THE RATTLE CALL: A FEMALE-SPECIFIC VOCALIZATION IN STELLER'S

JAYS

By

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ABSTRACT

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While the elaborate songs of male passerines are well documented for their role in intrasexual resource competition and mate attraction, vocalizations used in female competition are poorly understood. Research has suggested that the female-specific rattle call of Steller's jays (*Cyanocitta stelleri*) is used in competition for access to a territory and mate. I describe structural properties of the rattle call, and compare life history traits of individual females to rattle call occurrence. I used two rates to quantify rattle call occurrence from 20 females: rattles per observation period (RPO), and proportion of observations with a rattle call (POR) from August 2017 – April 2018 in Arcata, California.

Based on spectral analyses, rattle calling consisted of rapid-fire call notes given at $37 - 98$ notes per second (mean $= 68 \pm 17$ SE, $n = 16$) for $0.80 - 2.14$ seconds (mean $= 1.55$ s ± 0.39 SE, $n = 16$). Jays produced call notes at a peak frequency of 14,855 kHz ($\pm$ 2,716 kHz SE, $n = 16$) and fundamental frequency of 3,850 kHz ($\pm$ 205 kHz SE, $n = 16$). The rattle call was sometimes preceded by a series of guttural notes.

I observed 158 rattle calls from 18 of 20 females during 49 out of 162 focal animal observation periods. The likelihood of observing rattle calls depended on life history traits of the sender. I identified the receiver of the rattle call on 42 occasions; 18 rattle calls were directed at males (57%) and 24 were at other females (43%). When paired females rattled at a male, it was always at their mate. When unpaired, floater females rattled at a male, it was always at a territory owning male. Female Steller's jays were not observed rattle calling in the absence of conspecifics. Overall, novice females (i.e. beginning their first breeding season) had a higher rattle rate than experienced females. Floater females rattled in more observations than territorial females.

During back and forth rattle contests between novice and territorial females, novice females rattled as much as, or more, than their territorial opponents in several instances. In the two dyads where the territorial female did not rattle more than the novice intruder, the novice females ended up usurping the territorial females, and nesting in their territories with their mates.

Investigation into female vocalizations, such as the rattle call, may bolster our understanding of factors limiting survival and reproduction in females. The characteristics associated with higher rates of calling may indicate drivers for evolutionary change. In this case, floater females limited by nesting experience,

and paired females defending a territory apparently used the rattle call when

competing for access to mate, territory, and nesting resources.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

While the elaborate songs of male passerines are well documented for their role in intrasexual resource competition and mate attraction (Darwin 1859, Kroodsma and Byers 1991, Catchpole and Slater 2008), the traits and ecological contexts in which female birds invest energy into competition have received less attention (Langmore 1998, Amundsen 2000, Stockley and Campbell 2013, Cain and Rosvall 2014, Odom and Benedict 2018, Riebel et al. 2019). For example, when male birds sing, potential receivers within hearing range have access to information about the sender's ability and willingness to defend resources (Gil and Gahr 2002, Beecher and Brenowitz 2005, Catchpole and Slater 2008, Akçay et al. 2015). Interest in female vocalizations and competition has increased since the recent discovery that female song occurred in the common ancestor of modern-day songbirds, and that female song occurs in 32 of 44 modern-day songbird families (Odom et al. 2014, Price 2015, Odom and Benedict 2018, Riebel et al. 2019). The expression, utilization, and variation of female song may offer a greater understanding of the selective pressures driving evolutionary changes in social animals (Clutton-Brock 2007, Rosvall 2011, Cain and Rosvall 2014, Brunton et al. 2016).

Vocalizations serve in competition by indirectly conveying fighting abilities and directly conveying motive, or willingness, to fight (Shutler and Weatherhead 1991, Gil and Gahr 2002, Lane and Briffa 2018). Resource Holding Potential (RHP), or an individual's ability to win a contest over a limited resource (Allen and Krofel 2017), is generally based on intrinsic individual characteristics, such as body size, age, and

experience in an area (Mohamad et al. 2010, Lane and Briffa 2018). Resource Value (RV), or an individual's motivation to fight, is generally based on extrinsic characteristics, such as previous access to resources, timing of the contest, and historical reproductive success (Mohamad et al. 2010). Challengers may assess fighting capabilities of their opponent based on their RHP and RV before escalating to more costly and potentially damaging physical aggression (Maynard Smith and Parker 1976, Parker and Rubenstein 1981, Grafen 1990).

While both songs and calls may act as honest signals of RHP and RV, research has focused on the use of bird song, often defined as, "long, complex, vocalizations produced by males in the breeding season" (Catchpole and Slater 2008), rather than calls, in contest competition (Cate et al. 2002, Moskát and Hauber 2019). However, if song is defined by its function, "territorial and mate attracting" (Catchpole and Slater 2008), rather than its form, it provides a broader scope for understanding the significance of vocalizations in competition and selective processes. For example, male house sparrows (*Passer domesticus*) and male Eurasian collared-doves (*Streptopeila decaocto*) produce simple calls that function similarly to song in the context of territorial resource defense and mate attraction (Cate et al. 2002, Catchpole and Slater 2008). Female cuckoos (*Cuculus canorus*) produce a "bubbling" call used in territory signaling and mate attraction (Moskát and Hauber 2019). Female corvids (F. Corvidae; O. Passeriformes) produce a sex-specific call referred to as the "rattle" call, which has been observed in agonistic interactions between females (Brown 1964, Strahl and Brown 1987, Tarter 2008) and in the springtime during courtship (Brown 1964, Hope 1980, Conner 1985). In

corvids, the female rattle call is comprised of a series of rapidly repeated transient notes, comparable to the sound of running a finger down a plastic comb (Brown 1964, Hope 1980, Goodwin 1986).

