DO STELLER'S JAYS RESPOND TO HUMAN PROVIDERS?

By

Jessica Erin Guenther

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Committee Membership

Dr. Jeffrey Black, Committee Chair

Dr. Micaela Szykman Gunther, Committee Member

Dr. Barbara Clucas, Committee Member

Dr. Andy Stubblefield, Program Graduate Coordinator

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ABSTRACT

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Jessica E. Guenther

For millennia, humans and wildlife coevolved in a myriad of landscapes influencing each other through social interactions. Humans may be providing non-verbal signals in their facial features with gaze and head orientation that are perceived by non-human animals. The ability to follow human eye gaze and head orientation could enable non-human animals to access valuable resources, for example, birds provided with supplemental food. Few studies have quantified how closely birds in the wild watch and respond to 'familiar' humans who regularly provide food. From 2015-2019, Steller's jays (*Cyanocitta stelleri*) in Arcata, California were fed shelled peanuts and observed approaching human providers. In 2021, I investigated how free-ranging color-marked Steller's jays recognized and responded to five human social cues displayed, first, by a familiar human food provider, and second, by an unfamiliar human food provider. Steller's jays responded differently to the first and second human providers, but not to the cues they displayed (eye gaze and posture). The lack of response to human social cues could be broad-scale habituation of humans in the study area. Habituated Steller's jays exposed to regular supplemental feeding may recognize human faces and social cues, and may not be deterred by human gaze, whereas less-habituated individuals may be more

wary of human gaze direction. Understanding how wild animals perceive human

behavior at an individual and population level may minimize human-wildlife disturbance

and inform conservation practices.

ACKNOWLEDGEMENTS

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INTRODUCTION

For millennia, humans and non-human animals (hereafter animals) coevolved in the same or adjacent habitats while responding to each other's presence and behavior (Marzluff and Angell 2005, Kaltenborn and Linnell 2022). In rapidly changing environments, species that have a range of behaviors and learning capacity may have the potential to sustain themselves in various human modified environments (Beale and Monaghan 2004, Sih et al. 2012). Some animals take advantage of human's resources (waste and refuse), relative safety, or warmth and light in suburbs and cities (Niemelä et al. 2013, Goumas et al. 2020*a*). As urban areas expand, positive interactions between humans and wildlife may give rise to innovative behaviors in animals (Marzluff and Angell 2005, Lee et al. 2016, Magle et al. 2019, Harvey and Black 2021). In the United States, a human activity such as feeding wildlife, is a popular pastime in suburban settings, including stocking bird feeders with seed, millet, and suet in winter (Martinson 2003, Murray et al. 2016). Identifying and responding to the appearance of supplemental food that humans provide may improve health and body condition, and decrease starvation or nutritional stress in wild animals, birds in particular (Amrhein 2014, Wilcoxen et al. 2015, Murray et al. 2016).

Wild animals adept at monitoring conspecifics as well as heterospecifics (including humans) may obtain additional resources (Scheid et al. 2007) increasing the probability of persisting in urban settings (Sol et al. 2013). Possessing cognitive abilities can be essential to distinguish between threatening and non-threatening individuals,

avoiding unnecessary and costly fear responses (Greggor et al. 2016, Lee et al. 2016). Social learning is possessing the cognitive ability to recognize, expose, or support a behavior in an individual's repertoire (Cornell et al. 2012, McCune et al. 2022) which requires individuals to remember interactions and behavior of conspecifics potentially allowing animals to quickly respond to their environment (McCune et al. 2022). Social learning is defined by learning a new behavior through observational conditioning. Habituation, defined by repeated exposure to stimuli (*i.e.,* food) resulting in changing behavioral responses, may reduce fear responses and introduce new learned behaviors (Rankin et al. 2009, Uchida and Blumstein 2021). Wildlife habituated to supplemental feeding may result in continuous exposure to humans, therefore habituating wildlife to humans (Blumstein 2016). In urban settings where humans and some species interact consistently, some species may watch and respond to friendly and unfriendly humans and their postures (*i.e*., social cues) (Goumas et al. 2019).

Animals' awareness of individual humans has been described in a variety of domestic animals where they can discriminate between unfamiliar and familiar human providers and human visual cues (Davis and Taylor 2001, Belguermi et al. 2011, Hernádi et al. 2012). Domestic animals such as dogs and ferrets, can recognize human gestures or cues such as gaze direction, head orientation, and pointing (Hernádi et al. 2012, Kaminski and Piotti 2016). Similar to domestic species, wildlife in captivity can recognize heterospecific behavioral cues through visual signals to find hidden food (Polla et al. 2018, Goumas et al. 2020*a*). Birds, specifically corvids (*Corvidae*) in captivity have not

only demonstrated the ability to react to presence of eye gaze, but to also follow human eye gaze towards an object (Goumas et al. 2020*b*).

Corvids are well known for living alongside humans and responding to human social cues such as eye gaze and head orientation (Clucas et al. 2013, Walker and Marzluff 2015). A variety of species in the *Corvidae* family appear to use direct and indirect cues from humans to determine level of threat (Heinrich and Marzluff 1995, Clucas et al. 2013). One study found that hand-reared jackdaws (*Corvus monedula*) had a higher latency to retrieve food in the presence of an unfamiliar human provider as compared to a familiar food provider (Von Bayern and Emery 2009). The captive jackdaws in that study approached food items more readily when the unfamiliar person averted their eye gaze and body angle (von Bayern and Emery 2009). Another study demonstrated individual crows were warier when humans approached with a direct gaze (Clucas et al. 2013). American crows (*Corvus brachyrhynchos*) during capture memorized the mask worn by the captor and proceeded to mob and scold when the mask was worn nearby (Marzluff et al. 2010). Black-billed magpies (*Pica pica*) distinguished threatening versus non-threatening humans, where they exhibited aggressive responses to humans that were deemed as a threat (Lee et al. 2011).

Steller's jays (*Cyanocitta stelleri*), also in the family *Corvidae*, exploit anthropogenic food sources and can invade new habitats, increasing their interactions with humans (Marzluff and Neatherlin 2006). Steller's jays regularly cache or hide food items within their territory for later consumption (Rockwell et al. 2012, 2013), and neighboring Steller's jays will attempt to pilfer caches suggesting that they watch one

another (Kalinowski et al. 2015). Steller's jays possess the cognitive ability to recognize, respond, and anticipate conspecific's behaviors (Clayton et al. 2007, Rockwell et al. 2013, Kalinowski et al. 2015). Possessing the ability to watch conspecifics may lead to observing heterospecifics' behavior when it comes to anthropogenic food. Steller's jays have demonstrated behaviors that may suggest some individuals recognize human field workers and human eye gaze (*sensu* Gabriel and Black 2010).

In this study, I quantified the breadth and strength of free-ranging Steller's jay responses to human food provisioning and assessed whether individuals' strength of response was related to age, relative body size, sex, home range, seasonality, and prior experience of observing and participating in provisioning events. I also examined if habituation decreased approach latencies over time, and whether individual Steller's jays responded to postures and intentional gestures of familiar and unfamiliar human providers (*sensu* von Bayern and Emery 2009) while providing supplemental food at bird feeder locations.

MATERIALS AND METHODS

Study Area

The study area was located on Cal Poly Humboldt campus and surrounding neighborhoods in Arcata, California (40°52'15.4"N 124°04'36.0"W). The habitat consists of fragmented edge along a coastal redwood forest (*Sequoia sempervirens*). Previous studies have quantified a suite of individual differences among the 50-150 Steller's jay individuals in the population such as accessing food items, space use, willingness to take risks, and problem solving (Gabriel and Black 2010, Rockwell et al. 2012, Goldenberg et al. 2016, Harvey and Black 2021). A majority of these focal studies took place in the non-breeding season to avoid any potential bias due to Steller's jays breeding behaviors. In this urban population of Steller's jays, studies found a spectrum of bold to shy individuals, higher dominance for territory owners in close proximity to their nesting locations, and individuals participating in more risky behaviors after watching conspecifics perform the behavior first (Rockwell et al. 2012, Harvey and Black 2021). One study quantified that jays were consistent in their foraging behaviors over time even after different threat conditions (Rockwell et al. 2012).

Study Design

Prior to the Covid-19 pandemic, 19 feeders (Figure 1) placed throughout jay home ranges, were routinely stocked with peanuts and observers whistled to attract jays.

