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Condition explains individual variation in mobbing behavior

Mikus Abolins-Abols [iD] | Ellen D. Ketterson

Department of Biology, Indiana University, Bloomington, IN, USA

Correspondence
Mikus Abolins-Abols, Department of Biology, Indiana University, Bloomington, IN, USA
Email: mabolins@indiana.edu

Abstract

During mobbing, individuals approach predators with the apparent aim of reducing the risk of predation. The intensity of mobbing may depend on the costs and benefits of this behavior, which likely vary among individuals and between different social contexts. We studied whether Dark-eyed junco male mobbing behavior is related to social environment, individual condition, and age during experimentally induced mobbing events. Based on risk-taking theory, we predicted that individuals with high residual reproductive value—younger individuals and those in better condition—would show weaker mobbing behavior. We also expected to see weaker mobbing when the total number of individuals in the mobbing assemblage was small. All subjects were caught to assess condition and age. Focal males were then attracted to simulated mobbing events using heterospecific alarm calls. Social environment did not explain individual variation in mobbing behavior in focal juncos. Community-wise, the relationship between the closest approach and group size was not significantly different from chance. Junco males in better condition approached the predator less closely and were less likely to give alarm calls. Age did not explain variation in mobbing. Both the mean approach and probability of giving alarm calls by junco males were repeatable, in contrast to the size and composition of mobbing assemblages in junco territories, which were inconsistent. Our results show that variation in mobbing can be linked to individual state, which likely affects the costs and benefits of mobbing.

KEYWORDS
condition, juncos, mobbing, predation, risk, social environment

1 | INTRODUCTION

Mobbing is a widespread anti-predator behavior, where instead of avoiding predators, individuals approach the predator and give alarm calls, often attracting large groups of con- or heterospecific animals to the scene. The fitness benefits of this widespread behavior have been widely discussed and tested (Curio, 1978; Curio, Ernst, & Vieth, 1978; Flasskamp, 1978): In most cases, the primary and most important benefit of the mobbing is that it causes the predator to recognize that it is detected, leave the location, and avoid it in the future (Caro, 2005; Curio, 1978; Flasskamp, 1978). A potential additional long-term benefit of mobbing is the establishment and maintenance of social relationships between individuals that facilitate reciprocal help between family members and neighbors (Krams, Krama, Igaune, & Mänd, 2008;

Krams et al., 2013; Shields, 1984). Despite these benefits, mobbing incurs a potential immediate cost to the mobber: making one's self obvious to the predator increases the probability of attack and death (Curio & Regelmann, 1986; Krams, 2001). For mobbing behavior to be selectively advantageous, the immediate and future benefits of this behavior must outweigh any costs.

Mobbing behavior can vary considerably between situations and among individuals. Most research on the causes of variation in mobbing has been conducted across situations: mobbing behavior may vary seasonally (Cully & Ligon, 1986; Krams & Krama, 2002; Shedd, 1982), depend on the species of the mobber (Courter & Ritchison, 2012), or the predator that is being mobbed (Suzuki, 2016; Syrová, Michal, Vesel, Landová, & Fuchs, 2016; Welbergen & Davies, 2008). Propensity to mob also varies based on whether the individual whose life or nest is

in danger has previously assisted its neighbors during predator attacks in their territories: neighbors that have been assisted in mobbing in the past are more likely to reciprocate their help in the future (Krams et al., 2013). We know less, however, about what explains variation in mobbing among individuals in the same situation. Individual differences in response to a serious risk to survival as presented by a predator may have major consequences for lifetime fitness.

Optimality theory suggests that individuals should vary their risk-taking behavior based on the environmental and social contexts (extrinsic state), as well as their condition, sex, and age (intrinsic state) (Clark, 1994; McNamara & Houston, 1986). One of the most important extrinsic factors affecting mobbing is group size—individuals in larger groups tend to mob predators more actively (Curio & Regelmann, 1986; Krams, Bērziņš, & Krama, 2009; Wiklund & Anderrsson, 2016), suggesting that mobbing in large groups may make it safer (dilution effect) (Hamilton, 1971). In some bird species, mobbing behavior increases in the presence of a mate, presumably because the mate is a resource that needs protection (Regelmann & Curio, 1986). Predation defense intensity also increases with increasing age of offspring (Albrecht & Klvaňa, 2004; Patterson, Petrinovich, & James, 1980).