The female-specific rattle call in Steller's jays (*Cyanocitta stelleri*) has not been observed in males (Brown 1964, 1973). It is thought to provide designative information about the sender, such as species, age, sex, and location (Hope 1980). Hope (1980) suggested the acoustic form of Steller's jay rattle call revealed components of its function based on the way sound moves and is perceived throughout an environment. For example, the female rattle is atonal, delivered at a moderate volume, with abrupt onset for each transient note (Hope 1980). The volume allows the female rattle to be heard from a relatively far distance, with the continuous abrupt onset of notes allowing binaural location of the caller (Hope 1980). This is in accordance with the notion that threat calls must convey the location to be avoided in order to be effective, and that they are typically noisy, atonal, and sustained (Hope 1980).

This interpretation support Brown's (1964) conclusion that the rattle call in female Steller's jays was used as a territorial threat. Brown (1964) observed the rattle in aggressive contexts (e.g. in conjunction with supplanting) in 41 out of 49 rattle call observations on known-sex female jays. In aggressive interactions between two Steller's jays, the rattle was used the most out of any call; 74 rattles out of 107 calls from eight females (Brown 1964). Furthermore, Brown (1973), elicited rattle calls in a female Steller's jay by electrically stimulating the hypothalamus; the same region of the brain

that controlled crest raising and vigorous pecking with low thresholds of electrical stimulation.

The female rattle call has been documented for its use in aggression in Steller's jays, but it is unclear how the call functions within the territorial breeding system, mate guarding, and/ or mate selection. Hope (1980) and Brown (1964) observed the rattle in courtship contexts as well as in aggression. During spring gatherings from February – April, two or more Steller's jay pairs met on territorial boundaries to call, including rattle, and to perform ritualized sidling displays (Brown 1964, Hope 1980). While it is difficult to determine the function of the female-specific rattle call based solely on its acoustic structure and occurrence, life history traits linked to higher or lower rates of rattle calling may provide insight.

In socially monogamous species, such as Steller's jays, female reproductive success is enhanced by prolonged access to a mate and resources (Black 1996, Clutton-Brock 2007, Rosvall 2011). Birds that remain paired throughout breeding seasons benefit from reduced cost of searching for a mate, increased coordination of activities, site familiarity, and parental care (Black 1996, Gowaty 1996, Brunton et al. 2016). Whereas male reproductive success is limited by access to females, female reproductive success is limited by access to relatively higher quality resources that are often inaccessible in male-defended territories (Gowaty 1996, Clutton-Brock 2007). Thus, paired females benefit from the ability to defend their partnership against intruder females in competition, and unpaired females benefit from gaining partnerships with territorial males (Gowaty 1996, Cézilly et al. 2000).

In this study, I observed Steller's jays with known pair, territory, and nesting status to quantify differences in rattle call occurrence based on intrinsic Resource Holding Potential (RHP), and extrinsic Resource Value (RV) attributes of females. I describe the rattle call with regard to acoustic structure and context of use in individual female Steller's jays. I identify individual characteristics that might contribute to RHP and RV, and test for differences in rattle rates based on those traits. I also note changes to females' social status corresponding to rattle call occurrence.

More specifically, I conducted focal-animal observations on a color-marked population of Steller's jays to describe the acoustic attributes of this female-specific vocalization in terms of duration (s), note rate (notes per second), peak frequency (kHz), and fundamental frequency (kHz). I quantified the social context in which rattling occurred, including female-female competition, female-male within pair communication, and female-male mate selection. I described female characteristics that might contribute to RHP (Table 1), and tested for differences in rattle call occurrence between females with varying RHP by comparing female age, structural body size, duration of pair bond, and duration of territory ownership to two measures of rattle call occurrence: the number of rattle calls per observation (RPO), and the proportion of observations in which a rattle occurred (POR). I expected to find positive relationships between RPO, POR and female age, structural body size, duration of pair bond, and duration of territory ownership. I described three life-history traits that might contribute to RV (Table 1) and tested for differences in rattle call occurrence between females with varying RV by comparing female nesting status, pair status, and territory status to RPO and POR. Finally, I

compared RPO between females engaged in dyadic rattle contests, and described corresponding changes in females' partnership or territory status.

Table 1. Correlates of traits driving investment in contest competition, and support for their role in Resource Holding Potential (RHP) and relative Resource Value (RV) to an individual.

Driver	Trait	Correlates	Examples
RHP	Age	Older individuals won contests.	Kemp 2006, Tsai et al. 2014
	Structural size	Larger individuals won contests.	Lindström 1992, Bridge et al. 2000, Nijman and Heuts 2000, Brown et al. 2006, Gherardi 2006, Tsai et al. 2014
	Duration of pair bond	More aggressive birds had higher pairing success.	Kunc et al. 2006
	Duration of territory ownership	Owners had a competitive advantage over intruders.	Maynard Smith and Parker 1976, Shutler and Weatherhead 1991, Bridge et al. 2000, Nijman and Heuts 2000, Hoefler 2002, Lefevre and Muehter 2004, Kasumovic et al. 2011
RV	Nesting experience	Mating experience increased agonism.	Tsai et al. 2014
		Individuals with lower prior access to mating opportunities were more aggressive.	Brown et al. 2006, 2007
	Partnership status	For paired birds, maintaining pair status was more valuable than new partnerships.	Black 1996
	Territory status	Territory had greater value to owner than intruder.	Shutler and Weatherhead 1991, Alcock 1998, Bridge et al. 2000, Bradbury and Vahrenkamp 2011, Kasumovic et al. 2011
		Lack or necessity of resource increased its relative value.	Mohamad et al. 2010