Between 2015-2019, student observers recorded when individual jays approached them (< 5 m) while filling feeders or followed them when proceeding toward the next feeder. In 2020, for 11 months during the state-wide lockdown, feeders were not supplied, and Steller's jay monitoring was postponed. The 11-month hiatus resulted in a kind of 'natural experiment' that informed an index of 'prior training' for the jays receiving supplemental provisions in prior years. After the stimulus of feeding stopped, responses such as approaching humans may have partially recovered (Rankin et al. 2009). To refamiliarize ourselves to the Steller's jays after lockdown restrictions were lifted in the community, I, and a student assistant (CDC) supplied birdseed and shelled peanuts to 19 feeder sites in February and March 2021.
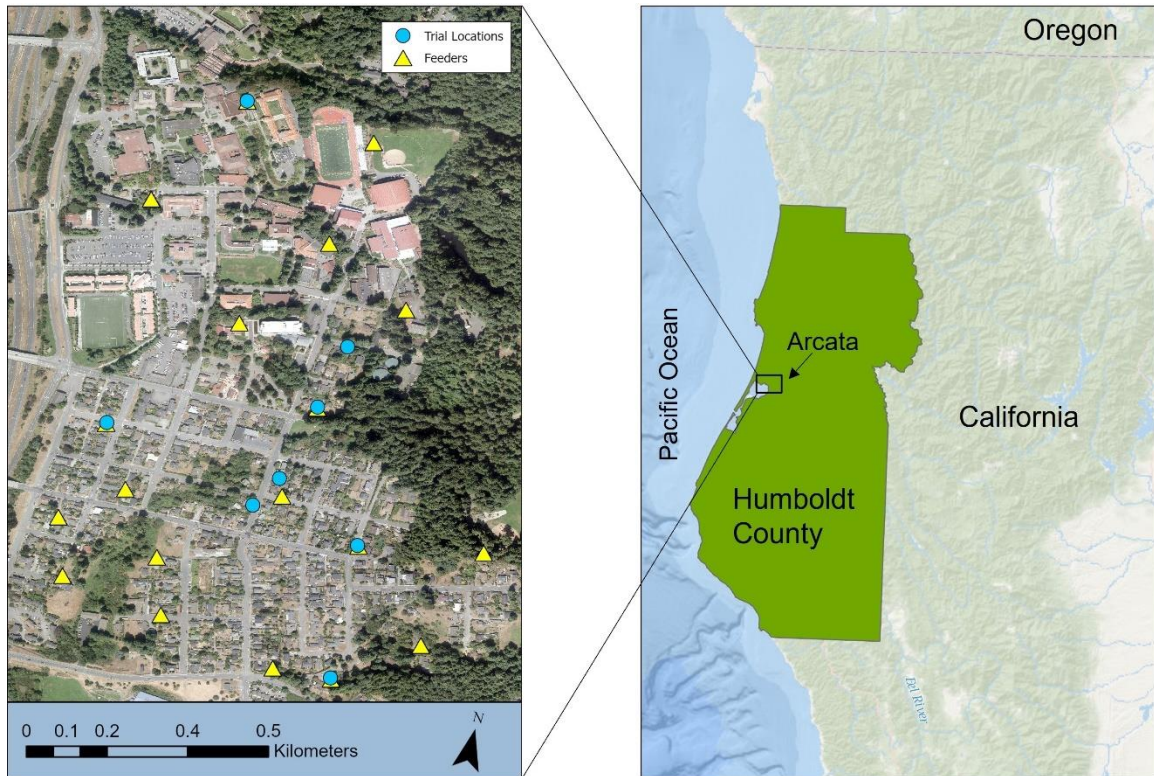
Figure 1. Map showing 19 feeder locations from 2015-2019 (indicated by yellow triangles) containing the Cal Poly Humboldt campus and in surrounding neighborhoods in Arcata, California, US. Blue circles indicate locations of trials within individuals' territories in 2021. Map of Northern California for location reference.

Jay Physical Characteristics

Over the past 25 years, Steller's jays in Arcata, CA have been captured and fitted with a U.S Geological Survey metal band and three unique combination of colored leg bands. Minimum age was classified for each bird as hatch year, second year, or adult ($\geq$ 3 yr) based on plumage and gape coloration (Pyle 1997). Body size was determined by averaging tarsus lengths measured to the nearest 0.1 mm with calipers. Sex of individuals (male (M) vs. female(F)) was determined by hearing sex-specific vocalizations (Hope 1980) and confirmed from DNA assessments (Overeem et al. 2014).

Historical Dataset Preparation

Historical approach trends

Resighting records of color-marked Steller's jays year-round from 2015-2019 were used to quantify the breadth and strength of free-ranging Steller's jay responses to human food provisioning. Color-marked jays that were observed approaching, were attributed a binomial approach response (1 = yes) if they approached a human provider within 5 meters. Color-marked jays that were present, but > 5 m from human providers were assigned as 'did not approach' (0 = no). Individuals that were observed approaching a human provider were also attributed an approach proximity between 0-5 meters. Physical characteristics (*i.e.* age, body size, and sex) were considered independent variables, as was observer provisioning (hereafter training), which incorporated three levels of "training" by prior student observers during 2015-2019; (1) if the observer

whistled to attract individuals, (2) if food was provided, and (3) and if the observed individuals watched food being provided at the time of each observation. Paired Steller's jays establish a home territory and defend the territory year-round (Gabriel and Black 2013). A home range variable was included since resident Steller's jays exhibit a higher dominance, and possible higher boldness within their home ranges (Brown 1963, West and Peery 2017). Home range was determined by using locations of known paired-bonded jays that were < 60 m away from their nest sites. Jays may attempt to approach supplemental food but may not approach humans outside of their nest area due to increased risk (West and Peery 2017). Because breeding and non-breeding season may affect number of sightings for different sexes due to females sitting on nests, I included a seasonal variable in historical analyses. To control for habituation, a cumulative habituation variable was created by counting the number of days an individual was exposed to any type of training (*i.e.,* whistling, peanuts provided, watching) per observation date resulting in an increasing habituation over time. Data were organized using Tableau Prep Builder 2021.3.2.

Social Cue Experiment

I assessed individual Steller's jays' response to postures and gestures from familiar and unfamiliar human providers (*sensu* von Bayern and Emery 2009) while providing supplemental food. I, and a student assistant (CDC) supplied birdseed and shelled peanuts to 19 feeder sites for a total of 28 days from February to March 2021, visiting 9-10 sites every other day and whistling to attract jays close enough to identify

color bands (*sensu* Gabriel and Black 2010). While present, CDC placed a novel wooden platform (38x45x17cm) < 10 m from existing feeders on the ground with 6-8 additional shelled peanuts (*sensu* Rockwell et al. 2012). I remained roughly 10 meters away to record bands, latency to approach (approaching the platform for the first time), platform duration (how long the individual spent on the platform), and if the individual approached within 5 meters of a human. If no jays were present, we left 6-8 peanuts in the feeders. We determined that 12 of the 19 feeder sites were no longer used by Steller's jays and installed new feeder sites within territories of 3 color-banded pairs.

Eight sites with 11 color-marked jays and mates were identified for the food provisioning experiment (Figure 1). Two females and two males did not have colored bands but were identified by accompanying their banded mates within their territories. Some non-banded individuals either had swollen ankles, feet, or toes which also allowed individual identification. Trials took place on five consecutive days between 0730 and 1100 for 2 weeks (Mar 22-Apr 4, 2021). Following von Bayern and Emery (2009), the now 'familiar' food provider (CDC) assumed one of five postures (Figure 2). Six peanuts were supplied on the platform and covered with a plastic solo cup with a 4-meter string attached to prevent premature participation. The cup was wrapped in a thin layer of bubble wrap to eliminate noise when pulled off the platform to avoid scaring the individuals. Once set, the 'familiar' food provider sat on a small chair or stool 4 meters away, sat motionless with a neutral facial expression for up to 6 minutes while assuming one of five postures for a 30-minute maximum trial duration. The order of postures (hereafter conditions) was randomized for each trial, including 1) eyes forward [EF], 2)

eyes averted [EA], 3) eyes closed [EC], 4) profile at 90˚ [PR], and 5) back [BA]

condition with body and head turned 180˚ away from the foraging platform (Figure 2).

Once in position, I whistled to attract the jays and if a jay was seen within 20

meters, the cup was pulled off the platform and the trial began. As the observer, I

remained roughly 10 m away to record bands, platform duration, latency to approach,

number of peanuts taken, and any emitted vocalizations. Once the target individual took a

peanut, the provider replenished the peanuts to 6, replaced the cup, and assumed the next

condition. Once the same individual was resighted within 20 meters, the trial started

again. Occasionally the individual would not be resighted for some time, resulting in

trials lasting longer than others.

Prior to trials, the familiar human provider sitting nearby had visited each jay

territory on 32 occasions in the prior 4 weeks. Each target individual was fed peanuts on

the platform by the familiar provider between 5-10 times. After all trials with a familiar

food provider were completed, the same procedures were employed with another student

assistant (MH) as an unfamiliar food provider and were completed in 5 days (Mar 21-Apr

4, 2021). For the Trial 2, the unfamiliar human provider had not previously visited the jay

territories.

