

MOBBING BEHAVIOR IN WILD STELLER'S JAYS (*CYANOCITTA STELLERI*)

By

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ABSTRACT

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Mobbing is a widespread anti-predator behavior with multifaceted functions. Mobbing behavior has been found to differ with respect to many individual, group, and encounter level factors. To better understand the factors that influence mobbing behavior in wild Steller's jays (*Cyanocitta stelleri*), I induced mobbing behavior using 3 predator mounts: a great horned owl (*Bubo virginianus*), common raven (*Corvus corax*), and sharp-shinned hawk (*Accipiter cooperii*). I observed 90 responses to mock predators by 33 color-marked individuals and found that jays varied in their attendance at mobbing trials, their alarm calling behavior, and in their close approaches toward the predator mounts. In general, younger, larger jays, that had low prior site use and did not own the territory they were on, attended mobbing trials for less time and participated in mobbing less often, but closely approached the predator more often and for more time than older, smaller jays, that had high prior site use and owned the territory they were on. By understanding the factors that affect variation in Steller's jay mobbing behavior, we can begin to study how this variation might relate to the function of mobbing in this species.

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INTRODUCTION

Mobbing is a widespread anti-predator behavior found in many vertebrates, especially birds (Godin and Dugatkin 1996, Krams and Krama 2002, Graw and Manser 2007). When confronted with a potential predator, birds may mob it by making rapid, stereotyped body movements, vocalizing, and closely approaching or diving at the predator (Cully and Ligon 1976, Krams et al. 2008, Dutour et al. 2016). Predators being mobbed may be confused or deterred and forced out of the area (Ficken 1989, Flasskamp 1994, Pavey and Smyth 1997). Mobbing may be done alone (Ostreiher 2003), but has been described as contagious, when neighbors and/or heterospecifics may be recruited to join (Beletsky and Orians 1989, Cornell et al. 2012, Hernández 2013). A mobbing individual may incur the costs of increased risk of injury or death for themselves (but see Hennessy 1986) or their kin, especially if mobbing alone (Sordahl 1990, Dugatkin and Godin 1992, Krams et al. 2008).

Mobbing may serve multifaceted functions beyond reducing potential predation risk, and expression of the behavior can vary both across and within species. For example, mobbing may signal an individual's quality or social status to potential mates (Arnold 2000). Subordinate Arabian babblers (*Turdoides squamiceps*) use mobbing to advertise themselves to conspecifics with whom they could disperse (Maklakov 2002). Juvenile or unfamiliar individuals may also learn about a predators' threat level by observing the mobbing of others (Francis et al. 1989, Cornell et al. 2012). The differences in life history traits between species may also influence mobbing behavior. For example,

scrub jays (*Aphelocoma coerulascens*) and Mexican jays (*A. ultramarina*) differ in their social organization, which led to differences in their formation of mobbing groups and the vigorousness with which they mob (Cully and Ligon 1976).

Individual differences such as sex (Sordahl 1990, Dugatkin and Godin 1992, Maklakov 2002), age (Montevecchi and Maccarone 1987, Sordahl 1990, Graw and Manser 2007), size (Berne 2011), personality (Gabriel and Black 2010), and prior site use (Beletsky and Orians 1989) may also impact mobbing behavior. For Steller's jays (*Cyanocitta stelleri*), alarm calling in the presence of a predator was correlated with risk-taking and exploration behaviors (Gabriel and Black 2010). Group dynamics such as dominance and territoriality (Cully and Ligon 1976, Maklakov 2002, Graw and Manser 2007) and social bonds (Griesser and Ekman 2005, Micheletta et al. 2012) may also impact mobbing behavior. Steller's jays live on year-round territories with a long-term partner, have site-centered dominance, and regularly travel outside their territories, where they can interact with dozens of conspecifics (personal observation, Brown 1963).

For species that do not lend themselves well to intensive behavioral study, the best way to understand the influences on a behavior may be to use parallels from similar species. By studying a wide range of factors that may influence a behavior, more parallels can be drawn between species. In Steller's jays (hereafter "jays"), their individual variation, mosaic of territory ownership (and related dominance hierarchies), and the variety in social connections between the pair bond and wider group dynamics make them ideally suited to study the influences of variation in mobbing behavior. In this study, I considered the influence of individual, group, and encounter level variables, such

as habituation (Arnold 2000), on jays' attendance during mobbing, participation in mobbing, and close approaches to predators during mobbing.

MATERIALS AND METHODS

Study Site

The study area was roughly 2.2 km² in Arcata, California on the fringe of a coastal redwood (*Sequoia sempervirens*) forest and contained coniferous-deciduous trees, housing, yards, streets, and other suburban structures (Fig. 1). The study area contained 11 permanent feeder traps (28 cm x 70 cm) stocked with bird seed and unshelled peanuts located across the study area (at least 150 m apart; Fig. 1). A sliding door comprised one wall of the feeder trap and allowed for an opening into the trap at one end. Peanuts were placed inside at the back of the trap, so birds usually had to enter all the way to retrieve food items.

