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Individual recognition, dominance hierarchies and winner and loser effects

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Winner and loser effects are defined as an increased probability of winning an aggressive interaction at time T, based on victories at time $T-1$, $T-2$, etc., and an increased probability of losing at time T, based on losses at time $T-1$, $T-2$, etc., respectively. Prior theoretical work on dominance hierarchy formation has demonstrated that when players are not capable of individual recognition, loser effects always produce a clear top-ranked (alpha) individual, but all other ranks in a group remain unclear; whereas winner effects always produce strict linear hierarchies in which the rank of each individual is clear. Paradoxically, however, when individual recognition—a phenomenon long thought to stabilize hierarchies—is possible, winner and loser effects have no impact on the probability of forming strict linear hierarchies.

Keywords: winner effect; loser effect; individual recognition; dominance hierarchies

1. INTRODUCTION

Models of aggression and dominance hierarchy formation often partition the effects that influence animal fighting behaviour into two compartments: intrinsic and extrinsic factors (Landau 1951*a*,*b*). Intrinsic factors refer to traits, such as size, that correlate with an animal's fighting ability in terms of physical prowess (i.e. its resource holding power (RHP) (Parker 1974)). Extrinsic factors generally refer to what have come to be known as winner, loser and bystander effects (Landau 1951*a*,*b*; McGregor *et al.* 1999; Mesterton-Gibbons 1999; McGregor & Peake 2000; see Chase *et al.* (1994) for a review of empirical work on winner and loser effects). Precisely how winner and loser effects impact fighting behaviour is not yet completely understood, but neuroendocrinological changes after victory or defeat are the probable proximate mechanisms (Allee *et al.* 1955; Rose *et al.* 1975; Hannes *et al.* 1984; Knapp & Moore 1996; Yeh *et al.* 1997; Oliveira *et al.* 2001; Summers *et al.* 2003; Yang & Wilczynski 2003).

Extrinsic factors have been the subject of less attention than intrinsic factors with regard to their influence on the outcome of dominance interactions. Moreover, empirical work has focused on the impact of winner and loser effects on pairwise interactions, rather than on dominance hierarchies (but see Chase *et al.* 2003). In a pair of influential papers, Landau (1951*a*,*b*) examined how extrinsic and intrinsic factors might explain the presence of the linear hierarchies that he believed were so common in nature, and found that except under extreme conditions, intrinsic factors alone could not produce the linear hierarchies that he felt were representative of nature. However, once extrinsic factors, such as winner and loser effects, were added to the model, hierarchies were much more similar to those found in nature.

Despite the importance and impact of Landau's (1951*a*,*b*) papers on research in the area of dominance hierarchies, several critical questions surrounding winner and loser effects, and how they interact, remain unanswered more than 50 years later. In particular, Landau (1951*a*,*b*) did not examine winner and loser effects independently, but considered only their impact on hierarchy formation when both were present. Furthermore, animals did not assess each other's fighting ability (RHP) in Landau's work.

In a prior model, the lead author found that when winner effects alone were examined, a strict linear hierarchy emerged in which all individuals held an unambiguous rank (Dugatkin 1997). When examining loser effects in the absence of winner effects, a clear alpha individual always emerged, but the rank of others in the group was unclear. In those models, individuals could not recognize one another. After winning or losing a fight, they raised or lowered their estimate of their fighting ability with respect to all other group members, not specifically with respect to the individual with which they had just interacted. Here, we describe the results of a computer simulation in which individuals in a group can recognize group mates and use information from prior aggressive interactions (wins and losses) to temper their future interactions with *specific* individuals, and examine how this affects the structure of dominance hierarchies (see Johnston (2003), Paintner & Kramer (2003), Petrulis & Eichenbaum (2003), Pfalzer & Kusch (2003) and Gherardi & Tiedemann (2004) for some recent studies on individual recognition across a wide array of taxa).

2. THE MODEL

A group of N animals within which randomly chosen pairs of individuals were pitted against one another in potentially aggressive contests was simulated, using an Apple Macintosh-based program written in TRUE BASIC. Discrete time intervals, $T = 1, 2, \ldots T_{max}$, were simulated,

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and at each interval $N/2$ interactions occurred (i.e. all group members were involved in contests). At the start of a simulation, each animal was assigned a score, which denoted the individual's assessment of its own fighting ability. This score was analogous to a player's estimate of its own RHP and is denoted as $RHP_{player\ i,\ self,\ T}$ (T is a counter that is initialized at 1 and increases by a single unit after each pairwise encounter). Individuals were aware of their own *initial* RHP value (RHP_{self}) and the initial RHP score of all other group members as well (RHP_{other}), but not the RHP of other group members as they changed as a result of winner or loser effects. In other words, player i always assumed that player j's RHP was whatever player j's initial RHP might have been.

