Repeatability of combat rate across different group compositions in male house finches

Masaru Hasegawa [a,*], **Mathieu Giraudeau** [b,**], **Russell A. Ligon** [b,***],
Nobuyuki Kutsukake [a], **Mamoru Watanabe** [c] **and Kevin J. McGraw** [b]

[a] Department of Evolutionary Studies of Biosystems, Sokendai (The Graduate University for Advanced Studies), 1560-35 Kamiyamaguchi, Hayama-machi, Miura-gun, Kanagawa 240-0115, Japan
[b] School of Life Sciences, Arizona State University, Tempe, AZ, USA
[c] Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Japan
[*] Corresponding author's e-mail address: perorobomusadiobe@gmail.com
[**] Current address: Biosciences, University of Exeter, Exeter, UK
[***] Current address: Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA

Abstract

Studies of animal contests have focused on the probability of winning an encounter, because it directly affects the benefits of competition. However, the costs (e.g., physiological stress) and benefits of competition should also depend on the number of aggressive encounters per unit time (combat rate, hereafter) in which the focal individual is involved. Using colourful and drab male house finches (*Haemorhous mexicanus*) from urban and rural sites, we showed that combat rate was repeatable across the same and different group sizes for birds who won competitions. In addition, colourful urban males exhibited the lowest propensity for frequent aggression (and hence low combat rate). However, male bill size (another trait we previously found to correlate with male competitiveness in this species) was not related to aggressive propensity. Combat rate can be predicted by male identity and some, but not all, predictors of male competitiveness.

1. Introduction

Animals often compete agonistically for access to limited resources (e.g., food, mates), even if competition is costly (e.g., physiological stress, risk of injuries, time/energy consumption; Hardy & Briffa, 2013). Theoretical and empirical studies have focused on factors determining the probability of winning aggressive encounters (e.g., competitiveness, asymmetry in resource value; Kokko, 2013). However, win/loss outcome is just one metric of competitive interactions, and there can be large inter-individual variation in the frequency of aggressive encounters (i.e., combat rate: e.g., Thompson, 1960a; McGraw et al., 2007; reviewed in van Oers & Naguib, 2013). Because the costs of competition can increase with the number of agonistic events (note that cost per event accumulates to be total cost of competition; Kokko, 2013), there may be strong selection on combat rate, and only those who benefit (e.g., procuring current and/or future resources) should continually persist in competitive battles.

Combat rate may vary as a function of the identity/phenotype of contestants. Depending on the social environment and resource value, individuals may frequently attack subordinate rivals (i.e., these differences predict differential agonistic behaviour: Kokko, 2013), enhancing variation in combat rate within populations. Such among-individual variation in frequent aggression (and thus combat rate) is also informative for opponents, if they can predict it using opponent identity or phenotype to avoid frequent aggression. Recent studies of animal personality (i.e., consistent among-individual variation in behaviour; Briffa et al., 2015) may shed light on whether or not combat rate can be predictable, because they reveal the repeatability of individual behaviours (i.e., predicting behaviours by individual identity; Réale et al., 2007; Bell et al., 2009; van Oers & Naguib, 2013; Briffa et al., 2015; note that we are not focusing on within-individual behavioural variation: Cleasby et al., 2015).

Personality studies often have focused on the behavioural propensity of isolated focal individuals (Webster & Ward, 2011). For example, in the context of aggression, aggressiveness is normally measured as the response of an animal to a conspecific model, in order to limit/remove variation in opponent behaviour (Briffa et al., 2015; e.g., by using caged animals, stuffed models, or mirror image: Barnett et al., 2012; Branch et al., 2015; Moreno et al., 2016; but see Santostefano et al., 2016 and citations therein). For this reason, these studies fail to account for potential social influences on measures

of aggressiveness (Webster & Ward, 2011). Thus, although repeatability between social behaviours including aggression should be studied in the actual interaction of conspecifics, it remains unclear whether and to what extent individual identity explains variation in focal behavioural traits in social interactions. Moreover, the size and membership of social groups change over time, but few studies have focused on the consistency of aggressive social interactions when the size and membership of social groups change (Webster & Ward, 2011; but see Harvey & Freeberg, 2007). To determine the ecological importance of frequent agonistic interactions, combat rate should be studied under multiple social conditions while tracking the identity/phenotype of participating individuals.