Study Species

The study population consisted of approximately 100 jays, the majority of which are individually marked. The population consisted of approximately 25 long-term pairs that lived on and defended year-round territories and approximately 50 additional regular visitors to the area that either owned territories outside of the study area or did not own territories (“floaters”). The relatedness between jays in this population, and the extent to which they may be cooperative, are currently unknown.

Jays often mob when confronted with a predator in their environment. Mobbing to force a predator out of the area would be adaptive for jays any time of year given that they live on year-round territories (Nijman 2004). Jays may mob alone, with their mate,

or as part of a larger group. Upon detecting a predator, jays may respond in several ways; by hiding or leaving the area, giving alarm calls, closely approaching the predator, or any combination of these (personal observation). Based on observations of natural mobbing events by jays, a jay is defined as “mobbing” if they make alarm calls in the presence of a predator and a “mobbing event” encompasses the mobbing of all jays from the first alarm call to approximately 2 minutes after the last call and/or when all jays have dispersed. When in conjunction with alarm calling, closely approaching a predator is also defined as a mobbing behavior, but jays may closely approach without producing alarm calls.

Prior to the start of regular monitoring and mobbing trials, jays were caught in feeder traps, fit with a unique combination of colored leg bands, and assessed for sex, age, and size. Sex was determined either through body measurements (Pyle et al. 1997), observations of sex-specific vocalizations, or nesting behavior. Minimum age was determined by plumage and gape characteristics at the time of first capture with birds becoming 2 years old on January 1 of their first winter (Pyle et al. 1997). Measurements of both tarsi over repeated captures were averaged to assess the size of the individual.

Regular Monitoring

Birds were regularly monitored throughout the study area, including at feeders, from April through September 2016. Jays typically habituate to human activities, which facilitates close observation of behaviors (Marzluff and Neatherlin 2006, Gabriel and Black 2010). Feeder traps were replenished several times a week. While at feeders the birds' relative behavior was quantified with indices of boldness, site use, and

territoriality. As one of several personality traits included in the species' behavioral syndrome (Gabriel and Black 2010), boldness was measured as willingness to enter and remain inside the feeder trap (*i.e.*, ranging from trap happy to trap shy). Boldness was scored from 1 - 6: 1) looks in but does not touch the feeder, 2) touches, but immediately jumps off the feeder, 3) reaches in for peanut, but only from the threshold of the feeder entrance, 4) quickly goes inside, retrieves a peanut, and leaves within 1 s, 5) goes inside to retrieve peanuts taking 1 - 3 s, and 6) goes inside to retrieve peanuts taking more than 3 s. Mean boldness score was shown to be consistent over time (Rockwell et al. 2012), so I calculated an average boldness score over the whole study period for each individual.

To reduce bias towards jays that were primarily resighted at feeders, such as those that live at the edge of the study area, site use was calculated at the feeder level rather than the individual level. For each feeder trap, a jay's site use was defined as the proportion of its resightings at that feeder, given the resightings of all jays at that feeder.

Jays have site centered dominance, where dominance decreases further from the territory center (Brown 1963). Territory centers were based on nest location midpoints (after Gabriel and Black 2010). Jay pairs had either 1 or 2 known nest locations for the 2016 season determined by observation of nest building activities. The midpoint tool in ArcMap 10.2.2 was used to find the midpoint between nests for pairs that had 2 nest locations. Territory ownership at each feeder was defined into 4 categories: "owners" own the territory the feeder is in, "near neighbors" own a territory adjacent to the feeder territory, "distant neighbors" own a territory away from the feeder, and "floaters" do not own a territory in the study area.

I used two indices to describe variation in sociality in this population of color-marked individuals (Farine 2015). Social degree score was defined as the total number of individuals with whom each jay interacted (*i.e.*, was recorded concurrently in the same 15 m radius during the 6-month study period). For each pair of birds observed together, social relationship scores were calculated. For each dyad, the social relationship score was defined as the proportion of a jay's resightings when both individuals in the dyad were present. For example, if a jay was observed 20 times during the 6-month study period and interacted with an individual during 5 of those observations, the dyad had a relationship score of 0.25. Relationship scores were highest between mates in long-term pair bonds and lowest between birds that were observed only once or twice (*i.e.*, a non-territory owning floater). A jay's highest dyad proportion, from among jays present at the same mobbing trial, was the relationship score used in analyses (see below).

Mobbing Trials

I used one-zero sampling (Martin and Bateson 2007) to measure 4 aspects of mobbing behavior, 1) attendance at mobbing trials, 2) participation in mobbing, 3) close approaches to predators during mobbing trials, and 4) proportions of close approaches. Jays were present for a mobbing trial if they were observed at least once during the trial within 25 m from the predator. Attendance was defined for each trial as the proportion of the trial length (dependent on the presence of jays, see below) given the trial maximum of 30 min. A jay participated in mobbing if they gave an alarm call within the observable area, up to 25 m from the predator. A jay closely approached if they came within 5 m of

the predator. Using the subset of birds that closely approached, I analyzed the approach proportion. Approach proportion was the number of intervals the bird approached within 5 m given the intervals they were present.

