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Winner and loser effects and the development of dominance relationships in young coyotes: An integration of data and theory

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ABSTRACT

Although it has been hypothesized that winner and loser effects may be important in the development of dominance hierarchies in diverse taxa, there are no studies of which we are aware that have investigated this idea for young mammals. In this study, we analysed winner and loser effects during the development of dominance relationships in three litters of young coyotes (*Canis latrans*). We found clear winner and loser effects that were rank-related. Highest-ranking (alpha) coyotes showed winner effects, lowest-ranking (omega) individuals showed loser effects, whereas there were no winner or loser effects for middle-ranking animals. We then modified Dugatkin's model for winner and loser effects and the structure of dominance hierarchies and found a high level of congruence between the empirical data and the predictions of the model. Indeed, theory predicted a relationship between winner and loser effects and position in a hierarchy. We hope our results will serve as a heuristic for further comparative studies of these phenomena in diverse taxa.

Keywords: canids, carnivores, coyotes, development, dominance, winner–loser effects.

INTRODUCTION

In various mammals (Bekoff *et al.*, 1981; Henry, 1986; Bekoff, 1989; Drea *et al.*, 1996; Holekamp and Smale, 1998) and birds (Drummond and Osorno, 1992; Piper, 1997; Drummond and Canales, 1998; Mock and Parker, 1998), young animals demonstrate high levels of aggressive behaviour that are associated with the development of dominance relationships. A major unresolved question concerns whether or not there is a 'training effect' due to an individual's experience as a 'winner' or a 'loser' (Drummond and Canales, 1998). The result of such training effects might be that current winners are more likely to win future interactions, whereas the converse applies to current losers.

Dugatkin (1997) has recently modelled winner and loser effects, defined as 'an increased probability of winning at time T, based on victories at time $T-1$, $T-2$, etc., and an

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increased probability of losing at time T, based on losing at $T-1$, $T-2$, etc., respectively' (p. 583). Drummond and Osorno (1992) reported such effects in the blue-footed booby (*Sula nebouxii*), in which winner and loser effects are reversible (Drummond and Canales, 1998). Hsu and Wolf (1999) also found evidence for winner and loser effects in fish (*Rivulus marmoratus*). In a review of the very limited literature on the subject, Chase *et al.* (1994) noted that loser effects were often clearer than winner effects (perhaps due to different methods of study; see Chase *et al.*, 1994, for a review of winner and loser effect studies).

Among various canids, there are large differences in the development of agonistic behaviour and dominance relationships. Specifically, coyote (*Canis latrans*) pups in captivity (and in the wild) are significantly more aggressive than are same-aged wolves (*C. lupus*) and most domestic dogs (*C. familiaris*) (Fox, 1971; Bekoff, 1974, 1977, 1978; Bekoff *et al.*, 1975). Indeed, between about 21 and 50 days of age, young coyotes form linear dominance relationships that persist over time. Furthermore, high-ranking, middle-ranking and low-ranking individuals show distinct behavioural profiles (or ontogenetic trajectories; Wiley, 1981) during the formation of dominance relationships with respect to patterns of initiation, escalation, termination of fights and pre-fight and during-fight assessments (Bekoff *et al.*, 1981). Although coyote dominance relationships have been studied extensively (Fox, 1971; Bekoff, 1974; Bekoff *et al.*, 1981), winner and loser effects have never been analysed in this species.

In the present study, we analysed winner and loser effects in three litters of young captive coyotes. We hypothesized that winner and loser effects would be evident based on past experiences of individual coyotes. Chase *et al.* (1994) suggested that winner and loser effects may be important in the development of dominance hierarchies in diverse taxa. However, except for a few studies of captive mice and rats (e.g. Ginsburg and Allee, 1942; Seward, 1946; Kahn, 1951; Scott and Martson, 1952; Bevan *et al.*, 1960), winner and loser effects have never, to the best of our knowledge, been analysed for any other mammalian species. We hope our results will serve as a heuristic for further comparative studies of this phenomenon.