Here we studied the repeatability of combat rate in social interactions of male house finches (*Haemorhous mexicanus*), a gregarious songbird species that is common throughout North America (Hill, 2002). For this purpose, we investigated the repeatability of combat rate across social contexts and the relationship between individual propensity of frequent aggression, which explains combat rate between dyads, and three male traits – habitat type (urban v. rural), plumage colouration (colourful v. drab), and bill size (all of which have been previously found to correlate with male competitiveness in this species; Hasegawa et al., 2014, 2015). House finches flock year-round but group membership is dynamic (i.e., free-entry group; Webster & Ward, 2011; see also Thompson, 1960b; Hill, 2002); thus this is a suitable study system for addressing consistency (i.e., the 'personality') of combat rate across social situations. Within flocks, males form dominance relationships, in which males who win previous encounters tend to win most subsequent encounters (sensu Vrontou et al., 2006), at least in controlled laboratory experiments (e.g., Belthoff & Gauthreaux, 1991; McGraw & Hill, 2000a,b; note that we can thus deem individuals as winners of a trial from a small number of aggressive encounters; see below). This pattern is different from the prediction based on sequential assessment of competitors (e.g., Enquist et al., 1990). In prior studies of house finches, winners/losers could be determined from a few (i.e., $\geqslant 5$; McGraw et al., 2007) aggressive encounters, but combat rate was highly variable within and among groups (Thompson, 1960a; McGraw & Hill, 2000a,b; McGraw et al., 2007; also see Results). Variation in competitiveness is also thought to depend on individual aggressive tendencies (Thompson, 1960a), but systematic evaluation of how combat rate links to individual identity/traits is lacking. We hypothesized that combat rate between
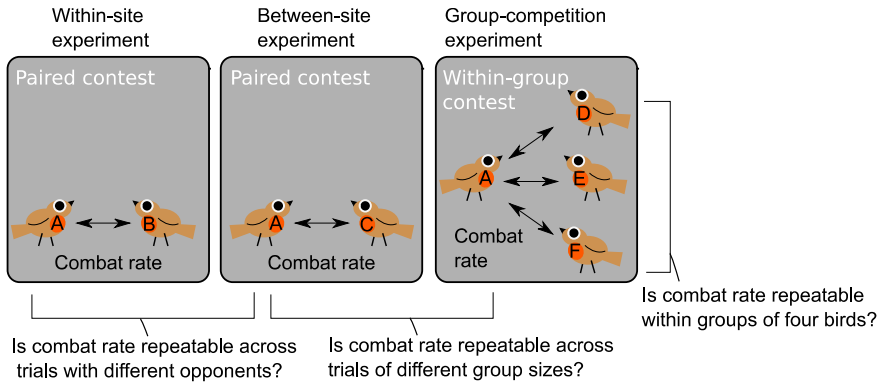
Figure 1. Schematic of our experimental design in which we pitted males in contest competitions across three social contexts. The same individuals are indicated by shared letters. Note that each individual was used only once per experiment.

dyads is explained, at least in part, by individual propensity (or "personality") for aggression, which further depends on male traits associated with resource value and social environment (and competitiveness).

Using a series of laboratory aggression trials (Hasegawa et al., 2014, 2015), we first studied the repeatability of combat rate, while also considering win/loss outcome, within groups of four unfamiliar birds (i.e., "group-competition experiment"; Figure 1). We predicted that males would exhibit consistent combat rate with different opponents within groups (at least for winners), if some males are more aggressive and more likely to beat group members than other males. We also studied the repeatability of combat rate in dyads ("within-site experiment" and "between-site experiment" in Hasegawa et al., 2014) and across trials with different group sizes (dyads and groups of four, for the "between-site experiment" and "group-competition experiment", respectively; Hasegawa et al., 2014; Figure 1; see the Methods section for detailed explanation for each experiment). Because male house finches form dominance relationships, and because of the apparent variation in aggressiveness among males, we predicted that combat rate was mostly determined by dominant individuals' (i.e., winners') identity even across different social environments (i.e., different opponents and different group size). Because losers' identity might also explain combat rate (i.e., aggressors' behaviours might be influenced by opponent phenotype; e.g., Wilson et al., 2011; Santostefano et al., 2016), we also studied whether losers have detectable repeatability of combat rate (though our small sample sizes pre-

vent us from comparing repeatability between winners and losers). Because winner (or loser) effects are not typical in this study system (Hasegawa et al., 2014), we were able to assess consistent individual behaviours without the confound of these effects.

Additionally, we considered bill size and plumage colour (Hasegawa et al., 2014, 2015) as predictors of individual propensity for frequent aggression, which is a latent variable that determines the observed combat rate between dyads. If males invest more in aggressive behaviours depending on these traits (i.e., if it is beneficial for these males to persist in competitive battles; Hasegawa et al., 2014, 2015), we could predict that these traits should be linked to individual propensity of frequent aggression. Because colourful urban males are less competitive than other male categories and smaller-billed males are more competitive than larger-billed males (Hasegawa et al., 2014, 2015; note that these relationships were mutually independent), we predicted a similar relationship between male propensity for frequent aggression and these traits (i.e., the propensity for frequent aggression would be low in colourful urban males compared to other males and would decrease with increasing bill size). Finally, in a "model-presentation experiment" (Hasegawa et al., 2014), we studied whether the propensity for frequent aggression can be predicted by the latency of a focal individual to approach a conspecific model (i.e., a well-known measure of aggressiveness in isolated individuals; e.g., Lack, 1965; Briffa et al., 2015). If the response of an animal to a conspecific model can be used as an index of aggressiveness in social interactions, this measure would predict its aggression in actual social interactions with live birds.

