

PROPENSITY OF PREDATOR MIMICRY IN WILD STELLER'S JAYS

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ABSTRACT

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Avian vocal mimicry has been described in a variety of contexts, suggesting its function is multifaceted within and across species; however, basic empirical data describing mimetic signal prevalence and context is lacking for numerous species. I examined occurrence and context of mimicked red-shouldered hawk (*Buteo lineatus*) calls over a 12-month period in a wild population of 49 individually color-marked Steller's jays (*Cyanocitta stelleri*) and reviewed the occurrence of the behavior in historic re-sight data. I documented mimicry of red-shouldered hawk calls in 14 of 49 (28.6%) jays during the study. Hawk mimicry occurred more often during the early breeding season when jays were within home territories, while mates were present and aggression was absent. Younger, larger, and bolder jays were most likely to perform imitations. These results suggest jays individually vary in mimetic propensity, and individuals' proclivity for mimicry may be influenced by social and ecological contexts, physical characteristics, and personality traits.

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INTRODUCTION

Vocal mimicry, where one species vocally copies the sounds of another, occurs among 15 – 20% of avian species (Marshall 1950). While potential functions for this phenomenon have received extensive speculation, there is a lack of empirical data supporting proposed explanations (reviewed by Kelley et al. 2008; Dalziell et al. 2015). Vocal mimicry has been described in both interspecific (Catchpole and Baptista 1988; Chu 2001; Flower 2011) and intraspecific contexts (Loffredo and Borgia 1986), suggesting multifaceted functions across species (Goodale and Kotagama 2006; Dalziell et al. 2015). Functional explanations for mimicry include threat avoidance, sexual selection, social affiliation, brood parasitism (Kelley et al. 2008), and kleptoparasitism (Flower 2011). A mimetic signaling system is comprised of the model (species being mimicked), mimic (species imitating the model), and audience (receiver of the signal) (Vane-Wright 1980; Dalziell and Magrath 2012). Audiences can include members of the model or mimic species, predators, or other competitors. To determine the functional significance of vocal mimicry in a given mimetic signaling system, we must determine what is copied, when, from whom, and the context in which mimicry occurs (Healy et al. 2009).

Some avian mimics appear to imitate sounds randomly (Hindmarsh 1986), while other species strategically imitate alarm calls or sounds produced by a predator (termed ‘predator mimicry’) (Goodale and Kotagama 2006; Kelley and Healy 2011; Goodale et al. 2014). Sri Lanka drongos (*Dicrurus paradiseus lophorhinus*) and Sri Lanka blue

magpies (*Urocissa ornata*) incorporate ‘danger mimicry’ – including predators’ vocalizations – into their own species-specific alarm calls (Goodale and Kotagama 2006; Ratnayke et al. 2009). Other corvids, including gray jays (*Perisoreus canadensis*), blue jays (*Cyanocitta cristata*), and Steller’s jays (*Cyanocitta stelleri*), also imitate raptor calls (Brown 1963; Hope 1980; Kennedy and Stahlecker 1993; Hailman 2009; Strickland and Ouellet 2011; Walker et al. 2016). Steller’s jays, in particular, are reported to mimic neighboring birds of prey, particularly red-shouldered hawks (*Buteo lineatus*) but also including red-tailed hawks (*Buteo jamaicensis*), Cooper’s hawks (*Accipiter cooperii*), and osprey (*Pandion haliaetus*) in Northern California (Brown 1963; Hope 1980; Walker et al. 2016; JM Black pers. comm.). In this study, I investigated whether the propensity to produce mimetic calls existed across individuals in a color-marked population of Steller’s jays and the contexts in which mimicking behavior occurred.

Gabriel and Black (2010) found that only some Steller’s jays (hereafter, ‘jays’) participated in alarm-calling behavior in the presence of a mock predator (common raven mount *Corvus corax*) while others did not. Producing vocalizations, including mimetic calls, may be risky as it may result in increased detection by predators (Edmunds 2000). Steller’s jays in this study population display a range of individual differences in willingness to take risks, as measured along a bold-shy continuum across multiple contexts, resulting in a gradient of personality types (i.e. behavioral syndromes; Gabriel and Black 2010, 2012b). Variation in willingness to take risks by individual jays has been linked to differences in sex, age, body size, boldness, and territory ownership (Gabriel and Black 2010, 2012b; Rockwell et al. 2012; Harvey 2015). Based on these findings, I

sought to test whether mimicking behavior varied in relation to these physical, personality, and social characteristics.

MATERIALS AND METHODS

Study Species

Steller's jays occupy fragmented forest patches, and are especially abundant along mixed-coniferous deciduous edges (Marzluff et al. 2004; Walker et al. 2016). They are known to frequently capitalize on recreational and suburban areas for foraging and breeding opportunities (Brown 1963; Marzluff et al. 2004; Marzluff and Neatherlin 2006). Steller's jay pairs are socially monogamous, remaining together year-round on territories defended through behavioral and vocal displays. They exhibit site-centered dominance, where dominance decreases with increasing distance from the nest; this results in overlapping home ranges and complex dominance hierarchies depending on where jays interact (Brown 1963; Walker et al. 2016). Thus, it is common to see neighboring jays alongside territory owners at valuable food resources in Steller's jay societies (Kalinowski et al. 2015). Additionally, jays cache food items for short and long-term storage throughout the year, relocating caches using spatial memory (Walker et al. 2016). Steller's jays are relatively tolerant of human proximity; they lend themselves well to examination of subtle behaviors, thus making jays a particularly well-suited species for behavioral studies. Prior research on this population has described a variety of individual variation in behavioral patterns, including behavioral syndromes (Gabriel and Black 2010), assortative mating (Gabriel and Black 2012b), optimal foraging (Rockwell et al. 2012), mate fidelity (Overeem et al. 2014), caching effort (Kalinowski et al. 2015), and

novel problem solving (Harvey 2015). This research was conducted under the Humboldt State University Institutional Animal Care and Use Protocol No. 15/16.W.40-A.

Study Site

I studied a suburban population of individually color-marked Steller's jays in Arcata, California (40°59'N, 124°06'W, Figure 1). The study area encompasses approximately 2.2 km², and is bordered to the east by second-growth coastal redwood (*Sequoia sempervirens*) forest. This population utilizes wooden feeding stations (71 x 35.5 x 28.5 cm) modified with sliding doors that allow for selective trapping of individuals (Gabriel and Black 2010). Stations are mounted in various places and heights on poles or fences distributed across the study area. They are regularly stocked with a wild birdseed mix including sunflower seed, millet, and raw unshelled peanuts, to facilitate re-sightings and selective capture of individuals. This population has been part of a local banding program since 1998, and has been intensively monitored for behavioral research since 2005.

