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The social implications of winner and loser effects

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Winner and loser effects have now been documented in a number of species. To our knowledge, experimental work, however, has focused exclusively on pairwise interactions, and not the extent to which winner and loser effects impact hierarchy formation. We report the results of experimentally manipulated winner and loser effects on hierarchy formation in a socially living species, the green swordtail, *Xiphophorus helleri*. Our results demonstrate that randomly chosen winners in pairwise aggressive contests were more likely to emerge as top-ranked individuals in a hierarchy, whereas randomly chosen losers were more likely to emerge as the lowest-ranking individuals, and that 'winner–neutral–loser' hierarchies were significantly overrepresented.

Keywords: winner effect; loser effect; dominance hierarchy; aggression

1. INTRODUCTION

Aggression and hierarchy formation are an integral part of everyday life for many social-living species. Winner and loser effects, in which 'winning begets winning' and 'losing begets losing' have now been demonstrated in several species (Chase *et al.* 1994). Surprisingly, although such winner and loser effects are thought to be very important in terms of how they influence hierarchy formation (Landau 1951*a*,*b*; Dugatkin 1997; Mesterton-Gibbons 1999; Hemelrijk 2000; Beacham 2003; Van Doorn *et al.* 2003*a*,*b*), experimental work has focused almost exclusively on pairwise interactions (for an exception see Chase *et al.* 2003), and not the extent to which winner and loser effects impact hierarchy formation. We report the results of experimentally manipulated winner and loser effects on hierarchy formation in a socially living species, the green swordtail, *Xiphophorus helleri* (Earley & Dugatkin 2002). We found that randomly chosen winners in pairwise aggressive contests were more likely to emerge as top-ranked individuals in a hierarchy, whereas randomly chosen losers were more likely to emerge as the lowest-ranking individuals.

2. MATERIAL AND METHODS

Each of the 20 trials that we undertook comprised two parts—a pairwise interaction component (part 1) and a hierarchy formation component (part 2). For part 1, we employed the 'randomly selected' technique for creating winners and losers (Chase *et al.* 1994). Prior work has shown that when swordtails differ significantly in total length, larger individuals win the vast majority of contests (Beaugrand *et al.* 1996). In our protocol, randomly selected male swordtails (of approximately equal mean lateral surface area (mlsa), measured as body length × body size + sword length) were assigned to one of three pairwise interaction treatments: (i) treatment 1: aggressive contests with a smaller individual (to create randomly selected winners: mlsa of focal = 4.38 cm^2; mlsa of smaller individual = 3.03 cm^2); (ii) treatment 2: contests with a larger individual (to create randomly selected losers; mlsa of focal = 4.37 cm^2; mlsa of larger individual = 5.84 cm^2); and (iii) treatment 3: no contests. Fish in treatment 3 (mlsa = 4.37 cm^2) experienced the same protocol as fish in treatments 1 and 2, but faced no opponent during the 'aggressive interaction' phase of part 1 trials, and were labelled 'neutrals'. Because winner and loser effects last for at least 24 h (Franck & Ribowski 1987), before the start of part 1, fish were isolated in individual 9.5 l tanks for 72 h to minimize the effect of any prior experience the fish may have obtained in stock tanks.

In part 1, two pairs of fish (one of which would produce a winner and the other a loser), and a single neutral fish were placed into one half of a 0.286 l tank (122 cm × 46 cm × 51 cm) divided lengthwise, and then subsequently subdivided into six equal compartments. An opaque partition separated pairs of fish (no fish was placed in the compartment adjacent to the neutral fish). After 30 min, the opaque partitions were lifted and aggressive/submissive acts were observed between the individuals in each of the two pairs (as in Earley & Dugatkin 2002). A fish was labelled 'dominant' when it undertook 10 unreciprocated acts of aggression against its opponent (Francis 1983). Only fish that were dominant to their smaller partner in treatment 1 were used as 'winners', and only fish that were dominated by their larger partner in treatment 2 were used as 'losers'. Once a winner (W), loser (L), and neutral (N) individual were obtained, all three fish were moved to the other half of the aquarium, which had three equal-sized sections separated by opaque partitions. After 5 min, the opaque partitions were lifted. Aggressive and submissive interactions were noted using 45 min focal animal samples on day 1, and 15 min samples every day after. A hierarchy was labelled stable if the rank of each fish remained unchanged for three days in a row. If no stable hierarchy was formed after 7 days, a trial was terminated—18 out of 20 trials produced stable hierarchies.

