

THE VOCAL REPERTOIRE OF THE WHITE-THROATED MAGPIE-JAY  
(*CALOCITTA FORMOSA*)

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Doctor of Philosophy

By  
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# THE VOCAL REPERTOIRE OF THE WHITE-THROATED MAGPIE-JAY

(*CALOCITTA FORMOSA*)

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From February 2003 through May 2005, I studied the vocalizations and communication system of the white-throated magpie-jay (*Calocitta formosa*) in Santa Rosa National Park, Area de Conservacion Guancaste, Guanacaste, Costa Rica. The goal of the study was to determine the size and function of the vocal repertoire of this species. I surveyed the repertoire as a whole, and used playback and observation to study three specific call types to determine their explicit function.

White-throated magpie-jays mob in response to low and high threat predators. Mobbing calls vary structurally and in delivery depending on the threat of the predator, with higher threat contexts elicit faster calling bouts and shorter calls. A playback showed that receivers pay attention to both variables, approaching if calls are short or given rapidly.

Female magpie-jays beg loudly early in the nest cycle, when they are fertile. Group members provision the female at low rates initially, but increase provisioning when eggs hatch. Provisioning is positively related to begging. Begging is the loudest signal in the vocal repertoire, and is variable in structure. Begging probably indicates the need of a female, but the structural and amplitude characteristics suggest that females have co-opted begging to signal their fertility.

Magpie-jays produce a distinct visual and vocal display in response to low-threat predators, the predator approach display. 134 call types were recorded during predator approaches, and the same call types were recorded in the hour before dawn. Production of and response to these calls is strongly male-biased, and males were

more likely to respond to playback when their mate was fertile. These loud calls may function as alarms, but the male bias and elaborate nature suggest males have co-opted them for self-advertisement.

Magpie-jays use fourteen functionally distinct call types, but use at least 150 structurally distinct types. Fourteen functional call types is not usual for a corvid, but such structural diversity is unprecedented in this group. Comparisons among nine corvids suggest that several aspects of social ecology can affect repertoire sizes.

## BIOGRAPHICAL SKETCH

Jesse Ellis was born September 23<sup>rd</sup>, 1978 in Minneapolis, Minnesota, to Suzanne Swanson and John Ellis. His childhood, spent in Saint Paul, Minnesota, was generally marked by an appreciation of the odd and strange, as well as a fascination with birds. His high school career was erratic: initially it was spent in class, but he unschooled himself for a large fraction of his four years, returning to the confines of the classroom only when necessary for his educational satisfaction. He graduated in 1997. In part due to his independent streak, he was awarded a Barbara Hirschi-Neely Scholarship to attend Lewis & Clark College, in Portland Oregon. There, his interest in birds, ecology and evolution were tied together into a love for behavioral ecology by his Animal Behavior professor, Dr. Kenneth Clifton. He spent a semester observing the biological oddities of Australia. His senior Honors Thesis focused on winter sociality in the Steller's Jay, and he earned his Bachelor of Arts in Biology in 2001, graduating with honors. That same autumn he began his graduate work at Cornell University in the Department of Neurobiology & Behavior.

*To my parents, who always let me bird.*

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## PREFACE

Communication is ubiquitous among animals, but few studies have been undertaken to determine why each species uses the specific number of signals that it does. This is the topic of my dissertation. My approach was to study the repertoire of a single species, the white-throated magpie-jay, in detail, to determine how its repertoire reflected its communicative needs. I then compared its repertoire to those of several species for which repertoires are well documented.

Several factors have been proposed to increase repertoire size. Aspects of sociality, including group size (McComb & Semple 2005; Freeberg 2006), group complexity (Blumstein & Armitage 1997) and dominance interactions (Rohwer & Ewald 1981; Popp 1987b; Popp 1987a) all select for larger repertoires. Sexual competition can affect repertoire size through both inter- and intra-sexual competition. Intersexual competition can select for signals for mediating conflicts and assessing rivals, while the need to attract mates and indicate quality can also increase repertoire size (Catchpole et al. 1984; Hack 1997; Johnson 2000). Environmental diversity can also influence repertoires; many species inform conspecifics about the movement and nature of predators and the presence of food (Strusaker 1967; Elgar 1986; Gyger et al. 1987; Gyger & Marler 1988). Indeed, humans represent the epitome of signaling about environmental diversity. Physiological and physical restrictions can decrease or limit repertoire size, but I do not treat those factors here, since their impact on communication can be difficult to measure.

In order to understand how these various factors affect repertoire size, we need to determine how repertoire size varies with the presence or absence of each factor. To do so requires some sort of standard currency for comparing repertoire sizes. Because

few studies have actually compared repertoires directly, no formal method exists for this task. Biological signals can vary considerably, as any field worker can attest (Figure 1). Such variation can complicate comparisons of repertoire size among species. To make such comparisons, I have devised a method for analyzing both the functions the repertoire performs and the structural variation within the repertoire. By parsing repertoires in this way, we can compare repertoire function in relation to various aspects of a species' biology despite different levels of structural variation within different repertoires.