Banding and Physical Measurements

All jays were initially captured in sliding-door feeding stations baited with raw peanuts in the shell. Unbanded birds were fitted with a U.S. Geological Survey metal band and a unique combination of three colored leg bands. Birds were processed and released at the trap site approximately 30-45 minutes after capture. Physical measurements during banding included tarsus length (mm). Minimum age was

determined for each individual, based on gape coloration and plumage patterns (Pyle et al. 1997). Sex of marked birds was determined by identifying sex-specific vocalizations (Gabriel and Black 2010).

Behavioral Observations

From 1 September 2015 until 31 August 2016 observational data were collected during opportunistic re-sightings of color-marked individuals. The occurrence and context of mimicry events was documented for all re-sightings. Mimicry events were denoted as jays performing imitations at least once within a survey occasion. Fourteen feeder locations across the study area (Figure 1) were surveyed several times weekly and stocked with peanuts in efforts to resight jays; if jays were seen or heard away from feeders, they were opportunistically observed. Surveys were conducted in the morning, when jays are most active. Re-sighted individuals were subject to continuous behavioral recording for the duration they were in view for each survey occasion. A single survey occasion constituted a minimum of 3 minutes of observation, and typically did not exceed 60 minutes.

During all mimicry events, I documented which individual jays performed imitations. Over September 2015 – August 2016, 100% of resighted jays that were observed performing imitations mimicked the red-shouldered hawk *kee-aah* call. The vocal array of red-shouldered hawks consists of seven recognized calls. *Kee-aah* is the most common call; the first syllable is accented, while a drawn out second syllable has a downward inflection (Figure 2). It sometimes denotes alarm, but is typically a call

used when announcing territories in early spring (Dykstra et al. 2008). In California, adults and juveniles call at any time of year, but calling becomes more regular and frequent between November and May, peaking in January through April (Dykstra et al. 2008).

Trap re-entry and boldness has been correlated to risk-taking and exploration responses among jays (Gabriel and Black 2010). Jays' willingness to re-enter feeder traps was monitored on a bold-shy continuum to generate an average boldness score for each individual. Boldness scores during each re-sighting occasion were assigned on a scale from 0 – 6: 0) observed, but not at a feeder location, 1) present at feeder but does not touch feeder, 2) present at feeder, tentative/touches but does not enter (maybe gets nut through the wire), 3) tentative, but reaches into feeder from threshold, 4) enters feeder all the way but quickly leaves (<1 s), 5) enters feeder all the way and spends time inside (< 3s), 6) enters feeder and stays (>3 s). Average boldness scores were calculated for each jay across all re-sightings in September 2015 – August 2016.

I also examined historic re-sighting data collected across 2006 – 2010 to document context of mimicry events in wild Steller's jays. Throughout this previous study period, jays were intensively monitored for behavioral research, but mimicry was documented in a haphazard fashion. I combined these data with behavioral data collected in September 2015 to August 2016, during which mimicry occurrences were the focus of data collection, to create a more robust dataset for context analysis. I compared monthly proportions of observations that included hawk calls using Spearman Rank Correlation to check similarity of the datasets from both study periods.

I recorded whether observed mimicry occurred during one of four seasons, corresponding to the reproductive cycle of jays. The pre-breeding season (January – February) is characterized by courtship and reaffirmation of the pair bond; the early breeding season (March – May) denotes continued courtship and is when first nests are established; the late breeding season (June – August) is when fledglings are present and later nest attempts may occur; the remainder of the year I denoted as the non-breeding season (September – December).

Previous re-sighting data and observations across September 2015 – August 2016 were used to determine pair status and territory centers (Gabriel and Black 2010). Males and females that regularly associated with one another and later attempted to nest were considered a pair (Gabriel and Black 2010). During all mimicry events, I recorded the “company” of jays: whether jays were alone, in the presence of their mates only, in the presence of other conspecifics only, or whether both mates and other conspecifics were present.

Territory holders were identified by performance of territorial vocalizations, displays, caching food items at the site, and displacing intruding conspecifics (Brown 1963; Walker et al. 2016). I recorded whether jays were territory holders or “floaters” – non-territory holding birds – and the “location” of jays during mimicry events with respect to territory; i.e. whether they were on home territories or territories belonging to conspecifics. All observations were monitored for aggressive interactions (i.e. direct supplantation/chasing of or by conspecifics). I noted whether any aggression was present at the time of a mimicry event.

I also observed whether any predators were present during mimicry events.

The following were considered to be predators: domestic cats (*Felis catus*), American crows (*Corvus brachyrhynchos*), common ravens (*Corvus corax*), and raptors (*Accipiter* spp., *Buteo* spp., and *Falco* spp.). This context model was restricted to mimicry observations from 2015 – 2016 as data on predator presence was not available for 2006 – 2010.

Statistical Analyses

I analyzed variation in predator mimicry in Steller's jays in two ways. First, I examined the context of observed mimicry incidents across different categories using Poisson generalized linear mixed models (GLMMs). My response variable for all models was the total count of observed mimicry events per category, for each jay; I fit separate models for each of the following fixed categorical predictors: season, company, location, aggression, and predator (Table 1). To account for non-independence between repeated individual counts, the focal identity of each jay was included as a random effect in all GLMMs. Because this study involved a wild population, some individuals were re-sighted and observed more frequently than others due to uneven attendance at survey locations. Mimicry events are unpredictable and relatively rare within this population; in order to preserve all opportunistic documentation of this behavior, I did not mandate a minimum number of re-sights for individuals to be included in this study. The total number of occasions each individual was re-sighted was summed across the 12 months of data collection. To account for variable levels of observation for different individuals, I

included the log (total number of observations per individual) as an offset term in all models. Offsets are often used in Poisson regression when measurement of rates is desired, where the rate is a count of events divided by some measure of that unit's exposure (Agresti 2013). In this case the offset is the count of hawk calls given by a jay divided by the total number of times that jay was observed. I calculated conditional and marginal R^2 values (following methods by Nakagawa and Schielzeth 2013) for all GLMMs to evaluate goodness of fit for each predictor variable. The conditional R^2 explains the variance of fixed effects and random effects combined, while the marginal R^2 explains the variance of the fixed effects alone.