Animals were housed and fed, and experiments were conducted in accordance with the animal care regulations at the University of Louisville.

3. RESULTS

In a group of three fish, six different stable transitive hierarchies are possible (W–L–N, W–N–L, N–L–W, N–W–L, L–W–N, L–N–W). The actual distribution of these six different possible hierarchies differed significantly from that expected by chance ($\chi^2 = 21.7$, d.f. = 5, $p < 0.001$); table 1 demonstrates that *hierarchies* with the winner holding the top rank, the neutral holding the middle rank and the loser holding the bottom rank were significantly overrepresented (11 out of 18 hierarchies; two-sided Fisher's exact test, $p < 0.02$). Furthermore, the distribution of winners, losers and neutrals into top, middle and botom positions in the hierarchy was different from that expected by chance ($\chi^2 = 13.3$, d.f. = 2, $p < 0.01$). Table 2 demonstrates that winners were more likely to occupy the top-ranked position (two-sided Fisher's exact test, $p < 0.05$), and losers the bottom-ranked position (two-sided Fisher's exact test, $p < 0.02$).

4. DISCUSSION

Winner and loser effects are almost always studied in the context of pairwise interactions (for an exception see Chase *et al.* 2003). However, many of the behavioural questions surrounding the evolution of aggression focus on dominance hierarchies, which may be more than a summation of all pairwise interactions. To examine the extent to which winner and loser effects obtained in pairwise interactions affect the structure of dominance hierarchies, we used fish of approximately the same size, randomly created winners,

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Table 1. The expected types of hierarchy if winner and loser effects had no impact on hierarchy formation versus the observed hierarchy formation.
(Winner–neutral–loser hierarchies were significantly overrepresented. Fisher's exact test, $^{*}p < 0.05$; n.s., not significant.)

hierarchy form	expected by chance	observed	statistical significance
winner–neutral–loser	3/18	11/18	*
winner–loser–neutral	3/18	2/18	n.s.
loser–winner–neutral	3/18	3/18	n.s.
loser–neutral–winner	3/18	1/18	n.s.
neutral–loser–winner	3/18	0/18	n.s.
neutral–winner–loser	3/18	1/18	n.s.

Table 2. The expected position of winner, loser and neutral fish if winner and loser effects had no impact on rank versus the observed rank.
(Winners were significantly overrepresented in the top position, and losers in the bottom position. Fisher's exact test, $^{*}p < 0.05$; n.s., not significant.)

	expected by chance	observed	statistical significance
top-ranked individual			
winner	6/18	13/18	*
neutral	6/18	1/18	n.s.
loser	6/18	4/18	n.s.
bottom-ranked individual			
winner	6/18	1/18	n.s.
neutral	6/18	4/18	n.s.
loser	6/18	13/18	*

neutrals and losers, and then put these three types of individuals together to record the establishment and stability of hierarchies, and the extent to which winner and loser effects impacted this process.

Our results with the green swordtail demonstrate that winners were more likely to assume the top-ranked position in a hierarchy, losers were more likely to emerge as the lowest-ranking hierarchy member, and W–N–L hierarchies occurred much more often than expected by chance. As such, to our knowledge, we provide the first controlled experimental evidence that winner and loser effects have important manifestations for hierarchy formation and structure. These results strongly suggest that information on intrinsic measures such as size and resource holding power are not sufficient to predict hierarchy formation (Bonabeau *et al.* 1996, 1999). Instead, a combination of intrinsic factors, with the extrinsic factors measured here (i.e. winner and loser effects) are necessary to make detailed predictions regarding hierarchy formation.

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