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Propensity of Predator Mimicry in Steller's Jays

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Simple Summary: Several species of birds are known to imitate or mimic the calls of other birds in a variety of contexts, but for many species, it is poorly understood why or how often this behavior occurs. We examined the occurrence and context of Steller's Jays mimicking the calls of Red-shouldered Hawks over a 12-month period. In a population of 49 individually color-marked jays, we documented the mimicry of Red-shouldered Hawk calls in 28.6% of the population (14 individuals). We also reviewed the occurrence of the behavior in historic observation data. Jays imitated hawk calls more often during the early breeding season when jays were within their home territories, while their mates were present, and while aggression towards other birds was absent. Younger, larger, and bolder jays were most likely to perform imitations. These results suggest jays individually vary in their likelihood to imitate hawk calls, and different individual jays may be more likely to perform imitations based on social and ecological contexts, physical characteristics, and personality traits.

Abstract: 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 are lacking for numerous species. We examined the occurrence and context of mimicked Red-shouldered Hawk (*Buteo lineatus*) calls over a 12-month period in a population of 49 individually color-marked Steller's Jays (*Cyanocitta stelleri*). We documented mimicry of Red-shouldered Hawk calls in 14 of 49 (28.6%) jays during this 12-month period. We also reviewed the occurrence of the behavior in historic observation data. Hawk mimicry occurred more often during the early breeding season when jays were within home territories, their 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.

Keywords: *Cyanocitta stelleri*; avian vocal mimic; mimetic signaling system; Red-shouldered Hawk; *Buteo lineatus*

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1. Introduction

Vocal mimicry, where one species vocally copies the sounds of another, occurs among 15–20% of avian species [1]. While potential functions for this phenomenon have received extensive speculation, there is a lack of empirical data supporting proposed explanations [2,3]. Vocal mimicry has been described in both interspecific [4–6] and intraspecific contexts [7], suggesting multifaceted functions across species [3,8]. Functional explanations for mimicry include threat avoidance, sexual selection, social affiliation, brood parasitism [2], and kleptoparasitism [6]. A mimetic signaling system is composed of the model (species being mimicked), mimic (species imitating the model), and audience (receiver of the signal) [9,10]. 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 [11].

Some avian mimics appear to imitate sounds randomly [12], while other species strategically imitate alarm calls or sounds produced by a predator (termed "predator mimicry") [8,13,14]. Greater Racket-tailed Drongos (*Dicrurus paradiseus*) and Sri Lanka Blue Magpies (*Urocissa ornata*) incorporate "danger mimicry"—including predators' vocalizations—into their own species-specific alarm calls [8,15], indicating predator mimicry may also function as a type of alarm call in other systems. Alarm calling occurs across a wide variety of taxa and is likely shaped by several major selective forces, including individual, kin, and sexual selection [16]. Other corvids also imitate predators (most notably raptor calls), including Canada Jays (*Perisoreus canadensis*) [17], Siberian Jays (*Perisoreus infaustus*) [18], Blue Jays (*Cyanocitta cristata*) [19], and Steller's Jays (*Cyanocitta stelleri*) [20–23]. Steller's Jays in particular are reported to mimic neighboring birds of prey, especially Red-shouldered Hawks (*Buteo lineatus*) but also Red-tailed Hawks (*Buteo jamaicensis*), Cooper's Hawks (*Accipiter cooperii*), and Osprey (*Pandion haliaetus*) in Northern California [20,21,23].

Steller's Jays (hereafter, "jays") are known to exhibit complex cognitive behaviors across multiple contexts, including foraging decisions [24], adjusting behaviors based on the presence of mates or other conspecifics [25], altering communication based on perceived predator risk [26], and novel problem-solving performance [27]. Mimicry behavior has been noted to play a role in sexual selection in other species; for example, female Satin Bowerbirds (*Ptilonorhynchus violaceus*) preferred males with larger mimetic repertoires [28]. Mimics may also imitate predators' calls to dissuade conspecific competitors from entering their territory [29]. Some mimics imitate predators to deceive competitors and steal food, or during aggressive interactions with competitors [6]. In some systems, predator mimicry may be an alarm signal given by a mimic to alert a predator that its presence has been detected, and thus any ambush will be unsuccessful (i.e., the "perception advertisement" hypothesis) [16].

Some Steller's Jays participated in alarm-calling behavior in the presence of a mock predator mount (Common Raven; *Corvus corax*), while others did not [30]. Producing vocalizations, including mimetic calls, may be risky as it may result in increased detection by predators [31]. Steller's Jays monitored in this 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) [30,32]. Variation in willingness to take risks by individual jays has been linked to differences in sex, age, body size, boldness, and territory ownership [24,27,30,32]. Male Steller's Jays sampled peanuts more often than females during foraging bouts; in other words, males engaged in riskier behavior, spending time comparing and selecting preferred food items at the cost of increased exposure time to potential predation [24]. Similarly, older, larger, and bolder jays engaged more often in food item sampling during foraging, illustrating a greater willingness to take risks among such individuals [24]. Territory-holding Steller's Jays exhibit a greater degree of social dominance compared to non-territory-holding individuals, as social dominance among jays is site-based [23].