Second, I examined what factors may influence mimetic propensity among 49 individuals by comparing total counts of observed mimicry occurrences in September 2015 – August 2016 as a function of individual characteristics (Table 2) using zero-inflated Poisson regression. I calculated mean measurements for left and right tarsus lengths (mm) of individuals included in analysis, to use as an indicator variable of body size. I compared total counts of observed mimicry events against the following predictor variables: sex, age, body size (tarsus length), average boldness, and territory ownership (0 = no, 1 = yes). To account for variable observation effort among individuals, I included an offset term, the log (total number of observations per jay), as an exposure variable in the model (essentially modeling the response variable as a rate: total count of hawk calls given by a jay, divided by the total number of times that individual was observed). To test for multicollinearity and potential confounding effects among continuous variables, I tested whether birds' average boldness scores, age, or body size (tarsus length) measures

were correlated using Spearman's rank correlation tests. Variables were sufficiently uncorrelated and none were excluded from analysis.

Classically, count data follow a Poisson distribution; however, the study of rare behavioral events often leads to the collection of data with a high frequency of zero counts (zero-inflation) (Welsh et al. 1996). Such data sets may also contain "false zero" observations due to sampling error during the course of data collection. Failure to account for these excess zeros causes bias in parameter estimates and their associated measures of uncertainty (Lambert 1992; Martin et al. 2005).

This dataset contained two classes of zeros: true zeros occurred when an observer recorded 0 total mimicry occurrences for an individual and that jay never performed any imitations. False zeros may have occurred when a jay did perform imitations, but was never observed doing so during any surveys. Due to the relative rarity of this behavior within this study population, and the elusive nature of observing rare behaviors, it is completely plausible that false zeros may exist in the data (Figure 3).

Zero-inflated Poisson regression is designed to deal with the two classes of zeros in the data by modeling the probability of a false zero versus true zero, given the predictor variables. Predictor variables are estimated in two ways. First, a binomial logit regression is used to determine the probability that zeros are false or true. Second, a Poisson distribution is used to model the true counts and true zeros (Linder and Lawler 2012). The same predictor variables were included in both the zero-inflated (logit) and Poisson portions of the model (Table 2).

I conducted likelihood ratio tests to evaluate the importance of each predictor for inclusion in the model, comparing the full model to a series of null models without the parameter of interest (χ^2). The least significant terms were dropped in turn until no further terms could be dropped. The optimal model was selected according to its lowest rank via Akaike's Information Criterion (AIC) further corrected for small sample size (AICc) (Burnham and Anderson 2002). I conducted Vuong's non-nested hypothesis test to compare the fit of the optimal zero-inflated Poisson model vs. its non-zero inflated analog (standard Poisson) to the data. It yielded a large, negative test statistic ($z = -3.17$, $P < 0.001$), providing evidence of the superiority of the zero-inflated Poisson model (Vuong 1989; Loeys et al. 2011). For visual interpretation of predictors in the model, I produced probability curves for each predictor by holding other predictors in the model constant and constraining them to mean values. All statistical analyses were completed in Program R 3.3.3 (R Development Core Team 2017).

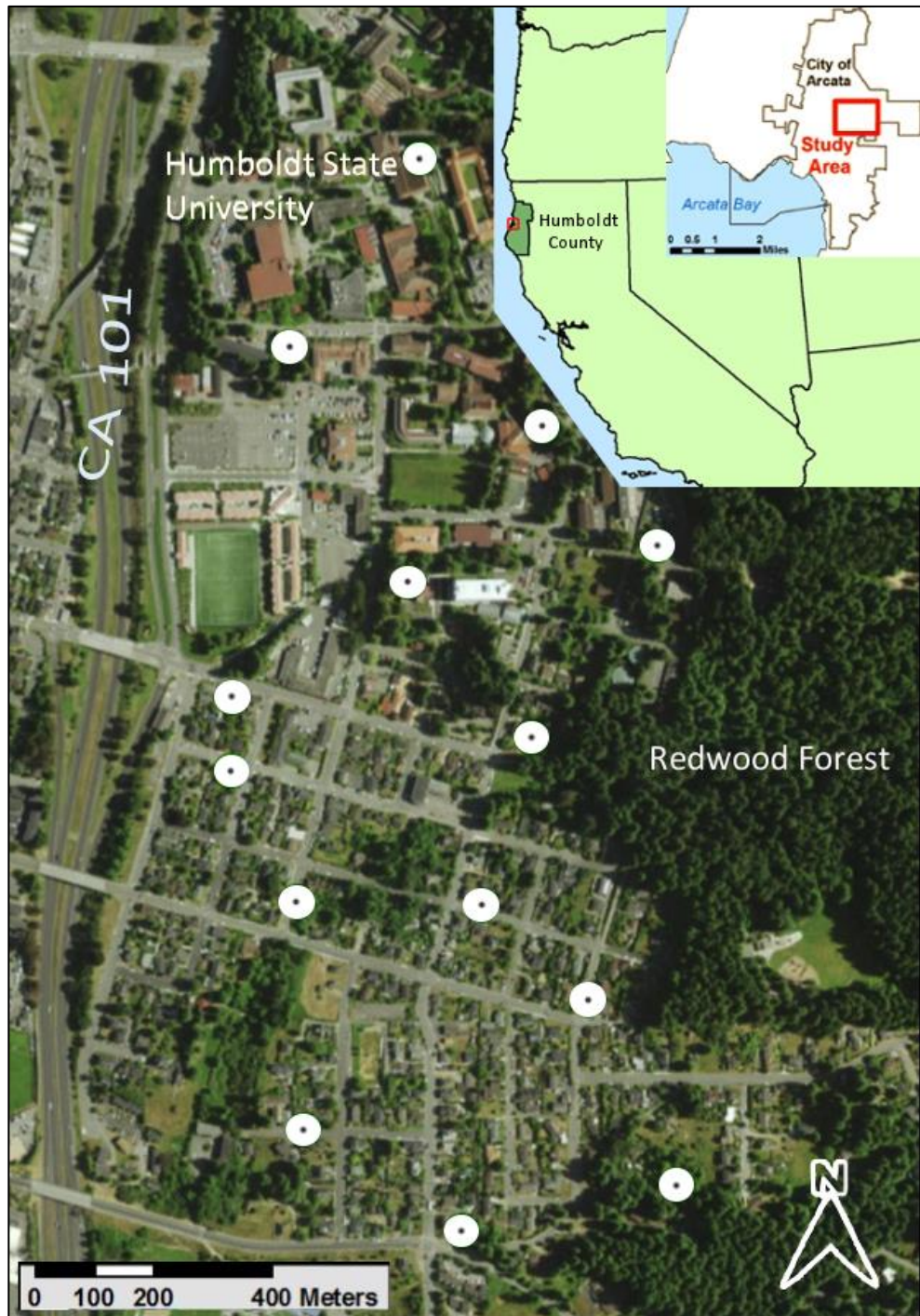


Figure 1. Location of Steller's jay study area (2006 – 2016) in Arcata, CA, USA.
 White points denote the 14 feeder locations visited during re-sight surveys.

