



Fighting ability and motivation: determinants of dominance and contest strategies in females of a passerine bird

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The communication of aggressive motivation or fighting ability has important fitness consequences for competing animals. Selection should favour rapid and honest communication between opponents to settle dominance relationships while avoiding prolonged and intense fighting. We investigated factors that influence fighting strategies and contest outcomes in female house finches, *Carpodacus mexicanus*, specifically focusing on the following questions. (1) What social contexts trigger an aggressive response? (2) Does body size and condition contribute to female fighting ability? (3) Do contextual factors, such as mate presence, nest status, nest proximity, and site experience contribute to fighting motivation? (4) Does contest intensity and duration increase as the differences in fighting ability between opponents decrease? (5) What is the relative contribution of fighting ability and aggressive motivation to the outcome of a contest? We found that aggression was triggered most frequently by female intrusions in the vicinity of nest and by extrapair female intrusions on an established pair. Female fighting and contest outcomes were strongly influenced by body condition and body size, and females were more motivated to initiate fights and won more contests when their mates were present. Females at the later breeding stages and those fighting closer to their nests were dominant and won more fights compared to females at earlier breeding stages or further from their nests. Females initiated a greater proportion of contests against opponents with similar local familiarity and breeding history. Escalated and prolonged contests, while rare, occurred exclusively between females of the most similar body size and condition. When differences in body condition between opponents are not easily perceived, contestants might escalate contests for more reliable assessments of relative fighting ability. Finally, body condition was not a strong determinant of contest outcome in the contexts with easily assessed differences in the resource value (e.g. mate presence), but without these motivational differences, body condition was the ultimate determinant of contest outcomes.

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What determines the outcome of aggressive contests between individuals is a topic of central interest to behavioural ecologists. Such contests can determine the access that an individual has to food, shelter and mates and, thus, have strong fitness consequences (Koskela et al. 1997; Watts 1998). Factors that can influence the

outcomes of aggressive encounters can be divided into those related to the phenotype of the animal, such as its size and weaponry and to the context in which the encounter occurs, such as site familiarity.

Many strategic decisions must be made once an aggressor initiates an agonistic confrontation. These decisions are based on the communication of information through morphological or behavioural signals of fighting ability and motivation. Without communication of these factors and accurate assessments of relative fighting potentials based on differences in fighting ability and motivation, interactions would have to be resolved with overt fighting. Because escalated contests are often costly for both combatants (Jakobsson et al. 1995), communication and

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assessment of fighting ability through initial display behaviours are advantageous for competing individuals (Caryl 1982).

Body size and condition are thought to be the best signals of fighting ability because size and condition often reflect individual strength (Breitburg 1987; Lindstrom 1988). In addition, fighting ability can be signalled by elaboration of armaments such as horn size in beetles (Lailvaux et al. 2005). In this study we investigated factors that influence fighting strategies and contest outcomes in female house finches, *Carpodacus mexicanus*, a socially monogamous passerine bird with obligatory bipaternal care (Hill 2002) and low levels of extrapair fertilizations (Oh & Badyaev 2006). House finches nest in semicolonial settlements and females display a complex array of contest behaviours (Thompson 1960; Jonart 2002). Contests are typically initiated with a series of postural threat displays including neck stretching and displacement towards the opponent that appear to function as rival assessment strategies. If a female is not immediately displaced by her aggressor, the contest escalates to prolonged chases and airborne battles lasting for several minutes (Thompson 1960; Jonart 2002).

Here we examine phenotypic and contextual factors that determine the outcome of aggressive interactions among females. Specifically we examine the role of females before interactions in determining the outcome of aggressive encounters. First, we investigated the effects of body size and condition on contest outcomes. Because contest initiation and escalation can vary with the asymmetry in perceived fighting abilities between competitors (Enquist 1985; Verrell 1986), contests between competitors of similar fighting ability should attain higher levels of contest duration and escalation (Maynard Smith 1982; Verrell 1986; Lindstrom 1991; Kura 1999). Second, we investigated the effects of individual differences in aggressive motivation by examining the social context of agonistic interactions. Specifically, we predicted that individuals should be more aggressive in the presence of their mate. Finally, we explored the effects of breeding stage of competitors, proximity to nest location, and prior site familiarity on contest outcomes (Verrell 1986; Wells 1988; Schuett 1997; Kura 1999). Whereas many theoretical and empirical studies have established that individuals' behavioural strategies during contests reflect fighting ability and motivation; only a few studies have explored the relative contributions of these factors to the contest outcomes in variable contexts. We tested the prediction that in specific competitive contexts motivational factors can outweigh the relative importance of fighting ability in the selection of opponent fighting strategies.