In this study, we sought to document the contexts in which predator mimicry occurred in this system and investigate whether mimetic calls were produced by all individuals. We examined whether predator mimicry was more likely to occur within a given season (time of year as related to the jays' breeding cycle) to evaluate whether mimicry may play a role in mate choice in this system. We also documented the "company" of jays, i.e., whether jays were more likely to mimic while alone, with a mate, or with non-mate conspecifics, to further elucidate whether sexual selection vs. intraspecific competition may play a role in this behavior. We investigated the location of mimicry events, i.e., whether jays were more likely to perform mimicry events while within their home territories, to investigate whether mimicry may function as a signal towards conspecifics during territory defense. We likewise examined whether jays were more likely to mimic during aggressive encounters (i.e., chasing or supplantation of competitors) to investigate whether mimicry may function in scaring competitors away from resources. Furthermore, we examined whether jays were more likely to mimic hawk calls in the presence of predators to explore whether such predators may be the target of a mimetic signal in this system.

We hypothesized that jays may exhibit predator mimicry across differing social and ecological contexts, as described above, and that individual jays may vary in their propensity to perform predator mimicry based on a suite of physical, personality, and social characteristics. We predicted male jays would be more likely to engage in the risk of producing mimetic calls compared to females. We additionally predicted that older, bolder, and larger jays may be more likely to perform predator mimicry. Lastly, we expected more dominant, territory-holding birds to engage in riskier behavior and thus predicted that territory-holding jays may be more likely to mimic predators compared to non-territory holders.

2. Materials and Methods

2.1. Study Site and Subjects

We 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 encompassed approximately 2.2 km^2; it included the Cal Poly Humboldt campus in addition to a portion of a suburban neighborhood to the south. The study area was bordered to the east by a second-growth coastal redwood (*Sequoia sempervirens*) forest. The human population density of Arcata was approximately 731 persons per square kilometer as of 2010 [33]. This Steller's Jay population utilized wooden feeding stations (71 × 35.5 × 28.5 cm) modified with sliding doors that allowed for selective trapping of individuals [30]. Stations were used year-round and were mounted in various places and heights on poles or fences distributed across the study area. Stations were 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 was part of a local banding program that started in 1998 and was intensively monitored for behavioral research starting in 2005; this paper summarizes data from 319 color-marked jays from the study area across both study periods (2006–2010 and 2015–2016; see Section 2.4). Potential avian predators common to the study area included Red-shouldered Hawks, Cooper's Hawks, Sharp-shinned Hawks (*Accipiter striatus*), American Crows (*Corvus brachyrhyncos*), and Common Ravens.

2.2. Study Species

Steller's Jays occupy fragmented forest patches and are especially abundant along mixed-coniferous deciduous edges [23,34]. They are known to frequently capitalize on recreational and suburban areas for foraging and breeding opportunities [22,34,35]. 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 [22,23]. Thus, it is common to see neighboring jays alongside territory owners at valuable food resources in Steller's Jay societies [25]. Additionally, jays cache food items for short- and long-term storage throughout the year, relocating caches using spatial memory [23]. Steller's Jays are relatively tolerant of human proximity; they lend themselves well to the 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 variations in behavioral patterns, including optimal foraging [24], caching effort [25], novel problem solving [27], behavioral syndromes [30], assortative mating [32], and mate fidelity [36]. This research was conducted under the Cal Poly Humboldt Institutional Animal Care and Use Protocol No. 15/16.W.40-A.