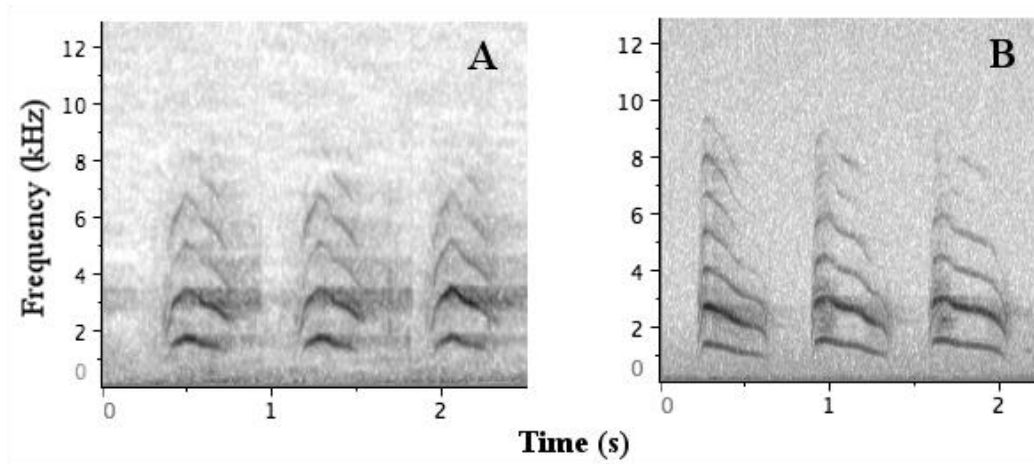


Figure 2. A) Spectrogram of a red-shouldered hawk *kee-aah* call, recorded March 2016 in Arcata CA; B) spectrogram of a Steller's jay imitation of the *kee-aah* call, recorded October 2015 in Arcata, CA. Calls were recorded with a Sennheiser MKH 70 P48 shotgun microphone coupled to a Zoom H4N Handy Recorder, sampling rate of 48 kHz and 24 bit resolution; spectrograms were generated using Raven Pro v1.4.

Table 1. Descriptive details differentiating context categories recorded during observation of Steller's jays performing mimicry events. Context data extracted from observed mimicry events across 2006 – 2010 and September 2015 – August 2016 in Arcata, CA. Predator context category pertains to observed mimicry events in 2015 – 2016 only.

Context category	Description
Season	Pre-breeding – reaffirmation of pair bond
	Early breeding – first nests established
	Late breeding – fledglings; late nest attempts
	Non-breeding – foraging
Company	Mimic is alone
	Mimic with mate only
	Mimic with other conspecifics only
	Mimic with mate and other conspecifics
Location	Mimic is in home territory
	Mimic is away from home
Aggression	No aggression present
	Aggressive encounter (supplantation/chasing by mimic or mimic being chased by conspecifics)
Predator	No predators present
	Predators (cats, crows/ravens, raptors) present

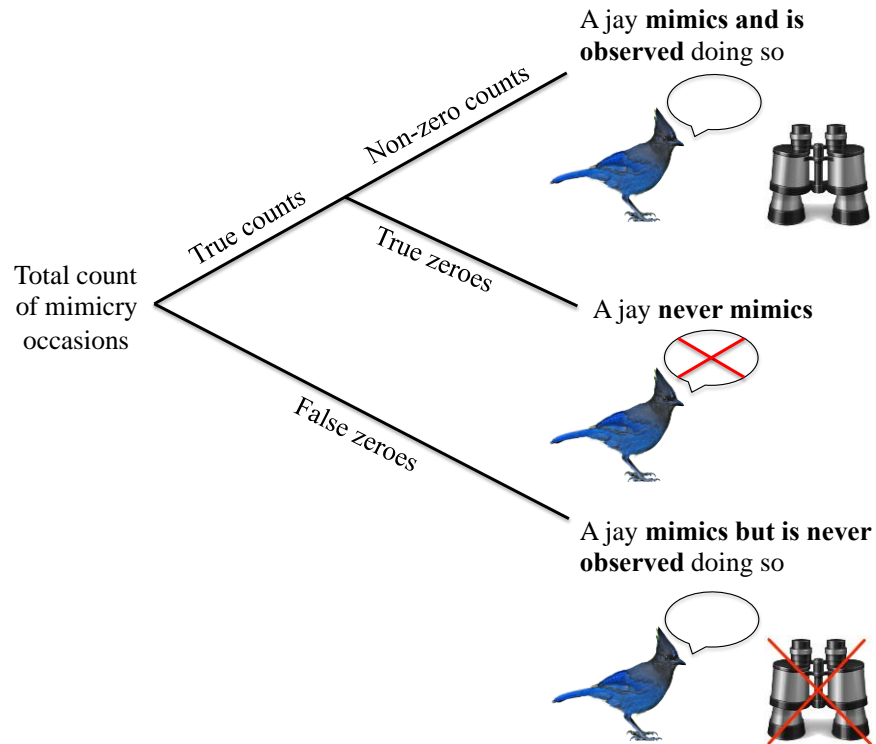


Figure 3. Schematic demonstrating logic of the zero-inflated Poisson model. A Poisson distribution is used to model the true counts (non-zero counts and true zeros), and a binomial logit regression is used to model the probability that zeros are false or true. Figure modified from Zuur et al. (2009) and Linder and Lawler (2012).

Table 2. Individual characteristics from 49 individual Steller’s jays observed over September 2015 – August 2016 in Arcata, CA, modeled as predictors in a zero-inflated Poisson model.

Predictor variable	Description
Sex	Determined by sex-specific vocalizations – Male (M), Female (F)
Age	Determined by gape coloration, plumage patterns; minimum age (yrs)
Body size	Proxy measure: averaged left and right measures of tarsus length (mm)
Boldness	Averaged across all observations 0 – observed, but not at feeder location 1 – present; does not touch feeder 2 – tentative/touches but does not enter 3 – tentative, reaches in through threshold 4 – enters completely; leaves <1s 5 – enters completely; leaves <3s 6 – enters and stays >3s
Territory Ownership	1 = yes; jay is a territory holder 0 = no; jay is not a territory holder (“floater”)

RESULTS

Mimetic occurrence across contexts

Examining the entire dataset (2006 – 2010, 2015 – 2016) to describe behavioral contexts in which Steller’s jay hawk mimicry occurred, 63 of 319 color-marked jays (19.7%) gave hawk calls on 163 occasions. In the 2015 – 2016 study period alone, 14 of 49 jays (28.6%) gave hawk calls on 65 occasions. The annual patterns of hawk calls in the two study periods (Figure 4) were moderately correlated ($r_s = 0.56$, $n = 12$, $P = 0.05$). The majority of hawk calls (52.8% of observations) were observed in the early breeding season (March – May), when first nests are established (Figure 5a).