For most of the trials I recorded behavior of both individuals of a pair in one trial.

Behavioral responses are independent of sex between pairs which validates assessing

mates simultaneously in the experiment (Gabriel and Black 2010). Most jays started to

lose interest in peanuts if the trial time was longer than 30 minutes. If the target bird did

not come back during a trial, the trial was discarded. If a bird was within 20 meters of the

platform, but never approached, they were given a maximum latency of 6 minutes (360 s) for that condition. The trial was then reset for the next condition until all conditions were tested. A couple of the trials had to be restarted another day because of disturbances from predators, or other humans walking by.

Figure 2. Human social cues displayed by human providers with neutral facial expression and body oriented toward the feeding platform, while sitting motionless 4 meters from provided food (peanuts). For 3 conditions (eyes facing [EF], eyes averted [EA]), and eyes closed [EC], the observer faced the food platform. For the profile [PR] condition, the observer's face (with the eyes facing forward) turned 90˚ angle from food platform, whereas in back [BA] condition, the whole body rotated 180˚ away from food platform (after von Bayern and Emery 2009).

Statistical Analysis

Historical approach trends

The 2015-2019 dataset describing observations of approach, mated pairs, and training did not meet normal assumptions, so a generalized linear mixed-effects models (GLMMs) was fitted with the *lme4* package in R to account for fixed-effect parameters and random effects that were nested within multilevel hierarchical data (Bolker et al. 2009, Nakagawa et al. 2017). To avoid artificially lowered measures and bias towards any group, I omitted individuals that had fewer than 25 observations in a year, which resulted in a total of 41 individuals for analysis, and 4 years of data (2016-2019). All linear effects models had scaled fixed numeric effects and individual ID held as a random factor (Benedict et al. 2021). Individual ID was considered a random factor to control for pseudoreplication since each individual had multiple observations. For all generalized linear mixed models, I calculated z statistic, a 95% confidence interval (CI), and a p value.

To understand the function of independent variables on an individual jay's probability to approach, a GLMM model was fitted with various fixed effects. I categorized every individual's approach in each observation as a binomial response based on if the individual approached or not (no = 0, yes =1). There were days where a jay did not approach and other days the individual did. To control for site-based social dominance, individuals were assigned a home range continuous variable (used as a fixed effect) by determining if an individual was near their nest location (< 60 m). To account for change in behavior between breeding and nonbreeding season, especially between

sexes (M/F), I included a binomial season variable and an interaction between sex and season. Breeding season consisted of months April through August, and nonbreeding season incorporated September through March. I included individual characteristics (*i.e.,* sex (M/F), age (1-17), body size (avg. tarsus length) as fixed effects, however, body size was missing for certain individuals, therefore was removed from final models due to not being significant (Odds Ratio = 0.69, 95% CI = 0.39-1.21, $p = 0.193$), which allowed for maximum number of observations for analysis (Benedict et al. 2021). An individual's age for each date was assigned to account for ageing over time. To assess if Steller's jays approached more with a type of training, training was divided into three categories; whistle, peanuts provided, and watched. I also included a cumulative amount of habituation, the number of days of any training up to date of observation, to control for the amount of habituation an individual was exposed to over time.

To understand if approaching humans was a function of individual characteristics, I conducted post-hoc tests comparing two groups of individuals (approached and never approached) using a binary logistic regression. I created a simplified dataset, containing each bird, sex, age, and if an individual ever approached (1 = yes, 0 = no). With approach as the response, a GLM model fitted with a binomial distribution was used since fixed predictors (*i.e.,* age, and sex) were categorical and quantitative.

Repeatability

Repeatability (*R*), the proportion of total variance accounted for within group differences, was calculated on a logit scale using a GLMM for flexibility and to control for confounding factors (Lessells and Boag 1987, Nakagawa and Schielzeth 2010). I

controlled for confounding factors such as seasonal, temporal, and physical characteristics changes from the long-term observational dataset limiting pseudo-repeatability and generating adjusted repeatability (Tkaczynski et al. 2020, Çakmakçı 2022). Repeatability of behavior can function as an indicator for personality, or behavioral differences among individuals across contexts with observational data over time (Gabriel and Black 2010, Wilson 2018). Estimating repeatability can determine if there is good evidence for consistent individual behaviors or if there are ecological factors that contribute to variation in behavior (Bell et al. 2009). Behaviors are repeatable when there is low within individual variation compared to high among individual variation, or when individuals act consistently over time and behave differently from each other (Bell et al. 2009).

Statistical analysis of repeatability of approaching humans was calculated using the R package *rptR* which generated adjusted repeatability estimates and confidence intervals from scaled variance components from the GLMM model (Blackburn et al. 2022). The GLMM model had a binary response variable (approach = 1, no approach = 0) with individual bird ID as the random factor. I used a logit link function with Laplace approximation to solve interactions of random effects and approximated true GLMM likelihood (Bolker et al. 2009, Rusyana et al. 2021). Parametric bootstrapping (N = 100) reduced uncertainty through replication which generated a 95% confidence interval and a *p* value for the approach response (Stoffel et al. 2017, Blackburn et al. 2022). Repeatability estimate was considered significant if the *p* value was less than 0.05 (Rudin

et al. 2018). I calculated approach for 35 individuals over 2016-2019 to identify if the proportion of variance was accounted for within or among individuals.

Historical approach proximity to human providers

Of the 35 individuals that approached at least once, I investigated if their average approach proximity was influenced by sex (M/F), age (1-17), training (*i.e.,* whistling, peanuts provided, watching), habituation, home range (< 60 m), season (breeding vs. nonbreeding), and an interaction of season and sex using a linear mixed-effects model (LMM) due to the continuous approach proximity variable and fitted with a Gaussian distribution. Each explanatory variable was scaled, and bird ID was set as a random factor. Approach proximity was recorded in meters and was grouped into five categories, 0-1, 1-2, 2-3, 3-4, and 4-5 meters to reduce measurement error.

There were many human providers over a period of 5 years, so trends in this dataset may be inconsistent or missing, due to human error. For example, some of the approach data were recorded in feet instead of meters, which was converted to meters for consistency. For the final analyses, data were only included if observations contained all accurate information and ones that were missing information or inconsistent were excluded.

Social Cue Experiment

To test whether Steller's jays recognize human eye gaze and head orientation, I conducted a generalized linear model (GLM) measuring latency of approaching the platform per human provider, and latency of approach for each condition. To control for potential familiarity with the trial itself, between the familiar and unfamiliar provider, I

included number of days between trials for each individual as a fixed effect (Nakagawa

and Schielzeth 2010). I also included sex and age as fixed effects. I investigated platform

duration (*i.e.,* time spent on platform) with the same fixed effects as the GLM condition

model to determine if individuals stayed longer on the foraging platform with different

providers and conditions. I calculated 95% confidence intervals and correlation

coefficients to interpret the certainty that the data reflects those relationships (Garamszegi

et al. 2009, Gabriel and Black 2010). All statistical analyses were conducted in Program

RStudio 2021.09.1 with R statistical version 4.2.1 (R Development Core Team 2020).

Ethical Note

This project was carried out under Cal Poly Humboldt Institutional Animal Care

and Use Committee (Protocol no. 15/16.W.48-A; 18/19.W.66-A; 20214W9). These

procedures were adapted from von Bayern and Emery's (2009) assessment of awareness

of human attentional cues in hand-reared jackdaws.

RESULTS

Historical Approaching Trends in Individuals

Thirty-five of 41 (85.4%) color-marked Steller's jays with 25 or more focal observations approached ≤ 5 m of a human observer during the 2015-2019 study period. Jays approached in 532 of 4520 observations (11.8%) with a mean approach proximity of 2.3 m ± 0.1 SE (N = 532) of observers. Annual number of observations per individual ranged from 25-179 (mean 65 ± 41 SE). Of the 35 individuals that approached observers at least once, 17 (49%) were female, and 18 (51%) were male. One female and five males did not approach.

The proportion of observations where individual jays (N = 35) approached human providers ranged from 0.01 – 0.45 (mean 0.12 ± 0.005 SE). Of the 35 individuals who approached a human provider, 17 (41%) had approached observers in more than one year, and five (12%) of those individuals approached in more than two years.