METHODS

Details of the methods used to observe individuals are reported in Bekoff *et al.* (1981). In this previous analysis of dominance relationships, three litters of coyotes, each consisting of six individuals, were observed from 21 to 50 days of age for about 150 h in a 6×8 m enclosure. Longitudinal data on identified individuals were recorded by hand or read into a cassette recorder. A list of actions is detailed elsewhere (Fox and Clark, 1971; Bekoff, 1974, 1978; Bekoff *et al.*, 1981). Coyotes show similar patterns of development regardless of the conditions in which they are observed, and there are parallels in wild populations (Fox 1971; Bekoff and Wells, 1986).

An individual was considered to be 'dominant' if it won (the other animal clearly submitted or retreated) a statistically significant higher percentage of fights with another individual (proportions tests: Sokal and Rohlf, 1969; Bruning and Kintz, 1977). Because sample size is incorporated into these analyses, there was no arbitrarily determined minimum 'cut-off' point for the percentage of interactions which individuals had to win. We used $P < 0.05$ (two-tailed test; $z_{crit} > 1.96$) to indicate significant differences between two percentages. The phrase 'no significant difference' or similar terms means that $z < 1.96$ and $P > 0.05$ [critical values of z for other levels of statistical significance are 2.58

($P < 0.010$) and 3.30 ($P < 0.001$)]. We analysed sequences of wins (W), losses (L) and draws (O) for the first, fourth and sixth ranked individuals in a hierarchy to test for winner and loser effects (fourth-ranking coyotes were chosen to represent middle-ranking animals).

We recognize that the ideal method for testing for winner and loser effects is a controlled environment in which randomly selected individuals are chosen to experience either 'wins' or 'losses'. Such individuals are then matched against others with no prior experience (see Chase *et al.*, 1994), and winner and loser effects are then measured. In our case, with coyotes, some elements of control were sacrificed to better match the natural conditions of dominance development. In fact, any attempt to achieve the perfect control needed to examine winner and loser effects in mammals in a way that is meaningful would be extremely difficult. That being said, the data we analyse are the next best thing to a controlled experiment, and they produce clear implications for our understanding of the development of dominance hierarchies.

RESULTS: DATA ANALYSIS

Data were cast into matrices so that the sequences win–win (WW), lose–lose (LL), win–win–win (WWW), lose–lose–lose (LLL), and so on could be analysed. Individuals had to engage in a minimum of 10 encounters for data to be used in our analyses. Conditional probabilities (reported here as percentages) were then calculated from matrix entries. For example, P (W/W) = given that an individual won its last fight, what is the probability that it wins its next fight? P (W/WW) = given that an individual won its last two fights in a row, what is the probability that it wins its next fight? And so on. Data were analysed for the highest-ranking (alpha), fourth-ranking and lowest-ranking (omega) individuals (see Table 1). There were no correlations between weight or gender and dominance (in accordance with Knight, 1978).

For alpha coyotes there were 144 rank-related agonistic encounters in which the next individual was a different coyote from the last, and 178 with all animals (i.e. 34 or 19.1% of the next encounters were repeats with the same individual as the last encounter). Repeat interactions with the same individual occurred mostly in the WW, OW and WWW categories. For WW interactions, the same percentage ($P > 0.05$) of encounters was won when the next interaction was with the same (77.8%) or a different (70.6%) coyote. Similarly, there was no difference in the percentage of OW encounters with the same (71.4%) or different (73.6%) coyote. However, for strings of WWW, two wins (WW) were followed significantly more often ($P < 0.001$) with a win over a different individual (92.9%) than over the same individual (50.0%). These data suggest that bullying the same individual repeatedly was not a major factor in subsequent wins by alpha coyotes.

There was a clear overall winner effect. Overall, the alpha coyotes won 82% of their fights. The percentages of occurrences of WW, WWW and WWWW were 72.1, 87.5 and 87.2%, respectively, and each of these is significantly greater than a probability of winning of 0.50 (the null hypothesis, given no impact of winner or loser effects; proportions tests, $P < 0.05$). However, it is possible that these high percentages might be due to alphas just being good fighters, even in the absence of winner effects. That is, these figures are necessary, but not sufficient, to demonstrate a winner effect for alpha. Other comparisons, however, provide a clearer picture with regard to alpha rank and winner effects. For example, the percentage of WWW (87.5%) is significantly greater than that of WW (72.1%; $P < 0.05$). This suggests that winning *per se* increases the probability of future wins. Furthermore,