METHODS

We studied a resident population of house finches in northwestern Montana, U.S.A. The study site has been maintained since 1994–1995 (for details of the study site and field protocol see Badyaev & Martin 2000; for history of this population see Badyaev 2005). The study site is a cluster of buildings and two sets of 74 identical

ornamental shrubs planted 4 m apart along two linear arrays in an open grassland. Finches used the 2–3 m high ornamental shrubs for nesting and several large coniferous trees at the edge of the complex for roosting. Each year from 1995 to 2004, at the onset of the breeding season, all birds in this isolated study population were captured, individually marked, and pair affiliations and nesting were monitored continuously (Oh & Badyaev 2006). Data for this study were collected in 2000–2001. Strong fidelity of adult house finches to the location of previous breeding and the isolation of the study site allowed us to assign birds' ages and to follow individual birds throughout their lifetime for most individuals (Jonart 2002; Badyaev & Duckworth 2003; Badyaev 2005). Nest construction begins in late February–early March and pairs can complete up to four nesting attempts during a breeding season of March–August.

Resident finches were recaptured reliably at regular intervals, and seven morphological traits were measured (bill length, depth, and width, tarsus length, wing length, tail length, and body mass). Upon initial capture each individual was assigned a unique combination of three colour bands and one aluminium band for identification. The lengths of left and right tarsi were measured twice to an accuracy of 0.02 mm and the mean of four measurements was used in subsequent analyses. We measured body mass with a balance to an accuracy of 0.05 g. Body condition was calculated as a ratio of body mass to tarsus length.

Behavioural Observations

Behavioural observations took place at least every other day between 0700 and 1200 hours with occasional observations between 1300 and 1500 hours. All resident pairs were monitored during these time periods and all behaviours were recorded from a parked car 5–10 m from the birds. Because this population of house finches has been exposed to vehicles daily, our presence did not interfere with their social interactions.

For each observed contest, an aggressive interaction ranging from postural displays to physical attacks, we recorded the identity of individuals involved as well as the initiator and the winner of the contest. We also recorded contestant persistence and the final level of contest escalation as a measure of investment into the contest (Sigurjonsdottir & Parker 1981; Austad 1983; Verrell 1986). We also recorded behaviours that triggered confrontations, specifically considering the following categories: (1) an intruder female prospecting for a potential nest site within 4 m of the initiator's active nest, (2) both females prospecting for potential nest sites in the same location, (3) an extrapair female receiving courtship display from the initiator's male, and (4) an extrapair female following or perching with the initiator and her mate.

Female Differences in Fighting Ability

Within dyads of competing females, we compared the body condition of the winners to the losers of contests. We observed variation in the aggressive tendencies of

individual dyads, with some pairs only competing a few times, while others engaged in repeated competitive interactions. To avoid pseudoreplication, we only used a single randomly selected contest per dyad ($N = 55$ contests). Condition estimates were log transformed to achieve normal distribution of data. Average body condition was compared with a two-tailed paired t test with the prediction that female contest winners would be in greater body condition. We used individual body mass as an indicator of female body size and used two-tailed paired t test to test whether the winners of contests were larger than the losers. To avoid pseudoreplication, we only used a single randomly selected contest per dyad ($N = 55$).

We also investigated the relationship between contestants' body condition difference and persistence and escalation of contests. We quantified contest escalation on a four-point scale: (1) a single displacement (i.e. a female displaces an opponent from a perch), (2) multiple displacements, (3) multiple displacements and prolonged chase, and (4) grappling fights in the air. Contestant persistence was estimated as the number of times opponents repeated aggressive behaviours during a contest.