To parse a repertoire for analysis, I use a hierarchical scheme based upon the probable function of each signal (Figure 0.1). I first use observations of context, sender production and receiver response to sort signals into widely accepted general signal classes. The signal classes I use pertain specifically to the information contained in the signal, and do not indicate anything about sender and receiver identity or the degree. Signal classes in my scheme are: predator related, food related, territory defense, conflict resolution, mate attraction, social integration and courtship. Within each general signal class, I determine number of functionally distinct signals. When structurally different variants produce similar responses and occur in similar contexts, I infer that these have the same primary function, even if such variation is meaningful in determining the degree of response, for instance. The total tally of functionally distinct signals is the functional diversity of the repertoire, while the total tally of structurally distinct signals is the structural diversity of the repertoire.

I have applied this approach to the highly diverse vocal repertoire of the white-throated magpie-jay. Numerous field workers have commented on magpie-jays' vocal prowess, raising the question of whether magpie-jays are saying many things (high functional diversity) or saying a few things many ways (low functional diversity and high structural diversity). Three chapters of my thesis deal with closer examinations of

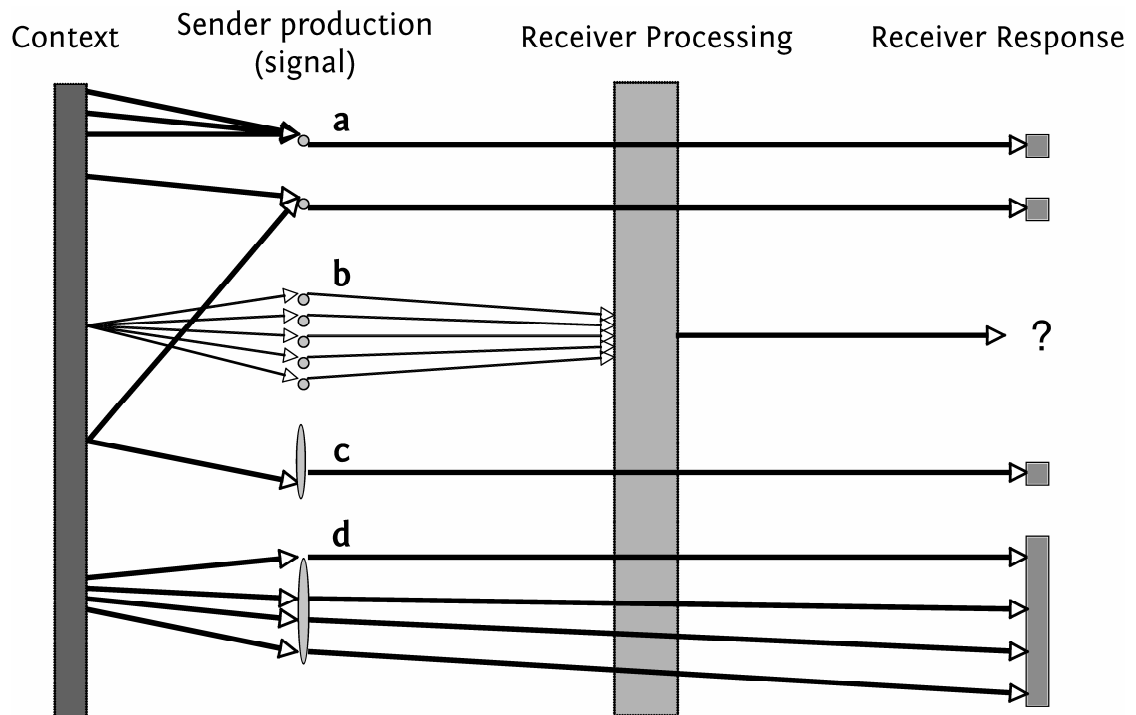


Figure 0.1. Sample mapping function for a repertoire, illustrating coding functions that can cause difficulty in determining repertoire “size”. Arrows indicate the correspondence between each level of the production and reception of a signal. Several different contexts can elicit the same signal type (a), or a single context can elicit multiple different signals (b). Variation within a signal can be epiphenomenal (c) or functional (d). Receiver responses (?) can also be difficult to determine.