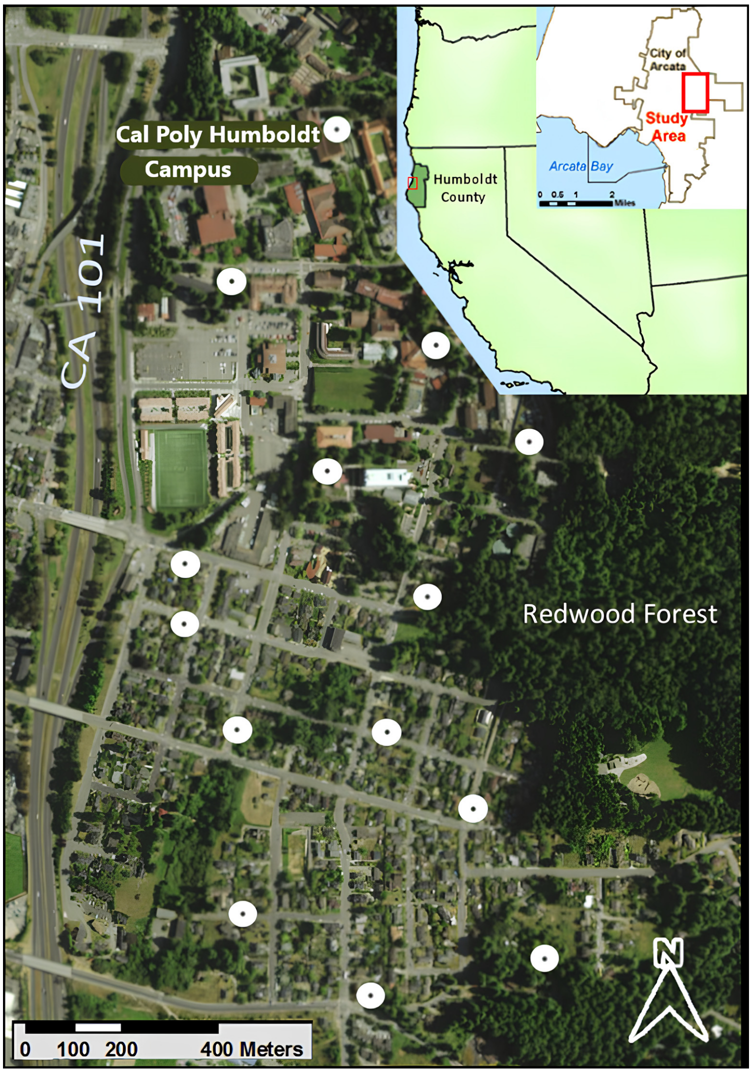


Figure 1. Location of Steller's Jay study area (2006–2016) in Arcata, CA, USA. White circles denote the 14 feeder locations visited during re-sight surveys. Red rectangles denote approximate study area location on inset maps.

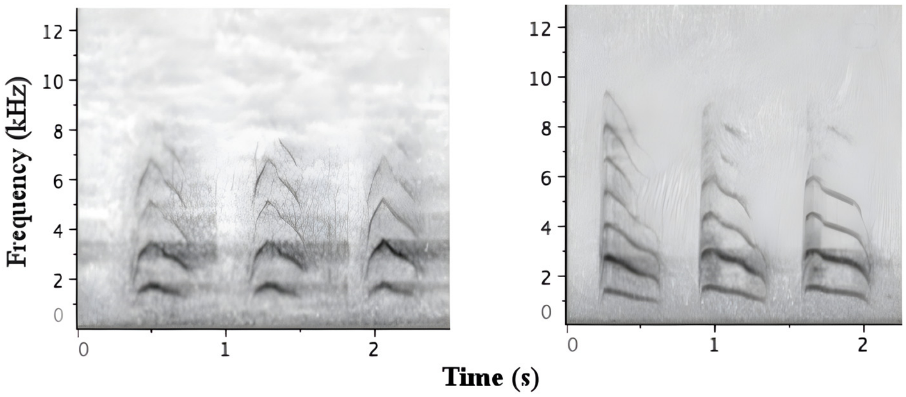
2.3. Banding and Physical Measurements

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 min after capture. As a proxy measure for body size, physical measurements of tarsus length (mm) were taken for each bird during banding. The minimum age was determined for each individual based on gape coloration and plumage patterns [37]. The sex of marked birds was determined by identifying sex-specific vocalizations [30] and differences in structural size and crest size, as males were generally larger than females (JMB et al. unpublished data).

2.4. 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 were 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 an effort to re-sight jays; if jays were seen or heard away from feeders, they were opportunistically observed. Surveys were conducted in the morning when jays were most active. Re-sighted individuals were subject to continuous behavioral recording for the duration they were in view for each survey occasion, for a minimum of 3 min of observation and typically not exceeding 60 min.

When mimicry events occurred, we documented which individual jays performed imitations and the type of predator/hawk call that was performed. From September 2015–August 2016, 100% of re-sighted 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 [38]. *Kee-aah* is the most common call for Red-shouldered Hawks, thought to be an alarm call during most of the year and a territorial declaration call in early spring [38]. The first syllable of *kee-aah* is accented, while the drawn-out second syllable has a downward inflection (Figure 2). In California, adult and juvenile Red-shouldered Hawks call throughout the year, but calling becomes more regular and frequent between November and May, peaking in January through April [38].



(**a**) (**b**)

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, with a sampling rate of 48 kHz and 24-bit resolution; spectrograms were generated using Raven Pro v1.4 [39].