Probability to approach was a function of age (z = 2.64, CI = 1.21-3.70, p = 0.008) suggesting older jays had a higher propensity to approach than younger jays (Figure 3). If an individual was observed in their home range, they were more likely to approach than if they were observed outside of their home range (z = 3.29, CI = 1.08-1.36, p = 0.001, Figure 4). Outside of breeding season, males and females had a similar likelihood of approaching (z = 0.38, CI = 0.66-1.84, p = 0.70); however, in breeding season males were more likely to approach than females (z ratio = -6.72, CI = -2.79- -

1.53, $p = < 0.001$). Female jays did not approach differently between breeding and non-breeding season ($z = 0.51$, CI $= 0.89$-1.21, $p = 0.61$). Males were more likely to approach during breeding than non-breeding season ($z = 2.18$, CI $= 1.02$-1.45, $p = 0.03$). Probability to approach was not influenced by the type of training (*i.e.,* occurrence of observer's whistle, watched food being provided, or peanuts provided) ($z = -1.19$, CI $= 0.86$-1.04, $p = 0.24$) or by the cumulative amount of habituation an individual was exposed to ($z = -0.49$, CI $= 0.82$-1.13, $p = 0.63$).

Post-hoc tests comparing jays' physical characteristics that approached at least once (N $= 35$) with those that never approached (N $= 6$) showed no difference for age ($z = 0.29$, CI $= 0.81$-1.36, $p = 0.78$) and sex ($z = -1.3$, CI $= 0.01$-1.59, $p = 0.19$). One female and five males never approached compared to 18 males and 17 females that did approach a human provider.
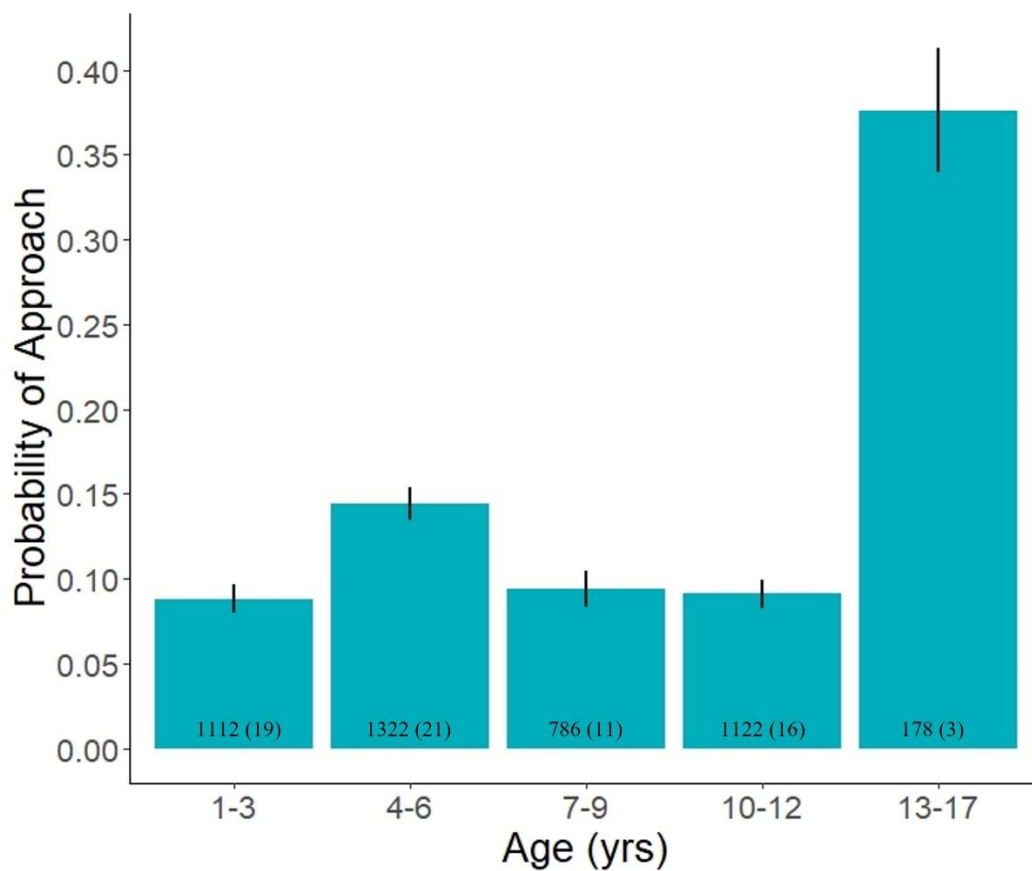
Figure 3. Probability of approach for all ages (N = 41) of Steller's jays during 2015-2019 in Arcata, CA. Age was bracketed to aid in visualization. Whiskers indicate standard error. Sample sizes include number of observations and number of birds in parentheses; some individuals contributed to more than one age category.
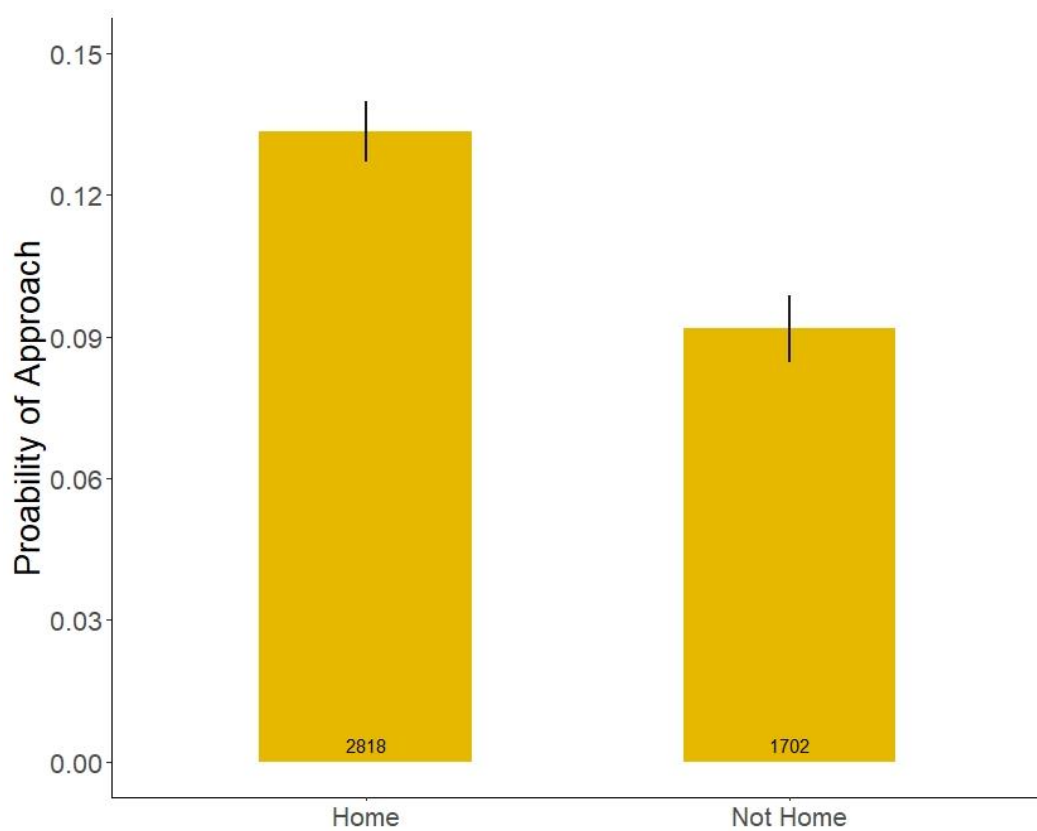
Figure 4. Probability of approach for Steller's jays (N = 41) when present within (Home) or in adjacent territories (Not Home) in 2015-2019 in Arcata, CA. Whiskers represent standard error. Bottom numbers represent number of observations.

Repeatability

Because the majority of the variation was found among individuals rather than within individuals, the probability of approaching human providers was primarily explained by individual bird identity (*i.e.*, the random factor in the model) (R = 0.171, SE = 0.051, CI = 0.093 – 0.266, *p* < 0.001, Figure 5a). Since the variation was found more with the random factor than the fixed effects, there was little ecological variation that contributed to the adjusted repeatability estimates (Figure 5b). These results suggest that individuals behaved consistently over time and acted differently from each other (Bell et al. 2009).