Although there is a rich literature on the relationship between intrinsic state and general risk-taking behavior (Lima & Bednekoff, 1999), there are few studies that explicitly investigate the effect of intrinsic factors on mobbing behavior (Berne, 2011). Both condition (Lima, 1986) and age (Avilés & Bednekoff, 2007) have the potential to affect the ability of animals to escape predation (due to either physical ability or experience) (Griesser & Suzuki, 2016) and therefore may affect the balance between the short-term risk and long-term benefit of mobbing behavior. Studies investigating variation in risk-taking behaviors during courtship and foraging suggest that animals with the most to lose (highest residual reproductive value (RRV): youngest individuals, individuals in highest condition) should behave most cautiously (Clark, 1994; Ghalambor & Martin, 2000, 2001).

In this paper, we investigated whether variation in extrinsic (mate presence, number of mobbers) and intrinsic (condition, age) factors explains variation in mobbing behavior in male Dark-eyed juncos (*Junco hyemalis*), a small songbird. We measured response to simulated mobbing events during the breeding season. If high RRV causes individuals to avoid danger during mobbing, we predicted that young individuals and individuals in a better condition would approach the predator less closely and make fewer alarm calls than older individuals or individuals in worse condition. Alternatively, individuals in a better condition may approach the the predator more closely than those in a worse condition if better condition enables individuals to be more vigilant or better at escaping risky situations. In accordance with the dilution effect (Krams & Krama, 2002) and mate-guarding (Regelmann & Curio, 1986) hypotheses, we also predicted that the presence of a mate and larger mobbing assemblages would be associated with more active mobbing by the focal junco males compared to when the mobbing groups were smaller or the female was absent. Finally, we predicted that at the community level the mobbing group size would be negatively associated with the closest approach by any individual, irrespective of species.

2 | METHODS

2.1 | Study site and species

All procedures described here were approved by the Bloomington Institutional Animal Care and Use Committee (BIACUC, protocol #12-050-08). We studied wild Dark-eyed junco males (*n* = 32) at the Mountain Lake Biological Station and surrounding forests in the Appalachian Mountains of Giles County, Virginia, USA (37°22′N, 80°32′W), from April 20 through August 10, 2015. We conducted an early (April 20–May 15) and late (July 15–August 10) breeding season census, where we banded each bird with federal aluminum as well as three additional plastic color bands. During the census, we made standard morphological measurements of each bird. Birds were released within an hour of capture. Following the early season census, we mapped the boundaries of junco males' territories using junco song playback and noting where males started/stopped responding to playback.

2.2 | Mobbing behavior

2.2.1 | Mobbing trials

We conducted simulated mobbing trials from May 15, 2015, to July 15, 2015. The trials were conducted in the estimated center of a focal male's territory, but were random with respect to the location of the nest because in most cases the location of the nest was unknown. Thirteen of 32 males were tested twice (45 total observations). If the nest location was known, the trial was conducted at least 15 m away from the nest. We conducted our trials in forest areas that had openings in the undergrowth to facilitate observations, but that had enough perches at various distances (0–50 m) from the stimuli. Mobbing trials conducted on the same day were carried out at least 200 m away from each other. We placed a taxidermied Cooper's hawk (*Accipiter cooperii*) on a tripod about 1.5 m from the ground and covered it with a camouflage cloth. Cooper's hawks are common forest predators that prey on juncos (Bielefeldt, Rosenfield, & Papp, 1992; Dunn & Tessaglia, 1994). We then broadcast a mix of alarm calls from six species that are common in the study site and are vocal participants in mobbing events (based on preliminary observations): Tufted Titmouse *Baeolophus bicolor*, White-breasted Nuthatch *Sitta carolinensis*, Blue-headed Vireo *Vireo solitarius*, Red-eyed Vireo *Vireo olivaceus*, Canada Warbler *Cardellina canadensis*, and Ovenbird *Seiurus aurocapilla*. Six species were chosen because the median number of species participating in the pilot trials was six. We used Altec Lansing Technologies IMT227 OrbitM speaker to broadcast the calls, which was placed right next to the hawk, and connected to an iPhone 4 (Apple Inc.) via a 15-m-long headphone cable. The volume of the playback recordings at 1 m was 90–94 dB as measured with a sound pressure meter. We used two unique alarm call recordings from each of the six species, which were obtained from xeno-canto.org (accession numbers: Tufted Titmouse: XC163235, XC60068; White-breasted Nuthatch: XC114591, XC162158; Blue-headed Vireo: XC194718, XC243385;