Trap re-entry and boldness have been correlated with risk-taking and exploration responses among jays [30]. 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: with (0) observed, but not at a feeder location; (1) present at a feeder but does not touch the feeder; (2) present at a feeder, tentative/touches but does not enter (maybe retrieves nut through the wire); (3) tentative but reaches into the feeder from the threshold; (4) enters the feeder all the way but quickly leaves (<1 s); (5) enters the feeder all the way and spends time inside (<3 s); (6) enters the feeder and stays (>3 s). Average boldness scores were calculated for each jay across all re-sightings in September 2015–August 2016.

We also examined historic re-sighting data collected across 2006–2010 to document the context of mimicry events in Steller's Jays. Throughout this previous study period, jays were intensively monitored for behavioral research, and mimicry was documented whenever observed, but not in a focused fashion. We combined these data with behavioral data collected from September 2015 to August 2016, during which mimicry occurrences were the focus of data collection, to create a more robust dataset for context analysis. We compared monthly proportions of observations that included hawk calls using Spearman's rank correlation to check the similarity of the datasets from both study periods.

We 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; and the remainder of the year we denote 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 [30]. Males and females that regularly associated with one another and later attempted to nest were considered a pair [30]. During all mimicry events, we 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 the performance of territorial vocalizations, territorial displays, caching food items at the site, and displacing intruding conspecifics [20,23]. We 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 their home territories or territories belonging to conspecifics. All observations were monitored for aggressive interactions (i.e., direct supplantation/chasing of or by conspecifics). We noted whether any aggression towards other birds was present at the time of a mimicry event.

We also observed whether any predators were present during mimicry events. The following were considered to be predators: domestic cats (*Felis catus*), American Crows, Common Ravens, and raptors (*Accipiter* spp., *Buteo* spp., and *Falco* spp.). This context model was restricted to mimicry observations from 2015–2016 only, as data describing predator presence were not available for the 2006–2010 study period.

2.5. Statistical Analyses

We analyzed variation in predator mimicry in Steller's Jays in two ways. First, we examined the context of observed mimicry incidents across different contextual categories using Poisson generalized linear mixed models (GLMMs). The response variable for all models was the total count of observed mimicry events per contextual category for each jay; we 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, we 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 all data collection periods. To account for variable levels of observation for different individuals, we 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 [40]. 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. We calculated conditional and marginal R^2 values following the described methods [41] for all GLMMs to evaluate the 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, we examined what factors may have influenced mimetic propensity among 49 individuals by comparing total counts of observed mimicry occurrences from September 2015–August 2016 as a function of individual characteristics (Table 2) using zero-inflated Poisson regression. We calculated mean measurements for the left and right tarsus lengths (mm) of individuals included in the analysis to use as an indicator variable of body size. We 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, we 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: the 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, we 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 the analysis.

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

Context Category	Description
Season	Pre-breeding—reaffirmation of the 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 the mimic or mimic being chased by conspecifics)
Predator	No predators present Predators (cats, crows/ravens, raptors) present

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 and plumage patterns; minimum age (years)
Body size	Proxy measure: averaged left and right measures of tarsus length (mm)
Boldness	Averaged across all observations 0—observed, but not at a feeder location 1—present; does not touch the feeder 2—tentative/touches but does not enter 3—tentative, reaches in through threshold 4—enters completely; leaves < 1 s 5—enters completely; leaves < 3 s 6—enters and stays > 3 s
Territory Ownership	1 = yes; jay is a territory holder 0 = no; jay is not a territory holder ("floater")

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) [42]. Such datasets may also contain "false zero" observations due to sampling errors during the course of data collection. Failure to account for these excess zeros causes bias in parameter estimates and their associated measures of uncertainty [43,44].

This dataset contained two classes of zeros: true zeros occurred when an observer recorded 0 total mimicry occurrences for an individual jay that truly 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 in a wild population, it is completely plausible that false zeros may exist in the data (Figure 3).