Historical Approach Proximity to Human Providers

Of the 35 individual Steller's jays who approached a human provider, approach proximity ranged between 0-5 m, mean 2.34 m ± 0.06 SE. Individual jays with fewer habituation events approached closer to a human provider (Figure 6, Table 1). Individual jays approached a human provider slightly closer during breeding season than in non-breeding season (Figure 7, Table 1). Other environmental and individual characteristics had little to no effect on individual approach proximity.
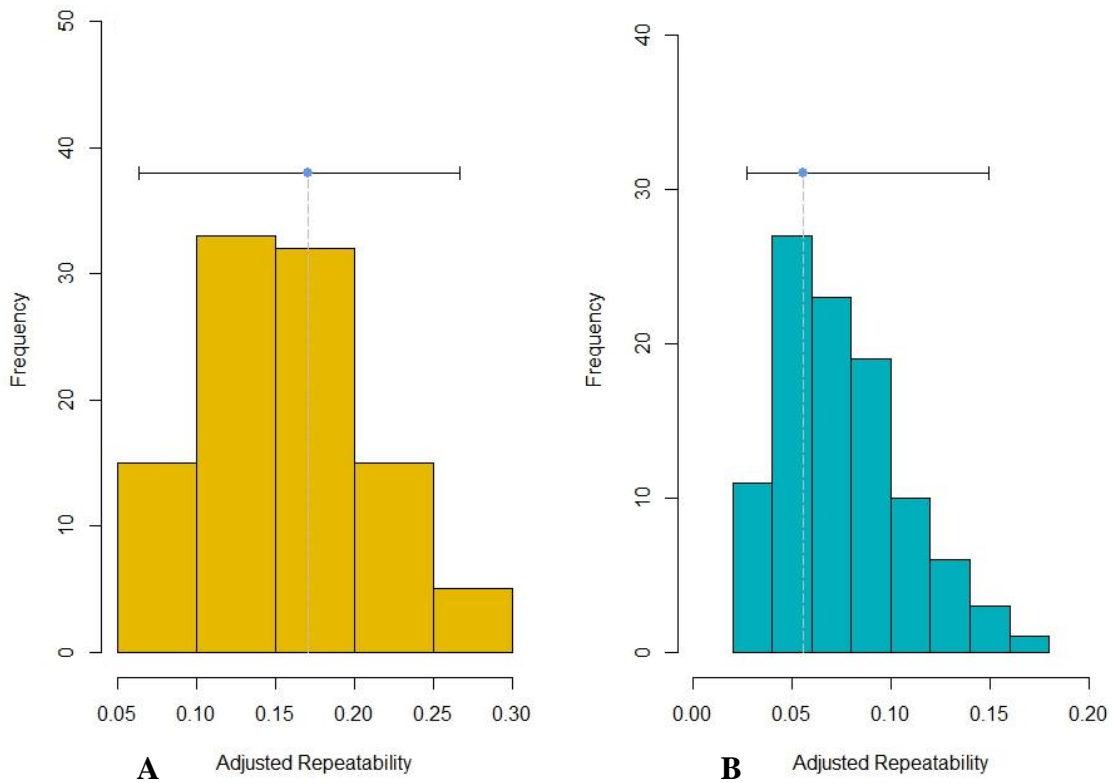
Figure 5. Repeatability of approach behavior among individual Steller's jays. Adjusted repeatability estimates for random factor Bird ID (A) versus adjusted repeatability for the fixed factors (B) from GLMM. The [2.5%,97.5%] confidence intervals are displayed by the horizontal line above resulting from 100 bootstrapping runs. Blue dot represents the calculated adjusted repeatability estimate.
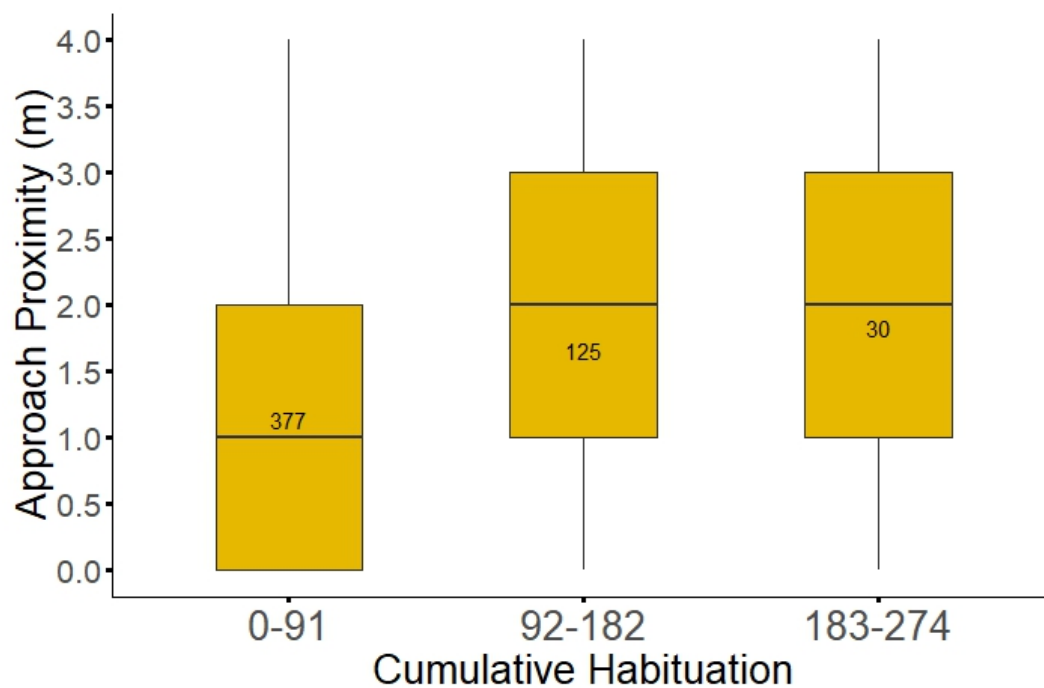
Figure 6. Cumulative habituation by date for Steller's jays that approached (N = 35) during 2015-2019 in Arcata, CA. Habituation was bracketed to aid in visualization. Thick horizontal line represents median value. Whiskers indicate quartile range of the data. Number of observations for each bracket of cumulative habituation represented within each boxplot.
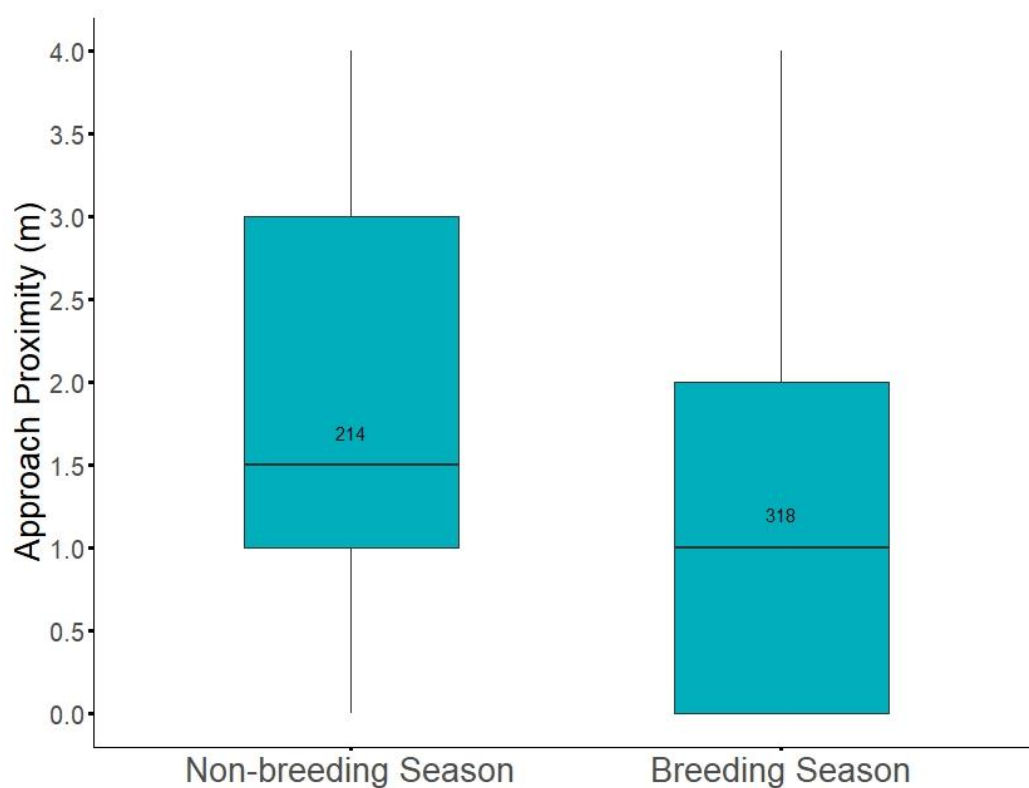
Figure 7. Approach proximity of Steller's jays that approached (N = 35) to human providers in their non-breeding and breeding season during 2015-2019, in Arcata, CA. Thick horizontal line represents median value. Whiskers indicate quartile range of the data. Number of observations for each season represented within boxplot.

Table 1. Effects of sex, age, home range, training, season, habituation, and an interaction of season and sex of Steller's jays (N = 35) approach proximity (<1 to 5 meters) to a human provider in Arcata, CA from 2015-2019.