In each contest, an animal could choose to either 'be aggressive' or 'retreat'. Players used a simple rule to determine which option to employ. Individual i assessed its own RHP and that of its opponent—individual j—and chose to be aggressive if $RHP_{player\ i,\ self\ versus\ j,\ T}/RHP_{other}$ was greater than or equal to the aggression threshold, labelled F. $RHP_{player\ i,\ self\ versus\ j,\ T}$ denotes player i's estimate of its own RHP when matched against player j at time T (Mesterton-Gibbons & Dugatkin 1995). If $F = 0$, animals always fought, regardless of who their opponent was; whereas if $F = 0.5$, they fought another individual whose RHP they assessed to be up to twice as great as their own, and so on. Thus, three outcomes were possible when player i met player j: (i) both player i and j met the aggression threshold and both decided to be aggressive (fights); (ii) player i met the aggression threshold, whereas player j did not (i attacked, j retreated), or vice versa (j attacked, i retreated); and (iii) neither player i nor player j met the aggression threshold, and hence neither opted to be aggressive. If both players opted to be aggressive, the probability that player i would defeat player j was given as

$$RHP_{player\ i,\ self\ versus\ j,\ T}/(RHP_{player\ i,\ self\ versus\ j,\ T} + RHP_{player\ j,\ self\ versus\ i,\ T}), \quad (2.1)$$

where $RHP_{player\ j,\ self\ versus\ i,\ T}$ equals player j's estimate of its own RHP when matched against player i at time T.

For all simulations, T_{max} was set to 1000, group size was set at either $N = 4$ or 8, and the initial RHP_{self} value for each group member was set at 10 (i.e. all group members started out with the same RHP value). Because the initial RHP values of others in the group were known, all animals assumed RHP_{other} to be 10 throughout the simulation. An animal was considered dominant to another if it defeated that individual in more than 50% of the encounters between the pair. In the model, an individual's assessment of its own RHP changed through time as a result of: (i) whether it won or lost a fight; and/or (ii) whether it retreated from an opponent, or whether its opponent retreated. In other words, winner and loser effects were a result of either (i) actually winning or losing a fight and (ii) simply retreating or having someone retreat from an attack. When player i won a fight against j, or had j retreat from its aggressive approach—i.e. when winner effects were in play—player i increased its own RHP with respect to player j by a factor of W, and so

$$RHP_{player\ i,\ self\ versus\ j,\ T} = (1 + W)\ RHP_{player\ i,\ self\ versus\ j,\ T-1}. \quad (2.2)$$

That is, when player i defeated player j, it increased its estimate of its own RHP against j, but did not increase its estimate of its RHP with respect to any other group members, reflecting the notion of individual recognition. Conversely, when player i lost a fight or retreated from an aggressive act by an opponent (j), its estimate of its own RHP with respect to j was lowered by a factor L and

$$RHP_{player\ i,\ self\ versus\ j,\ T} = (1 - L)\ RHP_{player\ i,\ self\ versus\ j,\ T-1}. \quad (2.3)$$

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. Indeed, numerous computer simulations undertaken show that relaxing this assumption does not qualitatively change the results presented below.

The parameter space explored was as follows: F varied from 0 to 1 (in steps of 0.25), W and L both ranged from 0 to 0.5, in increments of 0.1, and group size (N) was set at either 4 or 8. Hence, 300 unique combinations of parameters ($5 \times 6 \times 5 \times 2$) were simulated, and each of these combinations was run 500 different times, for a total of 150 000 simulation runs. Results from the simulations indicate that varying F and/or N had little qualitative effect on the outcome. In addition, varying W and L anywhere in the 0.25 to 1 range did not qualitatively affect results, and so here we report the case where group size was set at 4, and $F = 0.75$.

3. RESULTS AND DISCUSSION

The simulation output files were programmed to determine whether a linear hierarchy (alpha individual > beta > gamma > delta) existed in each group after 1000 interactions. In addition, the model was modified to consider the case of winner and loser effects, but no individual recognition: in these simulations individuals increased (winner effect) or decreased (loser effect) their assessment of their own RHP relative to everyone in their group (as in Dugatkin 1997). Results are shown in figure 1 and table 1. When individual recognition was in play, winner and loser effects produced hierarchies that were very similar to hierarchies formed when neither effect was in operation. These results are strikingly different from prior models of winner and loser effects in which no individual recognition was built into the simulations (Dugatkin 1997). In these models, all hierarchies were linear when W was in effect, and no hierarchies were linear when L was in play (figure 1).

From an evolutionary perspective, the results presented here are somewhat paradoxical. Individual recognition is thought to have evolved to allow for the detection of cheaters—individuals who bluff when involved in potential aggressive interactions—and to stabilize dominance hierarchies (Barnard & Burk 1979; Pagel & Dawkins 1997). Thus, the lack of individual recognition might be regarded as the primitive state in groups that may nonetheless have dominance hierarchies and individuals that respond to winner and loser effects. Once introduced into such a

Table 1. The win–loss matrices. (*a*) Winner effect = 0.3, no individual recognition. A clear linear hierarchy exists (D-> A-> C-> B) and all interactions are 'fights'. (*b*) Loser effect = 0.3, no individual recognition. A clear alpha individual (D) exists, but other ranks are indeterminate. All interactions are 'attack/retreats'. (*c*) Winner effect = 0.3, individual recognition. No linear hierarchy exists and all interactions are 'fights'. (*d*) Loser effect = 0.3, individual recognition. No linear hierarchy exists and all interactions are 'attack/retreats'.