MATERIALS AND METHODS

Study species

Steller's jays are a generalist non-migratory species that occupy mountainous evergreen forests, campgrounds, parks, and suburban areas in western North America (Walker et al. 2016). In northern California, Steller's jays form pair bonds in their first or second year, and once formed, pairs occupy territories year-round in socially monogamous partnerships, with both sexes participating in territory defense, resource acquisition, and brood rearing (Gabriel and Black 2010, 2012a). However, some extra-pair relationships have been detected among neighbors via examination of offspring DNA (Overeem et al. 2014).

Young jays disperse from their natal territory to 'float' in peripheral habitat on the fringes of defended territories, or pair with territory-holding individuals to gain access to food and nesting resources (Atwood 1980). For other jays species, dispersal is female-biased in predominantly male-defended territories (Greenwood 1980). Steller's jays exhibit site-centered dominance, where dominance is not related to contestants' relative body size, but is highest in the nesting area of a bird's territory, decreasing with distance from that point (Brown 1963). This creates a series of overlapping territories in which neighboring pairs regularly interact with one another, providing opportunities for researchers to observe social interactions. In the non-breeding season (September –

December), Steller's jays regularly make forays from their nesting area to forage and cache food items using their highly developed spatial memory (Walker et al. 2016).

Study Site

The study site, measuring approximately 2.2 km^2, had 15 feeder-traps distributed across neighborhoods at the forest-suburban edge of the redwood (*Sequoia sempervirens*) forest in Arcata, California (40°59′N, 124°06′W, Figure 1). Feeder-traps were mounted on posts or fence lines in the yards of private properties and on the Humboldt State University (HSU) campus. Feeder-trap locations typically contained one or two building structures, a lawn, a fence line, and a mixture of ornamental and native vegetation.

Members of the HSU wildlife department have marked and observed Steller's jays in this population since 1998 as part of a long-term study (Gabriel and Black 2010). Volunteers and researchers regularly provisioned feeder-traps with shelled peanuts to observe individual foraging behaviors (e.g. willingness to enter trap as an index of boldness) and social interactions (Gabriel and Black 2010, 2012b). They routinely recorded nesting dates, nest locations, number of nest attempts, and nest success during the nesting season from March - September (Gabriel and Black 2012a). They updated pair status (whether or not a Steller's jay was in a partnership with another Steller's jay) regularly based on presence of affiliative behaviors: nesting, joint perching, travelling together, courtship feeding, and partner vocalizations (Gabriel and Black 2010, 2012a).
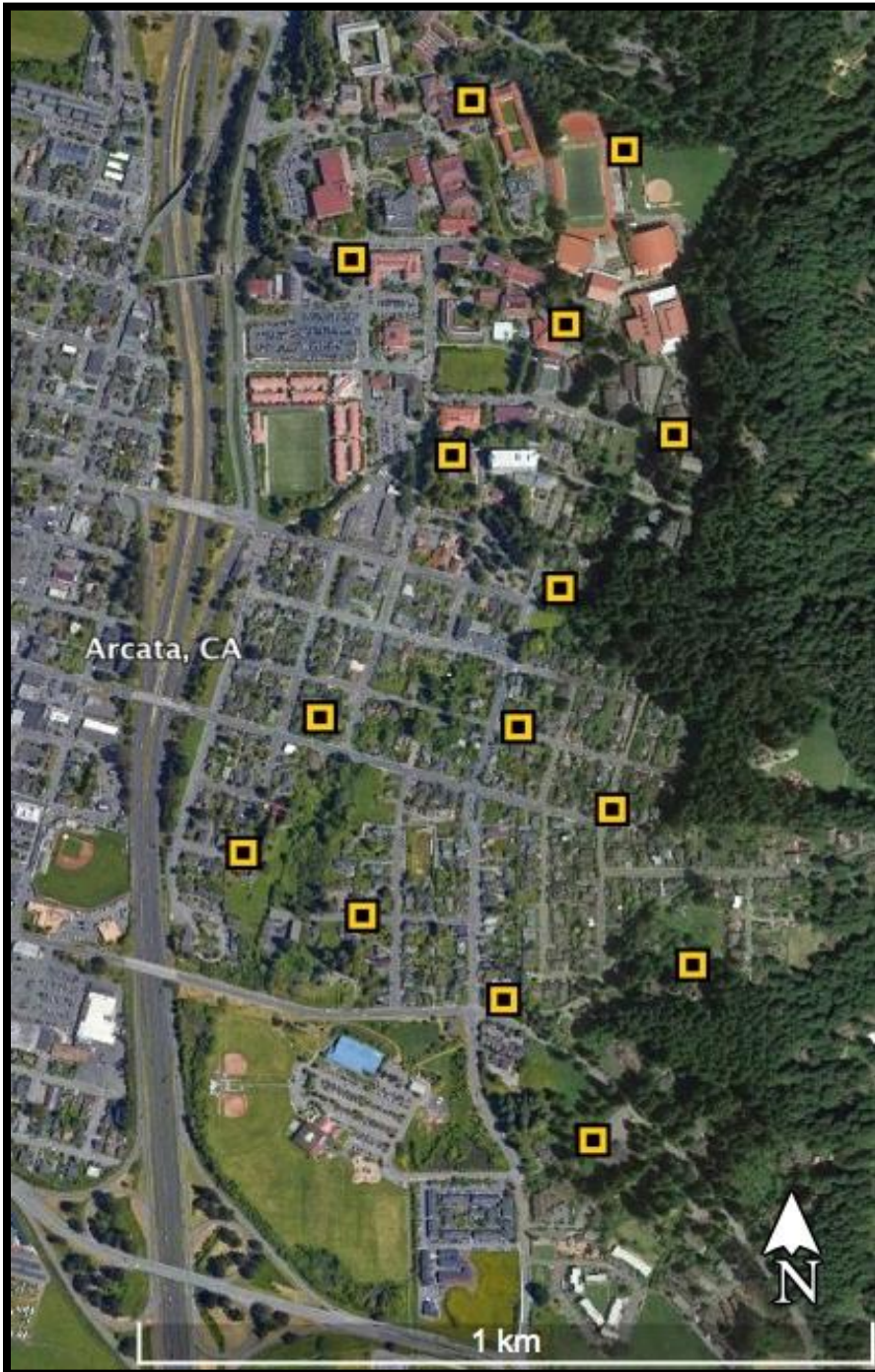
Figure 1. Locations and placement of Steller's jay feeder-traps and focal female
observations in Arcata, CA, US from August 2017 – April 2018.