Response	Effect	Estimate	Lower CI	Upper CI	p	Marginal R^2	Conditional R^2
Approach Proximity	Sex	-0.22	-0.51	0.08	0.15	0.130	0.401
	Age	-0.27	-0.59	0.04	0.09		
	Home Range	0.03	-0.07	0.13	0.55		
	Training	0.04	-0.06	0.13	0.45		
	Season	**-0.23**	**-0.39**	**-0.06**	**0.007**		
	Habituation	**0.30**	**0.18**	**0.42**	**<0.001**		
	Interaction: Season*Sex	0.09	-0.12	0.29	0.40		

Social Cue Experiment

Fifteen individual Steller's jays participated in the two experimental trials in March-April 2021; eight jays (53%) were males and seven (47%) were females. Eleven jays were color-banded and four were known unbanded individuals through association with color-marked mates. Seven of the 35 individuals that approached observers in 2015-2019 were involved in the 2021 experiment.

Trial duration for the first trial ranged from 2.4-30 min (mean 12.3 min ± 8.3 SE), and the second trial ranged from 1.7-23.2 min (mean 6.73 min ± 6.0 SE). Approach latency was a function of trial number (t = -2.586, CI = -95.25- -13.12, p = 0.01) with overall shorter latencies to approach in Trial 2 with the unfamiliar human provider (Figure 8). Number of days between the first and second trial (range 6-12 days) affected approach latencies (t = 2.59, CI = 3.96-28.62, p = 0.01), indicating that fewer days between the two trials resulted in lower approach latencies (Figure 9). Overall, latency to approach the platform was not a function of human social cues, indicating that jays were not generally deterred by postures or eye gaze directions presented by human providers (t = -0.03, CI = -14.74-14.30, p = 0.98). Interestingly, while holding all other variables constant, younger individuals had a lower latency to approach than older individuals (t = 3.56, CI = 6.07-20.97, p < 0.001, Figure 10). Males and females approached the platform with similar latencies (t = -0.89, CI = -75.09-28.62, p = 0.37).

Time spent on the feeding platform did not vary between Trial 1 (familiar) and Trial 2 (unfamiliar) (t = -0.67, CI = -4.11-2.01, p = 0.50), or when human providers

displayed different postures and eye directions ($t = 0.88$, CI = -0.58-1.54, $p = 0.38$;

Figure 11). Platform duration was not a function of individuals' age ($t = -0.17$, CI = -

0.60-0.51, $p = 0.87$) or sex ($t = -1.84$, CI = -7.29-0.23, $p = 0.07$). Not surprisingly,

individuals taking more than one peanut had a longer platform duration ($t = 2.67$, CI =