	A	B	C	D
(*a*)				
A	—	160	175	2
B	2	—	3	0
C	2	168	—	1
D	157	168	162	—
(*b*)				
A	—	0	0	0
B	0	—	1	0
C	0	0	—	0
D	162	163	170	—
(*c*)				
A	—	180	138	1
B	1	—	162	182
C	2	2	—	11
D	156	1	164	—
(*d*)				
A	—	172	0	162
B	0	—	160	0
C	171	0	—	166
D	0	169	0	—

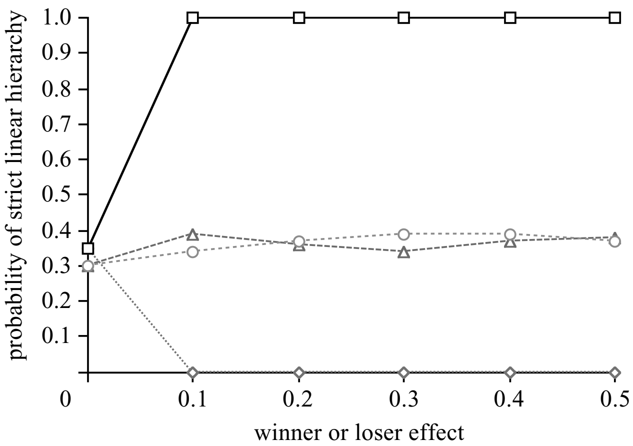

Figure 1. The probability of a linear hierarchy forming as a function of winner or loser effects. Squares: winner effect, no individual recognition; diamonds: loser effect, no individual recognition; circles: winner effect, individual recognition; and triangles: loser effect, individual recognition. At $X = 0$, neither winner or loser effects are in play. When no winner or loser effects are in play, the probability of a strict linear hierarchy is approximately 0.3—very similar to the probability obtained for the case of both 'winner effect, no individual recognition' and 'loser effect, no individual recognition'. A pair of individuals had to interact at least 10 times for their rank in relation to each other to be established; otherwise the relative rank of these individuals was ambiguous, and a linear hierarchy was not possible.

population, however, individual recognition negates the impact that winner and loser effects have on the probability of strict hierarchies forming.

One possible explanation for this paradox centres on the way in which pairwise interactions translate into broad changes in aggressive behaviour. When no individual recognition is possible in the model, winner effects create linear hierarchies because individuals raise their estimate of their own RHP in relation to *all* other group members after a win, but do not lower this value after a loss, and hence both players in a potentially aggressive interaction are likely to be above the aggression threshold. The individual with the higher estimation of its own RHP is more likely to win, leading to strict linear hierarchies. In the absence of individual recognition, loser effects quickly produce individuals (aside from the alpha individual) that refrain from being aggressive because of their low estimate of their own RHP after a few losses. In this scenario, linear hierarchies are never produced.

When individual recognition is possible, individuals no longer raise or lower their general estimate of their RHP, but rather increase or decrease their estimate of their RHP in relation to the individual that they have just encountered. As such, dyadic interactions do not affect the behaviour of interactants in the same broad way that they do when individual recognition is not possible, resulting in winner and loser effects having no impact on the formation of linear hierarchies. Given the ubiquity of dominance hierarchies in nature, the growing evidence that prior experience affects aggressive interactions, and the strong evidence for individual recognition in many social systems, models such as those developed here can be used to make explicit predictions about hierarchy formation, and can only enhance future field and laboratory research on aggression.

The results of our simulation support the notion that individual recognition mechanisms can interfere with the formation of linear dominance hierarchies (Gervet *et al.* 1993; Theraulaz *et al.* 1995; Bonabeau *et al.* 1996; Hemelrijk 2000). For instance, stable but weakly organized hierarchies emerge in populations composed of animals that modify their assessment of their own RHP relative to specific others (Hemelrijk 2000). Hemelrijk (2000) focused on how individual recognition mechanisms affect variation in dominance scores, but not hierarchy linearity *per se*, making it difficult to draw parallels between her simulation and ours. Using a completely different modelling technique than that described in this paper, Theraulaz *et al.* (1995) and Bonabeau *et al.* (1996), however, showed that when recognition of *all others* is possible (i.e. small groups), and when the past dominance history of a pair has a moderate to considerable impact on future fight outcomes, stable nonlinear hierarchies ($0.25 < h < 0.75$) become common.

We hope that the predictions generated from our model provide the impetus for examining empirically both the specificity of winner and loser effects and their subsequent impact on hierarchy structure.

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