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Extrinsic effects, estimating opponents' RHP, and the structure of dominance hierarchies

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We examined the impact of winner and loser effects on dominance hierarchy formation when individuals are capable of estimating their opponent's resource holding power (RHP). The accuracy of such estimates was a variable in our simulations, and we considered cases in which all individuals err within the same bounds, as well as cases in which some individuals consistently overestimate, while others consistently underestimate their opponent's fighting RHP. In all cases, we found a clearly defined linear hierarchy. In most simulations, the vast majority of interactions were 'attack–retreats', and the remainder of interactions were almost all 'fights'. Error rates had no effect on the linearity of the hierarchy or the basic attack–retreat nature of interactions, and consistent over and underestimation did not affect the ultimate position of an individual in a hierarchy.

Keywords: winner effect; loser effect; individual recognition

1. INTRODUCTION

Over the last two decades, behavioural ecologists have come to recognize that 'extrinsic' factors can have an effect on pairwise aggressive interactions, as well as on the structure of dominance hierarchies (Hsu *et al.* 2005). Extrinsic factors include winner and loser effects, wherein individuals increase or decrease their probability of winning as a function of prior experience, as well as bystander effects and audience effects (Landau 1951*a*,*b*; Bonabeau *et al.* 1999; Mesterton-Gibbons 1999; Beacham 2003).

In a prior model, one of us (L.A.D.) examined hierarchy formation when winner and loser effects were in operation. We found that when winner effects alone were examined, a strict linear hierarchy emerged in which all individuals held an unambiguous rank and fights were common (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 addition, when loser effects were in play, interactions were primarily of the form 'attack–retreat', wherein one animal opted to fight, but the other did not.

Here, we expand on the models described above, and consider the structure of dominance hierarchies when winner and loser effects are in operation, and individuals can assess the fighting abilities of opponents, and errors are made in assessment.

2. THE MODEL

Using Visual Basic, we simulated a group of four individuals, within which randomly chosen pairs of players were pitted against one another in potentially aggressive contests. Discrete time intervals, $T=1, 2, \ldots, T_{\max}$, were simulated. At the start of a simulation, each individual was assigned a score, which denoted its assessment of its own fighting ability. This score was analogous to a player's estimate of its own resource holding power (RHP) and is denoted as $\mathrm{RHP}_{\text{player i},T}$ (T denotes the number of encounters experienced, and is initialized at 1 and increased by a single unit after each interaction). Individuals are assumed to estimate their own initial RHP value correctly. This assessment of one's own fighting ability then changes as a function of wins and losses (as described below). In addition, on each encounter with a putative opponent, an individual estimates the fighting ability of that opponent—labelled individual j—but that estimate falls within certain error bounds of the true fighting ability of j. We denote the error associated with assessing an opponent's RHP as ε. The estimate of an opponent's RHP is randomly selected from the range $(1-\varepsilon)^*$ $\mathrm{RHP}_{\text{player j},T}$ to $(1+\varepsilon)^*$ $\mathrm{RHP}_{\text{player j},T}$. When ε is set at 0, an individual is assumed to have perfect knowledge of its opponent's RHP. We denote the estimate of an opponent's score after ε has been selected and applied as $\overline{\mathrm{RHP}}_{\text{player j},T}$. What cues individuals use to assess the fighting score of an opponent are not specified to allow for generality. Such assessment could be based on size, position, signals emitted by opponents and so on.

In each contest, an animal could choose to either 'be aggressive' or 'retreat.' Players use a rule to determine which option to employ. Individual i assesses its own RHP and that of its opponent and chooses to be aggressive if the assessment of its own RHP divided by its assessment of its opponent's RHP is greater than or equal to what we call the aggression threshold, labelled F. If $F=0$, animals always fight, regardless of who their opponent is; if $F=0.5$, they fight another individual whose RHP they assess to be up to twice as great as their own and so on. Three outcomes are possible when player i meets player j: (i) both individuals meet the aggression threshold and both decide to be aggressive (fights), (ii) i meets the aggression threshold, while j does not (i attacks, j retreats), or vice versa (j attacks, i retreats); and (iii) neither i nor j meets the aggression threshold, and hence neither opts to be aggressive (a 'double kowtow'). In our models, for a double kowtow to occur, it must be true that $F(1+\varepsilon)>1$.