Jays were more likely to give hawk calls when they were on home territories (81.0% of observations) compared to when they were on a neighbor’s territory (Figure 5b). Hawk calls were most often performed in the presence of a mate (49.7% of observations) (Figure 5c). Most hawk calls (84.7% of observations) occurred in the absence of aggressive encounters (following or chasing) with other jays (Figure 5d). Nearly all hawk calls (90.8% of observations) were observed when no predators (cats, crows/ravens, raptors) were present (Figure 5e); data on predator presence during mimicry events were not collected in 2006 – 2010.

Variation in hawk call mimicry was influenced by season, company, location, aggression, and predator contexts in Poisson GLMM regressions (season: $\chi^2 = 70.8$, $df = 1$, $n = 163$, $P < 0.001$; company: $\chi^2 = 49.8$, $df = 1$, $n = 163$, $P < 0.001$; location: $\chi^2 =$

72.3, $df = 1$, $n = 163$, $P < 0.001$; aggression: $\chi^2 = 82.9$, $df = 1$, $n = 163$, $P < 0.001$; predators: $\chi^2 = 50.1$, $df = 1$, $n = 65$, $P < 0.001$). Jays were 5.3 times (95% CI: 3.2 to 8.9 times) more likely to give hawk calls in the early breeding season compared to the non-breeding season (conditional $R^2 = 0.37$, marginal $R^2 = 0.22$); jays were not significantly more likely to perform hawk calls in the pre- and late-breeding seasons compared to the non-breeding season. Jays were 3.4 times (95% CI: 2.1 to 5.3 times) more likely to give hawk calls in the presence of their mate than when alone (conditional $R^2 = 0.33$, marginal $R^2 = 0.17$). Jays were not significantly more likely to give hawk calls in the presence of competitors only or the presence of a mate with at least one competitor than while alone. Jays were 4.5 times (95% CI: 3.0 to 6.7 times) more likely to perform imitations while on their home territories, than when away from home (conditional $R^2 = 0.55$, marginal $R^2 = 0.38$). Jays were 5.3 times (95% CI: 3.5 to 8.0 times) more likely to give hawk calls when they were not involved in an aggressive encounter with conspecifics (conditional $R^2 = 0.59$, marginal $R^2 = 0.43$). Jays were 9.8 times (95% CI: 4.2 to 22.8 times) more likely to perform hawk calls when predators were absent, compared to present (conditional $R^2 = 0.76$, marginal $R^2 = 0.61$).

Mimetic propensity and individual characteristics

I focused on the more precise 2015 – 2016 data set to describe propensity and individual characteristics of mimics. Five females and nine males were mimics (gave at least one hawk call), while 18 females and 17 males were non-mimics. Count of mimicry events (i.e. mimic rate; see Methods) was influenced by sex, age, body size (tarsus

length), and boldness, but not by territory ownership (sex: $\chi^2 = 4.1$, $df = 1$, $n = 49$, $P = 0.044$; age: $\chi^2 = 22.2$, $df = 1$, $n = 49$, $P < 0.001$; tarsus: $\chi^2 = 5.1$, $df = 1$, $n = 49$, $P = 0.024$; boldness: $\chi^2 = 12.0$, $df = 1$, $n = 49$, $P < 0.001$; territory: $\chi^2 = 0.4$, $df = 1$, $n = 49$, $P = 0.513$). The males were 52.4% less likely to mimic than the females (95% CI: 0.04% to 76.5%). Associated with each one-year increase in age, jays were 20.4% less likely to perform imitations (95% CI: 12.2% to 27.8%) (Figure 6a). Associated with each 1-mm increase in tarsus length, jays were 1.3 times more likely to perform imitations (95% CI: 1.0 to 1.6 times) (Figure 6b). Associated with each one-unit increase in boldness score, jays were 1.7 times more likely to perform imitations (95% CI: 1.2 to 2.4 times). Counts of observed mimicry peaked when boldness ~ 3.0 for females, and ~ 4.6 for males; males were estimated to mimic more than females when boldness > 3.8 . However, according to the model, counts of mimicry events were lowest when boldness scores were highest (Figure 6c).

The odds of recording a false zero were influenced by sex, boldness, and territory ownership, but not by age or body size (tarsus length) (sex: $\chi^2 = 8.6$, $df = 1$, $P = 0.003$; boldness: $\chi^2 = 8.9$, $df = 1$, $P = 0.003$; territory: $\chi^2 = 5.5$, $df = 1$, $P = 0.019$; age: $\chi^2 = 1.4$, $df = 1$, $P = 0.229$; tarsus: $\chi^2 = 0.9$, $df = 1$, $P = 0.346$). Compared to females, the odds of recording a false zero for males were estimated decrease by a factor of 0.03 (95% CI: 0.00 to 0.55). Associated with each 1-unit increase in boldness score, the odds of recording a false zero were estimated to increase by a factor of 10.8 (95% CI: 1.3 to 87.9) (Figure 6d). Compared to non-territory owners, the odds of recording a false zero were estimated to decrease by a factor of 0.07 for territory owners (95% CI: 0.02 to 0.90).