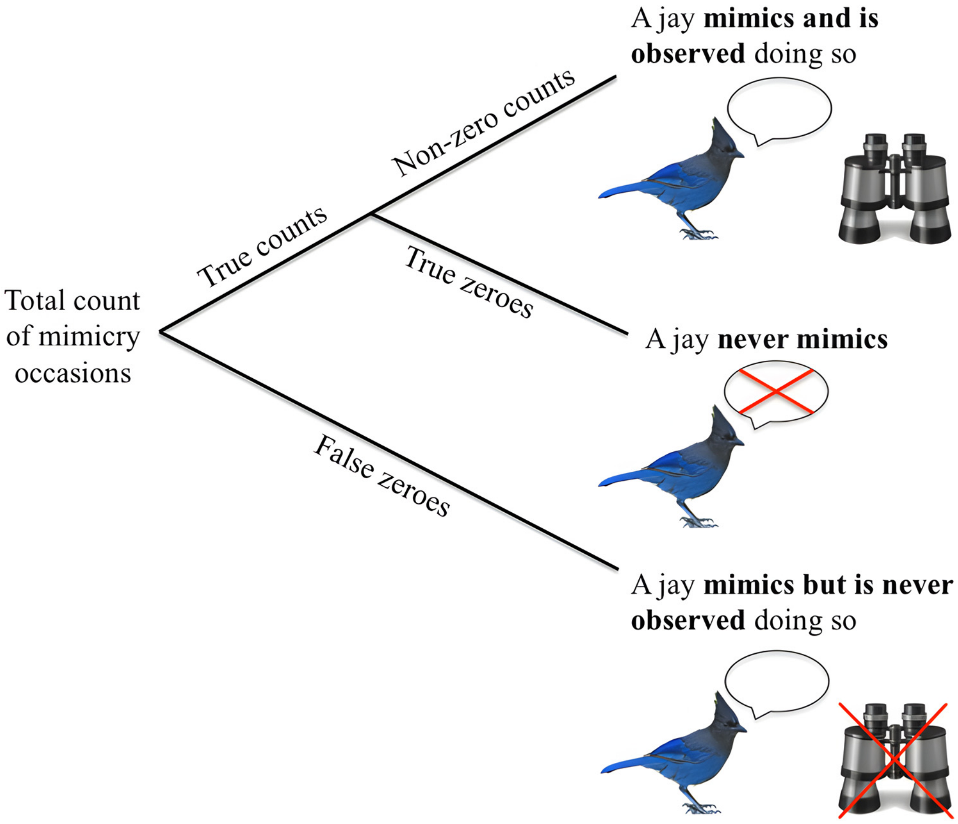


Figure 3. Schematic demonstrating the logic of the zero-inflated Poisson model. A Poisson distribution is used to model the true counts (non-zero counts and true zeros), and a binomial logit regression is used to model the probability that zeros are true or false. The figure is modified from other studies [45,46].

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 a 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 true or false. Second, a Poisson distribution is used to model the true counts and true zeros [45]. The same predictor variables were included in both the zero-inflated (logit) and Poisson portions of the model (Table 2).

We 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 by Akaike's Information Criterion (AIC) and further corrected for a small sample size (AICc) [47]. We 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 [48,49]. For visual interpretation of predictors in the model, we 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 v3.3.3 [50].

3. Results

3.1. 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 ($r_s = 0.56$, $n = 12$, $p = 0.05$).

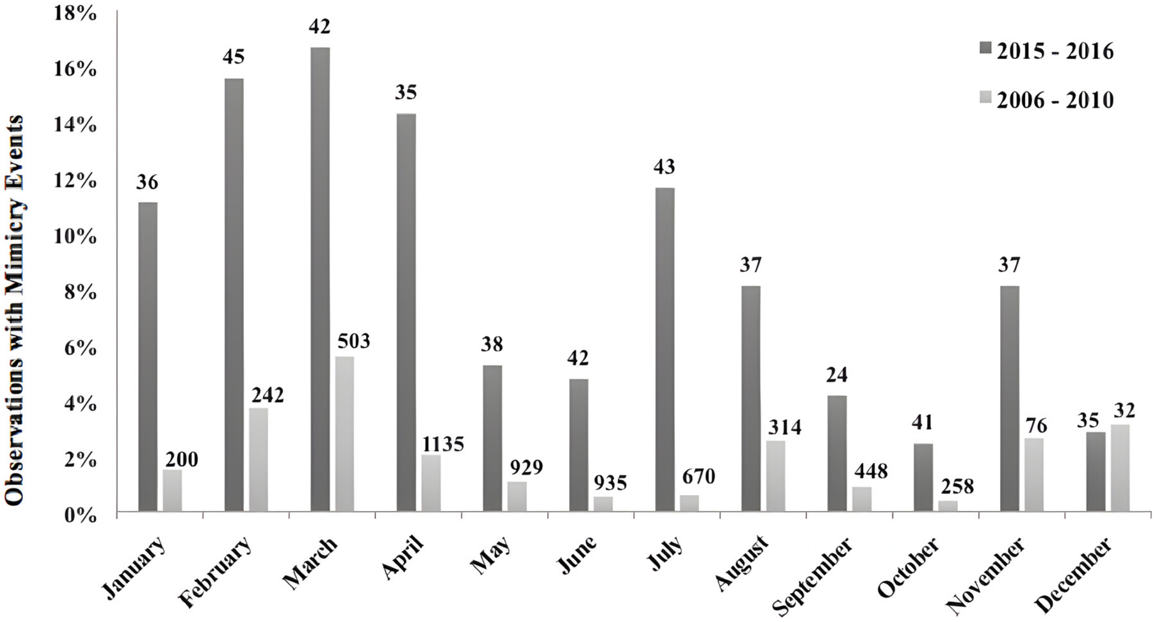


Figure 4. Proportion of observations in which Steller's Jays performed imitation Red-shouldered Hawk calls over two observation periods in Arcata, CA: 2006–2010 and 2015–2016. Imitations were performed by 19.7% of re-sighted jays over the entire data collection period (2006–2010 and 2015–2016) and by 28.6% of re-sighted jays in 2015–2016 alone. The numbers listed above each bar are the observation sample sizes from which percentages were calculated.