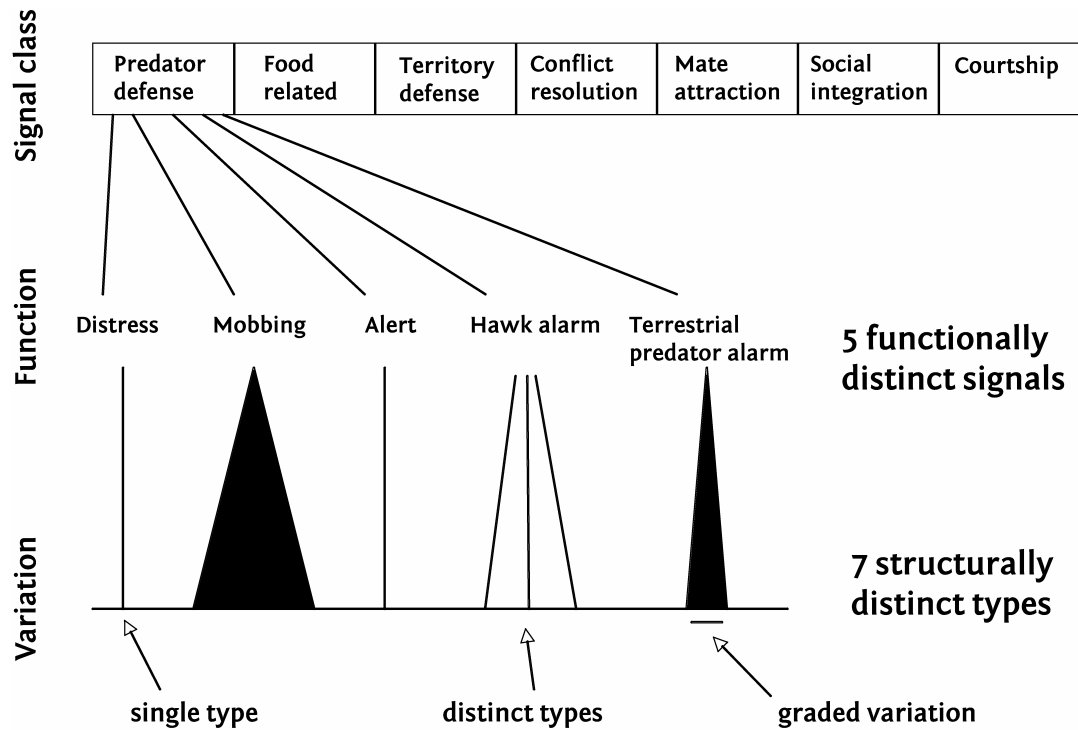


Figure 0.2. Example of repertoire classification for one signal class, predator defense signals. Within a single general signal class, predator defense, signals can be classified by general function, and variation within those functionally distinct types assessed. Such a classification scheme allows one to compare functions of repertoires, without large structural variation making comparisons meaningless.

the function and structural variation of specific signal classes. The first chapter looks at how relatively small variation within a single call type, the mobbing call, can transmit information about threat level. The second chapter analyzes in detail the function of a call, the adult begging call, that on the surface seems clear; to solicit feeding. However the phenology and structure of this call suggest it may perform a second function, advertisement. In the third chapter I ask whether the huge diversity of vocal signals that magpie-jay produce in response to low-threat predators are all variants of a single signal, or whether they have different functions. The final chapter presents the functional and structural diversity of the repertoire as a whole. I also assess how the repertoire of the white-throated magpie-jay compares to those of other corvids whose repertoires are well described. Together these studies analyze how variation with and between signal categories can affect repertoire size, and present a method for comparing them.

**Chapter 1: Which call parameters signal threat to conspecifics in White-throated  
Magpie-jay mobbing calls?**



## ABSTRACT

Variation in signals often encodes additional information beyond that provided by the main signal. Many species communicate degree of threat using such signal variation. However, multiple signal parameters often covary with threat level, and can be unclear whether receivers are using variation along one or more parameters when assessing threat level. White-throated magpie-jays (*Calocitta formosa*) vary several call parameters when mobbing, and here I report on an experiment testing whether such variation contains information used by conspecific receivers, and which parameters are salient to receivers. I collected data on natural mobbing sequences in two threat contexts and found that mobbing calls were highly variable in both length and inter-call interval, but on average, both parameters were shorter in high threat contexts, while call frequency did not differ. To determine how jays respond to such between-context variation, I conducted a playback experiment in which call length and inter-call interval were independently varied in a factorial design. This is one of the first studies to my knowledge to deconstruct and independently test covarying signal parameters in an anti-predator signaling system. Magpie-jays responded more often to treatments with either short call lengths or short inter-call intervals, in concordance with the natural calling data. However, the two parameters did not appear to act independently; responses were not additive, and short calls at short inter-call intervals elicited no stronger of a response than short calls at long intervals or long calls at short intervals. Receivers can use either parameter when assessing threat level. These data demonstrate that mobbing can signal threat level, that call length and call rate are

redundant, and that receivers need not use both to determine whether to approach.