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

$$\frac{\mathrm{RHP}_{\text{player i},T}}{\mathrm{RHP}_{\text{player i},T}+\overline{\mathrm{RHP}}_{\text{player j},T}}. \tag{2.1}$$

An individual's assessment of its own RHP changes through time as a result of whether it wins or loses a fight and/or whether it retreats from an opponent; or

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whether its opponent retreats from it. When winner effects are in play, and i wins a fight against j, or j retreats from its aggressive approach, i increases its own RHP, by a factor of *W*, and so:

$$\mathrm{RHP}_{\text{player i},T} = (1+W)\mathrm{RHP}_{\text{player i},T-1}. \quad (2.2)$$

Conversely, if loser effects are in operation, when i loses a fight or retreats from an aggressive act by an opponent (j), its estimate of its own RHP with respect to j is lowered by a factor of *L* and

$$\mathrm{RHP}_{\text{player i},T} = (1-L)\mathrm{RHP}_{\text{player i},T-1}. \quad (2.3)$$

Based on the result of prior simulations, we assume that winning a fight and having ones opponent retreat have the same effect on *W*, and that losing a fight or retreating has the same effect on *L* (Dugatkin 1997).

In our simulations, *T* was always set to 1000, *F* was set at either 0, 0.5 or 1.0, ε was set at 0, 0.25 or 0.75, and *W* and *L* both ranged from 0 to 0.5, in increments of 0.1. That is, there were 3 *F* values, 3 ε values, and 36 winner/loser combinations, for a total of 324 combinations of *F*, ε and *W*/*L*. For each of these 324 combinations, we ran the following:

(i) All individuals initiated with an RHP of 10.
(ii) All individuals initiated with an RHP of 10, but two individuals always overestimated an opponent's size (estimation of opponent's RHP ranges from $\mathrm{RHP}_{\text{player j},T}$ through $(1+\varepsilon)\mathrm{RHP}_{\text{player j},T}$) and two individuals always underestimated an opponent's size (estimation of opponent's RHP ranges from $(1-\varepsilon)^{*}\ \mathrm{RHP}_{\text{player j,T}}$ through $\mathrm{RHP}_{\text{player j,T}}$).
(iii) Initial RHP of the four individuals was 10, 12, 14 and 16.
(iv) Initial RHP of the four individuals was 10, 12, 14 and 16, but the two smaller individuals always overestimated an opponent's size and the two larger individuals always underestimated an opponent's size.
(v) Initial RHP of four individuals was 10, 12, 14 and 16, but the two smaller individuals always underestimated an opponent's size, and the two larger individuals always overestimated an opponent's size.

3. RESULTS

A number of general patterns emerged across our simulations:

(i) A clearly defined linear hierarchy was uncovered when winner effects, loser effects or both were in operation. Pairwise dominance was defined as defeating an opponent more than 50% of the time, but simulations indicate that individuals rarely defeated higher-ranking players at all (table 1).
(ii) When *F* was greater than zero, the vast majority of all interactions were of the form attack–retreat. The remainder of interactions were fights, with virtually no double kowtows recorded (as $F(1+\varepsilon)$ was usually less than 1). This was the pattern found for most combinations of winner and loser effects, and for most error rates used.
(iii) Of the fights that did take place, a large majority occurred early on in the 1000 interactions. For example, for the simulations presented in table 1*a–c*, there were 18, 19 and 9 fights, respectively, and 78.2% of all these fights occurred during the first 20 interactions of a simulation. This was the pattern found for most combinations of winner and loser effects, and for most error rates.
(iv) When all individuals were initiated at an RHP of 10 and they all had the same ε, error rates had no effect on the linearity of the hierarchy or the basic attack–retreat nature of interactions. That is, if we compare simulations in which the only difference is in ε—for example, if we contrast the case when all individuals are initiated at RHP 10, $F=0.5$ and $\varepsilon=0$ in one simulation, with the same case, except $\varepsilon=0.5$ in the other simulation—in both cases we see a linear hierarchy, in which the vast majority of interactions are of the form attack–retreat. This holds true for all comparisons in which the only difference between simulations is in the value of ε.
(v) When individuals were initiated at equal RHPs (10), a comparison of those who erred by always overestimating their opponent's RHP, and those who erred by underestimating, found no differences in the rank of such individuals. That is, consistent over and underestimating did not affect position in the hierarchy (table 2).