Table 1. Percentages of occurrence of win (W), lose (L) and draw (O) sequences as a function of dominance rank in infant coyotes

	Dominance rank		
Sequence	Alpha	Fourth	Omega
W/W	72.1 ($n = 86$)	40.1 ($n = 32$)	27.5 ($n = 40$)
L/L	37.5 ($n = 32$)	34.8 ($n = 66$)	51.3 ($n = 80$)
O/O	25.0 ($n = 60$)	35.4 ($n = 48$)	21.7 ($n = 46$)
W/WW	87.5 ($n = 48$)	36.4 ($n = 11$)	
L/LL		18.1 ($n = 22$)	78.9 ($n = 38$)
W/WWW	87.2 ($n = 39$)		
L/LLL			82.6 ($n = 29$)

Examples: P (W/W) = given that an individual won its last fight, what is the probability that it wins its next fight? P (W/WW) = given that an individual won its last two fights in a row, what is the probability that it wins its next fight? Only cases where $n \geq 10$ are listed. See text for statistical analyses.

WW (72.1%) is not significantly greater than OW (73.3%), suggesting that two wins rather than a single win is needed to produce winner effects. Lastly, WWWW (87.2%) is not significantly greater than WWW (87.5%), suggesting a levelling off of winner effects for alpha coyotes.

For fourth-ranking coyotes, there were 119 rank-related agonistic encounters in which the next individual was a different coyote than the last, and 141 with all animals (22 or 18.5% of next encounters were repeats with the same individual as the last encounter). Repeated interactions with the same individual were distributed almost evenly (≤ 3) in strings of WW, WL, WO, LW, LL, LO, OW, OL and OO encounters. No statistical analyses could be performed because of small sample sizes, but in all cases there were many more encounters with a new coyote in the next agonistic interaction.

Fourth-ranking coyotes won 43% of their fights. These individuals showed no winner or loser effects (winning did not beget winning and losing did not beget losing). For example, there was no significant difference in the percentage of occurrence of WW versus WWW ($P > 0.05$). Furthermore, the percentage of occurrence of LL was significantly less than the percentage of occurrence of LL ($P < 0.05$).

For omega (lowest-ranking) coyotes, there were 139 rank-related agonistic encounters in which the next individual was a different coyote than the last, and 166 with all animals (27 or 19.4% of the next encounters were repeats with the same individual as the last encounter). The only discernible pattern for interactions with the same coyote twice in a row occurred in the WL category, in which 8 of 19 (42.1%) losses for omega coyotes were to the same individual.

Omega coyotes won 8% of their fights and were generally very inactive and withdrawn. Clear loser effects emerged for omega individuals. For days 21–26, when there was a lot of fighting and dominance relationships were being established, LL (72%) was significantly greater than OOL (51.7%; $P < 0.05$), although this did not hold true for days 27–50. In addition, LLL (78.9%) occurred more frequently than LL (51.3%), but LLLL (82.6%) was not significantly greater than LLL. Overall, a loser effect appeared to kick in after a single early loss and the effects got stronger for two losses in a row, but then reached a plateau.

We also attempted to analyse WOW interactions and compare them to WWW and WW strings to determine if there were differences between double wins that immediately followed one another and those that did not. Unfortunately, there were too few data for WOW strings. However, when comparing WW and WO sequences for alpha, fourth-ranking and omega coyotes, we found that there were significantly fewer WO encounters than WW interactions for alpha individuals (11/59, 18.6%; $P < 0.0001$) compared with fourth-ranking (9/20, 45.0%) and omega coyotes (8/17, 47.1%).

A MODEL OF WINNER EFFECTS, LOSER EFFECTS AND POSITION IN A HIERARCHY

Our results suggest that, in coyotes, a winner effect exists for top-ranked individuals, a loser effect for bottom-ranked individuals and neither effect for those in the centre of a hierarchy. We decided to test whether theory would predict such a relationship between winner and loser effects and position in a hierarchy. That is, suppose that winner effects apply to some individuals, loser effects to others and neither effect to still others. Would we in fact expect those who experience winner effects to rise to the top of the hierarchy? Would those experiencing loser effects sink to the bottom?

