined hierarchy or no hierarchy at all (where wins and losses are randomly distributed among individuals).

Unfortunately, the published data on bystander effects are not of the form that can be plugged into the equations presented in this article. In principle, however, future experimental work could easily be constructed in a way to allow use of the equations presented here. For example, to measure bystander winner effects, for simplicity, one would begin in a system where no pure winner effects are in play and simple pairwise aggressive bouts were used to determine the value of Φ. Then individual i would be pitted against individual j (where i and j were of known RHPs) in part 1 of a trial, and any aggression that took place would be recorded. Then, at some point at which i and j had forgotten the initial encounter (this will vary across systems), i and j would be re-paired in part 2 of a trial, but only after i had been a bystander to a fight in which j emerged victorious. If repeated with many pairs of individuals, the difference between i's behaviors in different parts of a trial could be used to gauge WL. Similar sorts of experiments (but with i observing j lose) could be run to examine pure loser effects.

Once the sorts of experiments outlined above are complete, one could then further test the predictions from the models developed here in a comparative study in which hierarchy formation would be examined in species that had documented various combinations of bystander winner, bystander loser, pure winner, and pure loser effects. The types of hierarchies uncovered could then be compared to the results presented here and in Dugatkin (1997b). Unfortunately, the data for such comparisons do not yet exist. That is, although bystander winner, bystander loser, pure winner, and pure loser effects are evident in a wide variety of taxa (e.g., insects; Alexander, 1961; Burk, 1979; molluscs; Zack, 1975; fish; Beaugrand and Zayan, 1985; Francis, 1983; Frey and Miller, 1972; Johnsson and Akerman, 1998; Oliveira et al., 1998; birds; Drummond and Osorno, 1992; reptiles; Schuett, 1996, 1997 and rodents; van de Poll and Smeets, 1982), and despite some controlled studies of these phenomena (Bakker and Sevenster, 1983; Bakker et al., 1989; Beacham and Newman, 1987; Beaugrand and Zayan, 1985; Burk, 1979; Chase, 1982a,b, 1985; Chase et al., 1994; Cloutier et al., 1995, 1996; Francis, 1983, 1987; Frey and Miller, 1972; Hollis et al., 1995; Johnsson and Akerman, 1998; Oliveira et al., 1998; Schuett, 1996, 1997), no work to date has documented *both* pure and bystander winner and loser effects *and* the detailed nature of behavioral interactions when individuals are in *groups*. Hopefully, the results of this model will spur on such studies in the future.

Table 5

Joint bystander and pure loser effects. $N = 4$, BL = L = 0.3, ϕ = 0.5, 250 interactions (including double kowtows which score zero for each player involved in such an interaction)

	A	B	C	D
A	—	47	43	43
B	0	—	44	0
C	0	0	—	0
D	2	35	36	—

Entries in rows represent the sum of the number of times the row player defeated the column player in fights and attacked the column player.

Table 6

A summary of the effects of winner, loser, bystander winner and bystander loser effects on hierarchy formation

Model	Hierarchy structure
Pure winner only (Dugatkin, 1997b)	Clear linear hierarchy*
Pure loser only (Dugatkin, 1997b)	Only top rank clear
Bystander winner only	Only bottom rank clear
Bystander loser only	Random interactions**
Bystander winner and pure winner	Clear linear hierarchy*
Bystander loser and pure loser	Clear linear hierarchy*
Bystander winner, pure winner, bystander loser, and pure loser	Clear linear hierarchy*

* A clear linear hierarchy is one in which all positions in a hierarchy are clearly delineated. For example, if $N = 3$, a clear alpha, beta and gamma individual emerge.

** Random interactions denote the case where wins and losses are distributed evenly throughout a hierarchy. No position is clearly defined.

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