1.34-8.74, $p = 0.01$).
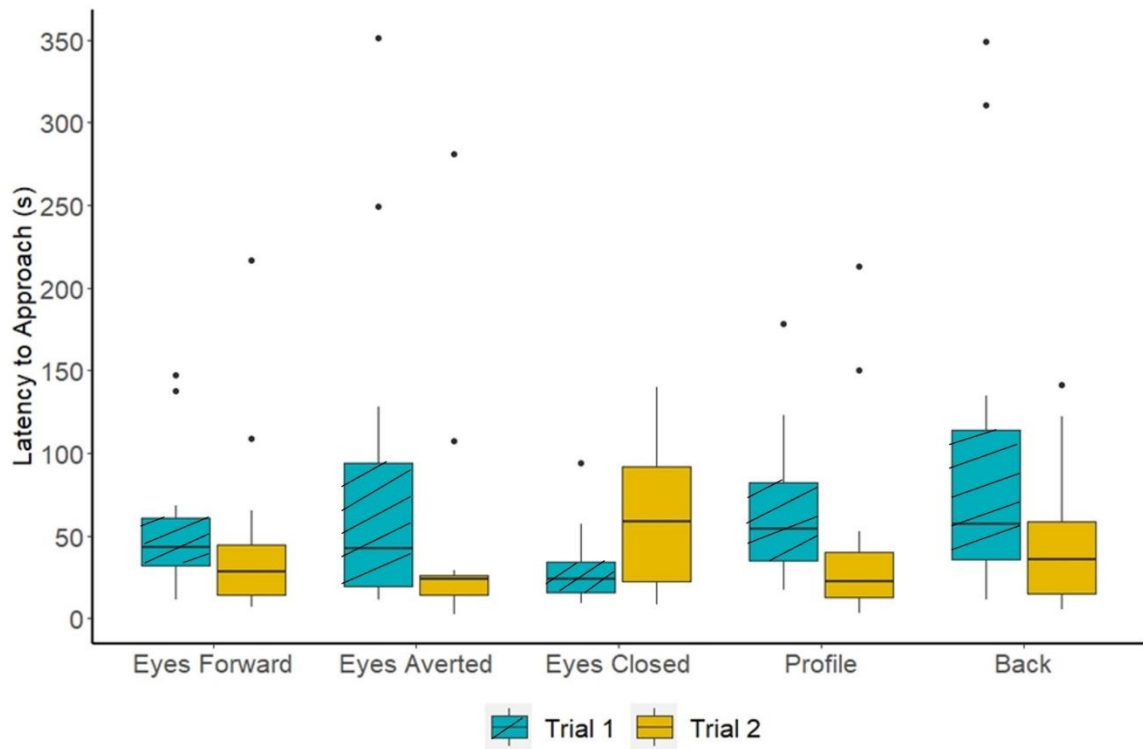
Figure 8. Latency to approach in seconds for 15 jays in all conditions (1 = Eyes forward, 2 = Eyes averted, 3 = Eyes closed, 4 = Profile, 5 = Back) for Trial 1 (familiar) and Trial 2 (unfamiliar), recorded during March-April 2021 in Arcata, CA. Maximum latency (360 s) was filtered to aid in visualization and outliers are represented in black circles. Thick horizontal lines indicate median values. Whiskers show quartile range of the data.
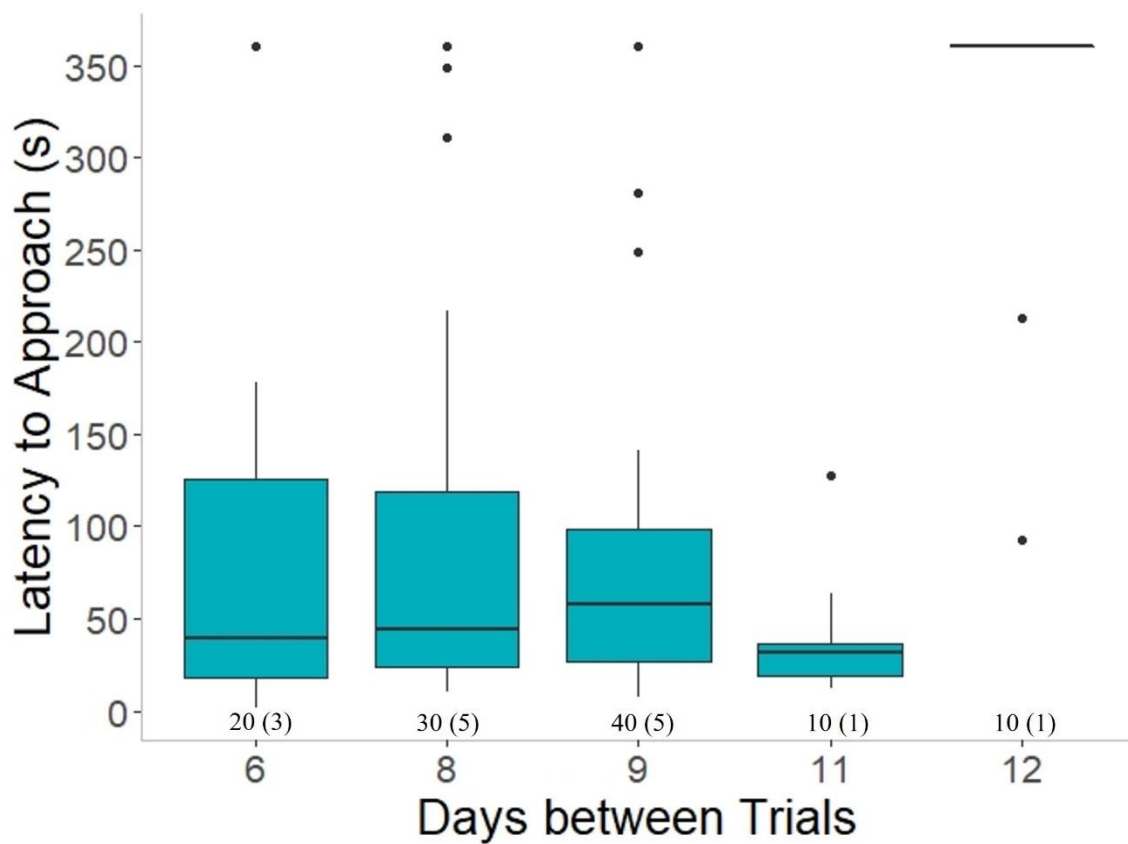
Figure 9. Latency to approach for number of days between trials during March-April 2021 in Arcata, CA. Thick horizontal line represents median value. Whiskers indicate quartile range of the data. Sample sizes include number of observations and number of birds in parentheses.
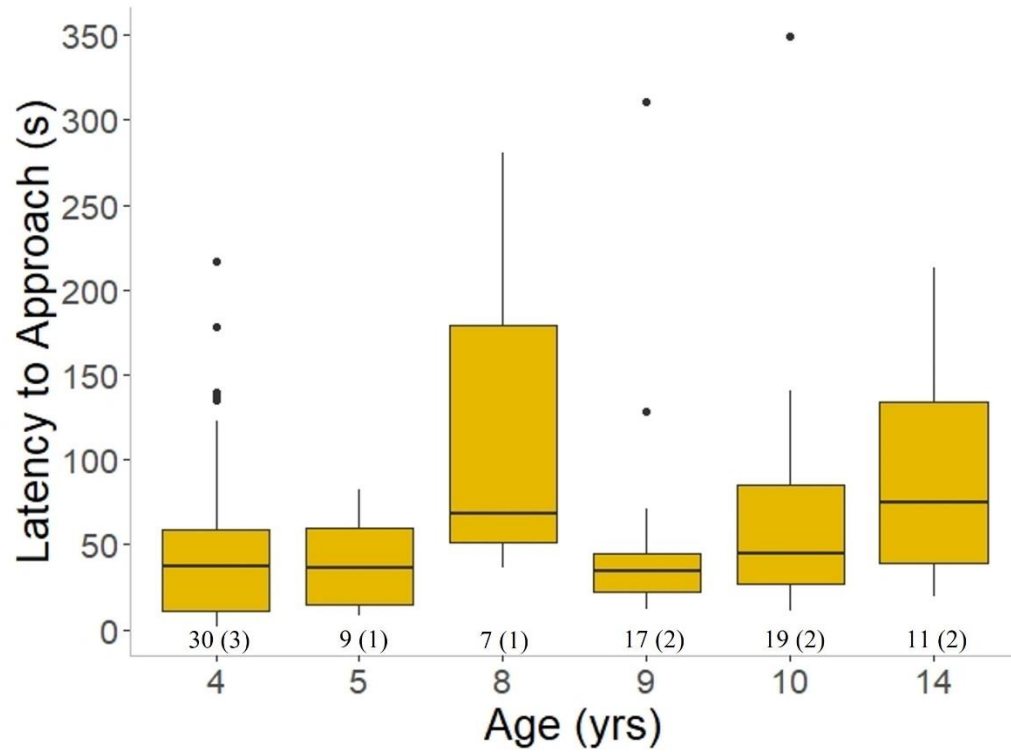
Figure 10. Comparison of approach latencies to an observer by age for 11 known-aged Steller's jays that participated in a total of 93 exposures to the experimental platform, March-April 2021 in Arcata, CA. Thick horizontal lines represent median values. Whiskers indicate standard error and black circles represent outliers. Sample sizes include number of observations and number of birds in parentheses.
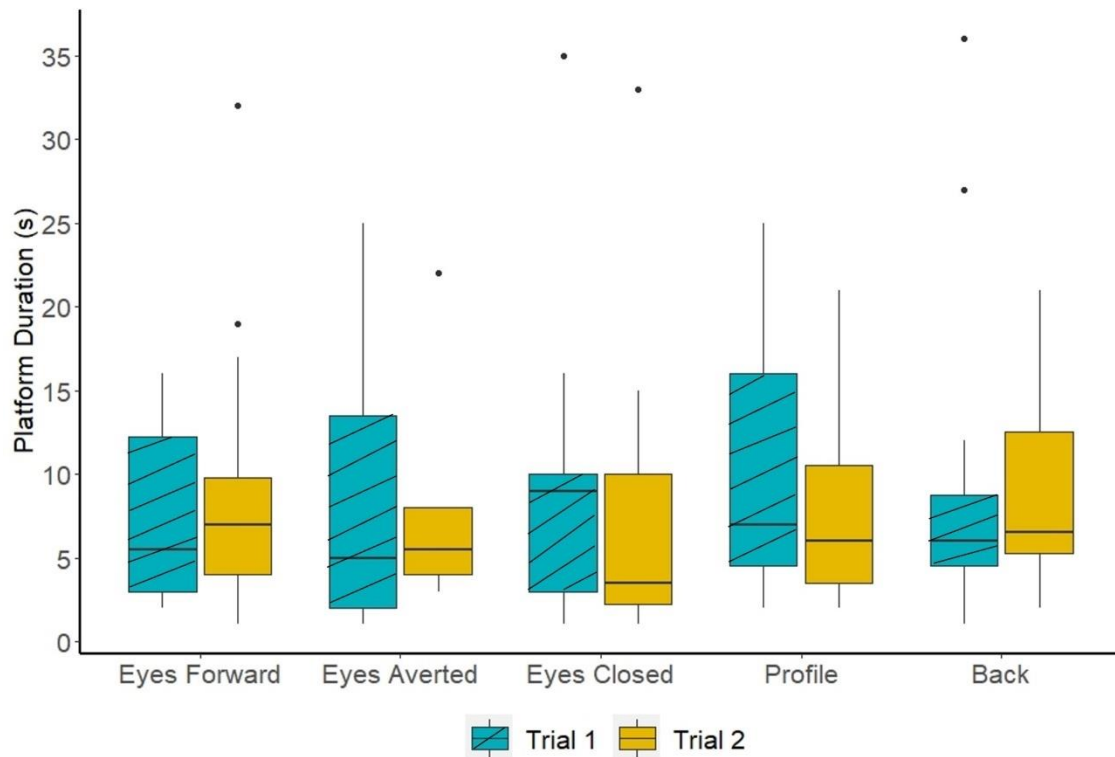
Figure 11. Platform duration in seconds for 15 jays in all conditions (1 = Eyes forward, 2 = Eyes averted, 3 = Eyes closed, 4 = Profile, 5 = Back) for Trial 1 (familiar) and Trial 2 (unfamiliar), recorded in March-April of 2021 in Arcata, CA. Individuals that did not approach the platform (0 s) were filtered out. Thick horizontal lines represent median value. Whiskers indicate quartile range of the data. Black circles signify outliers in the trials.

DISCUSSION

Approach Trends in a Population

Of the 41 color-marked Steller's jays involved in this study in Arcata, CA, 85%

approached a human provider. For years, this population of Steller's jays have been given

supplemental food (*i.e.,* peanuts and sunflower seed), which may have "trained" jays or

habituated them to recognize humans as food providers. Steller's jays in urban areas

where interactions with humans are common, may approach humans more often (Beale

and Monaghan 2004). Especially if individuals readily investigate new resources and

have exposure to social learning from conspecifics (Svartberg 2002, Kalinowski et al.

2015, Harvey and Black 2021). Learning to associate humans with food and having a

higher tolerance to human disturbance, may account for why Steller's jays have moved

into more human dominated environments (Samia et al. 2015, Blumstein 2016,

Goldenberg et al. 2016, West and Peery 2017).

Habituation events may lead species to become more tolerant to humans therefore

being able to coexist in human modified environments (Blumstein 2016), however, some

species sensitize rather than habituate to human disturbance (Blumstein 2013). Tolerance

to human disturbance may be influenced by habitat type, body mass, and diet (Samia et

al. 2015). Corvids in particular are generalist or opportunistic foragers by taking

advantage of human resources, and inhabit disturbed areas which may increase their

tolerance to humans (Marzluff and Neatherlin 2006). When Steller's jays approached a

human provider, they more often were older and within their home ranges. However, from the historical data (2015-2019), had less observations with older jays (13+), potentially biasing the data towards older individuals. As an individual ages, they were exposed to more habituation events (*i.e.*, whistling and feeding) suggesting older individuals may have become more habituated to humans thus possibly affecting likelihood of approach (Rockwell et al. 2012). Steller's jays may be more willing to take higher risks in their home territory where they enjoy the advantage of a homesite dominance (*sensu* Brown 1963, Harvey and Black 2021).

Differences between individuals, such as body size and sex, did not explain a significant proportion of individuals who approached human providers, coinciding with results from Harvey and Black (2021) where bird characteristics did not affect problem-solving behavior in Steller's jays. However, sex of the approaching individuals was influenced by seasonality; females sit on their nests during breeding season, resulting in more male sightings during this time.