Red-eyed Vireo: XC144678, XC103290; Canada Warbler: XC142760, XC30786; Ovenbird: XC140676, XC142342). Using random numbers generated by R (version 3.0.2; R Core Team 2013), we randomly chose one of the two recordings from each species and used the multitrack editor function in Adobe Audition (Adobe Systems Inc.) to overlay the six sound files so that all calls were broadcast simultaneously. Using the multitrack editor, we manually changed the volume of each species calls in the recordings, so that as the tape progressed, one species was 8 dB louder than others. We made 10 unique multitrack recordings, each 5 min long, and assigned them randomly to the behavioral trials. For males that were tested twice, we used different recordings. Research has shown that alarm calls by multiple species, including the Tufted Titmouse, may encode information about the specific threat the calls are directed to (Hetrick & Sieving, 2012; Nocera & Ratcliffe, 2010). In our study, recordings were chosen based on their quality, but not on specific spectral or temporal characteristics. Therefore, we do not know what threat was originally signaled by the alarm calls of birds whose recordings were used in this experiment. However, random track combinations used in this study controlled for any effects that information encoded in the specific alarm calls might have had.

The alarm calls were broadcast until we spotted or heard the focal male within 50 m (mean arrival time was 2.8 min, standard deviation (*SD*) = 3.35 min, *n* = 37). If the male did not arrive in 10 min, we stopped the trial. Once the male arrived, we remotely restarted the alarm call tape and revealed the hawk by removing the cloth with a string. The removal of the cloth also served to attract the focal male's attention to the hawk. Each mobbing trial lasted 5 min. At all times, the observer (MAA) sat concealed behind vegetation at least 10 m from the hawk.

2.2.2 | Control trials

To ensure that birds were attracted to the mobbing trials in response to the alarm call playback, as opposed to the playback itself, we conducted control trials on a different cohort of birds, where instead of alarm calls, we broadcast the long-range songs of the same species (xeno-canto.org accession numbers: Tufted Titmouse: XC100238, XC18385; White-breasted Nuthatch: XC13350, XC54710; Blue-headed Vireo: XC79006, XC135499; Red-eyed Vireo: XC243578, XC176354; Canada Warbler: XC79012, XC103276; Ovenbird: XC79093, XC100205). Instead of a hidden hawk, we put a nonthreatening stimulus (backpack) next to the speaker.

2.2.3 | Behavior of the focal male

We recorded the distance separating the focal male from the hawk or backpack throughout the trial using a construction rope with flagging that marked 1-, 2-, 5-, and 10-m distance from the speaker. This line was stretched from the speaker perpendicular to the location of the observer. Males never responded (approached or vocalized) to the speaker and backpack during control trials (see Results); therefore hereafter, we refer to methods that were used for mobbing trials only. We marked the time and distance of the male from the hawk

every time the male hopped or flew more than a meter. This allowed us to calculate the mean distance of the male from the hawk during mobbing. If a male moved to a distance greater than 50 m, we considered that the male had abandoned mobbing because juncos typically do not display anti-predator behaviors at this distance. For this reason, and the fact that it was not possible to see birds past this distance, we did not include the time spent further than 50 m in our calculation of the mean distance from the hawk. If during the trial, the observer lost sight of the focal male, upon respotting the male, the observer assumed that the male had just arrived at that location. We used the mean distance measure for the focal male behavior instead of the closest distance because closest distance estimates are likely to have higher error due to variability in perch availability and observer error. We also noted whether the males were giving alarm calls ("tiks"; Hostetter 1961, Nolan et al. 2002). Due to logistical challenges, we could not count the number or frequency of tiks, but simply noted whether males gave tik calls or not.