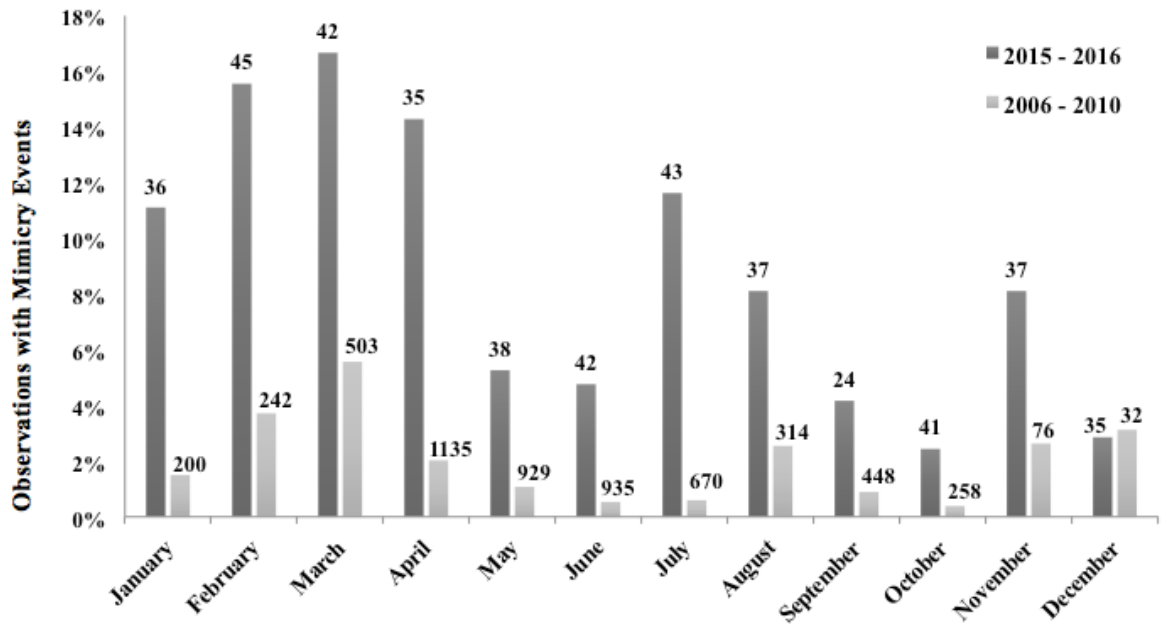


Figure 4. Proportion of observations in which Steller's jays performed imitation red-shouldered hawk calls over two observation periods in Arcata, CA: 2006 – 2010, and 2015 – 2016. Imitations were performed by 19.7% of re-sighted jays over 2006 – 2010 and 28.6% of re-sighted jays in 2015 – 2016. Numbers listed above each bar are the observation sample sizes, from which percentages were calculated.

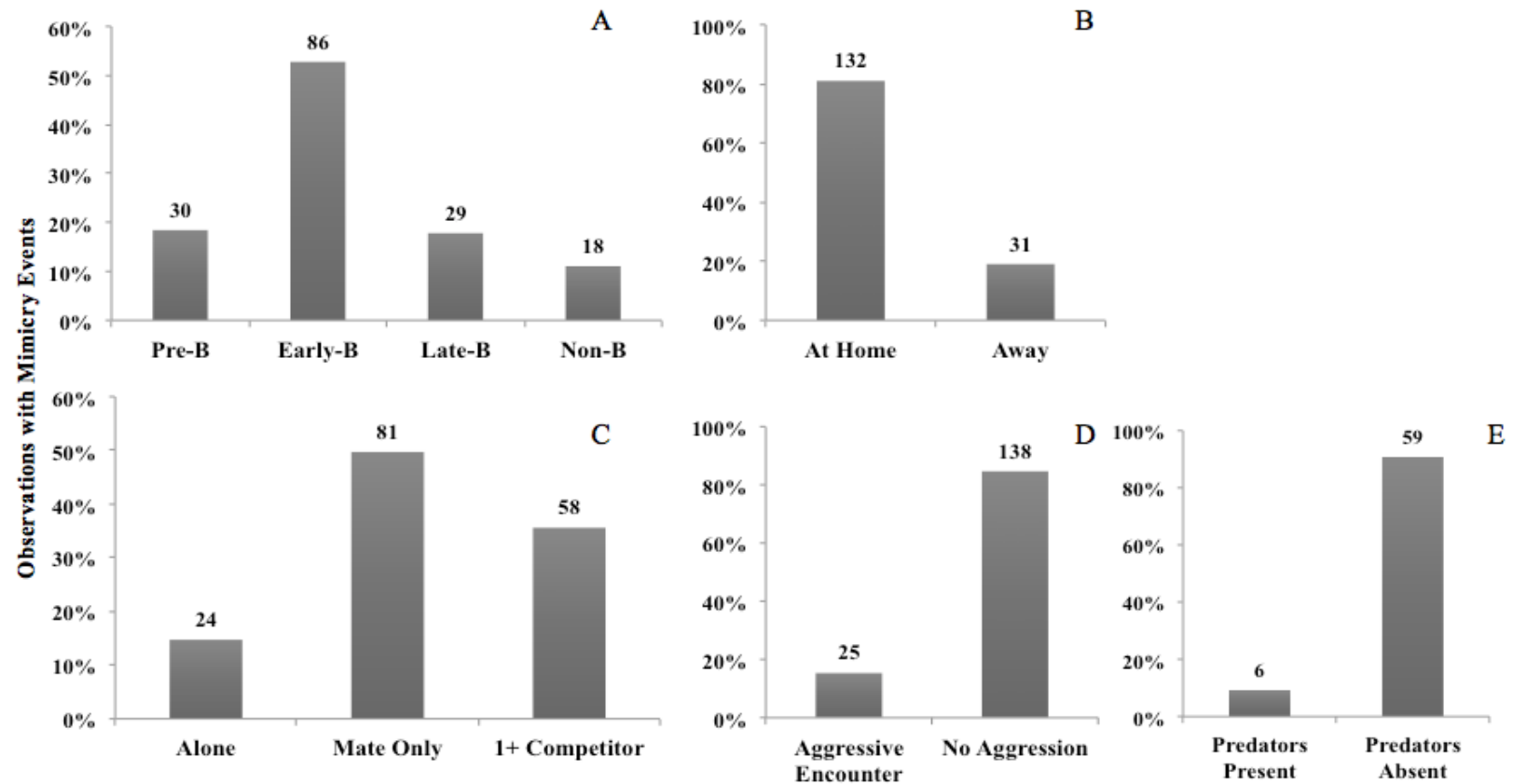


Figure 5. Proportion of mimicry events ($n = 163$) performed by Steller's jays observed over 2006 – 2010 and 2015 – 2016 in Arcata, CA across different contexts. A) Total mimicry events per seasons of the annual cycle; “-B” denotes “Breeding”. B) Total mimicry events on home territories vs. away from home. C) Total mimicry events performed while alone, when only a mate was present, and when at least one competitor (other conspecific) was present. D) Total mimicry events during an aggressive encounter vs. no aggression. E) Proportion of mimicry events ($n = 65$) performed by Steller's jays when predators were present vs. absent over 2015 – 2016 only in Arcata, CA. The number of observations on which percentages were calculated are given for each category.