2. Methods

We analysed combat-rate data from lab behavioural experiments (Hasegawa et al., 2014) in which we previously focused on aggressive encounters won and lost (i.e., deeming trial winners as those who won at least 2 more aggressive encounters than their counterpart). Uncertainty when assigning the winner and the loser of each interaction was at best small, because winners consistently won and losers consistently lost in our studies (e.g., only five of 335 (1%) and 5 out of 298 (2%) interactions were won by birds we deemed to be trial losers in within-site and between-site experiments; also see McGraw et al., 2007). Detailed information on bird capture sites, capture

dates, and housing procedures are described therein. In short, we captured 6 colourful and 6 drab males from each of two urban and two rural sites in the Phoenix, AZ, USA metropolitan area. These individuals were housed separately in indoor, animal-approved rooms in small wire cages on the Arizona State University campus. At capture, we measured bill length and bill width, from which we calculated overall bill size (PC1) using principal component analysis (Hasegawa et al., 2015). As before, we excluded the results of a misclassified individual and thus our final sample sizes were 11 urban colourful, 12 urban drab, 12 rural colourful, and 12 rural drab birds (i.e., 47 total birds: Hasegawa et al., 2014, 2015).

Trials were conducted for 30 min between 0600 and 0900 h. In a wire cage (0.77 m × 0.59 m × 0.50 m) containing multiple perches and a single food dish of sunflower seeds, individuals were subjected to a series of three competitive environments — a "within-site experiment", a "between-site experiment", and a "group-competition experiment". We compared aggression between colourful and drab males from the same habitat type (i.e., urban or rural) in the within-site experiment. In the between-site experiment, we staged agonistic encounters between urban and rural males while matching for colour type (i.e., colourful or drab: note that this species has sexually dimorphic colouration: Hill, 2002). During the group-competition experiment, we studied the relative aggressiveness of all 4 categories of birds (i.e., urban colourful, urban drab, rural colourful, and rural drab), by putting them into the same cage simultaneously. No bird was ever grouped with another male with whom he had previously competed. Lastly, we simultaneously presented each bird with a colourful and a drab house finch stuffed model ("model-presentation experiment") and monitored its behaviour (as latency to approach the conspecific model; see Figure 1 in Hasegawa et al. (2014) for experimental design). Because some males did not approach the model (i.e., land on a perch next to the mount), these trials were excluded from analyses (Hasegawa et al., 2014).

For the current study, we determined combat rate by counting the total number of aggressive encounters (e.g., chases, beak-jousting fights, perch displacements, avoidances; Hasegawa et al., 2014, 2015) experienced by each bird per unit time in each of the three experiments (within-site, between-site, and group-competition). In the group-competition experiment, each group contained 4 males and thus we determined combat rate between every dyad combination in the group.

2.1. Statistics

All data analyses were performed using the R statistical package (version 3.5.0; R Core Team, 2018). The repeatability of combat rate across the experiments was analysed with a Poisson error distribution (sensu Hasegawa et al., 2014). For this purpose, we used the "rptPoisson" function in the latest version of "rptR" package (see Nakagawa & Schielzech, 2010; Stoffel et al., 2017 for detailed information; note that this function accounts for overdispersion). In addition to estimating repeatability, we added SE and 95%CI (Confidence Interval) estimated by parametric bootstraps, together with the p value from a significance test based on likelihood-ratios. That is, we used combat rate as a response variable and male identity as the random factor (no other variables were included in the model). We showed original scale repeatability (Nakagawa & Schielzech, 2010) and estimated repeatability for winners and losers separately. We did not adopt more sophisticated approaches to simultaneously estimating repeatability for both participants (e.g., Wilson et al., 2011; Santostefano et al., 2016) because of small sample sizes and because our purpose was not to compare repeatability between winners and losers but to study whether combat rate can be separately repeatable for winners and losers.

To study individual propensity for frequent aggression and male competitiveness, a hierarchical Bayesian inferential approach was used (sensu Hasegawa & Kutsukake, 2015; Hasegawa et al., 2015). We used a Bayesian extension of the Bradley–Terry model proposed by Adams (2005), modified by Hasegawa et al. (2015). Based on results from the within- and between-site experiments, we estimated the attained competitiveness values, or 'dominance index' (d in the model), which is estimated relative to all other group members (Adams, 2005; see also Shev et al., 2012). In short, let Pij be the probability that individual i dominates individual j, then the probability that individual i wins against individual j is given by $\text{logit}(Pij) = di - dj$. Competitiveness in each trial (attained competitiveness: d) would be determined by $d = mu + \varepsilon$, where $mu = $ inherent competitiveness of each bird (hereafter, "competitiveness"). Term ε denotes the residual competitiveness, representing additional unquantified within-individual variation. Detailed information is described in Hasegawa et al. (2015). At the same time, we also estimated individual propensity for frequent aggression (b in the model), a latent variable determining the observed combat rate. The combat rate from

each experiment was designated as a response variable (as Poisson error distribution with log link), with winners' identity as a random factor. To account for overdispersion (Hasegawa et al., 2014), "observation level random effect" (*obs* in the model) was included in the model (Gelman et al., 2014). Combat rate was explained by attained frequent aggression of winners in each trial, $b2$. This parameter is further determined by individual propensity for frequent aggression (i.e., b), with additional unquantified residual number of aggressive encounters representing all other unquantified variation. In other words, combat rate was decomposed as winners' propensity for frequent aggression and residual variation. The full algorithm can be found in Appendix A. Although combat rate and the probability of winning are mathematically independent variables, it should be noted that these may not be independent biologically if aggressive birds happen to fight and win more (see Results).