I used predator mounts to elicit mobbing behavior in color-marked jays at 11 feeder traps (after Maklakov 2002, Gabriel and Black 2010, Courter and Ritchison 2012). To prevent habituation, three predator mounts were introduced over the course of the study, including great horned owl (*Bubo virginianus*, “owl”), common raven (*Corvus corax*, “raven”), and Cooper’s hawk (*Accipiter cooperii*, “hawk”) (*sensu* Conover 1985, Montevecchi and Maccarone 1987). A jay mount laying on its side was added to the base of the hawk mount to resemble a recent capture. Movement of all the mounts at least once per minute provided additional realistic stimulus to jays, a feature also recommended to prevent habituation (McClean et al. 1986, Billings et al. 2017). The owl mount was mechanized to rotate its head via remote control. The raven was mounted in a flying position and swung freely from a frame (after Gabriel and Black 2010). The hawk mount was bobbed remotely via fishing line, to imitate plucking of the jay kill.

The predator mount, initially covered with a cloth, was placed approximately 5 m from the feeder and within 5 m of adjacent perches (*e.g.*, trees, fences, etc.), which jays regularly used when approaching or leaving feeders. Trials began when at least one individual of the local territory-owning pair arrived at the feeder and took a peanut to cache nearby (Kalinowski et al. 2015). I removed the covering from the mount before jays returned to the feeder. Trials were a maximum of 30 minutes long, consisting of 15

intervals of 2 minutes each. Trials either lasted 30 minutes or until no jays were < 25 m from the predator or observable (*e.g.*, out of sight in a bush).

Trials were conducted between 08:50 and 10:45 hrs during the non-breeding season from October 8 to December 24, 2016, when jays are less territorial, regularly visit nearby feeders, and after molt has completed (Brown 1963, Flasskamp 1994). Each of the three predator types was presented at the 11 feeders before trials with the next predator type began (owl 1st, raven 2nd, hawk 3rd). An average of 27 days elapsed before trials were conducted again at the same location (min = 8 days, max = 46 days). Sequential trials were separated geographically ensuring that no birds were exposed to the same predator type more than twice. For example, trials at 1 of the 4 northern feeders were typically followed by a trial at either 1 of the 4 eastern or 1 of the 3 western feeders (Fig. 1). All experimental procedures were approved by the Humboldt State University Institutional Animal Care and Use Committee (Protocol #15/16.W.42-A).

Analysis

I used generalized linear mixed models (GLMM) with binomial error distributions to test the influence of 12 predictor variables (see below) on attendance at mobbing trials, participation in mobbing, close approaches to the predator mount, and the proportion of close approaches using “glmer” in the R package “lme4” (RStudio Team 2015). Eleven responses by jays to mock predators were excluded due to interference from a non-target species (*e.g.*, ravens). After testing that no predictor variables correlated more than 0.6, I included all predictor variables and relevant two-way interactions in the initial models.

Interactions included predictor variables with some relevant biological connections, such as sex and tarsus or site use and territory category. Non-significant ($P < 0.05$) coefficients were sequentially removed from initial models and top models were selected based on the lowest Akaike's information criterion score corrected for small sample size (AICc, Table 1). I used a Wald z test to test the statistical significance of each coefficient in top models. Because individual birds mobbed on several occasions and both feeder locations and predator types were repeated throughout trials, these factors were included as random variables. Feeder location was repeated for each predator type, therefore the feeder location term was nested within predator type. The results of interaction terms were not presented here because a sole component variable was responsible for significance in all cases and in the case of the attendance analysis, the interaction term was responsible for multicollinearity in the model. Tukey's post hoc tests were performed to test for statistical differences between groups in significant categorical variables using the "glht" function in the R package "multcomp" (RStudio Team 2015).

Predictor variables included 5 individual and 3 group level variables collected from capture (sex, age, tarsus length) and regular monitoring (boldness score, site use, territory category, social degree, social relationship). To assess variation present during the mobbing trials, I included 4 additional encounter level predictor variables. Encounter level variables included the trial number (indicating the progression of trials and possibility of habituation over time), the number of birds present at the trial (including those for which data was not included in analysis), whether a bird was present at the

feeder before the start of the trial, and the individual history of the bird (*i.e.*, the count of how many times they had seen that predator type).

Table 1. Top models as determined by lowest AICc value analyzing 4 mobbing behaviors in Steller's jays. Mobbing behaviors observed October – December 2016 in Arcata, CA. All models included the random variables bird ID, predator type, and feeder location nested within predator type.