Banding and Individual Characteristics

Over the last 22 years, our graduate laboratory has captured Steller's jays in the sliding door feeder-traps (71 x 35.5 x 28.5 cm) and fitted them with a combination of three unique colored leg bands and one U.S. Geological Survey metal leg band. We captured birds using a string and pulley system and released them at the capture site within 30 minutes of capture. We assigned sex using the presence of breeding season sex-specific diagnostics (presence of brood-patch in females or cloacal protuberance in males from March – September), known partner status (if the bird was paired with a known male or female, assuming no same-sex partnerships), or observation of sex specific vocalizations in the field (female rattle or male clink call) (Hope 1980). Previously, other members involved in this long-term study determined sex on DNA extracted from blood samples for 32 birds sexed as female (rattle call) and 34 sexed as male (clink call), with 100% and 91% accuracy, respectively (Overeem, Gabriel and Black unpublished data).

We assigned age based on gape coloration and/ or feather condition at the time of capture (Pyle et al. 1997). We measured left and right tarsus lengths (mm) using calipers. I used an average of adult (after hatch year / after second year) tarsus length measurements across captures as an index for body size (hereafter "structural size") for each female (Freeman and Jackson 1990).

Female Observations

I conducted 20-minute focal observations on all known-female Steller's jays ($n =$ 20) in the study population from August 2017 – April 2018. I created an observation schedule by randomly selecting females using a random number generator. After the first round of observations in which I did not detect some females after 10 – 15 minutes of searching, I observed females on a priority basis; I sought females with the fewest number of completed focal observations before females that had more time under observation. To find a selected female I provisioned the feeder closest to the female's historical nesting area with a constant supply of peanuts. I observed floater females opportunistically, when present at feeders. I began observation immediately when the focal female appeared. I recorded the number of times a focal female gave the rattle call ("rattled"), and the band combination of the bird receiving the call. I considered the bird to be the receiver if the calling female's body position, eye gaze, body movements (e.g. chasing, supplanting), or ritualized 'sidling' display (see Brown 1964) was oriented toward it. If I could not identify any one receiver, or if it appeared as though the female was rattle calling to all Steller's jays in an area, then I recorded the receiver as 'unknown' or 'all'. I defined a call as an uninterrupted series of notes. I also recorded the number of rattles directed at the focal female or her mate by a non-focal female during the observation period.

I ended observations after 20 minutes. I ended the observation early and discarded the data if the focal female was out of sight for more than five consecutive minutes

during an observation period. I considered a female to be in-sight if I could see the body and bill movement, or if I could guarantee that a rattle call was coming from a visually obstructed female. For example, if a female landed on a branch directly overhead, and the branch obstructed the female's body from view, I still considered the female in-sight as long as I could see her leave, or other birds appear.

Acoustic Recording

I recorded rattle calls using a Zoom H4N Handy Recorder and Sennheiser MKH 70 P48 shotgun microphone (sampling rate 48 kHz, 24 bit resolution) opportunistically, when traveling between observation points, and during female focal observations by setting the microphone to record on a tripod approximately 5 m from the feeder trap prior to observation.

Statistical Analysis

I measured spectrograms of rattle calls to describe the duration (s), note rate (notes per second), peak frequency (kHz), and fundamental frequency (kHz), of rattle calls using Raven Pro v1.4 software (Bioacoustics Research Program 2011). Terminology for acoustic qualities follows Hope (1980). I was unable to identify sender and receiver identities in some audio recordings. Therefore, rattle call recordings were used only to describe acoustic aspects of the call, and not individual variation based on female characteristics.

My data did not meet assumptions of parametric tests, therefore, I used non-parametric statistical analyses that are robust against non normal distribution, small sample sizes, and outliers to analyze rattle occurrence data (Siegel 1956) on females with at least three completed focal observations using Program R 3.3.3 (R Development Core Team 2017). I quantified two measures of rattle occurrence using averages for each female across observation periods: rattles per observation period, and proportion of observations in which a rattle occurred.