Repeatability

Most of the variation in approaching behavior was explained by the individual Steller's jay. Some behaviors that are influenced by the environment may decrease repeatability; however, approach in Steller's jays was repeatable suggesting that environmental variance may allow for more behavioral expressions among individuals, thus increasing repeatability (Bell et al. 2009). For example, Australian magpies (*Cracticus tibicen dorsalis*) level of cognition for an associative learning task changed

due to changing environmental conditions (*i.e.,* heat stress). Repeatability of cognitive

ability was high within conditions, but low between conditions suggesting that cognitive

performance was negatively affected under heat stress (Blackburn et al. 2022). Potential

effects on variation were controlled by including all confounding factors (*i.e.,* age, sex,

home range, season, habituation, training, and an interaction of sex and season) in the

GLMM model (Çakmakçı 2022). Measuring repeatability can also check the reliability of

data, and if the variance cannot be reduced completely, knowing the source of variation

within data provides a better interpretation for behavior (Rudeck et al. 2020).

Historical Approach Proximity to a Human Provider

Approach proximity to a human provider decreased during breeding season

compared to non-breeding season (Figure 7). During breeding season, males have a

smaller area of dominance but are also responsible for feeding the female (Brown 1963).

Anthropogenic food (*i.e.,* peanuts) are a high value resource, and perhaps individuals risk

approaching humans closer for higher rewards. Repeated exposure to harmless humans

can cause urban animals to decrease their fear responsiveness to humans (Uchida and

Blumstein 2021). Urban birds have shown to have reduced fear and faster approaching

times towards objects especially if it offers a reward (Greggor et al. 2016).

Social Cue Experiment

Approach latency was a function of trial number, where Steller's jays had a lower

latency to approach in the second trial even though the food provider was not familiar to

the jays. This result could be attributed to those individuals having already been habituated to humans over the past few years during 2015-2019 observations. A total of 15 Steller's jays participated in the social cue experiment, and statistical results failed to support the hypothesis that Steller's jays respond to human eye gaze and head orientation in either of the two human food providers (Figures 8 and 11). In the experiment, the unfamiliar food provider was tested after the familiar provider to ensure that Steller's jays remembered the feeding routine involved in the prior 4 weeks. Animals that recognize individual humans are suggested to possess high cognitive abilities and have frequent encounters with humans (Lee et al. 2016). Corvids, such as Steller's jays, are known to possess high cognitive abilities, use visual communication, and dominate areas with frequent human interactions (Emery 2006, Clayton et al. 2007, Goldenberg et al. 2016, Harvey and Black 2021). Not being deterred by an unfamiliar human provider could suggest that individuals associate humans with food, thus increasing their tolerance and habituation to humans (Uchida et al. 2019). This population of Steller's jays have been exposed to many different human food providers over the years possibly habituating them to unfamiliar people.

Von Bayern and Emery (2009) found that 10 human-reared, captive jackdaws generally responded differently to human eye gaze and head orientation of an unfamiliar human, (e.g., jackdaws) and had longer approach latencies or did not approach when the unfamiliar human's eyes were directed straight ahead. However, when in the presence of the familiar human who had raised the birds from chicks, latencies to approach were quicker with no differences among human eye gaze or head orientation. Hand rearing of

chicks may have habituated jackdaws to humans more than if a wild population was tested. Jackdaws were also tested separately without any interactions with other conspecifics unlike in a wild population where interactions are common. Although jackdaws seemed sensitive to human eye gaze, this response could have evolved from within species communication between bonding partner and competing conspecifics (Von Bayern and Emery 2009). Some traits though, such as dominance and explorative behavior (*i.e.,* personality) expressed in captivity can also be expressed in the wild for certain species (Herborn et al. 2010). Subsequent studies could compare the gaze and head orientation experiment between captive, hand raised Steller's jays to see if behavioral decisions change based on different habituation conditions.

Latency to approach the platform increased with the duration between the two trials with different food providers. The number of days between the two trials ranged from 6 to 12 days. If stimuli (*i.e.,* peanuts) are removed after a feeding period, responses may partially revert, extending approach latencies and altering behavioral responses (Rankin et al. 2009, Blumstein 2016). Although individuals were habituated over years to many providers, the 2020 year-long lockdown paused all supplemental feeding, possibly allowing behavioral responses to change. For habituation to occur, repeated exposure is required, so intermittent exposure may not lead to habituation (Blumstein 2016).

In a prior experiment involving peanuts provided on a platform in a previous cohort of Steller's jays, but in this same population, older individuals that had experienced prior food provisioning tended to take multiple peanuts and often used more complex behaviors (Rockwell et al. 2012). In this current study, we tested adult territory-

owners who were established in long-term territories and already familiar with available

food sources (Rockwell et al. 2012). During 2015-2019, older individuals were likely to

approach more, but in the experiment with two different food providers, Steller's jays

that were in range of 4-9 years of age had decreased latencies to approach than older (9+

years) individuals. The difference between the datasets could be attributed to lack of

consistent number of older individuals participating the in the social cue experiment.

Also, the one older individual (14 yrs) that participated was not observed with a mate

unlike the other jay participants. This could suggest that older, possibly unmated Steller's

jays are less risk averse and invest their energy elsewhere (Dammhahn and Almeling

2012, Gabriel and Black 2013).

Similar to the historical dataset, during the experiment neither conditions nor

different providers deterred jays in spending less time on the platform, only when an

individual took more than one peanut did their platform duration increase. Steller's jays

that take greater risks in familiar territory (*i.e.,* home range) tended to take multiple

peanuts more frequently (Gabriel and Black 2010, Rockwell et al. 2012). During the

2015-2019 period, Steller's jays were captured, color-marked to identify individuals, and

measured to assess their physical characteristics. Since more dominant, explorative

individuals often take risks, they were more likely to be captured and recaptured during

2015-2019, effectively altering the distribution of behavior making it difficult to assess

studies relating to behavior (Gabriel and Black 2010).

There was one older female, who had a history of approaching but did not

approach the platform in the experiment with different food providers. This female

attempted to approach only when profile and back condition (*i.e.,* less threatening

conditions) were presented (observational data) suggesting that she may understand

human eye gaze and head orientation. This individual was 14 years old suggesting that

older individuals may be more risk averse. In the 2015-2019 dataset, jays that were older

than 9 had longer latencies to approach humans. We did not assess relative boldness or

measures of risk taking as done in previous years in this population of Steller's jays

(Gabriel and Black 2010, Rockwell et al. 2012). We anticipate shyer or more risk-adverse

individuals may exhibit different behaviors when exposed to human eye gaze like having

longer latencies to approach a novel food item or be too fearful to approach (Goumas et

al. 2019).

In summary, the historical dataset (2015-2019) included individual birds that had

been captured in baited feeder traps for initial banding (Rowland 2020, Harvey and Black

2021). With the potential risk of capture, this may have changed Steller's jay behavior by

affecting the likelihood of approaching humans. In contrast, prior to the human social cue

experiment in 2021, Steller's jays had not been captured for at least a year and had been

"trained" to come to the wooden platform provided with peanuts on 32 occasions over a

4-week period. During the human social cue experiment, the average jay was not deterred

by either head orientation or gaze directions presented by human providers. Interestingly,

jays during Trial 2 came more, not less, quickly to the wooden platform when the

unfamiliar human provided peanuts and sat nearby. This result does not need to imply

that jays cannot distinguish between familiar and unfamiliar providers. It is more likely

jays had been increasingly familiarized to the feeding routine and showed less inhibition

to approach in the later part of the study (*i.e.,* habituation). Furthermore, the jays in this population may have little "fear" and attribute minimal risk to humans in this "friendly human" study area. Urban species, including Steller's jays, may not approach human resources if there is conflict or a risk to individuals (Goumas et al. 2019). Herring gulls (*Larus argentatus*) possibly learned human gaze aversion after being chased away from food resulting in associating human gaze as a potential danger (Goumas et al. 2019). Future studies examining birds' tendencies of responding to human social cues may consider including differing levels of risky human behavior (*sensu* Cornell et al. 2012).

Conservation Implications

Understanding how Steller's jays perceive humans may help minimize human-wildlife disturbance and allow for better implementation of conservation management measures (Goumas et al. 2020*b*) as it pertains to native and endangered species (West et al. 2019). Steller's jays have gained attention for occupying human-dominated areas such as campgrounds in California and for being a potential nest predator of the threatened Marbled murrelet (*Brachyramphus marmoratus*) (Marzluff and Neatherlin 2006, Goldenberg et al. 2016, West et al. 2019). If Steller's jays habituate to humans and lose their fear responses, human-dominated areas that border protected areas may see an increase in jay populations, thus increasing the pressures for sensitive species (Lapiedra et al. 2017, West et al. 2019). More broadly, effects of human disturbance in human-modified environments may give further insight to wildlife behavioral flexibility and how

it affects population dynamics and interactions (Sih et al. 2012, Lapiedra et al. 2017,

Ortiz-Jimenez et al. 2022).

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