Response Variable	Model	Δ AICc	df	Weight
Attendance	Boldness Score + Site Use + Territory Category + Trial Number + Boldness Score : Site Use	0	9	0.59
	Boldness Score + Site Use + Territory Category + Trial Number + Individual History + Boldness Score : Site Use	1.7	10	0.25
	Sex + Boldness Score + Site Use + Territory Category + Trial Number + Individual History + Boldness Score : Site Use	3.5	11	0.10
Participation	Territory Category + Trial Number + Presence Before Trial + Individual History	0	8	0.44
	Territory Category + Trial Number + Individual History	1.2	7	0.25
	Territory Category + Social Relationship + Trial Number + Presence Before Trial + Individual History	2.1	9	0.15
Close Approach	Sex + Age + Site Use + Territory Category + Trial Number + Number of Birds Present + Individual History + Sex : Site Use	0	12	0.69
	Sex + Age + Site Use + Territory Category + Trial Number + Number of Birds Present + Presence Before Trial + Individual History + Sex : Site Use	2.1	13	0.23
	Sex + Age + Site Use + Territory Category + Trial Number + Number of Birds Present + Presence Before Trial + Individual History + Sex : Site Use + Site Use : Territory Category	4.8	14	0.06
Close Approach Proportion	Tarsus + Trial Number + Presence Before Trial	0	7	0.40
	Tarsus + Presence Before Trial	0.9	6	0.26
	Tarsus + Boldness Score + Trial Number + Presence Before Trial	1.5	8	0.18

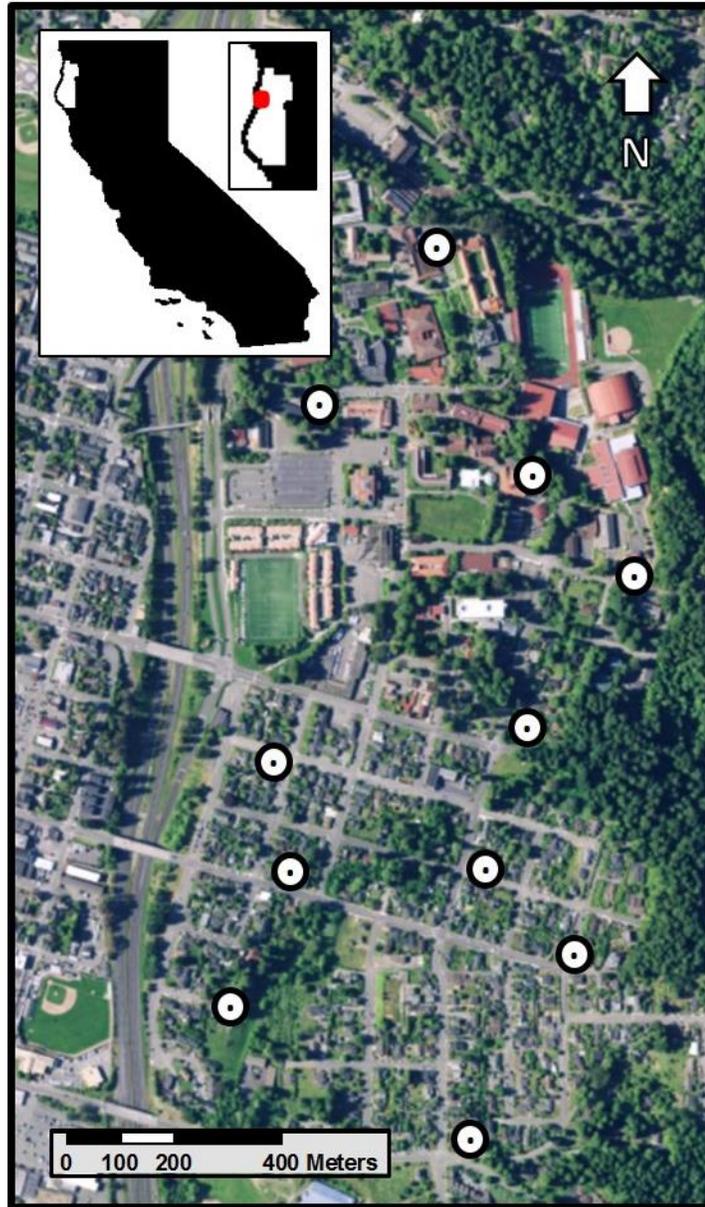


Figure 1. Location of Steller's jay study area in Arcata, CA, USA from April – December 2016. White dots indicate the 11 feeder and mobbing locations used during mobbing trials. Basemap courtesy of Esri, DigitalGlobe, GeoEye, i-cubed, USDA, FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

RESULTS

Steller's jays varied in their responses to mock predators at the individual, group, and encounter levels. Over 32 trials, 33 color-marked jays were observed to respond to mock predators 90 times. Individual jays had from 1 to 5 repeated observations during different mobbing trials. Mobbing was initiated (*i.e.*, the first alarm call given) by 18 of 33 jays and mobbing occurred in 75% of 32 trials. Twelve observations of participation were from 6 individuals who participated in every trial they attended and 19 observations of no participation were from 9 birds who never participated. Thirty observations of close approaches to the predator were from 12 individuals who always closely approached and 6 observations of no close approaches were from 4 individuals who never closely approached.