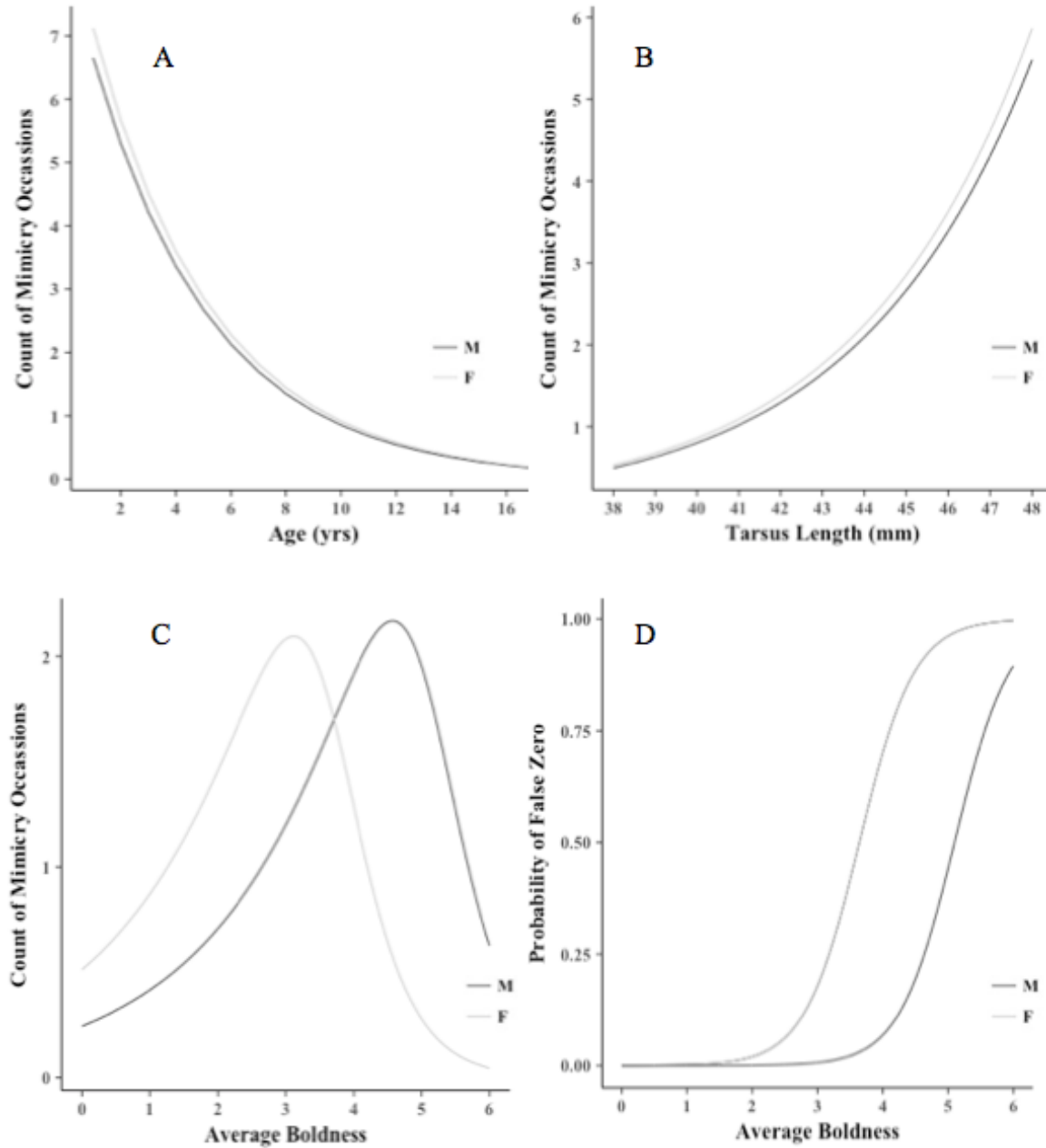


Figure 6. Zero-inflated Poisson regression model curves predicting counts of mimicry events (i.e. mimic rate) as a function of different predictors for male and female Steller's jays ($n = 49$) in Arcata, CA from 2015 – 2016. A) Predicted counts of mimicry events in response to age. B) Predicted counts of mimicry events in response to tarsus length. C) Predicted counts of mimicry events in response to average boldness score. D) Logit portion of Zero-inflated Poisson regression model depicting the probability of recording a false zero count of mimicry occurrences in response to average boldness score.

DISCUSSION

Mimetic occurrence across contexts

Steller's jays in this study mimicked red-shouldered hawks in a variety of distinct contexts. Most mimicry of hawk calls was observed in the jays' early breeding season (March – May), when first nests were being built and territory boundaries were established. Jays' proclivity for predator mimicry in this season may suggest mimicked hawk calls function in nest and/or territory defense. Dalziell and Welbergen (2016) noted female superb lyrebirds (*Menura novaehollandiae*) produced more hawk calls during nest defense situations than while foraging. In this case, superb lyrebirds mimicked the collared sparrowhawk (*Accipiter cirrocephalus*) and gray goshawk (*Accipiter novaehollandiae*). Dalziell and Welbergen (2016) speculated that by imitating predators, female lyrebirds “cried wolf” (see Igic et al. 2015), suggesting mimicry facilitated the acoustic illusion that dangerous raptors were present, thus decreasing the attractiveness of their territories either to other predators or conspecifics.

March – May was also when red-shouldered hawk territorial *kee-aah* calls were most prevalent in our study area (*sensu* Dykstra et al. 2008). Perhaps jays imitate hawks more frequently at this time of year because hawk calls are a more prominent feature of the jays' soundscape in the early spring. This idea could be experimentally tested by presenting jays with playback of red-shouldered hawk calls at other times of year, and documenting whether playback elicits more mimicry from jays. Additionally, responses

of different audiences (predators, neighboring jays) to playback of hawk calls may explicate the intriguing “crying wolf” hypothesis.

Vocal mimicry in some systems may be explained by sexual selection. The production of copied sounds requires a mimic to effectively alter its vocal motor pattern to match that of the model species (Zollinger and Suthers 2004). Learning and retaining a heterospecific sound may be neurologically demanding (Garamszegi et al. 2007; Zann and Dunstan 2008). Accurate mimicry, therefore, may be an honest indicator of physical and cognitive performance (Nowicki et al. 2002; Coleman et al. 2007; Garamszegi et al. 2007). Since most mimicry occurred in the early breeding season for Steller’s jays, it is possible the behavior plays a role in mate choice or pair bond maintenance of long-term partnerships (*sensu* Black 1996). Steller’s jays form long-term stable pair bonds, and in California, pairs remain together on territories year-round (Brown 1963; Walker et al. 2016) with both males and females participating in territory defense (Gabriel and Black 2012b). The honest signal idea could be examined by studying the occurrence and accuracy of mimicked hawk calls in Steller’s jays (e.g. quantifying variation in spectrograms of imitated hawk calls via acoustic analyses) in relation to pair bond tenure and cohesiveness (*sensu* Black 2001).