2.3 | Intrinsic state variables

To assess condition, we used the residuals from a mass–tarsus regression, a measure that standardizes mass for the structural size of the animal (measured by tarsus), and is widely used to assess condition in birds (Labocha & Hayes, 2011). These measures were made during the spring census, which preceded the behavioral trials. The spring and late summer mass–tarsus regression residuals of the same individual were positively correlated (Pearson's *r* = .51, degrees of freedom (*df*) = 17, *p* = .03), indicating that individual differences in condition were consistent across the breeding season. However, only a subset of individuals from the mobbing trials was captured in the late season census; therefore, we used only the spring values in our analyses. The mass–tarsus residuals were positively correlated with another estimate of condition, a visual index of pectoral muscle volume (Pearson's *r* = .36, *df* = 40, *p* = .02), which is a more direct measure of condition in songbirds (Brown, 1996; Meddle, Owen-Ashley, Richardson, & Wingfield, 2003; Tonra, Marra, & Holberton, 2011). While more direct, visual inspection of pectoral muscle volume lacks precision and resolution, therefore we did not use this index in our analyses.

Age was estimated based on census records and plumage coloration. For a fraction of individuals (18 of 25), we knew their precise age based on when they were banded as nestlings or juveniles. For others (7 of 25), we knew only their minimum age based on plumage and when they had first been banded as adults; thus, we might have underestimated the age of some individuals. Models with and without individuals of estimated age gave quantitatively similar results, but models without individuals of estimated age had lower power. In our final analyses, we therefore included both individuals with known age and individuals with estimated minimum age.

2.4 | Social environment

Nearly all males in our study population had known mates, and we noted whether the mate of each male participated in the mobbing.

Because our focus was on males, we could not assess the behavior of the mate with certainty; therefore, we simply noted her presence/absence in each trial. We also counted other birds (con- and heterospecific) that came to the mobbing trial. As the observer was focused on the focal junco male, the mobbing community estimates are based on birds that were active participants (moving or vocalizing) of the mobbing group.

2.5 | Community-level patterns

To draw community-level inferences about the effect of the mobbing group size and composition on mobbing behavior, we calculated the total number of participants and species richness of the mobbing groups (R package vegan (Oksanen et al., 2015)) and investigated the relationship of these variables to the closest approach of any individual (irrespective of species) during each mobbing bout.

As larger groups have an increased probability of containing individuals that make close approaches to the predator compared to smaller groups, a negative relationship between group size and closest approach distance may arise by chance. To assess this possibility, we compared the observed relationship between the closest approach and the mobbing group size from the true dataset with a simulated expected relationship that was strictly probabilistic and ignored any psychological effect group size may have on individuals' behavior.

The simulated relationship was derived by randomly sampling approach distances of hypothetical mobbing groups 1–11 individuals in size (same as the observed range) from a dataset that included all closest recorded approaches of mobbing participants, irrespective of species (n = 215). This larger dataset contained multiple species per trial, but was not complete: It was not possible to record the location of every bird at the mobbing event because our focus was on the focal junco males. However, the large sample size of this dataset should approximate the mobbing participant approach distances that we did not record. We then took the closest approach distance from each of the hypothetical mobbing groups (n = 44 to match the sample size of the real dataset).

We then ran an ANCOVA to compare the slopes of the observed and simulated expected relationships. If the expected slope was significantly steeper (more negative) than the slope from the observed data, that would indicate that individuals were less bold in larger groups than expected by chance. If the simulated slope was significantly less steep (less negative) than the slope from the observed data, that would indicate that individuals were more bold in larger groups than expected by chance. Repeated simulations of the expected relationships gave qualitatively and quantitatively equivalent results.