Responses to mock predators were recorded from 13 females, 17 males, and 3 birds of unknown sex. Jays ranged in age from 2 to 16 years (mean = 7.2 years \pm 0.6 SE, n = 33). Jays ranged in tarsi lengths from 40.4 to 45.4 mm (mean = 43.1 mm \pm 0.3 SE, n = 33). Based on 1,948 observations with feeder traps (mean = 59.0 observations per bird \pm 14.0 SE), average boldness scores ranged from 2.0 to 5.6 (mean score = 3.9 \pm 0.2 SE, n = 33). From 755 observations at the 11 feeders (mean = 68.6 visits \pm 12.3 SE), site use ranged from 0.01 to 0.67 (mean proportion = 0.16 \pm 0.2 SE, n = 33). I recorded responses to mock predators 54 times from territory owners, 21 times from near neighbors, 6 times from distant neighbors, and 9 times from floater jays. Territory midpoints for each pair averaged 112.4 m from their home feeder (\pm 19.5 m SE, n = 11), 295.5 m from their

neighbors' feeders (± 22.4 m SE, $n = 27$), and 802.5 m from all other feeders (± 30.2 m SE, $n = 105$). Social degree ranged from 4 to 24 individuals (mean = 14.2 ± 1.1 SE, $n = 33$ birds in the population). Social relationship scores ranged from 0 to 0.7 (mean relationship score = 0.3 ± 0.03 SE, $n = 90$).

Responses to mock predators were described and assessed in the following four ways; attendance, participation, close approaches to the predator, and the proportion of close approaches to the predator. Below I present the results from the top model for each of these analyses.

Attendance

Variation in trial attendance was a function of site use, trial number, boldness score, and territory category (Table 2). Both prior site use and trial number explained a significant amount of variation in trial attendance. For every 10% increase in a bird's share of sightings at a feeder, its odds of maximum attendance decrease by 10%. With every sequential trial, the odds of a bird attending for the maximum trial duration were 17% lower. Neither boldness score nor territory category explained a significant amount of variation in attendance (Table 2).

Participation

Variation in participation was a function of territory category, trial number, presence before trial, and individual history (Table 2). Territory category explained a significant amount of variation in participation. Jays that did not own the territory at the

mobbing location were 80% less likely to participate (Fig. 2). Trial number also explained a significant amount of variation in participation; with every sequential trial, the odds of participation were 13% lower. Neither presence before trial nor individual history explained a significant amount of variation in participation (Table 2).

Close Approaches to the Predator

Variation in whether jays closely approached the predator mount was a function of the bird's age, site use, the trial number, the number of birds present at the trial, individual history, sex, and territory category (Table 2). Age and site use explained a significant amount of variation in close approaches to the predator. For every year increase in age, the odds of a bird approaching the predator decrease by 19% (Fig. 3a). For every 10% increase in the bird's share of sightings at a site, its odds of approaching the predator were 10% lower (Fig. 3b). Trial number, the number of birds present at the trial, and individual history all explained a significant amount of variation in close approaches to the predator. With every sequential trial, the odds of approaching the predator were 6% lower. For every 1 bird increase in the number of birds present at the mobbing trial, the odds of approaching the predator were 10% lower. For birds that were seeing the predator for the second time, the odds of it approaching the mock predator were 48% lower. While sex was significant in the model (Table 2), the statistical differences were between birds of unknown sex and birds of known sex. Sex did not explain a significant amount of variation in close approaches to the predator when the top model was rerun without birds of unknown sex included in the data. While territory

category was significant in the model (Table 2), a Tukey's post hoc analysis showed that there were no statistical differences between territory categories in the amount of variation they explained in close approaches to the predator.

Proportion of Close Approaches to the Predator

For those birds that approached the predator during a trial, variation in the approach proportion was a function of tarsus length, presence before trial, and trial number (Table 2). Tarsus length explained a significant amount of variation in the close approach proportion; for every 1 mm increase in tarsus length, the odds of a jay approaching the mock predator during every interval in which they were present were 176% higher. Jays are sexually size dimorphic, but a post hoc analysis showed no clear distinction between the sexes in their tarsi lengths as they related to approach proportions. Neither presence before trial nor the trial number explained a significant amount of variation in approach proportions (Table 2).

Table 2. Statistical results for top models, as determined by lowest AICc value, analyzing 4 mobbing behaviors (response variables) in Steller's jays. Mobbing behaviors observed October – December 2016 in Arcata, CA. Significant predictors are bolded. Predictors related to encounter level variation are italicized. All models included the random variables bird ID, predator type, and feeder location nested within predator type. *Groups within categorical predictors showed no significant differences after Tukey's post hoc analyses.

Response Variable	Residual df	Predictor	Coefficient \pm SE	<i>z</i>	<i>P</i>
Attendance	81	Boldness Score	-1.324 \pm 1.272	-1.041	0.298
		Site Use	-68.534 \pm 30.816	-2.224	0.026
		Territory Category	1.365 \pm 1.022	1.336	0.182
		<i>Trial Number</i>	-0.189 \pm 0.069	-2.758	0.006
Participation	82	Territory Category	-1.594 \pm 0.524	-3.043	0.002
		<i>Trial Number</i>	-0.135 \pm 0.066	-2.038	0.042
		<i>Presence Before Trial</i>	2.646 \pm 1.635	1.619	0.105
		<i>Individual History</i>	-2.583 \pm 1.399	-1.847	0.065
Close Approach	78	Sex*	-1.151 \pm 0.008	-150.600	<0.005
		Age	-0.208 \pm 0.008	-27.700	<0.005
		Site Use	-5.963 \pm 0.008	-780.500	<0.005
		Territory Category*	-0.268 \pm 0.008	-35.100	<0.005
		<i>Trial Number</i>	-0.060 \pm 0.007	-8.800	<0.005
		<i>Number of Birds Present</i>	-0.106 \pm 0.008	-14.100	<0.005
		<i>Individual History</i>	-0.655 \pm 0.008	-85.700	<0.005
Close Approach Proportion	52	Tarsus	0.567 \pm 0.219	2.594	0.010
		<i>Trial Number</i>	-0.059 \pm 0.033	-1.783	0.075
		<i>Presence Before Trial</i>	-2.219 \pm 1.155	-1.921	0.055