Effect of Differences in Resource Value or Motivation on Contest Outcomes

For each contest we recorded the presence of the contestants' current partners. Partners of fighting females were classified as 'present' if they were within 8 m (a distance of two potential nest sites) of the contest and 'absent' if they were more than 8 m away. The distance was selected based on the linear layout of the nesting area (Jonart 2002). When pairs were more than 8 m apart they were partially visually isolated from each other and responded less to their mates' extrapair interactions (Lindstedt et al. 2007). For each resident female we compared the proportion of fights initiated with her male present versus the proportion of fights she initiated when her male was absent. To test for differences in the breeding stage between the opponents, we divided the nesting cycle into six discrete stages: (1) prospecting for nest site, (2) nest building initiation, (3) nest lining, (4) egg laying, (5) incubation, and (6) brooding.

For each dyad we recorded the distance from the location of the contest to competing females' nest sites and compared the mean distance of winners to the mean distance of losers to their nests (using a randomly selected contest per dyad) with a two-tailed paired t test ($N = 34$). We also compared the average site experience of the contest initiators and winners with the average site experience of contest losers with a two-tailed paired t test ($N = 66$). We subtracted the losers' years on the site from the winners' years on the site for each observed contest.

The Relative Contribution of Fighting Ability and Motivation to Contest Outcome

We examined a subset of contests in which the mates of the contest initiators were present while their opponents'

mates were absent. This was done to investigate the relative contribution of body condition (a proxy of fighting ability) in contests with observable differences in individual fighting motivation (mate presence). For this subset of contests, we compared body condition between the winners and losers with a two-tailed paired t test. To test the strength of body condition as a predictor of contest outcome in a different context, we investigated the retreat strategies of females in a subset of contests in which both competitors' mates were present (equal fighting motivation). We carried out a two-tailed paired t test to examine the difference in mean body size between winners and losers of contests. Finally, we examined inter-relationships among the factors influencing the contest outcome.

RESULTS

Contests were consistently initiated with assessment displays, and only rarely escalated to fights until one individual retreated from the location of the contest. Individual dyads vary in their tendency to initiate agonistic interactions with a half of all dyads observed in multiple interactions throughout the breeding season. The variability of dominance relationships is evident in the average ratio of wins/losses among those competitors engaging in multiple challenges ($\bar{X} \pm SE = 0.66 \pm 0.07$, $N = 26$). The females who initiated contests always won them. Contests ($N = 171$) were most frequently (40%) provoked by a female prospecting near the nesting site of the aggressor, 14% of aggressive interactions were initiated in response to simultaneous nest prospecting by two females, 11% in response to their mates' extrapair displays towards other females, and 36% of contests were initiated in response to an intruding extrapair female.

Body Mass and Body Condition in Relation to Fighting Ability and Contest Outcome

Contest winners were in better body condition than females that lost contests, and the initiators and winners of contests were significantly heavier than females that retreated from contests (Table 1). Absolute difference in body condition between opponents did not correlate with either the degree of escalation (Spearman rank correlation: $r_s = -0.96$, $N = 137$, $P = 0.27$; Fig. 1) or contest persistence ($r_s = -0.06$, $N = 137$, $P = 0.51$; Fig. 2). However, escalated and longer contests occurred exclusively between opponents with minimal differences in body condition (Figs 1 and 2).