2.6 | Statistics

2.6.1 | The mean distance of the focal male to the hawk

We used linear mixed models (LMMs, R package nlme (Pinheiro, Bates, DebRoy, & Sarkar, 2015)) with type-III (marginal) sums of squares to test for the relationship between the mean distance of the focal male to the hawk and explanatory variables (age, condition, presence of a mate, number of individuals of other species). Some junco males were tested more than once; therefore, we included individual identity as a random factor in our models.

2.6.2 | Alarm calls by the focal male during mobbing

We first tested the relationship between alarm call behavior and explanatory variables (age, condition, presence of a mate, number of individuals of other species) using logistic regression. However, logistic regressions with individual as a random factor resulted in overfitted (nonsensical) models. In attempt to take individual identity into account, we ran generalized estimating equations (GEEs, R package gee (Carey, Lumley, & Ripley, 2012)), which can include random effects, but lack the power of generalized linear models (GLMs). GEEs relax assumptions of GLMs and provide z scores for the average effect of predictors on the mean response of the population (Zeger, Liang, & Albert, 1988).

2.6.3 | Community-wide behavior

We tested the relationship between the closest approach by any bird (junco or other) and characteristics of the community (species of the closest individual, total number of mobbers, species richness in the mobbing group) using linear models (LMs).

2.6.4 | Repeatability

We estimated the repeatability (R) and its standard error (SE) of junco mobbing behavior, mate presence, and mobbing group size and richness using the R package rptR (Schielzeth & Nakagawa, 2013). The critical alpha value was $p \leq .05$. All models were tested for variance inflation (R package usdm (Naimi, 2013)) to ensure that model predictors did not show collinearity.

3 | RESULTS

### 3.1 | Control vs. mobbing trials

None of the 71 control trials attracted junco males to the speaker. In 25 of 71 control trials (35.2%), the focal male was singing nearby. Of 66 mobbing trials, males were actively mobbing the hawk or singing nearby in 46 trials (69.7%). This difference in male recruitment to the trials between treatments was significant (Fisher's exact test, p < .001), indicating that males were attracted to the mobbing alarm calls specifically. We therefore do not conduct further analysis of control trials.

3.2 | Mean distance to hawk

Variation in the mean distance from the hawk during mobbing was significantly positively correlated with condition (LMM, $F_{1,16}$ = 7.67, n = 29,
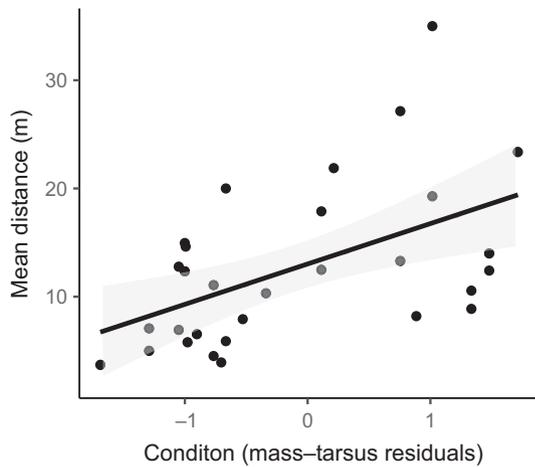
FIGURE 1 Individuals in lower condition approached the predator more closely than individuals in better condition ($p = .01$). The gray shaded area denotes 95% CI for the fit
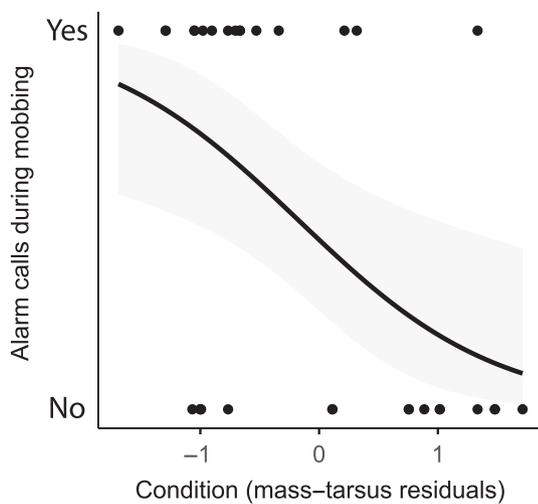