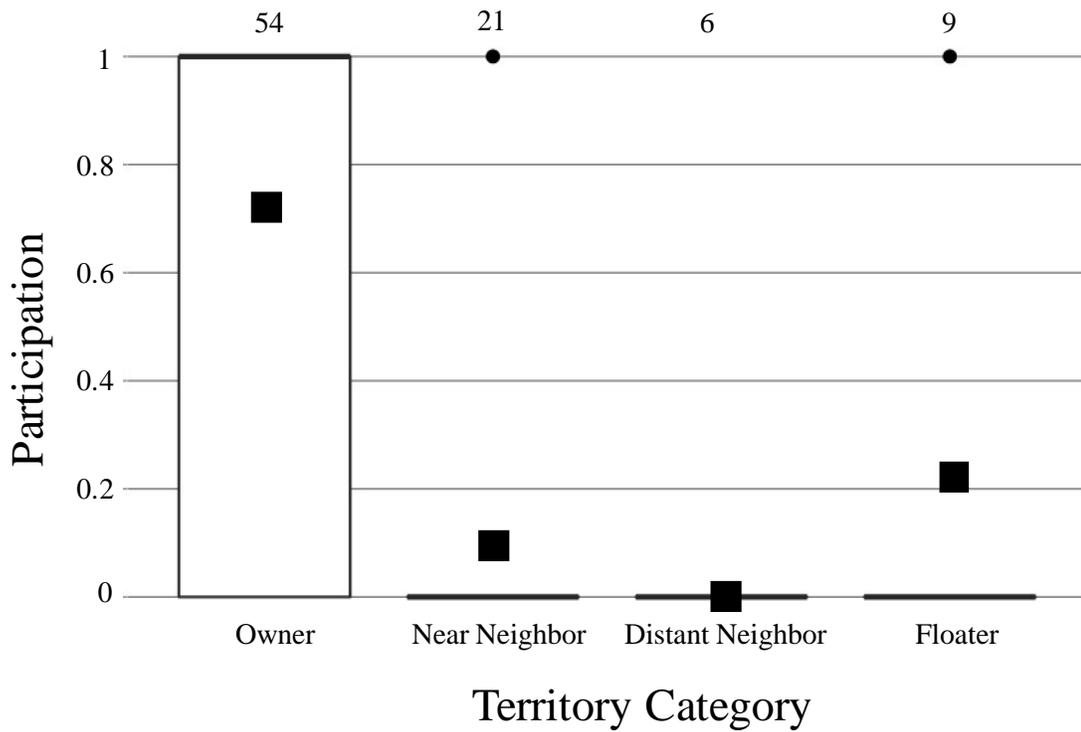


Figure 2. Boxplots of the proportion of participation for Steller's jays during mobbing trials in Arcata, CA from October – December 2016 across different territory categories. Upper and lower limits of the box indicates 25% and 75% quartiles, respectively. Black bars indicate median values. Black squares indicate mean values. Black circles indicate outliers. Numbers above columns indicate sample sizes.