Effects of Contextual Factors on Contest Outcome

Females initiated a greater proportion of contests when their mates were present compared to when they were absent (paired t test: $t_{12} = -3.57$, $P = 0.002$, Fig. 3). The winners of contests were at more advanced stages of their breeding attempt than the opponents who retreated from contests and were significantly closer to their nest site

Table 1. Paired *t* test analyses of differences in fighting ability and motivation between the winners and losers of female house finch contests

	Winners	Losers	<i>N</i>	<i>t</i>	<i>P</i>	<i>d</i> -Score
	Mean±SE	Mean±SE				
Fighting ability						
Body mass (g)	27.1±0.52	25.9±0.53	55	1.93	0.03	0.41
Body condition (g/mm)	1.28±0.13	1.21±0.15	55	2.67	<0.01	2.28
Fighting motivation						
Nest status (stage 1–6)	3.36±0.22	2.71±0.23	171	4.28	<0.01	0.38
Nest proximity (m)	3.17±5.02	8.63±12.75	34	−3.85	<0.01	0.56
Site experience (years)	1.44±0.01	1.61±0.01	66	−1.28	0.10	0.38

than the females who retreated from the contests ($t_{33} = -2.0$, $P = 0.03$; Table 1). Difference in prior site experience of opponents did not predict contest outcome (Table 1). Females initiated a majority of contests against other females with similar site experience (chi-square test: $\chi^2_4 = 95.15$, $P = 0.005$; Fig. 4). There were no correlations among the factors contributing to contest outcome (Table 2).

Relative Contribution of Fighting Ability and Fighting Motivation to Contest Outcome

When we examined the effect of fighting ability on contest outcome for only those contests where the initiators' males were present, we found that body condition was a weak determinant of the strategies of the contestants (paired *t* test: $t_{12} = 1.431$, $P = 0.09$). When we examined the relative role of fighting ability as a predictor of interaction outcome in a subset of female contests where asymmetries in aggressive motivation were removed,

body condition was a strong predictor of contest victory ($t_{42} = 3.024$, $P = 0.002$).

DISCUSSION

Female–female aggression, while rarely explored, may have strong physiological and social consequences for a semicolonially breeding species (Bernhardt et al. 1998; von Holst 1998; Wiley et al. 1999; Jasnow et al. 2001). Our observations indicate that extrapair intrusions were the most common instigators of female aggression. Extrapair behaviours are frequent in this species (Jonart 2002; Oh & Badyaev 2006; Lindstedt et al. 2007) potentially imposing a trade-off for males between investment in within-pair breeding and pursuit of extrapair copulations. Such a trade-off might be especially pronounced during incubation when females are confined to nests and particularly dependent on male provisioning.

Within competing dyads of female house finches, contests were initiated and won by larger females and females in better condition. Females would benefit from

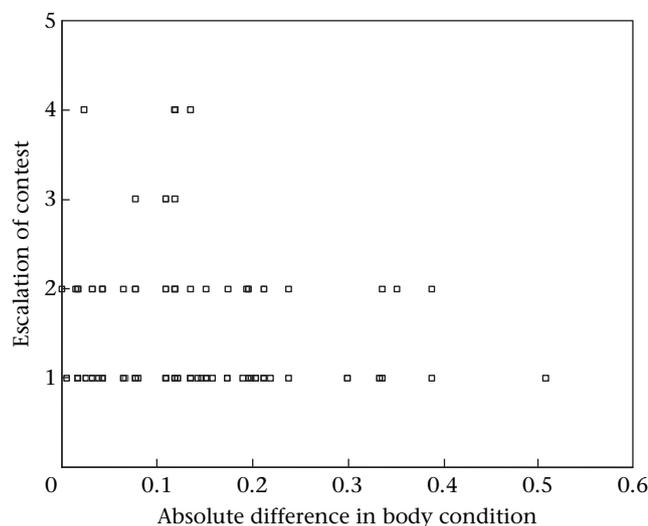


Figure 1. Scatter plot of the relationship between absolute differences in body condition and the level of contest intensity (escalation). Escalation values are graphed in increasing intensity: (1) single displacement, (2) multiple displacements, (3) multiple displacements and chases, and (4) multiple displacements, chases, and physical airborne attack.