A total of 240 000 Monte Carlo iterations per chain, including 80 000 burn-in iterations, was performed, and one of every 40 steps was sampled from the remaining 160 000 steps, yielding 4000 samples per calculation trial (as in Hasegawa et al., 2015). The calculation was repeated three times, so in total 12 000 samples were obtained for each estimate, using software WinBUGS 1.4 (Lunn et al., 2000; see also Appendix A). The reproducibility of the MCMC simulation was assessed by calculating the Brooks–Gelman–Rubin statistic (Rhat), which should be <1.2 for all parameters (Kass et al., 1998). Model estimates (and their relationship with other male attributes) are presented as posterior means, 95% credible intervals (CrIs), and MCMC-based p values (p_{MCMC}: "mcmc.pval" in R package "MCMC.qpcr"). All analyses were carried out in R using the "coda" package (Plummer et al., 2006).

3. Results

3.1. Repeatability of combat rate in the group-competition experiment

We first asked whether combat rate was repeatable for individual birds in the group-competition experiment when they fought against different opponents. We found that the combat rate of males had significant repeatability when they defeated two or more opponents (original scale repeatability $\pm$ SE = 0.55 ± 0.18, 95% CI = 0.10, 0.81, N_{male} = 15, $p < 0.001$; Figure 2a; see Methods; also see Hasegawa et al. (2014) for rank determination) and when
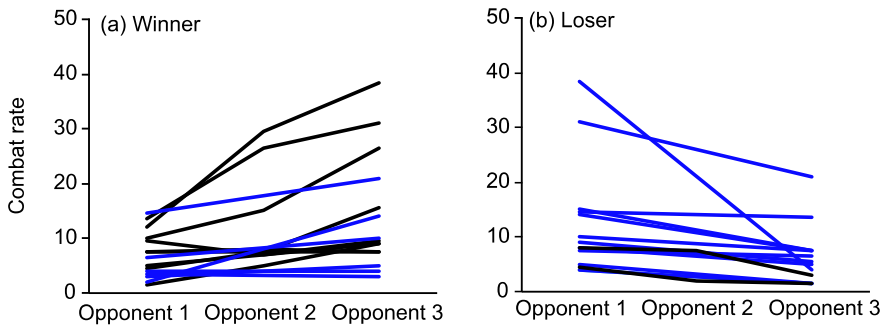
Figure 2. Combat rate (measured as the number of competitive interactions per 30 minutes) was repeatable for winners (a) and for losers (b) against different opponents in the group-competition experiment. Each line denotes the same individual. See detailed information in text. Males that won (or lost) against three opponents are in black and males that won (or lost) against two opponents are in blue.

they lost to two or more opponents $(0.43 \pm 0.22$, 95% CI $= 0.00, 0.77$, $N_{male} = 14$, $p = 0.03$; Figure 2b).

Also, for second- and third-ranking males in groups (i.e., who were dominant to some opponents but subordinate to others; note that first- and fourth-ranking males were always dominant to others or always subordinate to others, respectively), we calculated the repeatability of combat rate. When they won (or lost) against multiple opponents, we used average combat rate, not to be confounded by repeatability of winners (and losers: i.e., to study repeatability when they change their role, i.e., winner and loser). For these males, we found low, non-significant repeatability of their combat rate against different opponents $(0.12 \pm 0.20$, 95% CI $= 0.00, 0.64$, $N_{male} = 11$, $p = 0.33)$.

3.2. Repeatability of combat rate in paired contests (i.e., within- v. between-site experiments)

When we compared the combat rates of individual birds from the within-v. between-site experiments, we found a significant, high repeatability when males won both of their trials (original-scale repeatability $\pm$ SE $= 0.61 \pm 0.20$, 95% CI $= 0.23, 0.85$, $N_{male} = 15$, $p < 0.01$; Figure 3a). On the other hand, the repeatability was low and non-significant for males who lost both trials $(0.00 \pm 0.12$, 95% CI $= 0.00, 0.41$, $N_{male} = 14$, $p = 0.50$; Figure 3b) and for those who won one and lost one trial $(0.00 \pm 0.14$, 95% CI $= 0.00, 0.51$, $N_{male} = 12$, $p = 0.50)$. This was also the case when we calculated the repeatability of combat rate for males who won the first and lost the second
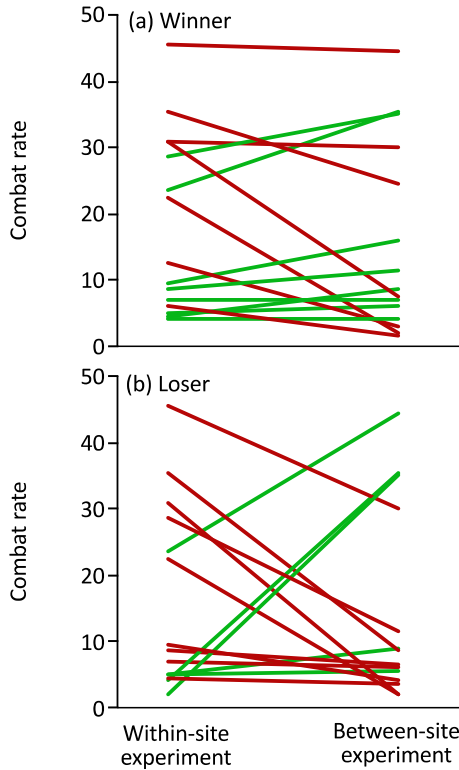
Figure 3. Combat rate was repeatable for winners (a) but not for losers (b) between two paired contests (within-site experiment and between-site experiment). Each line denotes the same individual. See detailed information in text. Positive sloped lines are green and negative sloped lines are red.