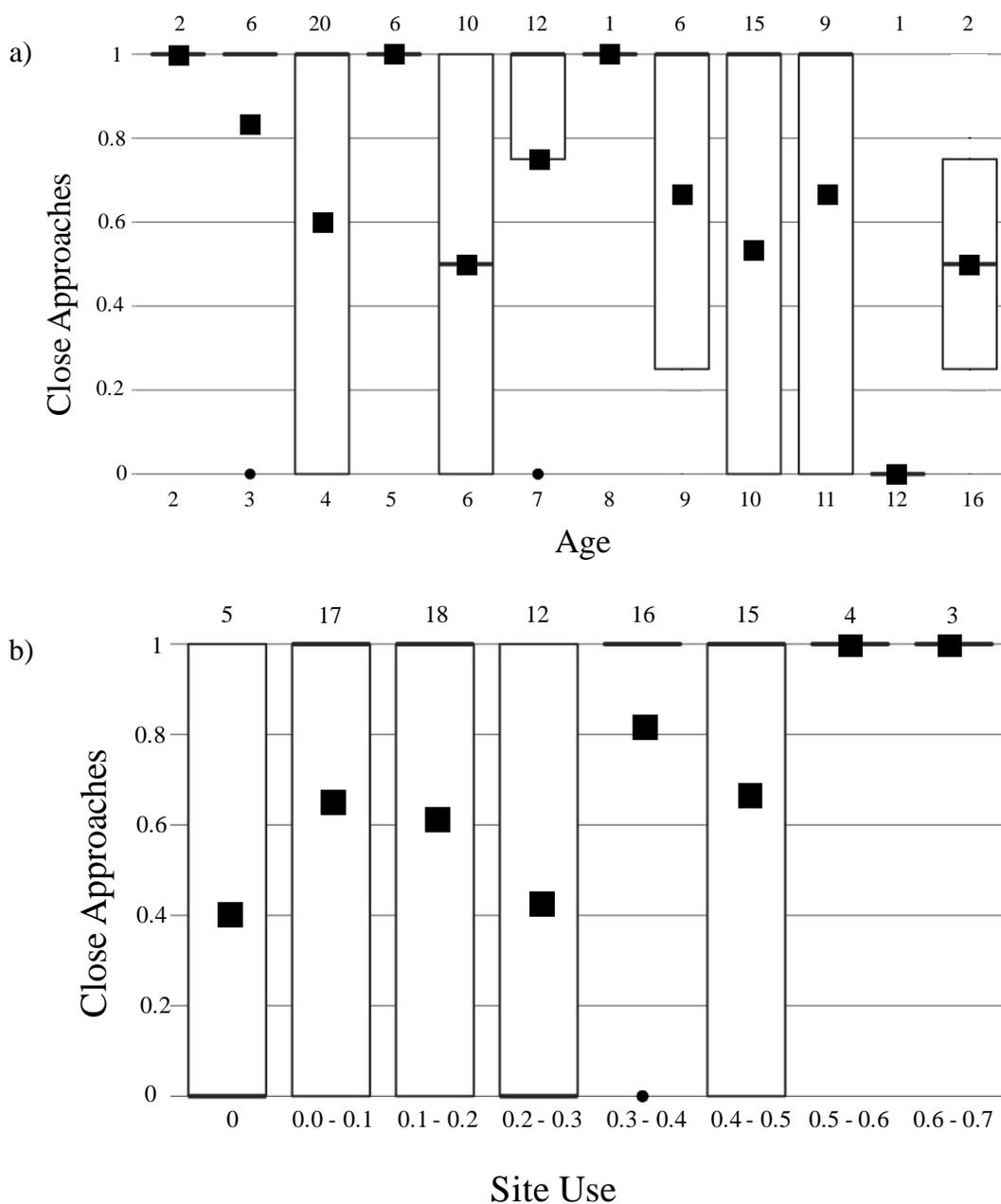


Figure 3. Boxplots of the variation in close approaches to a mock predator during Steller's jay mobbing trials in Arcata, CA from October – December 2016 across a) age ranges and b) prior site use. Upper and lower limits of boxes indicate 25% and 75% quartiles, respectively. Black bars indicate median values. Black squares indicate mean values. Black circles indicate outliers. Numbers above columns indicate sample sizes. For b) site use numbers have been lumped for ease of visual understanding.

DISCUSSION

Steller's jays' mobbing behavior in this study varied as a function of several individual, group, and encounter level variables. Whereas, Gabriel and Black (2010) described variation in one aspect of mobbing behavior, I have described variation in all 4 aspects of mobbing behavior studied here. Several of the factors studied here explained variation in some aspect of mobbing behavior and these factors were not the same for all mobbing behaviors.

While age-related differences in mobbing behavior have been found between juveniles and adults in species ranging from gray jays (*Perisoreus canadensis*; Montevecchi and Maccarone 1987) to meerkats (*Suricata suricatta*; Graw and Manser 2007), I found variation even within adult Steller's jays. Among adult jays, older birds were less likely to closely approach the predator. Birds may closely approach a predator to learn about its threat level and motivation (*i.e.*, whether it is hunting or not; Dugatkin and Godin 1992). Since approaching a predator is a dangerous behavior, a bird may not approach unless it requires more information about the threat level or intention of the predator (Curio and Regelman 1985, Fishman 1999). In my study area, older birds may have had more experience observing local predators and other threats than younger birds. Perhaps older jays, with more experience observing threats, require less information about a predator to assess the threat it poses and are therefore less likely to closely approach. Alternatively, birds may closely approach a predator to advertise their fitness to conspecifics (*sensu* Maklakov 2002). Jays in this study population are known to

engage in extra-pair copulations (Overeem et al. 2014). However, it is unknown whether jays advertise their quality to potential mates through mobbing behavior or whether younger birds are more likely to do so.

Larger birds in my study were more likely to closely approach the predator for each interval they were present (*i.e.*, they had higher close approach proportions). If larger birds are less vulnerable, as suggested by Dugatkin and Godin (1992), they may be more likely to behave boldly in risky situations.

Jays that had higher site use were less likely to attend the trial for the maximum duration (*i.e.*, had low attendance proportions) and were less likely to closely approach the predator mount. Jays more familiar with a site may be better able to evade predators, as was found in eastern chipmunks (*Tamias striatus*; Clarke et al. 1993). A jay familiar with the area may be better equipped to find a safe refuge away from the predator (*sensu* Clarke et al. 1993) and therefore seek a refuge sooner than their less familiar counterparts. Similarly, a jay with low prior site use may be less well equipped to find a safe refuge and therefore choose to keep the predator in view (Flasskamp 1994) and learn more about its threat level by closely approaching (Curio and Regelmann 1985, Fishman 1999).