Keywords: predator defense, mobbing, alarm, *Calocitta formosa*, urgency, threat level

Variation in signaling systems has proven both a boon and a thorn in studies of communication. Some variation is probably epiphenomenal, while some has been shown to be functional, but it can be difficult to determine which is which. Anti-predator signals have provided clear examples of the functional variation. In several systems, there is not a specific “alarm call”; rather, discrete variation in multiple parameters creates wholly distinct call types, which are associated with distinct predator types (Cheney & Seyfarth 1990; Pereira & Macedonia 1991; Evans et al. 1993). In others, variation is continuous, and indicates the threat level presented by the predator (Macedonia & Evans 1993; Blumstein 1995; Warkentin et al. 2001; Randall & Rogovin 2002). The information provided in both types of systems allows receivers to act adaptively in the face of danger. Another anti-predator behavior, mobbing, occurs when a sender encounters a potential predator and approaches it while giving distinctive calls and displays, recruiting conspecifics and often driving away the predator (Curio 1978; Caro 2005). Calls given during mobbing can also vary. For example, recent studies showed that the black-capped chickadee and the Arabian babbler (Naguib et al. 1999; Baker & Becker 2002; Templeton et al. 2005) vary several calling parameters according to the level of threat a particular predator presents. Presumably, if such variation is functional, particular call variants should elicit responses appropriate to the context in which those variants are produced. However, when multiple signal parameters vary, it may be important to determine which is actually carrying the information.

Why should mobbing calls vary with threat level? In group living species, not all group members may be present at the time a predator is discovered. Naguib et al (1999) hypothesized that if the predator is not a high threat, group members can avoid paying opportunity costs of approaching when they do not need to. Conversely, knowing that a predator is high threat could allow vulnerable conspecifics to avoid

that area. Variation in calls given during mobbing could also signal the likelihood of attacking the predator, which could correlate with perceived level of threat.

Three studies that have tested for threat signaling in mobbing calls all found that at least two call parameters vary with threat level. Baker and Becker's (2002) study of the *chick-a-dee* call in black-capped chickadees (*Poecile atricapilla*) found that calling rate and the A to B syllable ratio varied with threat, and Templeton et al. (2005) found that both rate and fine-scale details of harmonic weighting of the D note in the same call also were related to threat level. In Arabian babblers (*Turdoides squamiceps*), both calling rate and note ratio varied (Naguib et al. 1999). None of these studies tested both variables independently. This phenomenon raises the question of how receivers determine threat level. Are multiple call parameters salient, or need they only evaluate one? Here I present data on vocal variation in mob calls, and conspecific responses to mob call variation in the White-throated Magpie-jay (*Calocitta formosa*). Magpie-jays live in cooperatively breeding groups with female helpers; unpaired males disperse and float among territories (Innes & Johnston 1996; Langen 1996; Langen & Vehrencamp 1999). Magpie-jays give a variety of calls in response to high-flying raptors, but give distinctive harsh calls (Figure 1.1) while mobbing arboreal predators and terrestrial predators and some perched raptors. Known arboreal predators of adults include the collared forest-falcon (*Micrastur semitorquatus*), white-faced capuchins (*Cebus capuchinus*) and boas (*Boa constrictor*), while nest predators include the former three species, black iguanas (*Ctenosaura similis*) and white-nosed coatis (*Nasua narica*). Magpie-jays also mob terrestrial threats such as coyotes (*Canis latrans*) and humans. Calls given during mobbing attract conspecifics and often other birds. Mobbing calls are not easily confused with any other call in the magpie-jay repertoire, because no other magpie-jay call is as noisy or broad-band (Ellis, unpublished data), but within this category, calls

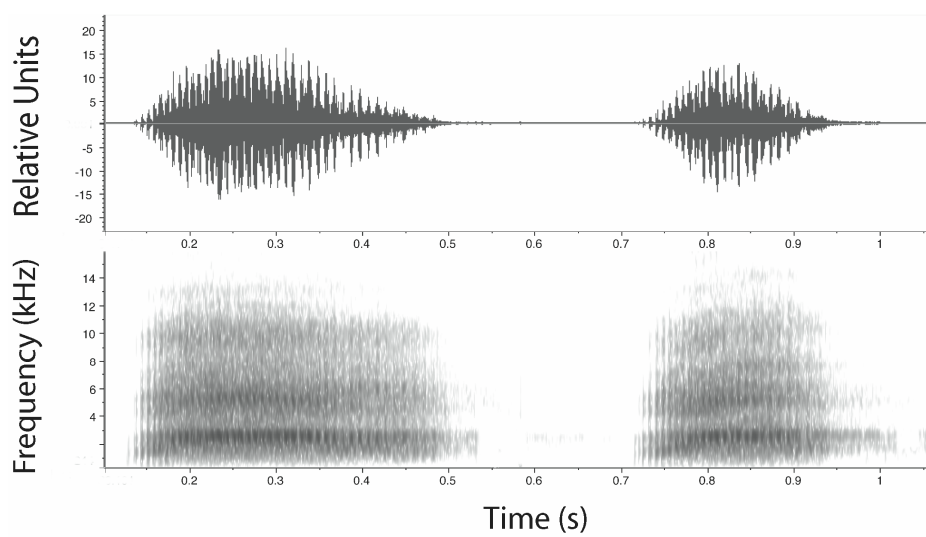


Figure 1.1. Mobbing calls. Length in seconds. Calls are harsh and noisy. Note the difference in length of the two calls, and the similar structures of the two.