It is important to bear in mind that we are not asking whether winning *per se* brings an individual up the hierarchy ladder and losing *per se* causes an individual to fall to the bottom. Obviously, winning is better than losing if the goal is to be at the top of the hierarchy. Here we are modelling whether winner *effects* and loser *effects* have implications for hierarchy formation. In an attempt to model this question, we modified Dugatkin's (1997) simulation of hierarchy formation and winner–loser effects.

Rules and parameters

We model groups of either six or nine individuals. Within groups, 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, interactions occur. At the start of a simulation run, each animal is given a score that measures that individual's assessment of its own fighting ability. This score is analogous to a player's estimate of its own fighting ability (or resource-holding power; RHP; Parker, 1974; Parker and Rubenstein, 1981). Individuals are aware not only of their own initial RHP value, but those of all other group members as well. An individual's assessment of the RHP of *others* does not change through time, and this value is labelled RHP_{other}. An individual's assessment of its own RHP, however, does change through time as a result of whether it wins or loses a fight. A player's assessment of itself is labelled $RHP_{player\ i,\ self,\ T}$ (where, again, T is a counter that is initialized at 1 and increases by a single unit *after* each pairwise encounter).

In each contest, an animal can choose to either '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:

$$\mathrm{RHP}_{\text{player } i,\ \text{self},\ T}/\mathrm{RHP}_{\text{other}} \geq F \tag{1}$$

where $\mathrm{RHP}_{\text{player } i,\ \text{self},\ T}/\mathrm{RHP}_{\text{other}}$ will be referred to as 'relative RHP' and F will be called the 'aggression threshold' ($F \geq 0$; see Mesterton-Gibbons and Dugatkin, 1995, for details). For example, if $F = 1$, individuals will fight anyone with an RHP they assess to be smaller than their own; if $F = 0$, animals will always fight, regardless of the RHP of their opponent; if $F = 0.5$, individuals fight anyone up to twice their size, and so on. Given this, three outcomes are possible when player i meets player j:

1. Both players (labelled i and j) meet the aggression threshold and both decide to fight.
2. Player i meets the aggression threshold whereas player j does not, or vice versa. In this case, we will say that one player was aggressive, but that the other player 'retreated'.
3. Neither player i nor player j meets the aggression threshold; hence, neither opts to fight. This will be referred as a 'double kowtow'.

If both players opt to be aggressive (fight), the probability that player i will defeat player j is defined as:

$$\mathrm{RHP}_{\text{player } i,\ \text{self},\ T}/(\mathrm{RHP}_{\text{player } i,\ \text{self},\ T} + \mathrm{RHP}_{\text{player } j,\ \text{self},\ T}) \tag{2}$$

When player i wins a fight, it increases its own RHP by a factor of W and so

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

This will be referred to as the winner effect. Conversely, when a player loses a fight, RHP is lowered by a factor L and so

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

As such, L measures loser effects.

W and L were each increased from 0.1 to 0.5 in increments of 0.1. F took one of two values, 0.5 or 0.75, and $T_{\max}$ was set to 500. An animal was considered 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™.

In Dugatkin (1997), for a given simulation, *every* individual in a group had the same winner (or loser) effect, and the implications of winner effects versus loser effects on hierarchy formation were examined. The results of these simulations suggested that, when winner effects alone were important, there was a hierarchy in which all individuals held an unambiguous rank. 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.

Here, based on the general patterns uncovered in the coyote data, we modified Dugatkin's (1997) model such that, in any group of size n, $n/3$ individuals are affected by winner effects, $n/3$ by loser effects and $n/3$ by neither effect. This allowed us to examine what impact winner and loser effects have on position in hierarchy. In addition, we built in a cost to fighting. This cost is not paid when one or both individuals choose to retreat, but is incurred by *both* individuals when they each independently decide to fight one another. The cost was set

at 0, 0.5, 1 or 5 RHP units (e.g. if the cost was 1, then individuals with an RHP of 100 had this value decreased to 99 after a fight). Neither of these effects (the cost or the random assignment of winner and loser effects) were modelled in Dugatkin (1997). Our hypothesis, based on the coyote data, is that winner effects should push individuals to the top of a hierarchy and loser effects should work in the opposite direction.