Jays were more likely to perform imitations on home territories as opposed to neighboring territories, and when mates were present. Perhaps predator mimicry in Steller’s jays serves as a warning alarm for a partner’s benefit. This is consistent with the “mate protection hypothesis” as proposed for great tits (*Parus major*) and willow tits (*Parus montanus*) (Hogstad 1995; Krams et al. 2006) where survival of a mate is

important to both partners in long-term pair bonds. Additionally, if mimicry functions as an honest signal of quality in jays, it follows that most hawk calls would be performed on home territories when a mate (or potential mate) is present (as opposed to when jays are alone or in the presence of same-sex conspecifics).

Flower (2011) documented the use of vocal mimicry by fork-tailed drongos (*Dicrurus adsimilis*) to deceive and kleptoparasitize other species. Steller's jays in my study did not perform hawk calls in the presence of potential heterospecific competitors at feeder stations. The majority of imitations occurred in the absence of aggressive encounters (following or chasing) with other jays. Mimicry was even less likely to occur when jays were with non-mate conspecifics. This suggests predator mimicry was unlikely to serve a function in deceiving competitors, or direct supplantation or conflict with conspecifics in this system either in competition for resources or intrasexual competition.

Nearly all mimicry events in 2015 – 2016 were observed when no predators (cats, crows/ravens, raptors) were present. A factor that must be taken into consideration is that humans might be “predators.” Human observers were present during all surveys in my study, and though these suburban jays were habituated to humans, humans cannot be ruled out as the target of a mimicked signal (see Kelley et al. 2008). Previous studies on this population of jays have documented individual variation in degrees of explorative and risk-taking behaviors (Gabriel and Black 2012a, 2012b; Rockwell et al. 2012; Harvey 2015). Anecdotally, one male jay performed a hawk call while being handled during banding, while another male consistently performed hawk calls whenever observers approached the feeder. Perhaps these two particular jays gave hawk calls during stressful

situations in an attempt to deter humans, as an acoustic aposematic signal. It would be interesting to further examine how human presence may influence predator mimicry in this system.

Mimetic propensity and individual characteristics

The most intriguing finding regarding Steller's jay hawk mimicry was that less than a third of the color-marked population produced the behavior. Upon examining the individual characteristics of the 14 Steller's jays that performed imitations in 2015 – 2016, I confirmed that the behavior appeared in both sexes, across all age and body size classes, and throughout the jays' bold-to-shy behavioral spectrum. I further examined the rate at which jays produced hawk calls most often, to reveal patterns in birds' proclivity for predator mimicry within each of these categories.

Mimetic propensity may vary between sexes. Female jays were more likely to imitate than males; however, difference between the sexes was insubstantial with respect to age and body size (Figure 6a, b). Other studies have demonstrated mimicry may vary with respect to sex. Territorial male violaceous euphonias (*Euphonia violacea*) mimicked heterospecific calls, while females did not; in contrast, mimicry was performed by both sexes in thick-billed euphonias (*Euphonia lanirostris*) (Morton 1976). Additionally, while both male and female superb lyrebirds perform mimetic vocalizations, the sexes imitate different species within different contexts (Dalziel and Welbergen 2016).

Younger jays were more likely to perform imitations. A mimic's ability to reproduce model calls with high fidelity may be positively correlated with age. Zann and Dunstan (2008) established adult male superb lyrebirds were more accurate mimics than juveniles of indeterminate sex. Older male satin bowerbirds (*Ptilonorhynchus violaceus*) produced higher-quality bouts of mimicry than younger males, implying learning and practice influences mimicry (Loffredo and Borgia 1986). Thus, younger jays may be mimicking more often as they learn and practice these calls. Acoustic analyses of recorded hawk imitations would reveal whether variation in call quality exists among different age classes.

With increasing tarsus length, i.e. larger body size, jays were more likely to perform imitations. There is an allometric relationship between body size and syrinx size, affecting the range of fundamental frequencies a bird is able to produce (Ryan and Brenowitz 1985). Larger syrinxes vibrate at a slower rate, producing lower frequency sounds more effectively than high frequency sounds (Wallschläger 1980). Mason and Burns (2015) determined larger tanagers (Aves: family Thraupidae) produced lower-frequency vocal displays than smaller birds. Larger jays may be better physiologically equipped to mimic vocalizations of the larger-bodied red-shouldered hawk. Additionally, less vulnerable – i.e. larger – prey are more likely to take risks (Dugatkin and Godin 1992).

Bolder jays were more likely to perform imitations, with bolder females more likely to mimic than bold males (Figure 6c). Bolder individuals tend to react more aggressively toward threats and engage in risky behavior, as shown in great tits (Verbeek

et al. 1996; van Oers et al. 2004). However, likelihood of imitation increased with boldness only to a point, then decreased for the boldest individuals; the model yielded a peak in counts of mimicry incidents observed when boldness scores were ~ 3 for females, and ~ 4.6 for males. Males were estimated to mimic more than females when boldness > 3.8 . The negative trend observed for the boldest individuals may indicate these birds take higher risks by remaining silent. Kareksela et al. (2013) demonstrated that silent willow tits took greater risks than those that vocalized in the presence of a predator, as pygmy owls (*Glaucidium passerinum*) only attacked silent dummy birds. This may also suggest female jays take greater risks than males concerning predator mimicry behavior.

Since predator mimicry was rare in this study population, it is quite possible some jays who mimicked were never observed doing so. In other words, their total count of mimicry was a “false zero”. It is important to account for these false zeros and try to understand what processes might influence our ability to document this rare behavior.

The probability of recording a false zero increased with increasing boldness score; i.e., it was more likely that mimicry events performed by bolder jays were undetected by observers. This may be confounded by the possible effect of bolder birds undertaking greater risk by remaining silent, described above, especially if human observers are regarded by jays as “predators”. The probability of recording a false zero was higher for females than males. For about a month during the breeding season, breeding females were observed less often while they incubated eggs and brooded chicks. This increased the likelihood that mimicry events weren’t observed. The probability of recording a false zero was higher for “floater” individuals than for territory holders. Territory-holding

individuals were more reliably re-sighted, due to their consistent defense of a particular location; thus, it is more plausible that mimicry may have gone undetected for “floater” individuals that were less routinely observed. In sum, future studies of this system should be aware that detecting mimicry may be more difficult for individuals that are bolder, female, or “floater” birds and adjust sampling effort accordingly to document mimicry most effectively.

Avian vocal mimicry, a spectacular form of communication among birds, remains poorly understood due to the lack of observational and descriptive data on mimics. This study has chronicled patterns of predator mimicry observed in wild Steller’s jays across various contexts and individual characteristics, and lays the foundation for more detailed investigations of mimicry in this system. More empirical data are necessary, particularly examining the acoustic structure and accuracy of mimicked hawk calls. Experimental playbacks documenting responses of predators and jays to imitations will elucidate the potential functional significance of predator mimicry in Steller’s jays.

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