can vary subtly. One of the most variable parameters is the duration of the call (which I term call length). Calling rate can also vary widely – sometimes calls are given seconds apart, but others, less than 2 tenths of a second apart. The main frequency band of calls can also vary to some degree, with most calls emphasizing the first harmonic but some having maximal energy in the third harmonic. My goals were to test if variation in these parameters varies with threat level, and if so, whether conspecifics use this information to determine their response, and which call parameter is most important in eliciting responses.

## **METHODS**

### **Study Site and Subjects**

Fieldwork was conducted at the Santa Rosa unit of the Guanacaste Conservation Area, Guanacaste, Costa Rica (10°50' N, 85°37' W), from February to May 2004 and 2005. Site details can be found in Langen & Vehrencamp (1998) and Berg (2004). Approximately 50% of subjects were individually color marked with metal leg-bands, either as nestlings or as adults, as described in Berg (2005). Most unbanded group members were recognizable by distinctive facial patterns, and could be sexed by face pattern and behavior (Langen 1996). I studied 12 social groups over the two years of this study. Group sizes ranged from two to five (mean  $2.75 \pm SE$  0.88).

### **Field Recordings**

*Data collection:* In 2004 and 2005, I recorded vocalizations by magpie-jays *ad lib* from 10 of the 12 study groups in a variety of contexts. Recording equipment

consisted of a Sennheiser MK67 shotgun microphone and a Marantz PMD 690 digital recorder set to a 48kHz sampling rate. Magpie-jays at the headquarters of Santa Rosa National Park are accustomed to humans, yet still give mobbing calls on occasion when they encounter researchers in the field. Recordings were made at distances of 5 m to 15 m while following groups as they pursued daily activities, or while checking nests, which was done twice weekly while the nest was active. I defined a mobbing event as such when a magpie-jay approached a known stimulus (an observer) and gave mobbing calls. Nest checks were designated high threat; an assistant and I examined nest contents with a mirror on an extendable pole, provoking strong mobbing responses by magpie-jays. Mobbing calls given in response to observers over 25 m from the nest were designated low threat; mobbing events that occurred when observers were within 25m of a nest but not checking it were not used in this analysis. I analyzed 11 high threat events (855 calls) and 25 low threat events (1033 calls); 36 individuals were recorded in total.

*Acoustic Analyses:* I measured call lengths and inter-call intervals by hand-selecting mobbing calls using XBAT 0.6.1 sound analysis software (xbat.org: Bioacoustics Research Program, Cornell Lab of Ornithology) and calculating differences between start and end time for each box (call length) and end time and start time between boxes (inter-call interval). Spectrogram settings for selection were FFT size = 512, window size = 1, window function = Hanning, and FFT overlap = 0.5, giving .011 s time resolution and 93.75 Hz frequency resolution. Inter-call intervals and call length were log transformed to meet requirements for normality.

To calculate center frequency, I used the XBAT Energy Distribution Measurement plug-in. This algorithm calculates the aggregate power spectrum across frequency within a selection box by summing the power values in each frequency bin

in the spectrogram, and then generates descriptive statistics by treating the aggregate as a probability density function. Descriptive statistics are generated using a user-specified percentage of the aggregate, rather than using a fixed statistic such as inter-quartile range. The center frequency is effectively the median frequency, with half of the user-specified fraction of energy above that frequency and half below (Cortopassi 2006a; Cortopassi 2006b). I used 95% of the call energy to find the center frequency, and spectrogram settings were FFT size = 2048, window size = 1, window function = Hanning, and FFT overlap = .5, giving a frequency resolution of 23 Hz and time resolution of .043 s. To eliminate low frequency wind noise, I designated a frequency window of 600Hz to 10kHz.

*Statistical Analyses:* I defined a recording session of a predator encounter as an event. Within events, calls often occurred naturally in bouts. Bouts were defined as any set of calls with inter-call intervals of less than two seconds. I chose two seconds as a cutoff because log-frequency analysis indicated that 2s was probably a conservative estimate of the inter-call intervals that separate bouts (Sibley et al. 1990). Approximately 93% of the intervals were lower than 2s, and events always included multiple bouts. To be included in analysis, bouts had to have four or more calls. While this excluded some calls, it allowed accurate, unskewed calculations of inter-call intervals and patterning within bouts that could vary with threat level, and reflects natural calling patterns. Within bouts, I assigned each call an order, allowing me to detect patterns within calling bouts that might differ between threat levels. The mean order and standard deviation of each bout were calculated, and then I standardized the order of each call in a bout with the formula  $(\frac{x_i - \bar{x}}{\sigma})$ , where  $x_i$  is the order of the  $i$ th call in a bout,  $\bar{x}$  is the mean order for that bout and  $\sigma$  is the associated standard deviation. Standardization allowed me to examine changes from the beginning of a bout to the



end without distortion due to differing bout lengths, and compensates for average calls per bout being higher in high urgency contexts.