For every combination of parameters (winner effect, loser effect, F and cost), 10 simulations were run.

RESULTS OF THE SIMULATION

The results of the simulations were clear. For ease of explanation, we break down the results into two sections.

Group members have identical initial RHPs

In these runs of the simulation, all group members began with the exact same RHP (arbitrarily set to a value of 100). This was meant to mimic a case where all group members begin interactions with the same fighting abilities, as measured by size, fat reserves, 'weapons' (horns, etc.), or whatever the appropriate currency for the species being examined experimentally. Individuals randomly chosen to experience winner effects end up at the top of hierarchies (alpha in three-player hierarchies, alpha or beta in six-player hierarchies and alpha, beta or omega in nine-player hierarchies). Players randomly assigned loser effects always ended up at the bottom of their group's hierarchy structure, and individuals experiencing neither winner nor loser effects ended up in the middle slots of a hierarchy (see Table 2). This held true for all strengths of winner and loser effects, for all values of the aggression threshold examined, for all costs and for all group sizes.

Group members have different initial RHPs

The results described above are robust and generally apply to the case where initial fighting abilities were different among individuals within groups. Two different initial distributions of RHP were examined. In both cases, the same initial distribution of RHP within groups was used, but whether large individuals had winner or loser effects was manipulated. For example, for the case of $n = 6$, the initial distribution of RHP was 100, 100, 150, 150, 200, 200. In one case, individuals with RHP 100 were assigned winner effects, those with RHP 200 loser effects, and those with RHP 150 neither winner nor loser effects. In the second case, however, the larger individuals were assigned winner effects, the smaller individuals loser effects and the middle-ranking individuals no effects. In the latter case, results were similar to simulations in which RHP did not differ across individuals – those assigned winner effects always rose to the top of the hierarchy and those assigned loser effects always sunk to the bottom of the hierarchy. In the former case (when losers were assigned high initial RHPs, etc.), about 50% of the simulations produced results similar to the case when all individuals had similar RHPs. However, in approximately 50% of the simulation runs, individuals with loser effects, as well as those with neither winner or loser effects, were not confined to the bottom two ranks and were able to rise as high as beta in a hierarchy (see Table 3). This suggests that, under some conditions, high RHP can overcome loser effects (to some extent). It is important, however, to note that the alpha individual in a group was always one of the individuals with winner effects.

Table 2. Winner and loser effects and hierarchy structure with 500 potential interactions (including double kowtows which score zero for each player involved in such an interaction)[a]

		A	B	C	D	E	F
(a)	**A**	**0**	**25**	**33**	**34**	**43**	**39**
	B	**2**	**0**	**30**	**48**	**26**	**23**
	C	2	1	0	12	36	40
	D	1	0	17	0	29	29
	E	*0*	*0*	*0*	*0*	*0*	*0*
	F	*0*	*0*	*0*	*0*	*0*	*0*
(b)	**A**	**0**	**1**	**32**	**24**	**30**	**31**
	B	**27**	**0**	**27**	**35**	**36**	**38**
	C	0	1	0	7	12	7
	D	1	0	7	0	16	11
	E	*1*	*1*	*0*	*0*	*0*	*1*
	F	*0*	*0*	*0*	*0*	*0*	*0*
(c)	**A**	**0**	**26**	**34**	**42**	**33**	**46**
	B	**1**	**0**	**40**	**31**	**31**	**33**
	C	0	1	0	0	2	0
	D	0	0	1	0	6	3
	E	*0*	*0*	*0*	*0*	*0*	*0*
	F	*0*	*0*	*0*	*0*	*0*	*0*

[a] Entries in rows represent the number of times the row players defeated the column player. Defeats include both losing fights and retreating. Individuals with winner effects are shown in **bold**, those with loser effects in *italics* and those experiencing neither effect are shown in plain text. $n = 6$, $F = 0.75$, $W = L = 0.4$ for all cases. Initial RHP of all players equal (100). (a) Cost = 0; (b) cost = 1; (c) cost = 5.