FIGURE 2 Individuals in lower condition were more likely to give alarm calls during the mobbing event than individuals in better condition ($p = .05$). The gray shaded area denotes 95% CI for the fit

$p = .01$; Figure 1). Neither the age of the males (LMM, $F_{1,16} = 2.93$, $n = 29$, $p = .11$), presence of a mate at a trial (LMM, $F_{1,8} = 0.04$, $n = 29$, $p = .84$), nor the number of other con- or heterospecific birds present at a trial (LMM, $F_{1,8} = 0.02$, $n = 29$, $p = .88$) explained significant variation in the mean distance from the hawk. The mean distance from the hawk was significantly repeatable ($R = .22$, $SE = .21$, $p = .05$).

3.3 | Alarm calls

The probability of male juncos giving alarm calls during the mobbing trial was higher for males in lower condition (GEE, robust $z = 1.95$, $n = 31$, $p = .05$; Figure 2). The alarm calling probability did not differ between males of different ages (GEE, $z = -1.03$, $n = 31$, $p = .30$). Neither the presence of a mate (GEE, $z = 0.50$, $n = 31$, $p = .66$) nor the number of other mobbers (GEE, $z = 1.09$, $n = 31$, $p = .28$) explained the presence or absence of alarm calls. Males that gave alarm calls came closer to the
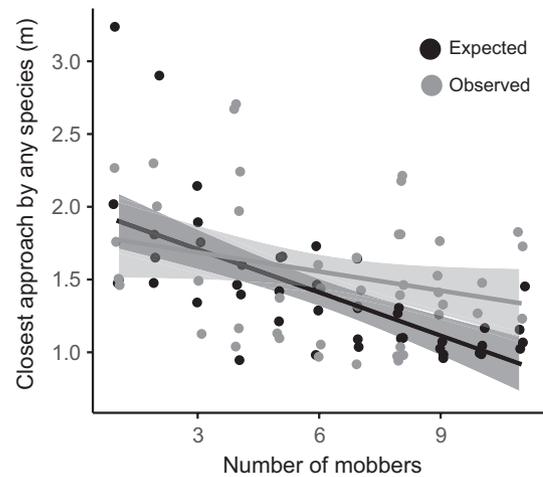
FIGURE 3 Larger mobbing assemblages tended to have individuals that approached the predator more closely (observed data, gray dots, light gray best fit line and CI, $p = .06$), but this relationship was not different from a simulated expected relationship (black dots, dark gray best fit line and CI) where closest approach and group size were linked purely by chance. The gray shaded area denotes 95% CI for the fit

hawk (paired t-test, $t = -4.16$, $df = 11$, $n = 43$, $p < .01$). The probability of giving alarm calls was repeatable ($R = .75$, $SE = .36$, $p = .03$).

3.4 | Community-wide mobbing behavior

The closest distance of any species (as opposed to just the focal junco male) to the hawk during mobbing was nearly significantly negatively associated with the number of individuals that participated in mobbing: In larger groups, birds tended to come closer (LM, $F_{1,43} = 3.71$, $n = 45$, $p = .06$; Figure 3). Species identity did not predict the closest approach (LM, $F_{15,28} = 0.93$, $n = 45$, $p = .55$). However, the observed relationship between the closest approach and group size was not significantly different from a simulated probabilistic relationship between closest approach distances and hypothetical mobbing assemblages (Figure 3, ANCOVA, $F_{3,85} = 3.76$, $n = 80$, $p = .06$). Species richness of the mobbing groups was positively correlated with group size (Fig. S1). After controlling for group size, species richness of the mobbing groups was not related to closest approach distance (LM, $F_{2,42} = 1.52$, $n = 45$, $p = .22$). Neither group size nor species richness was repeatable between repeated trials in the same junco male's territory (number of mobbers: $R = 0$, $SE = 0$, $p = .33$; richness: $R = 0$, $SE = .17$, $p = .50$). Species composition of the mobbing assemblages is reported in the Supplementary Material.