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 their 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.

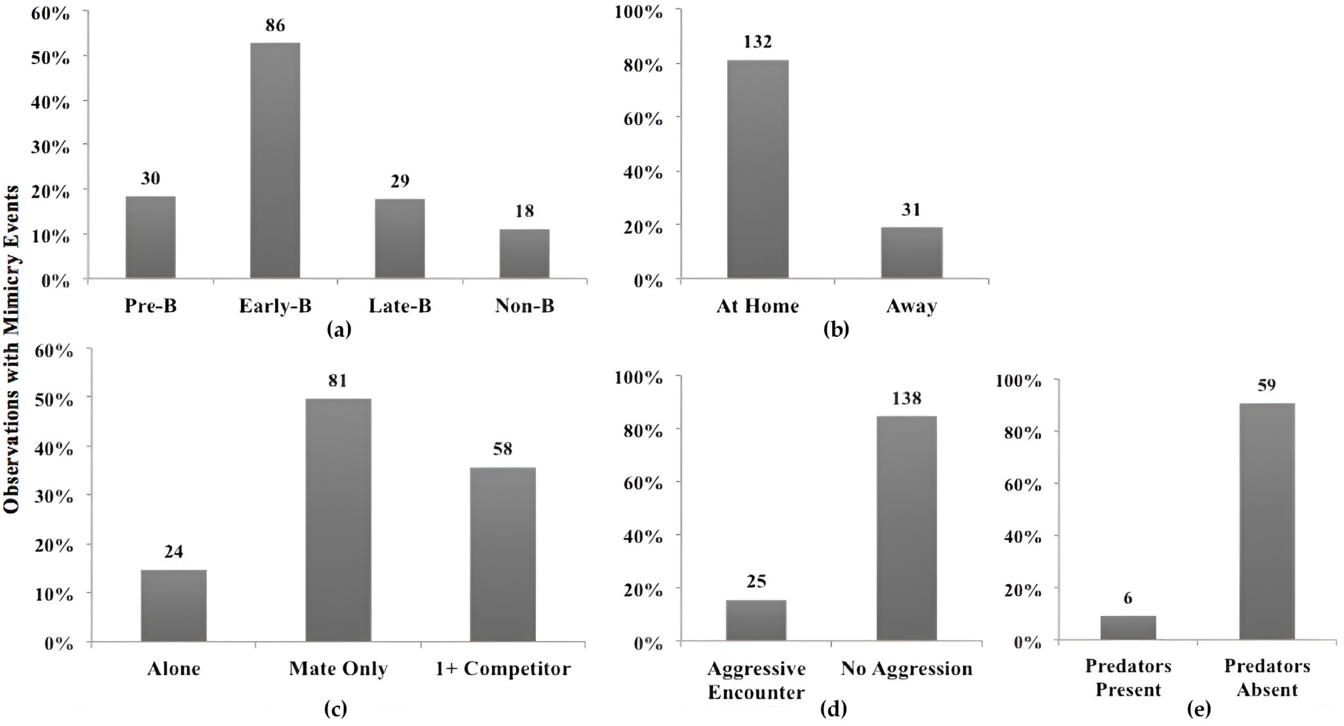
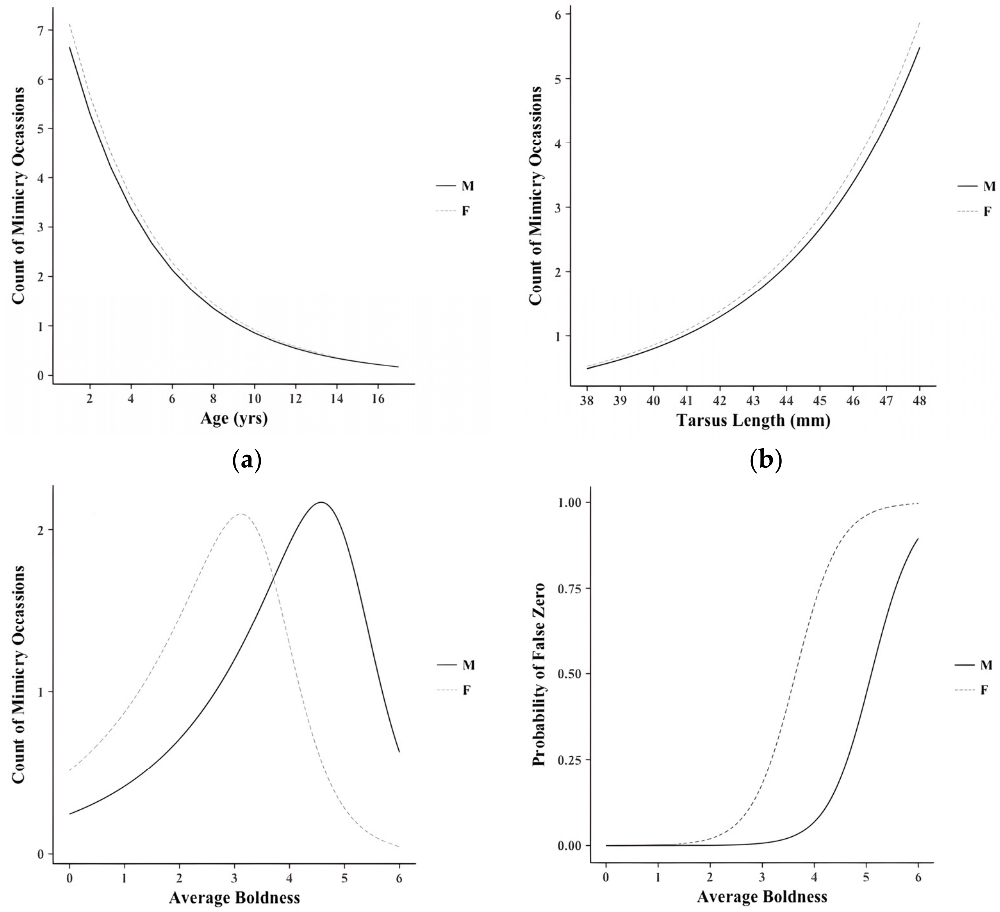