Analysis focused on three questions: 1) Does call length, inter-call interval, or center frequency differ between predator threat levels? 2) Are there temporal patterns in call length, inter-call interval, or center frequency within bouts that reflect threat level? 3) What are the relationships between these three variables? I analyzed the effects of threat level on each dependent variable and the temporal patterns in bouts using multi-level mixed models with PROC MIXED in SAS (SAS Institute Inc., Cary, NC, USA). Each dependent variable (call length, inter-call interval and center frequency) was tested separately (Littel et al. 1996; Singer 1998). Threat level and within-bout order were considered fixed effects, and I controlled for event and bout in the following manner. Each recording had a hierarchical structure; events were associated with a single threat level, and each bout was associated with a single event. To control for the lack of independence of calls within events and bouts, and because I wanted to assess the effects of threat level at the event level, rather than at the call level, I blocked for both event and bout. This tests the effects of threat level against a denominator degrees of freedom related to the number of events rather than the number of calls. Event was treated as a random effect in the models, because I was not testing for differences between bouts. To block for bout and to test for changes within bouts, I fitted a random intercept model to the data. Such a model estimates the linear slope of the dependent variable against the within-bout order and tests whether the average slope of all bouts is significantly different from zero. It uses degrees of freedom associated with the number of bouts rather than the number of calls. The interaction between urgency and within-bout order tests whether there are different temporal patterns for each urgency level. For example, does call length decrease more or less rapidly in high urgency situations, if it changes at all?

## **Playback Experiments**

*Data Collection:* I designed the playback experiment to test conspecific responses to different call rates and inter-call intervals. Experiments were conducted in 2004. The playback experiment was a 2x2 factorial design in which call length and inter-call interval were varied in four treatments. Calls were recorded from known individuals within the study site, calling in response to the investigator located 5-15 m away. Exemplars were selected for good signal-to-noise ratio and were amplified or attenuated to equal amplitudes. All stimulus construction was accomplished using Syrinx-PC (J. Burt, Seattle, WA). All recordings were high-pass filtered at 800 Hz to reduce background wind noise; the minimum frequency of magpie-jay mobbing calls is approximately 1000 Hz. Long calls were ~300 to ~500 ms in length (mean  $355 \pm 67$  ms), and short calls were ~190 to ~220ms (mean  $213 \pm 18$ ms). Inter-call intervals for the two interval treatments were 0.10 s (fast) and 1.0 s (slow). These call lengths and inter-call intervals are natural, but represent extreme ends of a continuous, unimodal distribution of each measure (see results). Calls were arranged in bouts of ten calls, with an inter-bout interval of 2 s to approximate natural calling patterns. Total duration of playback was 1 min. I was limited to using 8 to 11 original calls for each stimulus, and created subsequent ten-call bouts by systematically rearranging the original calls, avoiding using the same call consecutively or in the same order as previous bouts. All call exemplars within a single stimulus came from the same individual to control for potential effects of switching caller identity during a trial. Exemplars were taken from individuals non-neighboring territories, so that all subjects were unlikely to be intimately familiar with the source individual. I knew the histories of stimulus individuals for at least one year prior; recorded males were not known floaters the year before. While responses could be modified by territoriality, all

treatments were from probable strangers, and any differences in response would reflect differences in treatment.

Three short-call playback stimuli and five long-call stimuli were created. Both long and short inter-call interval treatments were created for each. I could not entirely eliminate pseudoreplication by creating a unique stimulus for each trial. I must assume that variation within the population is adequately sampled by the stimuli I recorded. Each stimulus was used 2 or 3 times. All calls were recorded in contexts in which jays called in response to humans away from nests (i.e. low threat), a restriction that controlled for untested structural differences between calls given in high and low threat contexts. To assess whether frequency might co-vary with call length in the playback stimuli, I measured each unique call within a stimulus using Raven sound analysis software (Charif et al. 2004) to calculate the frequency of highest amplitude. I tested for differences in frequency between short-call and long-call treatments using a two-tailed t-test. There were no differences in the frequency of highest amplitude between long calls (mean  $2566 \pm \text{SE } 92$  kHz,  $n = 50$ ) and short calls (mean  $2560 \pm \text{SE } 78$  kHz,  $n = 30$ ;  $t = 0.261$ ,  $df = 78$ ,  $p = 0.8$ ) within the playback stimuli (See Results for information on call frequencies in natural calling sequences).