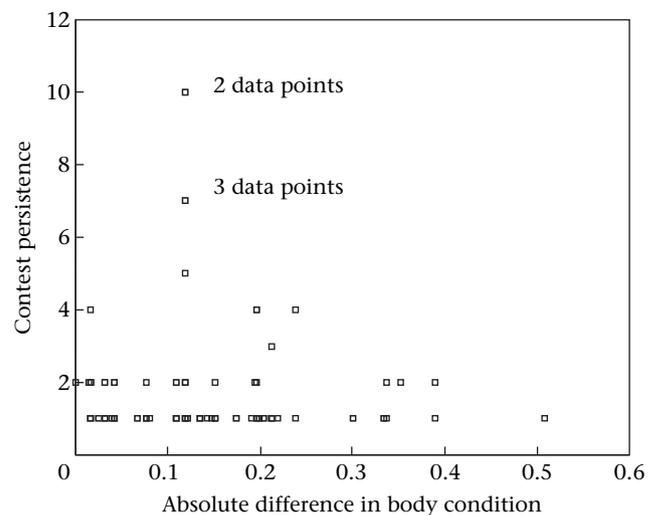


Figure 2. Scatter plot of the effect of body condition differences (winners' mass/tarsus – losers' mass/tarsus) on the persistence of female finch contests, measured as repetitions of the aggressive display. Females were more persistent and less likely to terminate a contest with similarly sized opponents.

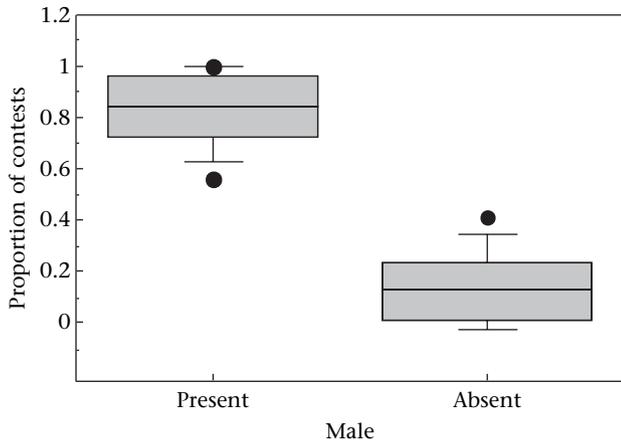


Figure 3. Box plot of the proportion of contests that female house finches initiated with their partners present compared to the proportion that they initiated with their partners absent ($t_{12} = -3.57, P < 0.01$).

information about their opponents' relative fighting abilities to avoid repeated and escalated contests and to establish dominance relationships. This may be accomplished through physical contact or behavioural displays rather than morphological assessment. Parker & Rubenstein (1981) have emphasized the importance of assessment ability and its role in facilitating multiple-staged aggressive contests of various lengths. Specifically, they showed that all information is accumulated at some cost, and contest intensity (e.g. escalation or persistence) is positively correlated with quantity and quality of this information. Information about relative fighting ability and motivation, and thus the probability of winning a contest, is more readily assessed for contestants with larger differences in fighting ability or motivation. Our results similarly illustrate the relationship between relative differences in fighting intensity and duration among dyads. Female house finches rarely escalated contests to levels of physical contact or long duration, but escalated contests were exclusively between females of similar sizes.

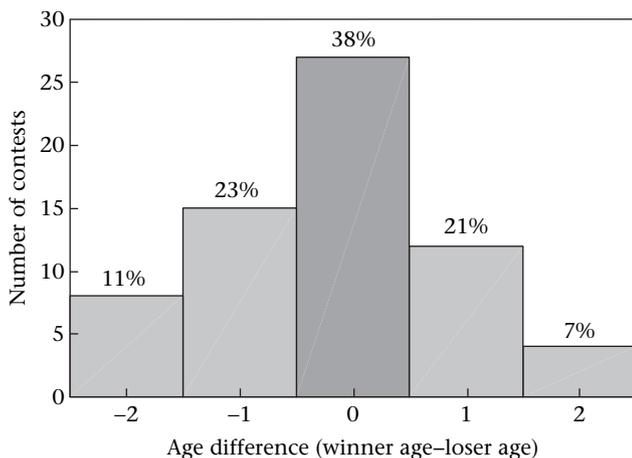


Figure 4. Histogram of the distribution of age differences (winners' age - losers' age) as a function of contest initiation. Significantly more contests were initiated among females within the same age category ($\chi^2_4 = 95.15, P < 0.01$). Asymmetry in age between opponents did not predict contest initiation or outcome.