I tested for differences in timing of rattle use by comparing winter (August - December) and spring (January - April) RPO and POR rates using two-way Mann-Whitney *U* tests. I investigated receiver context by comparing female, male partner, non-partner male RPO and POR using Kruskal-Wallis tests. I defined partner males to be the mate of the female producing the rattle call, and non-partner males as any male receiver that was not paired to the female producing the call.

I tested how intrinsic female qualities (RHP) affect rattle occurrence by conducting a series of Spearman correlation tests between RPO, POR and continuous variables: female age, structural size, duration of pair bond, and duration of territory ownership. Age was a continuous variable that I calculated using the number of years elapsed since a bird's initial capture, plus one year for birds captured as AHY, or plus two years for birds captured as ASY. I used nesting records to calculate the duration of territory ownership for Steller's jay females. I assigned unpaired, floater females with no mate or territory a pair-bond duration / territory ownership duration of zero. Figure 2

shows median and ranges for age, pair duration and territory duration of Steller's jay

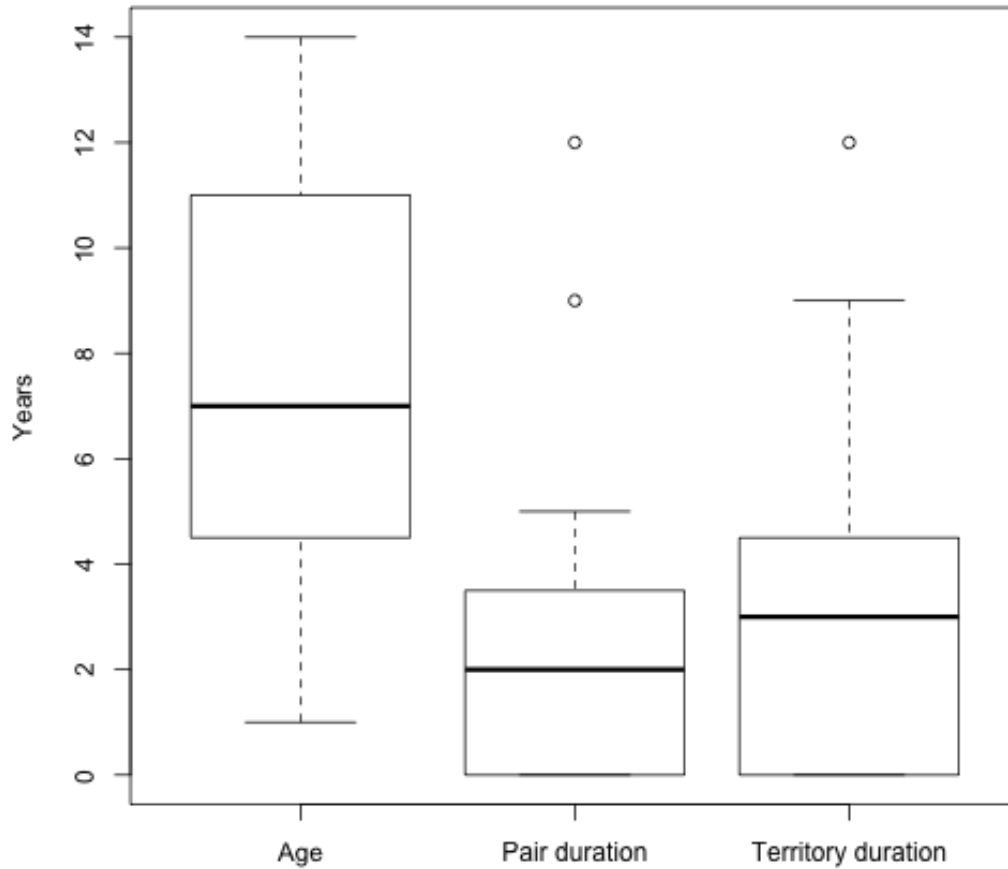females in this study.

Figure 2. Age, duration of pair bond, and duration of territory ownership for Steller's jay females in Arcata, California from August 2017 – April 2018. The bars represent the median of the data, the boxes delineate upper and lower quartiles (25% and 75%), the tails extend to minimum and maximum values, and the points above pair duration and territory duration are outliers.

I tested how extrinsic female qualities (RV) affect rattle occurrence by testing for differences in RPO and POR based on females' life history traits: pair, territory, and nesting status (Table 2). I tested for differences in RPO and POR based on partner status (paired, unpaired), on territory status (territorial, floater), and on nesting status (novice or experienced), using Mann-Whitney U tests. I also tested for differences in territorial rattle rates compared to intruder rattle rates within a females' territory. Most of the territorial females in the study area were paired ($n = 11$), except for three cases in which an unpaired, previously paired female maintained defense of an area. One novice female entering into her first nesting season was paired throughout the study period. She was assigned "novice" status for nesting analyses, and "paired" status for partnership analyses.

When two females engaged in back-and-forth rattle contests, or 'dyads' during an observation period, I tested the influence that pair, territory, and nesting status had on sender and receiver RPO. I noted corresponding changes to territory and partnership statuses.

Ethical Note

This project was carried out under approved federal bird handling licenses and Humboldt State University's Institutional Animal Care and Use Committee (Protocol no. 16/17.W.49-A). Homeowners of Arcata granted permission to access their private properties for Steller's jay observation and feeder placement.

Table 2. Definitions and sample size for groups of female Steller's jays (*Cyanocitta stelleri*) observed in focal animal observations, based on females' pair, territory, and nesting history in Arcata, California from August 2017 - April 2018.