4 | DISCUSSION

Optimal mobbing effort, like any other behavior, is predicted to depend on the costs and benefits of performing the behavior. These costs and benefits depend on the extrinsic and intrinsic state, which may differ among individuals (McNamara & Houston, 1986; Sih et al., 2014). Most

attention to date has focused on how mobbing varies across situations or how social state may affect mobbing behavior (Cully & Ligon, 1986; Krams et al., 2013; Welbergen & Davies, 2008). Here, we show that body condition, an intrinsic factor, is a better predictor of an individual's mobbing intensity than extrinsic social factors, such as the presence of a mate or individuals of other species. During a simulated mobbing situation in the wild, male juncos in better condition stayed farther away from the hawk mount and were less likely to give alarm calls than were individuals of lower condition. Both approach distance and probability of giving alarm calls were repeatable among junco individuals, but mobbing group size and species richness were not. This suggests that mobbing behavior is consistent within individuals and inconsistent at the community level and that high-condition individuals are risk-averse in contrast to the more risk-prone low-condition animals.

The relationship between risk-taking and condition has received considerable attention in optimal foraging theory (Barnard & Brown, 1985; Nonacs & Dill, 1990; Real & Caraco, 1986), where the condition of an animal is often assumed to be a good indicator of the RRV of the individual—the better the condition, the more likely the animal is to survive (Naef-Daenzer, Widmer, & Nuber, 2001) and reproduce (Marra, Hobson, & Holmes, 1998; Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004) in the future. In this framework, low-condition animals have relatively more to gain from risk-taking than high-condition animals. High-condition individuals, on the other hand, are predicted to remain vigilant so as not to jeopardize their current high RRV ("asset protection principle") (Clark, 1994; Houston & McNamara, 1989).

If applied to our mobbing behavior study, the asset protection principle suggests that high-condition individuals have relatively less to gain from mobbing than low-condition individuals—actively participating in mobbing events may jeopardize their high expected future reproductive success. It is less clear what low-condition individuals might gain from mobbing, however. The two major (not exclusive) benefits to mobbing are removing the predator from the vicinity (Curio, 1978) and building social relationships with other individuals to ensure cooperation during future mobbing events (Krams et al., 2008). Low-condition individuals might gain relatively more (or lose relatively less) from initiating or actively contributing to mobbing than high-condition individuals if mobbing protects their current reproductive investment at the expense of survival: causing the predator to leave the vicinity may reduce the predation risk to their current mate or nest, which may be more valuable to them than to high-condition individuals, who may be more likely to find another mate and breed in the future if the current reproductive attempt fails. Alternatively, low-condition individuals may value better "social standing" among mobbing participants more than high-condition birds, because that social standing may increase the probability that other birds will help them in the future mobbing events. Songbirds have been shown to change their mobbing effort in a way that is consistent with interspecific recognition and reciprocity among heterospecific individuals (Krams & Krama, 2002). High-condition individuals, on the other hand, might avoid taking immediate risks during mobbing, relying on a potentially better ability to escape predators.

An important alternative explanation for the observed positive correlation between condition and mean distance from the hawk is that heavier males may remain further away from the hawk because being heavier may result in impaired maneuverability and coming closer may compromise their ability to escape. However, a number of observations from this study argue against this interpretation. First, there was a positive correlation between the visual estimate of the pectoral muscle volume and male condition. Pectoral muscle enables flight, and thus, a heavier muscle is more likely to enable better maneuverability than hinder it. Second, we also investigated whether an estimate of wing-loading (wing length divided by mass), which should relate to maneuverability, is a better predictor of mean distance than mass alone. We found that while mass is significantly positively related to approach distance (mass and condition measures gave nearly identical results in this study), wing-loading was not (Supporting information). Therefore, it is unlikely that the observed positive relationship between approach distance and condition was related to maneuverability.