trial (0.00 ± 0.19, 95% CI $= 0.00, 0.67$, $N_{male} = 6$, $p = 0.50$) and those who lost the first and won the second trial (0.00 ± 0.19, 95% CI $= 0.00, 0.69$, $N_{male} = 6$, $p = 1.00$), though sample sizes were small in these analyses.

3.3. Repeatability of combat rate between paired contests and the group-competition experiment

Mean dyadic combat rate was 1.6 times lower in the group-competition experiment (mean $\pm$ SE $= 8 \pm 1$ aggressive encounters per 30 min) than in the between-site experiment (mean $\pm$ SE $= 13 \pm 3$ aggressive encounters per 30 min). Thus, to control for the mean difference, which confounds the measure of repeatability (see Nakagawa & Schielzeth, 2010), we divided the combat rate by 1.6 for the between-site experiment, which rendered it

comparable to the average combat rate of winners and losers in the group-competition experiment.

After this procedure, combat rate was significantly moderately repeatable in instances where males won paired contests and against some (i.e., $\geqslant 1$) opponents in the group-competition experiment (i.e., average combat rate as winners for first-, second- and third-ranking males: original-scale repeatability $\pm$ SE $= 0.48 \pm 0.24$, 95% CI $= 0.00, 0.85$, $N_{\text{male}} = 13$, $p = 0.031$; Figure 4a). Again, the repeatability was low and non-significant when males lost paired contests and against some opponents in the group-competition experiment (i.e., average combat rate as losers for second-, third- and fourth-ranking males: original-scale repeatability $\pm$ SE $= 0.00 \pm 0.13$, 95% CI $= 0.00, 0.43$, $N_{\text{male}} = 16$, $p = 1.00$; Figure 4b). We then calculated the repeatability of combat rate for males who won in the between-site trial but lost against some opponents in the group-competition experiment (see above), and for males who lost the between-site experiment but won against some opponents in the group-competition experiment (see above), and found relatively low, non-significant repeatability (0.11 ± 0.14, 95% CI $= 0.00, 0.49$, $N_{\text{male}} = 21$, $p = 0.25$). This was also the case when we separately calculated the repeatability of the former category (0.22 ± 0.22, 95% CI $= 0.00, 0.73$, $N_{\text{male}} = 12$, $p = 0.19$), and the latter category (0.00 ± 0.17, 95% CI $= 0.00, 0.56$, $N_{\text{male}} = 9$, $p = 1.00$).

Although we investigated combat-rate repeatability for the two adjacent experiments (i.e., between-site and group-competition experiment here), a similar pattern was found when we examined combat rate in the within-site and group-competition experiments [i.e., significant repeatability for winners (0.59 ± 0.18, 95% CI $= 0.15, 0.84$, $N_{\text{male}} = 18$, $p < 0.01$) but not for losers (0.05 ± 0.14, 95% CI $= 0.00, 0.47$, $N_{\text{male}} = 16$, $p = 0.41$) and for males who won in the between-site trial but lost against some opponents in the group-competition experiment, and for males who lost the between-site experiment but won against some opponents in the group-competition experiment (0.22 ± 0.19, 95% CI $= 0.00, 0.64$, $N_{\text{male}} = 18$, $p = 0.15$)].