DISCUSSION: THE RECIPROCAL RELATIONSHIP BETWEEN DATA AND THEORY

We believe that the approach we have taken here in integrating theoretical and empirical work has general heuristic value. In 1997, Dugatkin produced a model of dominance hierarchies that took into account winner and loser effects. This was one of the first such models (since a pair of papers by Landau, 1951a,b) and was meant to be quite general. The model did not attempt to focus on one empirical system, but rather to spur on those already working on aggression to reappraise their interpretations in light of new theory. On this front, the model was successful, as it led to the current study.

Once the 1997 model was published, Bekoff realized that winner and loser effects could potentially help understand the dynamics of aggression in coyotes. The next important step came when we realized that not only could the coyote data be analysed in the contexts of winner and loser effects, but that the data also suggested new directions for the theory. While the original model examined winner and loser effects, it did not allow for individual differences in winner and loser effects *within groups*. That is, either every one in a group experienced winner (or loser) effects, or no-one did. Yet the coyote data suggest that some individuals in a group may experience winner effects (not due merely to bullying the same individual repeatedly), some may experience loser effects and yet others neither of these effects. It also seems reasonable to assume that this is true of other social groups,

Table 3. Winner and loser effects and hierarchy structure with 500 potential interactions (including double kowtows which score zero for each player involved in such an interaction)[a]

		A	B	C	D	E	F
(a)	**A**	**0**	**29**	**30**	**31**	**39**	**29**
	B	**4**	**0**	**31**	**26**	**27**	**28**
	C	5	1	0	14	31	34
	D	2	0	5	0	41	33
	E	*3*	*2*	*0*	*1*	*0*	*0*
	F	*1*	*0*	*0*	*0*	*0*	*0*
(b)	**A**	**0**	**0**	**0**	**0**	**0**	**0**
	B	**32**	**0**	**36**	**35**	**27**	**26**
	C	34	0	0	12	44	31
	D	32	3	6	0	35	36
	E	*1*	*1*	*0*	*0*	*0*	*0*
	F	*6*	*3*	*0*	*3*	*3*	*0*
(c)	**A**	**0**	**32**	**35**	**29**	**35**	**36**
	B	**1**	**0**	**29**	**31**	**26**	**22**
	C	0	1	0	5	1	0
	D	0	3	12	0	0	1
	E	*0*	*4*	*4*	*0*	*0*	*0*
	F	*1*	*0*	*4*	*2*	*0*	*0*
(d)	**A**	**0**	**0**	**0**	**0**	**0**	**0**
	B	**36**	**0**	**18**	**30**	**22**	**29**
	C	33	0	0	11	0	0
	D	41	1	11	0	0	0
	E	*1*	*2*	*3*	*3*	*0*	*0*
	F	*10*	*2*	*5*	*4*	*3*	*0*
(e)	**A**	**0**	**4**	**38**	**27**	**30**	**26**
	B	**40**	**0**	**37**	**26**	**29**	**34**
	C	2	2	0	3	1	0
	D	3	4	3	0	1	0
	E	*1*	*0*	*0*	*0*	*0*	*0*
	F	*4*	*1*	*6*	*5*	*1*	*0*
(f)	**A**	**0**	**23**	**28**	**20**	**36**	**36**
	B	**0**	**0**	**0**	**0**	**0**	**0**
	C	4	20	0	2	0	0
	D	5	19	2	0	0	0
	E	*2*	*1*	*1*	*0*	*0*	*0*
	F	*4*	*8*	*5*	*5*	*6*	*0*

[a] Entries in rows represent the number of times the row players defeated the column player. Defeats include both losing fights and retreating. Individuals with winner effects are shown in **bold**, those with loser effects in *italics* and those experiencing neither effect are shown in plain text. Initial RHP of winner effect individuals = 100, initial RHP of loser effect individuals = 200 and initial RHP of individuals with neither winner or loser effects = 150. $n = 6$, $F = 0.75$, $W = L = 0.4$ for all cases. (a) Cost = 0, winner effect individuals on top of hierarchy. (b) Cost = 0, individual with neither winner or loser effects occupies beta rank. (c) Cost = 1, winner effect individuals on top of hierarchy. (d) Cost = 1, individual with loser effects occupies beta rank. (e) Cost = 5, winner effect individuals on top of hierarchy. (f) Cost = 5, individual with loser effects occupies beta rank.

including sibships (e.g. Drummond and Osorno, 1992; Drummond and Canales, 1998; Mock and Parker, 1998), although we have not explicitly built identity by descent into our model.