Another interpretation for mobbing behavior observed in this study is that instead of responding to the hawk, junco males may have been trying to defend their territories against the heterospecific individuals whose calls were broadcast through the speakers. Hence, the individual variation in behavior might not represent variation in response to risk, but variation in response to intruders. However, junco male behavior directed to the hawk and speaker was completely different from their territorial behavior (observed after the mobbing trial, M. Abolins-Abols and E.D. Ketterson, in prep.): Junco males approached conspecific intruders more closely, sang more, and flew over territorial intruders more than they did over the hawk and alarm call speaker. This suggests that junco male behavior during mobbing trials was shaped more by response to the risk than response to the territorial intruders, although we cannot completely exclude the latter possibility.

An important intrinsic factor that is predicted to relate to RRV and, therefore, risky behavior is age. Life-history theory suggests that investment in current reproduction will depend on the prospect of survival to the next breeding event (Williams, 1966). Specifically, the terminal investment hypothesis states that if older animals have lower RRV, they should invest more in current reproduction (Clutton-Brock, 1984). This is predicted to lead to more risk-taking in older individuals (Billing, Rosenqvist, & Berglund, 2007; Ory, van Son, & Thiel, 2015). In juncos, male survival to the next breeding season is low in their first year, but preliminary data show that it stays relatively constant in individuals older than two years (N. Gerlach, pers. com.). Furthermore, older males in this population have higher nest success and longer breeding seasons (Reed et al., 2006). This suggests that RRV might not decrease with age in juncos and that older individuals should not take more risks than young individuals (Cameron, Linklater, Stafford, & Minot, 2000). Our data are consistent with this interpretation, showing that age does not explain significant variation in either approach distance or alarm call frequency.

We did not find any association between the behavior of focal junco males and the presence of a mate during the trial or the number of other con- and heterospecific individuals that attended the mobbing, suggesting that junco behavior is not influenced by social factors. At the community level, the closest approach by a bird of any species to the hawk was nearly significantly correlated with the total number

of birds mobbing. This pattern has been demonstrated before (Krams et al., 2009; Wiklund & Anderrsson, 2016) and is consistent with the dilution effect, whereby the risk to any one individual decreases with increasing group size, and individuals approach predators more closely (Curio & Regelmann, 1986; Hamilton, 1971; Krams & Krama, 2002). However, the observed relationship was not significantly different from a simulated probabilistic relationship between the closest approach and group size, suggesting that the observed relationship may be negative purely by chance. In fact, the simulated relationship had a near-significantly more negative slope, suggesting that birds in real mobbing groups may behave more cautiously than expected by chance. The closest approach by a bird of any species was not associated with the species richness of the mobbing group.

Neither mobbing group size nor species richness was repeatable between trials in the same junco territory, suggesting that mobbing assemblages are inconsistent. The behavior of the focal juncos, in contrast, was significantly repeatable. The consistent among-individual variation in mobbing behavior further supports our conclusion that variation in mobbing behavior is more likely to depend on intrinsic factors, rather than environmental conditions.

It is important to note that our inference about the effect of the group size in this experiment may be confounded by the experimental design—it is likely that alarm calls in the playback were perceived as real individuals by the focal junco males and other mobbers. The perceived group size thus might have been larger than the number of actual mobbing individuals. Although this does not change the relative group size—all mobbing playback tapes included calls from individuals of six species—this means that the perceived mobbing group size may never have been fewer than six individuals. Any change of mobbing behavior in groups that are smaller than six individuals might not have been detectable using our design.

In summary, we show that condition—an intrinsic factor—is a better predictor of variation in mobbing behavior in junco males than social factors (presence of a mate and other individuals). These results suggest that the relative importance of the costs and benefits of mobbing behavior may differ among individuals that have different RRV. It is unclear, however, exactly what such benefits might be, because the "asset" that individuals are protecting during mobbing might be their survival, their nest, or their social standing. Applying the optimality framework to socially complex situations where animals may be working toward protecting multiple assets may shed light on this question.

CONFLICT OF INTEREST

The authors do not have any conflict of interest to declare.

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