3.4. Male aggressiveness, competitiveness and plumage/bill traits

Using a Bayesian approach based on data from the within- and between-site experiments (Hasegawa et al., 2015), we found that "latent" male aggression frequency (i.e., individual propensity for frequent aggression; see Methods), which determines the observed combat rate in the model, was positively correlated with inherent male competitiveness (see Methods; $r = 0.30$,
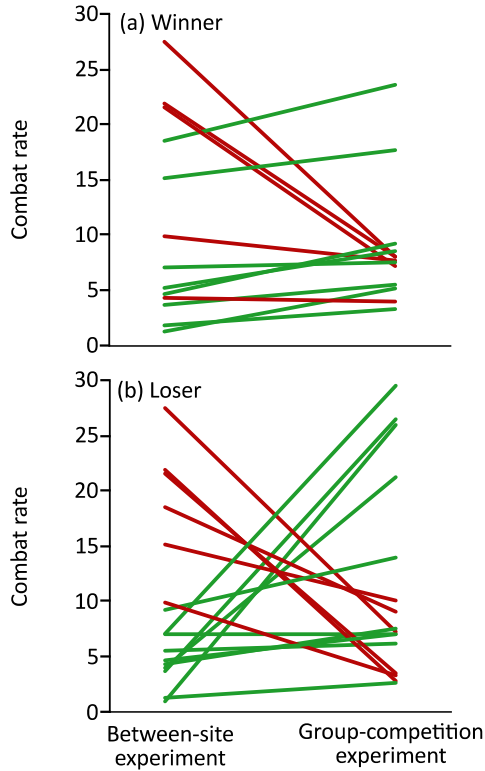
Figure 4. Combat rate was repeatable for winners (a) but not for losers (b) between the paired contest (between-site experiment) and within-group contest (group-competition experiment) after controlling for 1.6 times less competition in the within-group contest (see text). Each line denotes the same individual. Positive sloped lines are green and negative sloped lines are red.

95% CrI $= 0.01, 0.56$, $p_{MCMC} = 0.032$; Figure 5), explaining 9% of the total variance (i.e., "aggressiveness" explains a small portion of competitiveness; note that individual propensity for frequent aggression can be estimated solely for winners: $n = 31$). However, mean relative competitiveness of opponents (i.e., competitiveness of winner minus loser) was not significantly correlated with latent male aggression frequency ($r = 0.24$, 95% CrI $= -0.11, 0.54$, $p_{MCMC} = 0.14$). This was predictable because relative competitiveness of opponents showed non-significant repeatability (repeatability $= 0.36$ (95% CrI $= -0.11, 0.74$, $p_{MCMC} = 0.10$) and 0.28 (95% CrI $= -0.21, 0.69$, $p_{MCMC} = 0.23$), respectively), indicating that individual "inherent" competitiveness statistically matters more than the dis-
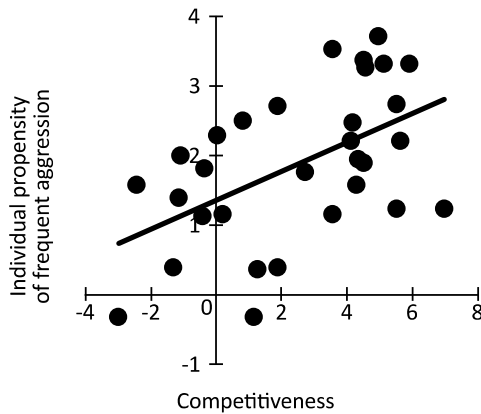
Figure 5. The propensity for frequent aggression in paired contests by winners was partially explained by male competitiveness. For illustrative purpose, only posterior mean values together with the simple regression line for these values are represented (note that actual statistics in the text are based on each of 12 000 iterations).

crepancy in competitiveness between contestants in determining combat rate.

We also found that urban colourful males had a significantly lower latent aggression frequency than other groups (i.e., $p_{MCMC} \leqslant 0.01$; Figure 6a), and that bill size did not significantly predict latent aggression frequency ($r = -0.10$, 95% CrI $= -0.26$, 0.07, $p_{MCMC} = 0.25$; Figure 6b). Because male competitiveness was still negatively related to bill size in those 31 birds ($r = -0.31$, 95% CrI $= -0.56$, -0.02, $p_{MCMC} = 0.030$; see Hasegawa et al. (2015) for all 47 males), the lack of a significant relationship between latent aggression frequency and bill size was not due to reduced sample size.