Stimuli were played on a Panasonic SL-SX320 portable CD player. Sound output was amplified with a HarmonKardon CA212 automotive amplifier and broadcast with a JBL Control 1Xtreme loudspeaker within the range of natural amplitude for these calls (tested with a RadioShack sound amplitude meter; 88 dB SPL at one meter). I recorded and narrated response behaviors on a Sony TRV87 Hi-8 video camera with an Audiotecnica AT815b shotgun microphone. At the start of each trial, individuals were identified visually with Swarovski WB 8x32 binoculars. All trials were conducted from 0600 to 1100 hrs and 1500 to 1800 hrs, periods when jays were most active. Sequential trials to a group were separated by at least two days to

reduce habituation. Each group received all four treatments in random order. Stimuli were broadcast from at least 50 m within the boundaries of the territory. I hung a speaker in vegetation approximately 2m above the ground, within the range of heights at which jays encounter predators. Observations were made 25 m from the speaker and the group; once the approaching individuals had passed me on their approach to the speaker, I moved closer to the speaker to estimate closest approaches. Habitat in the study site was deciduous tropical dry forest, and during the study, foliage was generally not present. Playbacks were conducted along the edges of patches of forest, so that groups were visible continuously and could approach as close as they preferred without having to land on the ground. I began broadcasting when the focal group was 45-55m from the speaker and after no focal birds had given calls for at least two minutes. Flagging was placed at 10 and 5 m from the speaker in the direction of the group prior to playback to allow me to estimate distances to the speaker on approach. I aborted the trial if predators appeared at any time before or during playback.

I tested 10 groups of magpie-jays, and recorded responses for every magpie-jay visible during the trial. Response variables collected include: closest approach, latency to approach within 10 m of the speaker, time spent at or less than 10 m from the speaker, and any vocal responses by focal birds. I also tracked group size and the number of birds from the group responding to playback. The test period continued five minutes after the end of playback. If no subject had responded at this point, time to approach was scored as 360 s for each individual (see statistical analyses, below).

*Statistical Analysis:* Only the behavior of the first bird to respond was analyzed, because the responses of other group members may have been influenced by the response of the first individual. Results for groups were qualitatively similar to those for first responders. Time spent at or less than 10 m from the speaker was also

dependent on the behavior of other group members, so I did not analyze this variable further. I recorded the time taken by a responder to approach within 10 m of the speaker, and the closest approach in response to each combination of treatments. All models included the call length factor (short versus long), the inter-call interval factor (fast versus slow), the interaction between length and inter-call interval, group ID, and treatment order. To analyze approach latency data, I used a Cox proportional-hazards model in JMP v5.1 (SAS Institute Inc., Cary, NC, USA), a survival/failure analysis that accounts for failures by subjects to respond to treatment. In this case, a lack of response by the end of the treatment period (6 min from initiation of stimulus playback) was scored as 360 s, but also treated as having failed to respond, and subsequently censored in analysis. Survival analysis accurately accounts for the score of 360, despite the fact that the subject did not actually respond at this time. Closest approach data were highly bimodal and I analyzed them using logistic regression. For closest approach, responses of greater than 10 m were scored as 0, and those closer than 10 m as 1, effectively testing whether the subject responded or not. To test if there were treatment effects on those individuals that did respond, I analyzed response latency and closest approach in the subset of cases where approaches were elicited using a mixed model (see Results below). Means are reported  $\pm$  SE. Duty cycle, a measure of time spent actually broadcasting sound (time emitting sound/total stimulus duration), was also tested as an explanatory factor for each response measure. However, because duty cycle is dependent both call length and call rate, the three measures cannot be included in the same model.

## RESULTS

### Call variation in natural contexts

The rate at which calls were given was highly variable, and the length of individual calls often varied by a factor of two or more (Figure 1.1). Mean event time was  $78 \pm 61$  s, and mean number of calls per recorded event was  $52 \pm 39$ . The number of calls per bout was higher for high urgency contexts (high urgency: mean  $18.1 \pm 2.2$ , low urgency mean  $7.2 \pm 1.4$ ;  $F_{1,34} = 20.4$ ,  $P = 0.0002$ ) Natural calls vary in length, ranging from 0.13 to 0.71 s long, with a mean of  $0.280 \pm 0.002$  s. The average inter-call interval within an event was  $0.67 \pm 0.03$  s, with a median of 0.23 s, ranging from as little as .05 to over 2s (see Methods). The difference between the mean and median reflects the fact that most calls were usually closely spaced but included some large gaps. Mean center frequency was  $2559 \pm 4.5$  Hz. Call duration was positively correlated with inter-call interval but explained little of the variation ( $r^2 = 0.02$ ,  $F_{1,1675} = 28.5$ ,  $P < 0.0001$ ).