Given the results of the coyote analysis, Dugatkin's model was modified such that winner and loser effects could be parsed out differentially to members of a group. Recall that alpha coyotes showed winner effects and omega coyotes displayed loser effects. Consequently, we hypothesized that, if we began our model with three classes of individuals, those experiencing winner effects should rise to the top of a hierarchy and those experiencing loser effects should sink to the bottom of a hierarchy. The model supports this hypothesis.

Of course, the model we generated does not mimic exactly the coyote system. Nonetheless, our model still predicts what is observed in the coyotes' dominance hierarchies (but not in less stable non-linear hierarchies formed among young wolves; M. Bekoff, unpublished data). This holds true even though the model did not use any data generated by the coyote system *per se*, thus avoiding questions of circularity. That is, our model of the impact of differential allocation of winners and losers within groups was developed in *light* of the coyote data, but the coyote data themselves were *not* part of the model. Without the original model the coyote data would have never been re-analysed in the light of winner and loser effects, and without the coyote data the model would never have been modified to address a new, interesting question regarding winners and losers.

It is important to realize that our model does not attempt to examine the *evolution* of winner and loser effects, but rather their *effect* on hierarchy structure given that such effects are present. For example, one might inquire as to why loser effects still exist under the conditions outlined in the model. After all, if loser effects put an individual at the bottom of the hierarchy, should not natural selection have eliminated them? Our model itself cannot answer this question directly, since it is not a classic cost–benefit model, and we are simply assuming the existence of winner and loser effects (based on the coyote work and many other studies outlined in the Introduction). However, in the spirit of motivating future work in this area, we offer two possible answers to this question. Both obviously need to be tested and are meant only as springboards for further experimentation.

First, it may be the case that being at the bottom of the hierarchy is not always costly. Very few studies have provided detailed data on the costs and benefits associated with different positions in a hierarchy and, until such work is completed, it is only an assumption (albeit a very reasonable one) that being at the top of a hierarchy has the greatest benefit–cost ratio associated with it. One area that has received a lot of attention concerns possible reproductive advantages associated with being a dominant individual. More specifically, are dominant individuals more reproductively fit than subordinate animals? It is extremely difficult to collect reliable data for most animals, especially long-lived, wide-ranging individuals. Despite impressions that are often reported as facts, and heated debates among researchers, with few exceptions (see, for example, Dewsbury, 1982; Drickamer *et al.*, 1996; Frank, 1997; Pusey *et al.*, 1997; Alcock, 1998) field studies have not found high positive correlations between dominance status and lifetime reproductive success (Clutton-Brock, 1988; Berger and Cunningham, 1994; Altmann *et al.*, 1996; Byers, 1997; Alcock, 1998; Takahata *et al.*, 1999).

In one long-term study, Frank (1997) reported that high-ranking female spotted hyaenas (*Crocuta crocuta*) when compared to low-ranking females 'give birth at an earlier age, have shorter intervals between litters, and more of their offspring survive to adulthood' (p. 59); the top-ranking matriline raises 2.5 times as many sons and 2.75 times as many

daughters to reproductive age. Such data, however, are rare. In general, associations between dominance rank and reproductive success are complex, and variations in age and sex need to be accounted for, as does the instability of an individual's dominance status over time (Altmann *et al.*, 1996).

Second, it could be that being at the top of a hierarchy is favoured by natural selection, but that winner (and loser) effects are assigned to individuals in a way that is inaccessible to natural selection. For example, aggressive tendencies have long been associated with various androgens in males (e.g. Nelson, 1995). Male hormones, however, can be affected by such random events as fetal position in a mother's womb (vom Saal, 1989; Clark *et al.*, 1993; Houtsmuller *et al.*, 1994). Under such a scenario, individuals might essentially be assigned winner or loser effects in a random manner (matching the assumption of our model), with natural selection unable to act on such effects. In such instances, individuals must simply make the best of a bad (in the case of loser effects) or a good (in the case of winner effects) situation.

We hope that the present study will serve as a springboard for future research on winner and loser effects. Furthermore, we hope that our analyses provide convincing evidence of how theory and empirical data can be used to develop a more integrated approach to the study of behaviour.

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