Figure 5. Proportion of mimicry events (n = 163) performed by Steller's Jays observed over 2006–2010 and 2015–2016 in Arcata, CA, across different contexts. (**a**) Total mimicry events per season of the annual cycle; "-B" denotes "breeding". (**b**) Total mimicry events on home territories vs. away from home. (**c**) Total mimicry events performed while alone, when only a mate was present, and when at least one competitor (another 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 is given for each category.

Variation in hawk call mimicry was influenced by season, company, location, aggression, and predator contexts in Poisson GLMM regressions (season: χ^2 = 70.8, df = 1, n = 163, $p < 0.001$; company: χ^2 = 49.8, df = 1, n = 163, $p < 0.001$; location: χ^2 = 72.3, df = 1, n = 163, $p < 0.001$; aggression: χ^2 = 82.9, df = 1, n = 163, $p < 0.001$; predators: χ^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 in 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).

3.2. Mimetic Propensity and Individual Characteristics

We focused on the more precise 2015–2016 dataset to describe the propensity and individual characteristics of mimics. Five females and nine males were mimics (they gave at least one hawk call), while 18 females and 17 males were non-mimics. The 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). The counts of observed mimicry peaked when the boldness score was ≈ 3.0 for females and ≈ 4.6 for males. However, according to the model, counts of mimicry events were lowest when boldness scores were highest (Figure 6c).



(**a**) (**b**)

(**c**) (**d**)

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 the average boldness score. (**d**) Logit portion of a zero-inflated Poisson regression model depicting the probability of recording a false zero count of mimicry occurrences in response to the average boldness score.

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 to decrease by a factor of 0.03 (95% CI: 0.00 to 0.55).

Associated with each one-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).

4. Discussion

We sought to investigate whether mimetic calls were produced by all individuals and demonstrated that not all Steller's Jays in this population mimic hawk calls. We hypothesized mimicry would occur across a variety of social and ecological contexts; our findings demonstrate predator mimicry in this system may function in nest/territory defense, mate choice, and/or mate protection. Moreover, in this population, predator mimicry is unlikely to serve a function in deceiving competitors, either in competition for resources or intrasexual competition, and is unlikely to serve as a direct signal towards predators. We further hypothesized that individual jays may vary in their propensity to perform predator mimicry based on physical, personality, and social characteristics. Younger, larger, and bolder jays were most likely to perform imitations, indicating individual jays do in fact vary in their proclivity to mimic hawks.