Table 1. All individuals were initiated at RHP=10. $F=0.5$, $L=0.2$, $W=0$. A, B, C and D refer to four individuals, but do not imply a rank in a hierarchy (i.e. individual A is not necessarily the top-ranked individual). Entries in each cell denote the number of times the row player either fought and defeated, or attacked (and caused a retreat in), the column player. (*a*) $\varepsilon=0$, (*b*) $\varepsilon=0.25$, (*c*) $\varepsilon=0.75$. (*a*) 982 attack–retreats, 18 fights, 0 kowtows. (*b*) 981 attack–retreats, 19 fights, 0 kowtows. (*c*) 991 attack–retreats, 9 fights, 0 kowtows. Similar results are obtained when *L* and *W* are looped through all possible combinations from $L=0$ to 0.5, and $W=0$ to 0.5. The absence of double kowtows is due to the fact that $F(1+\varepsilon)<1$ for all cases in this table.

individual	A	B	C	D
(*a*)				
A	—	162	191	149
B	0	—	167	1
C	0	1	—	0
D	1	164	164	—
(*b*)				
A	—	174	182	151
B	0	—	1	1
C	1	140	—	0
D	1	168	181	—
(*c*)				
A	—	0	0	161
B	178	—	172	149
C	162	0	—	178
D	0	0	0	—

Table 2. All individuals were initiated at RHP = 10. $F=0.5$, $L=0.2$, $W=0$. (*a*) $\varepsilon=0$, (b) $\varepsilon=0.25$, (c) $\varepsilon=0.75$. In this case, A and B only underestimate, and C and D only overestimate. Similar results are obtained when L and W are looped through all possible combinations. (*a*) 968 attack–retreats, 32 fights, 0 kowtows. (*b*) 974 attack–retreats, 26 fights, 0 kowtows. (*c*) 974 attack–retreats, 26 fights, 0 kowtows. The absence of double kowtows is due to the fact that $F(1+\varepsilon)<1$ for all cases in this table.

individual	A	B	C	D
(*a*)				
A	—	172	155	162
B	0	—	175	0
C	2	2	—	2
D	3	157	170	—
(*b*)				
A	—	151	160	160
B	0	—	175	1
C	0	1	—	0
D	3	186	163	—
(*c*)				
A	—	162	1	174
B	4	—	1	159
C	149	166	—	183
D	0	1	0	—

(vi) When individuals were initiated at different RHPs (10, 12, 14 and 16), ε had no effect on position. When all four individuals had the same ε value—including the case when $\varepsilon=0$—the vast majority of simulations found that the individuals that started with RHP scores of 16 and 14 occupied the top two ranks in the hierarchy at the end of a simulation, and the individuals that were initiated with RHP scores of 12 and 10 occupied the lower two ranks. Most interactions were of the form attack–retreat. This type of hierarchy (two individuals with higher initial RHP occupy the top two ranks in the final hierarchy) and the attack–retreat behaviour noted were also found both when smaller individuals were underestimators and larger individuals were overestimators, and when smaller individuals were overestimators and larger individuals were underestimators.

4. DISCUSSION

Our results suggest that when individuals can estimate their opponent's fighting abilities, strict linearity hierarchies should emerge, and that within these hierarchies, aggressive interactions are of the form attack–retreat, rather than fight. These results are different from prior models of winner and loser effects in which individuals were not able to estimate their opponent's fighting ability and how it changed over time (Dugatkin 1997). In those models, all hierarchies were linear when W was in effect; when L was in play, a clear top-ranking individual emerged, but it was impossible to assign rank to any other group member. In addition, when winner effects were in operation in prior models, the typical aggressive interaction was a fight, rather than an attack–retreat. As such, the estimation of opponents' RHP that we model here appears to both stabilize linear hierarchies and to minimize the number of fights between individuals in a hierarchy.

When ε was greater than zero in our simulations, every individual made errors, although in some simulations we modelled consistent overestimators and consistent underestimators. ε had little effect on the general patterns we uncovered—hierarchies when $\varepsilon>0$ were similar in structure to hierarchies when ε was zero. In addition, when ε was greater than zero, over and underestimating had no impact on the rank of an individual.

Given the evidence that many hierarchies in nature have a strong linear component, and that dangerous fights are the exception rather than the rule, we hope that our model will spur on continued research in the area of winner and loser effects and hierarchy formation. In addition, our results that estimating an opponent's fighting score produces linear hierarchies with few fights suggests that future work examining hierarchy formation from a more cognitive perspective, including experimental work on animals' abilities to estimate various features of potential opponents, may be fruitful.

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