3.5. Frequent aggression and latency to approach the stuffed model

In our "model-presentation" experiment ($N = 23$ birds, in which latency to approach the conspecific model and latent aggression frequency can be estimated), we found that latency to approach the conspecific model was not significantly correlated with either latent aggression frequency ($r = -0.13$, 95% CrI $= -0.40$, 0.34, $p_{MCMC} = 0.53$) or male competitiveness index ($r = -0.24$, 95% CrI $= -0.52$, 0.09, $p_{MCMC} = 0.12$).
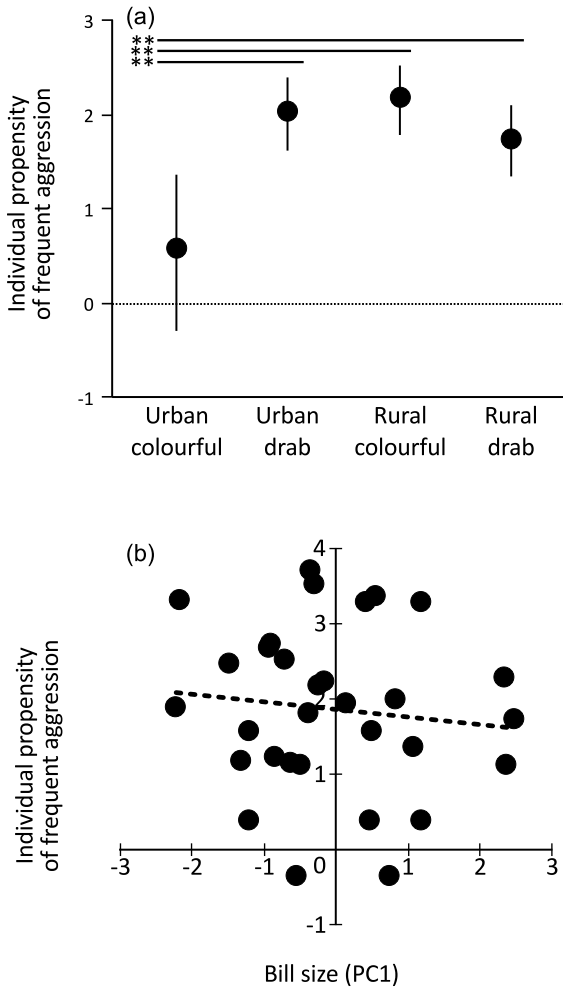
Figure 6. The propensity for frequent aggression by winners was explained by plumage/urbanization category of males (a) but not by male bill size measured by PC1 (b). For the upper panel, posterior means and 95% credible intervals are presented. $^{**}p_{\text{MCMC}} \leqslant 0.01$ (see text for detailed information). Sample sizes for urban colourful, urban drab, rural colourful and rural drab males are 4, 10, 9 and 8, respectively. For the lower panel, only posterior mean values together with the simple regression line for these values are represented (note that actual statistics in the text are based on each of 12 000 iterations).

4. Discussion

Our finding that combat rate was repeatable for winners in our behavioural trials (Table 1) indicates that being a "bully" is a personality trait in house

Table 1.

Combat-rate repeatabilities for winning and losing males across our different competition experiments.

Males tested	Within-group competition	Within v. Between	Between v. Group-competition
Winners	$0.55 \pm 0.18^*$	$0.61 \pm 0.20^*$	$0.48 \pm 0.24^*$
Losers	$0.43 \pm 0.22^*$	0.00 ± 0.12	0.00 ± 0.13
Winner for some trials and loser for others	0.12 ± 0.20	0.00 ± 0.14	0.11 ± 0.14

Values are represented as Mean $\pm$ SE. Please see text for detailed information. * indicates significant repeatability.

finches. Because combat rate was repeatable for both winners and losers in the group-competition experiment (Table 1), frequent aggressive interactions may induce aggression from other group members towards losers (in other words, combat rates among group members are inter-dependent, though we could not completely exclude the common elements of the asocial environment, such as air temperature, in each experimental setting). Since winner/loser status can be determined from a few (i.e., 5; McGraw et al., 2007) aggressive encounters in this species, large variation in combat rate among males (see Figures 2 and 3; also see Hasegawa et al., 2014) is not a simple by-product of the processes determining dominant/subordinate status. Likewise, since combat rate was not repeatable for males who lost at least one of the trials in our experiments (i.e., both between the paired trials and across trials with different group sizes), individual variability in combat rate was not simply due to differences in activity (or more precisely, differences in activity alone could not explain repeatability of winners; Wilson et al., 2011, 2013). This finding is consistent with the previous report in this study system (Thompson, 1960a) that a male's intrinsic propensity for aggression should determine his combat rate.

The fact that we observed moderate repeatability (ca. 0.50) for the combat rate of winners even across different social contexts also indicates that aggressive propensity is relatively stable with changing group composition, at least over a relatively short period of time. In other words, across group sizes, about half of the total variance in combat rate could be explained by a winners' aggressive tendency alone. Latent aggression frequency of winners was also positively related to male competitiveness index, but could not

be predicted by one of the two correlates of competitiveness (i.e., bill size), further supporting the idea that frequent aggression is not concomitant with high competitiveness. As with win/loss outcomes, combat rate might also depend on the relative competitiveness of opponents, but this was not the case (also see Figure 5). Lastly, individual propensity for frequent aggression, which determines combat rate, was partially independent of latency to approach the conspecific models (a classic measure of aggressiveness; e.g., Lack, 1965; Briffa et al., 2015), indicating that there are several axes of "aggressiveness" (i.e., different personality traits: Carter et al., 2013), at least in this study system.

The partial independence of aggression frequency and the latency to approach the conspecific models may be governed by endocrinological mechanisms, because initial aggression towards conspecifics and its persistence thereafter can be controlled by different hormones in birds (e.g., Wingfield, 1994; Heimovics et al., 2015; also see Wilson et al., 2011, p. 11 for a similar difference in the proximate control of agonistic behaviours in fishes). For example, breeding and non-breeding male song sparrows (*Melospiza melodia*) are equally aggressive towards territory intruders, but only breeding males remain aggressive for hours, perhaps because non-breeding males become temporarily aggressive due to oestradiol, i.e., aromatized testosterone, which does not bind to androgen receptors but to oestrogen receptors (Heimovics et al., 2015; also see Wingfield & Soma, 2002). Although aggressiveness is often assumed to be enhanced by increased testosterone secretion, there may be several physiological mechanisms (e.g., aromatization of testosterone, other hormones, neurotransmitter systems) by which some, but not all, aspects of aggression are linked to male characteristics (Lynn, 2008; Barron et al., 2015).