Life-history trait	Status	Definition	n
Partnership	Paired	Female was observed foraging, travelling, nesting, or displaying affiliative behaviors (e.g. courtship feeding, soft-calling) with the same male throughout the study period.	12
	Unpaired	Female was not observed foraging, travelling, nesting, or displaying affiliative behaviors (e.g. courtship feeding, soft-calling) with a male partner.	8
Territory	Territorial	Female maintained territory; defended observation area surrounding feeder-trap.	14
	Floater	Female did not have territory; used peripheral habitat.	6
Nesting	Experienced	Female had historically nested but could be either paired or unpaired (widowed or divorced) during data collection.	17
	Novice	Female that had never nested.	3

RESULTS

Between August 2017 and April 2018, I observed 158 rattle calls from 18 out of 20 focal females during 49 of 162 (30%) observation periods. Females produced 1-20 rattles per observation period in observations that contained rattles (mean = 3.23 RPO ± 0.58 SE, n = 18. Individual females rattled in an average of 35% (± 0.06 SE, n = 20) of their observations. Rattles were directed at both females and males, while perched, flying, supplanting, being supplanted, and aggressive sidling (see Brown 1964). I did not observe any known-male Steller's jays produce the rattle call.

Based on measurements of spectrograms, rattling consisted of a series of rapid notes given at 37 – 98 notes per s (mean = 68 ± 17 SE, n = 16) for 0.80 – 2.14 s (mean = 1.55 s ± 0.39 s, n = 16). Notes had an average peak frequency of 14,855 kHz (± 2,716 kHz SE, n = 16) and an average fundamental frequency of 3,850 kHz (± 205 kHz SE, n = 16; Figure 3). I observed a short duration guttural note preceding the rattle as described by Brown (1964, 1973) on several occasions. I identified the receiver of the rattle call 42 times; 18 rattles were directed at other females (43%), and 24 were directed at males (57%). I observed paired females (n = 10) rattle calling at their mate, and not at non-partner males. Unpaired females (n = 8) rattle called at territory owning males (n = 7), and not at floater males. Rattle behavior (RPO, POR) was not significantly different between non-breeding and pre-breeding seasons; however, there was a tendency for higher average RPO in the spring (mean = 3.48 ± 1.14 SE, n = 19) than the winter (mean = 1.41 ± 0.64 SE, n = 17) (U = 125, P > 0.20).

Rattle occurrence varied with female nesting status and territory status but not with partner status. Novice females had higher rattle rates (mean RPO = 8.11 ± 2.30 SE, $n = 3$; mean POR = 0.778 ± 0.11 SE, $n = 3$) than experienced females (mean RPO = 2 ± 0.62 SE, mean POR = 0.28 ± 0.06 SE, $n = 17$) (U = 47, P < 0.05) (Figure 4). Floater females rattled in a higher percentage of observations (mean POR = 0.57 ± 0.13 SE, $n = 6$) than territorial females (mean POR = 0.26 ± 0.06 SE, $n = 14$) (U = 17.5, P < 0.05). However, within a female's territory, the territory owner rattled more on average (mean = 2.55 RPO ± 0.39 SE, $n = 29$) than intruding territorial or floater females (mean = 0.93 RPO ± 0.33 SE, $n = 29$; U = 164.5, P < 0.01).

Back and forth rattle calling between two females (aka 'dyads') occurred on five occasions, when a territorial female and a floater, novice female took turns rattling at one another, or rattling at the territorial female's mate, within her territory (Table 3). Two of the novice females, and one of the territorial females were unpaired; the other novice female and two territorial females were paired. The two unpaired, novice females produced as many, or more rattle calls (mean = 4.25 RPO ± 1.31 SE, $n = 2$) than the paired territorial females (mean = 2.5 RPO ± 0.29 SE, $n = 2$) during four independent observations of these dyads. The paired, novice intruder was in a dyadic rattle interaction with an unpaired, territorial female. The novice female rattled three times to the unpaired territorial female's four rattles (Figure 5). The unpaired, novice females that rattled as much as or more than the territorial females in these dyads were later observed in partnerships with the territorial females' mates.