4.1. 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. Female Superb Lyrebirds (*Menura novaehollandiae*) produced more hawk calls during nest defense situations than while foraging [29]. In this case, Superb Lyrebirds mimicked the Collared Sparrowhawk (*Accipiter cirrocephalus*) and Gray Goshawk (*Accipiter novaehollandiae*). The authors of one study [29] speculated that by imitating predators, female lyrebirds "cried wolf" [51], 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, as documented elsewhere [38]. 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 the year and documenting whether playback elicits more mimicry from jays. Additionally, the responses of different audiences (predators, neighboring jays) to the 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 [52]. Learning and retaining a heterospecific sound may be neurologically demanding [53,54]. Accurate mimicry, therefore, may be an honest indicator of physical and cognitive performance [28,53,55,56]. 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 [57]. Steller's Jays form long-term stable pair bonds, and in California, pairs remain together on territories year-round [20,23], with both males and females participating in territory defense [32]. 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 by acoustic analyses) in relation to pair bond tenure and cohesiveness [58].

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 (*Poecile *montanus*) [59,60], where the 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).

The use of vocal mimicry by Fork-tailed Drongos (*Dicrurus adsimilis*) to deceive and kleptoparasitize other species has been documented [6]. Similarly, brood parasitic Common Cuckoos (*Cuculus canorus*) mimic the calls of Eurasian Sparrowhawks (*Accipiter nisus*) during laying, which is thought to threaten and deceive hosts while female cuckoos lay their eggs [61,62]. Steller's Jays in this 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 heterospecific competitors, 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 predators may have been observed by jays but were missed by human observers during some mimicry events. It is also possible that predators may have left the area immediately prior to the arrival of human observers, and as such, the predator's presence was not documented during the observation of a given mimicry event. Another key consideration is that humans might be "predators." Human observers were present during all surveys in this study with no effort to conceal themselves from jays; though these suburban jays were habituated to humans, humans cannot be ruled out as the target of a mimicked signal [2]. Previous studies on this population of jays have documented individual variation in degrees of explorative and risk-taking behaviors [24,27,32,63]. 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.

4.2. 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, we confirmed that the behavior appeared in both sexes, across all age and body size classes, and throughout the jays' bold-to-shy behavioral spectrum. We further examined the rate at which jays produced hawk calls to reveal patterns in birds' proclivity for predator mimicry within each of these categories. However, it is important to note that only 14 jays performed mimic calls; this is a small sample size, and consequently, our results regarding mimetic propensity and individual characteristics should be taken with caution.

Mimetic propensity may vary between sexes. Female jays were more likely to imitate than males; however, the difference between the sexes was insubstantial with respect to age and body size (Figure 6a,b). Other studies have demonstrated that 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 laniirostris*) [64]. Additionally, while both male and female Superb Lyrebirds perform mimetic vocalizations, the sexes imitate different species within different contexts [29].

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. For example, adult male Superb Lyrebirds were more accurate mimics than juveniles of indeterminate sex [54].

Older male Satin Bowerbirds (*Ptilonorhynchus violaceous*) produced higher-quality bouts of mimicry than younger males, implying that learning and practice influence mimicry [7]. Thus, younger jays may be mimicking more often as they learn and practice these predator-imitation 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 physiologically able to produce [65]. Larger syrinxes vibrate at a slower rate, producing lower-frequency sounds more effectively than high-frequency sounds [66]. For instance, larger tanagers (Aves: family Thraupidae) produced lower-frequency vocal displays than smaller birds [67]. Larger jays may be better physiologically equipped to mimic the vocalizations of the larger-bodied Red-shouldered Hawk. Additionally, less vulnerable—i.e., larger—prey are more likely to take risks [68].

Bolder jays were more likely to perform imitations (Figure 6c). Bolder individuals tend to react more aggressively toward threats and engage in risky behavior, as shown in Great Tits [69,70]. However, the likelihood of imitation by jays increased with boldness only to a point, then decreased for the boldest individuals. The negative trend observed for the boldest individuals may indicate these bolder birds take even higher risks by remaining silent. For example, 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 [71].

Since predator mimicry was rare in this study population, it is quite possible that 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 an 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, as 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 performed by breeding females were not 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 in this study system.

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 Steller’s Jays and lays the foundation for more detailed investigations of mimicry in this system. Our examination of mimetic propensity as related to individual characteristics was based on a small sample size of 14 birds, and as such, further study of additional individuals is needed. Overall, mimicry behavior was rare in this system, and greater observation effort may be needed to reduce the likelihood of false zeros when categorizing individuals as mimics vs. non-mimics. Particularly, mimicry events may be more difficult to observe in female individuals, bolder individuals, and non-territory-holding birds; thus, sampling design should take this into account. Related to the contexts in which jays performed hawk calls, human observers during this study may have missed predators that were detected by jays during mimicry events, or the human observers themselves may have been regarded as predators. Further study examining the context of jays performing mimicry events in the presence of assorted predator mounts or out of sight of human observers may shed further light on this question. More empirical data are needed, particularly examining the acoustic structure and accuracy of mimicked hawk calls in this system. Finally, experimental playbacks documenting the responses of predators and jays to imitations may help further elucidate the potential functional significance of predator mimicry in Steller's Jays.

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