From the viewpoint of subordinates, predictable combat rate of winners can reduce the cost of competition because weak competitors can avoid frequent aggression by monitoring opponents' identity (via past experience or eavesdropping on others' competitions) or phenotype (i.e., drab males from urban sites were frequent aggressors). In fact, in our previous work, lean urban males avoided drab male models (Hasegawa et al., 2014), which could be interpreted as an adaptive response to avoid frequent aggression from other group members. One component of contest behaviour — "fighting ability" — is typically the focus of research (Chaine et al., 2011), but recently it has been shown that contest behaviour is comprised of multiple behavioural

parameters, which are signalled by multiple traits (e.g., defence ability and aggressiveness: Bókony et al., 2006; long-term and short-term dominance: Galván & Sanz, 2008, 2009; aggressive encounter and escalation: Chaine & Lyon, 2008; Chaine et al., 2011, 2013). Our study adds another important axis, frequent aggression, to our understanding of animal contests.

From the viewpoint of dominants, why do some but not all dominants repeatedly attack opponents? A possible explanation is the differential benefits/costs of frequent aggression in dominant males, who in fact consist of several kinds of individuals (e.g., drab urban males, rural males or short-billed males; Hasegawa et al., 2015). Some dominants should repeatedly attack other males, driving opponents (and eavesdroppers) away, and thus take advantage of securing immediate and future resources. Other dominants may minimize costly social interactions after they dominate opponents, maximizing the amount of time available for other activities (e.g., foraging; see Heimovics et al. (2015) for the same explanation for seasonal variation in persistent aggression). For example, frequent aggression of drab urban males and rural males could be explained if they have greater incentive to engage in aggressive competitions that increase survival and reproduction in their harsh social/asocial environment (e.g., disadvantage at mate choice or food shortage; Hasegawa et al., 2014), whereas short-billed males might simply have competitive advantages via the high manoeuvrability at short-range jostling (Hasegawa et al., 2015). As another explanation, Hasegawa et al. (2015) proposed that short-billed males are highly motivated in competitions to compensate for the disadvantages posed by scramble competition (i.e., limited ability to husk large, valuable seeds) or mate attraction (i.e., differential song characteristics in relation to bill size; Badyaev et al., 2008; Badyaev, 2014; Giraudeau et al., 2014), but this is unlikely because bill size was not linked to the winner's propensity for frequent aggression in this study. By closely investigating individual propensity for aggression in addition to the probability that the focal individual won, we could infer the cause of competitiveness and thus have better knowledge of animal contest tactics than previous approaches using simple comparisons of aggressive encounters won and lost (e.g., Hasegawa et al., 2014) or using the probability of winning alone (e.g., Hasegawa et al., 2015).

In summary, we showed that combat rate in male house finches is highly consistent among winning individuals but not strongly linked to competitiveness or to latency to approach the conspecific models, at least over a

relatively short period of time. Although behavioural studies frequently assess the latter two measures as primary indicators of fighting ability and examine their relationship with other behavioural propensities (e.g., proactive/reactive; van Oers & Naguib, 2013) or phenotypic traits (e.g., ornaments; Senar, 2006), combat rate (and its determinant, winners' propensity for frequent aggression) should also be included in future analyses. In male house finches, aggression frequency was not correlated with one of the two previously established predictors of competitiveness, indicating its functional difference within competitive contexts. Clearly, the current experiment is based on small sample size, which prevents accurate computation of repeatability (and further analyses of repeatability such as comparison of repeatability between winners and losers). It remains to be clarified whether and how animals integrate information about opponents' aggressive propensity (as well as their own competitiveness) and how they behave based on this information during social interactions.

Acknowledgements

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Appendix A: WinBUGS specification of the Bradley–Terry model modified from Hasegawa et al. (2015).

```
model {
  for (i in 1:48) { n[i] <- win1[i] +win2[i]
  win1[i]~dbin(p[i],n[i])
  logit(p[i])<-(d[ind1[i]]-d[ind2[i]])
  n[i]~dpois(lambda[i])
  log(lambda[i])<-b2[ID[ind1[i]]]+obs[i]
  obs[i]~dnorm(0,tau4)}

  for (i in 1:32){b2[ind11[i]]~dnorm(b,tau3)}
  for (i in 1:48){r[i]~dnorm(0,tau2)}
  for (i in 1:96){d[i]~dnorm(mu[i],tau) I(-15,15)
  mu[i]<-r[ID[i]]}

  b<-0
  tau<-pow(sigma,-2)
  tau2<-pow(sigma2,-2)
  sigma~dunif(0,1000)
  sigma2~dunif(0,1000)
  tau3<-pow(sigma3,-2)
  sigma3~dunif(0,1000)
  tau4<-pow(sigma4,-2)
  sigma4~dunif(0,1000)
  }
```