A total of five females changed pair and/or territory status during the observation period from August 2018 to April 2019. Nesting status could not be changed unless a female nested during the study. Four females gained partners during the study period: the two aforementioned novice females that usurped two territory holding females, and two experienced, unpaired territory holders that were widowed / divorced from their previous partner prior to data collection. One of the territorial females that were usurped by a novice female immediately re-paired in a neighboring territory. Both females that were usurped had been in long-term partnerships (4 and 12 years) within their territory. I could not find any differences between females that changed status and females that maintained the same status based on RPO or POR.
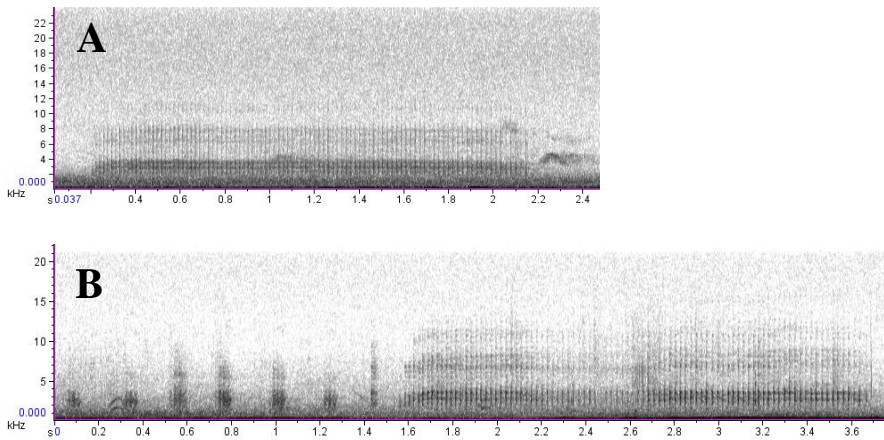
Figure 3. A) Spectrogram of female Steller's jay rattle call, with duration 1.95 s, note rate 50 notes/ sec, peak frequency 11865 kHz, and fundamental frequency 3594 kHz recorded in February 2018 in Arcata, California; B) spectrogram of Steller's jay female rattle call preceded by repeated guttural note recorded in February 2018 in Arcata, California. Calls were recorded using Sennheiser MKH 70 P48 shotgun microphone. Acoustic analyses were conducted using Raven Pro v1.43.
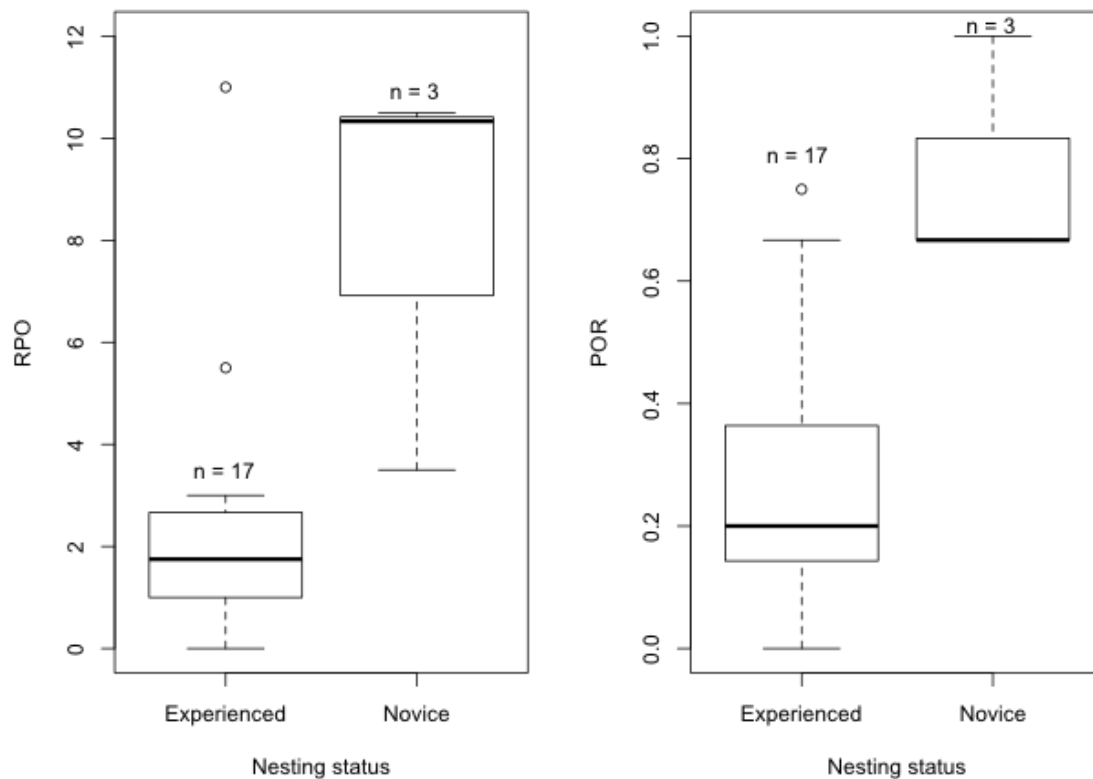
Figure 4. Median number of rattle calls per observation period (RPO) and average
proportion of observation periods (POR) in which female Steller's jays with
different nesting statuses produced rattle calls in Arcata, California from August
2017 – April 2018. The bars represent the median of the data, the boxes delineate
upper and lower quartiles (25% and 75%), the tails extend to minimum and
maximum values, and the points above experiences females are outliers.

Table 3. Dyadic rattle call interactions between paired, territorial female Steller's jays
within their territories, and intruder female Steller's jays. The first and third
columns, Territorial and Intruder, show the females' unique band-combination
identities. The second and sixth, 'rattle' columns show the number of rattles each
female made during a single observation period. The territory and paired columns
refer to whether or not the intruding female was territory owning (yes = Y, or no
= N). The last column describes behaviors exhibited by the females during their
interaction. All data were collected between August 2017 and April 2018 in
Arcata, California.

Territorial	Rattles	Intruder	Territory	Paired	Rattles	Behaviors
LRMG	3	BOMY	N	N	3	Both females engaged in aggressive sidling while calling.
LRMG	2	BOMY	N	N	4	Both females engaged in aggressive sidling while calling.
MWPP	3	HYML	N	N	4	MWPP remained perched while calling, HYML flew around and called from several perches.
MWPP	2	HYML	N	N	8	MWPP remained perched while calling, HYML flew around and called from several perches.
PLMP	2	LHMB	N	Y	3	PLMP followed and supplanted LHMB until LHMB left.