In jays, territory owners are generally dominant (Brown 1963), and in my study, territory-owning jays were more likely to participate in mobbing. Territory owning ring-billed gulls (*Larus delawarensis*) engaged in mobbing while neighboring gulls spectated (Conover 1987). Neighbors may derive less benefit by moving a predator out of the area if by doing so they drive the predator into their own territories (Cully and Ligon 1976).

Sex, boldness score (*i.e.*, a trait describing personality), the number of social connections (*i.e.*, social degree), and the strength of those social connections did not explain a significant amount of variation in any aspect of mobbing studied here. The results of this study do not preclude the option that these variables influence mobbing behavior in jays. The differences between my study design and natural mobbing events, which often occur high in tree tops (personal observation), may have prevented these variables from being significant in any of my analyses. The similar roles of male and female jays in territory defense and mate choice (Gabriel and Black 2012) may explain why there were no significant differences in mobbing behavior between the sexes (Dugatkin and Godin 1992).

It is interesting that the aspects of mobbing behavior studied here were not a function of the birds' boldness to enter the feeder traps given that Gabriel and Black (2010) found that other types of risk-taking and exploration behaviors were correlated with alarm calling behavior. Gabriel and Black (2010) used only one predator type to study alarm calling, whereas I used three. It is possible that each predator type presented a different threat level to jays during mobbing trials given that the diet and hunting strategies differ between the predator types used here (Conover and Perito 1981, Griesser 2009, Dutour et al. 2016). However, a Tukey's post hoc analysis showed no differences between predator type for any of the 4 mobbing behaviors studied here. Anti-predator strategies that are influenced by personality have been shown to differ based on the perceived threat level. For example, Öst et al. (2015) found that among female eiders (*Somateria mollissima*) of similar boldness, females at a higher risk from predators

preferred to rear their broods in larger groups. Personality may have explained variation in mobbing behavior in Steller's jays, but the interaction between personality and perceived threat levels could have prevented a clear relationship.

The social environment, as measured by the number of social connections (*i.e.*, social degree) and the strength of those connections, did not explain a significant amount of variation in any aspect of mobbing behavior. Variation in social degree may have been influenced by reduced female movement during the breeding season, when social connections were monitored. Also, there may not have been enough variety in the composition of mobbing groups to determine if social relationship strength influences mobbing behavior. Jays were present at mobbing trials either with their mate (55.5%), without their mate (22%), they had no mate (15.5%), or they mobbed alone (7%, $n = 90$). Also, in only 2 of the 25 instances where a jay pair was present together at a trial, did the individuals in the pair differ in whether or not they mobbed. Given that jays in this study mobbed even when alone, it may be that jays react to the presence of a predator regardless of their sociality or the social environment around the predator. Or, given that the majority of responses to mock predators were of jays at the trial with their mate and the fact that pairs rarely differed in their responses, it may be that the bond between a mated pair is the only social factor that matters in determining mobbing behavior. The results of this study do not preclude the option that mobbing may serve an alternative function that would be influenced by a different social environment than was experienced by mobbing groups here. For example, this population of jays has less need to form

dispersal coalitions (Maklakov 2002), alert offspring to predator presence (Griesser and Ekman 2005), or attempt to attract a mate (Arnold 2000).

Even though encounter level predictors (trial number, number of birds present, presence before trial, individual history) were not the focus of this study, they were included in analyses of mobbing behavior to gain a broader understanding of the behavior. As trials progressed, jays in this study were less likely to attend trials for their maximum duration, less likely to participate, and less likely to closely approach the predator. By using different predators, habituation to any one of them may have been reduced, but the presence of more predators in general may lead to habituation and reduced mobbing intensity (Mirza et al. 2006). Contrary to studies that found an increase in mobbing intensity with larger mobbing groups (Ostreiher 2003, Krams et al. 2009), with more conspecifics present, jays in this study were less likely to closely approach the predator. In this study, individuals that had seen the predator mount before, were less likely to closely approach the predator. In this study, presence before the trial was the only encounter level variable that did not explain a significant amount of variation in mobbing behavior. Similar to other studies (Kennedy et al. 2009, Gabriel and Black 2010), on few occasions did a jay who had not been observed in the area prior to mobbing, arrive after mobbing had begun.

Mobbing behavior serves multifaceted functions in many of the species for which it has been studied (Cully and Ligon 1976, Arnold 2000, Maklakov 2002). To better understand these functions, we must first understand how a species varies in its mobbing behavior. In my study, the mobbing behavior of Steller's jays varied in relation to the

birds' age, size, site use, and territory ownership, suggesting the risks and benefits of mobbing likely differ across individuals varying in these factors. Research can begin to explore how this variation might relate to differences in individual risk assessments or multifaceted functionality in Steller's jays. For example, a study testing whether jays cooperate in mobbing could target non-territory owning jays, who were less likely to participate in mobbing in my study, and observe the circumstances under which they do assist with mobbing, and whether this assistance is reciprocated. Additionally, this study provides further evidence that Steller's jays can be used as a model study species for behavioral research and questions about mobbing behavior in wild animals.

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