Table 2. Correlations between variables that account for intrinsic and motivational determinants of contest outcomes

	Body condition	Body mass	Nest status	Nest proximity	Site experience
Body condition	1.000	0.246	-0.374	0.303	-0.287
Body mass	0.246	1.000	0.062	-0.151	0.334
Nest status	-0.374	0.062	1.000	-0.042	0.103
Nest proximity	0.303	-0.151	-0.042	1.000	-0.183
Site experience	-0.287	0.334	0.103	-0.183	1.000

These results are consistent with studies that found positive relationships between contest intensity and information gathered from each successive stage of a fight (Enquist & Leimar 1983; Marden & Rollins 1994).

The triangular shape of the relationships between contest duration or escalation and the extent of asymmetry in fighting ability observed in this study (Figs 1 and 2) and in other studies (Robertson 1986; Wells 1988) are consistent with results of the Parker & Rubenstein's (1981) model. Evolutionary stable retreat strategies can be predicted based on relative size differentials, such that when contestants differ strongly in size, there is only a single evolutionary stable strategy by which contestants should respond (retreat if you are smaller and lose the first round). However, when contestants are similarly matched or when differences are undetectable, a series of mixed strategies (elevate contest to higher levels for more information, or retreat at any level) can be evolutionarily stable. Alternatively, the assessment may not be accurate in a system lacking conspicuous morphological badges of fighting ability, especially among opponents of similar body size and condition (Enquist & Leimar 1983). It is possible that dyads that engage in multiple contests throughout the breeding season may be most similar in fighting ability, thus requiring reassessment.

Differences in fighting motivation can also influence contest behaviours and outcomes (Parker 1984; Verrell 1986; Wells 1988; Lindstrom 1991). In female house finches, individuals initiated and won a greater proportion of agonistic interactions when their mate was present, suggesting that elevated aggression in the presence of a mate may function as a means of pair maintenance or reflect resource value, mate quality (Wells 1988; Lindstrom 1991).

Females at more advanced breeding stages won more contests than females at less advanced stages, and the female closer to her current nest site had a greater probability of winning and was dominant over the female competing further from her nest site. Prior site experience of female competitors had an opposite effect on contest behaviours than we originally predicted. Females initiated the greatest proportion of their contests against opponents with similar site experience. These results contradict studies that have shown a significant role of site experience in determining contest outcomes (Wells 1988; Schuett 1997). Furthermore, our results suggest that females are most aggressive towards opponents within their own

cohort probably due to shared competition over a limited resource. Alternatively, females within the same cohort have similar breeding and social histories and thus similar perceived reproductive value (motivation) and fighting abilities.

The extent to which body condition influenced contest initiation and outcome was dependent on the context in which the fight occurred. Differences in body condition between opponents had a weak effect on outcome of interactions in which the winner's partner was present and differences in aggressive motivation were therefore easy to assess. Females in lesser body condition defeated females in greater body condition when the perceived value of the contest outcomes was greater than that of their opponents'. Because mate presence is readily observable and may be used to resolve contests without escalation, females might reduce contest costs by selecting contest strategies based on mate presence asymmetries rather than differences in fighting ability.

Conversely, body condition (intrinsic fighting ability) was a reliable indicator of outcome of contests with lesser value asymmetries. This is expected when both opponents perceive their resource value as relatively high. Contests may also require escalation because females might select their strategy based on cues of fighting potentials that might not be easily and accurately assessed. Under these circumstances, fighting behaviour might be influenced by body condition asymmetries.

Variation in the frequency of aggressive interactions, with some pairs re-establishing their relationship through numerous interactions over the course of the breeding season, might reflect the dynamic nature of dominance relationships. Repeated encounters might enable reassessment of opponent fighting motivation and persistence throughout the breeding season. The average ratio of dyadic wins and losses corroborates the suggestion that dominance might be interchangeable within a dyad, and that fighting strategies might instead be influenced by additional extrinsic factors such as individual's social history (Johnsson & Åkerman 1998).

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