DISCUSSION

Researchers are beginning to document the occurrence, drivers, and mechanisms of female competition. While sexual selection based on male song has been the model for studying honest signaling, secondary sex traits, fitness limitations, and adaptation in songbirds, this study focused on female competition using the rattle call. The rattle call is produced only by female members of the family Corvidae, and has been documented in contexts of sexual selection: female-female aggression and female-male courtship (Brown 1964, Hope 1980). I identified characteristics that were associated with competition in other species: inherent traits that influence an individual's resource holding potential, and life history traits that influence an individual's willingness to compete for a resource in question. I found differences in rattle call rates for female Steller's jays based on nesting experience, and territoriality, and observed changes in those life history statuses for some birds following dyadic rattle contests. Continuing long-term research on this individually marked population of Steller's jays afforded me the opportunity to seek answers regarding the factors limiting female fitness, and how the female-specific rattle adaptation is used in our study population.

On average, female Steller's jays in this Arcata, Humboldt County, CA population produced rattle calls with a faster note rate (68 notes per s) and slightly shorter duration (1.55 s) than those observed by Hope (1980) in Alameda and Contra Costa Counties, CA in the 1970s (e.g. 41 notes per s, and 1.83 s duration; Hope's 1980). This could be the result of a local dialect, difference in methods for acoustic measurements, or

from small sample sizes in both studies. Future investigation into variation in rattle calls among populations could use a larger sample of acoustic recordings across geographic areas, with females of different nesting, partnership, and territory statuses.

Observing individually marked Steller's jays allowed me to compare rattle rates with regard to sender and receiver life history characteristics (*sensu* Johnston 1997). Paired females rattled at their male partner, and unpaired females (floaters) rattled a territory-owning males and females. Floater females rattled more than territorial females in general. Novice females (those that had not yet nested) rattled more than experienced females. Territorial females rattled more than intruders, except when the intruder was a novice female. Two novice females changed from unpaired, floater novices to paired, territorial novices after producing as many or more rattle calls than the territorial female over the course of two dyadic interactions each.

Female Steller's jays rattled at other females, at territory owning males, and at their mates, if paired. Paired females did not rattle at males that were not their mates. I did not observe females rattling at unpaired, floater males. Assuming the rattle has energetic costs great enough to dissuade females from calling indiscriminately, this might indicate the rattle is used toward male receivers to gain or maintain access to territorial resources.

Previous research on contest competition describes relationships between an individual's intrinsic qualities that improve likelihood of winning contests for limited resources (RHP) and investment into competition (Table 1). I did not observe a difference in rattle call occurrence based on intrinsic female characteristics relating to RHP. Female

age, structural size, duration of territory ownership, or duration of partnership were not significant predictors of RPO or POR. Steller's jay dominance hierarchies conform to the 'bourgeois' strategy, where territory ownership is more important than body size in contest competition (Brown 1963), which might explain why structural size did not predict rattle occurrence. Conversely, duration of territory ownership did not influence rattle call occurrence on a population level. Territory owners generally rattled more than intruders during one-on-one interactions.

An individual's willingness to enter into competition depends on the relative value of the resource in question (Enquist and Leimar 1987, Hurd 2006). Territorial females and novice females had higher rattle rates than other females in some contexts. Dyadic interactions between paired-territorial, and intruder females followed resource defense theory (see Alcock 1998, Bridge et al. 2000) in which paired-territorial females invested more in rattle calling than intruders. However, novice-floater females rattle called more than paired-territorial females in dyadic interactions. I observed territory / partnership changes for the two paired, territorial females that were twice 'out-rattled' by intruders. Both paired, territorial females were in long-term partnerships (5 + years) with their mates. After the interaction I observed one female with another male in a neighboring territory, and did not see the other again. The novice females that rattled more than the paired, territorial females nested with the (previously) paired territorial mates of the former females.

Paired, territorial females have the most to lose by being out-competed (Shutler and Weatherhead 1991, Alcock 1998, Bridge et al. 2000, Kasumovic et al. 2011). In

socially monogamous birds, including Steller's jays, reproductive performance is suggested to be enhanced by coordinated participation in mutual tasks of pair members, such as fighting for and obtaining food, caring for young, watching for predators, and defending a territory (Black 1996, Gabriel and Black 2012*a*, *b*, 2013). Even so, copulations outside the pair bond and/ or intra-specific nest parasitism can result in extra-pair offspring in the nest (Birkhead and Møller 1995, Griffith et al. 2002). In this study population, Overeem et al. (2014) quantified 15.2% of Steller's jay nests contained extra-pair young. Thus, when extra-pair behavior poses a threat to partnerships and subsequent access to resources, paired, territorial females are expected to engage in competition against intruder females (Gowaty 1996, Clutton-Brock 2007).

Novice females might have the most to gain from winning a contest. They have limited access to resources in territories defended by male and female pairs. If the rattle call has been adapted for sexual selection, a contest providing novice females with coordinated resource defense, increased mating opportunities, male parental care, and experience in nest building and brood rearing would increase individual fitness (Black 1996). I observed two instances of partner 'divorce', where a female's partnership ended without death of her mate. Both were preceded by two contest competitions between a dyad, where the intruding female rattle called more than the territorial resident. I am reporting this is anecdotal evidence to provide direction for future research. It is unclear to what extent this was a result of female-female competition as opposed to male choice, as males were present bystanders during 80% of female-female rattle battles. A study on the outcomes of dyadic rattle contests could reveal other applications.

While the rattle call of female Steller's jays is harsh compared to the melodious trills and whistles of conventional bird song, it appears to serve similar functions in female-female contest competition, potential mate selection via unpaired-floater to territorial male communication, and within-pair communication via paired female to paired male communication.

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