I found that call lengths in high threat contexts were shorter than in low threat contexts, (high threat:  $0.259 \pm 0.003$ ; low threat:  $0.300 \pm 0.002$ ;  $F_{1,34} = 6.39$ ,  $P = 0.016$ ; Figure 1.2a). Call length decreased during bouts and although there was a tendency for length to decrease more in high threat contexts, the interaction term was not significant (within-bout order:  $F_{1,124} = 24.4$ ,  $P < 0.0001$ ; within-bout order\*threat:  $F_{1,124} = 1.28$ ,  $P > 0.05$ ). Inter-call intervals were shorter in high threat contexts (high threat:  $0.288 \pm 0.012$ ; low threat:  $0.426 \pm 0.012$ ; threat level:  $F_{1,34} = 8.64$ ,  $P = 0.006$ ; Figure 1.2b). There was no effect of within-bout order ( $F_{1,124} = 1.34$ ,  $P = 0.25$ ), nor any difference in changes over a bout by threat context (threat\*within-bout order:  $F_{1,124} = 1.12$ ,  $P = 0.29$ ).

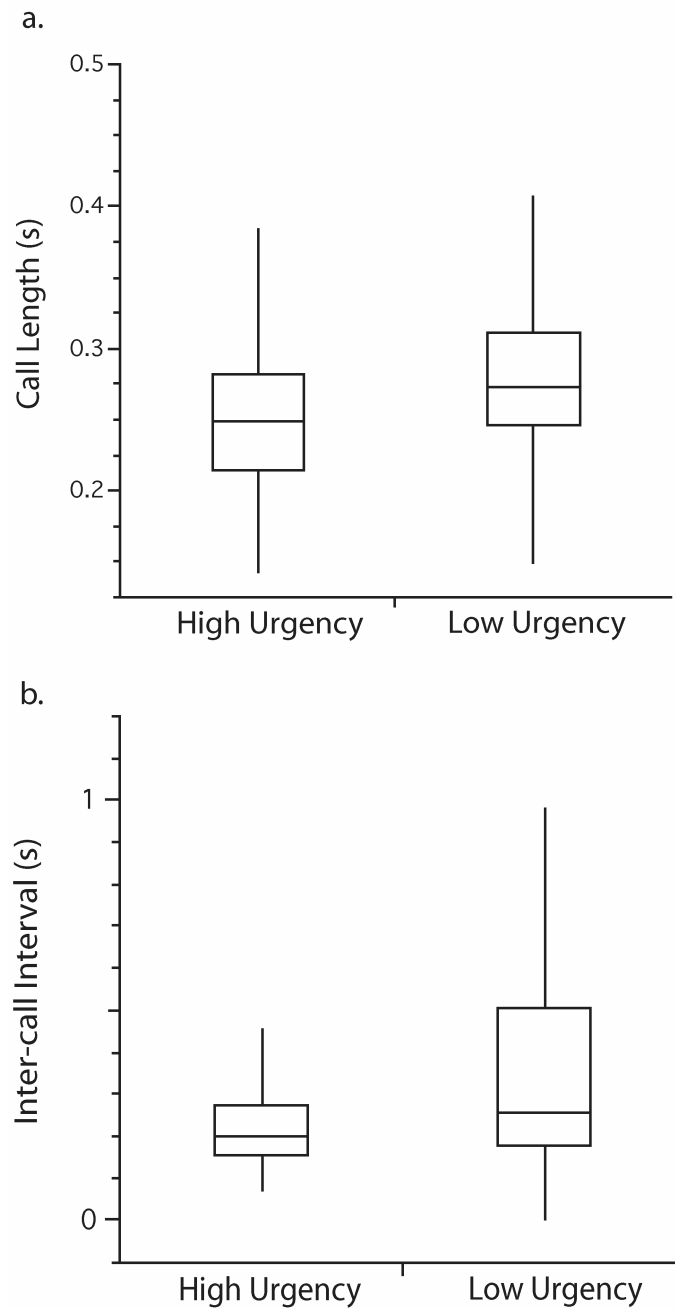


Figure 1.2. The effect of predator threat level on call production in natural calling sequences. Both graphs show significant differences. Median and inter-quartile range are shown. a) Call length in high and low threat contexts. b) Inter-call interval in high and low threat contexts.

### Receiver responses to call variants

Magpie-jays responded to playback stimuli in two ways. They either quickly approached the speaker or did not approach at all. Approaching magpie-jays generally came within 10 m of the speaker in less than one minute (Figure 1.3a). Magpie-jays never gave calls when searching for the source of the sound. Approaching individuals often remained alert for the length of the playback, but when playback ceased they immediately lost interest in the area around the speaker. At this point, birds began foraging, assumed resting postures or engaged in social interactions.

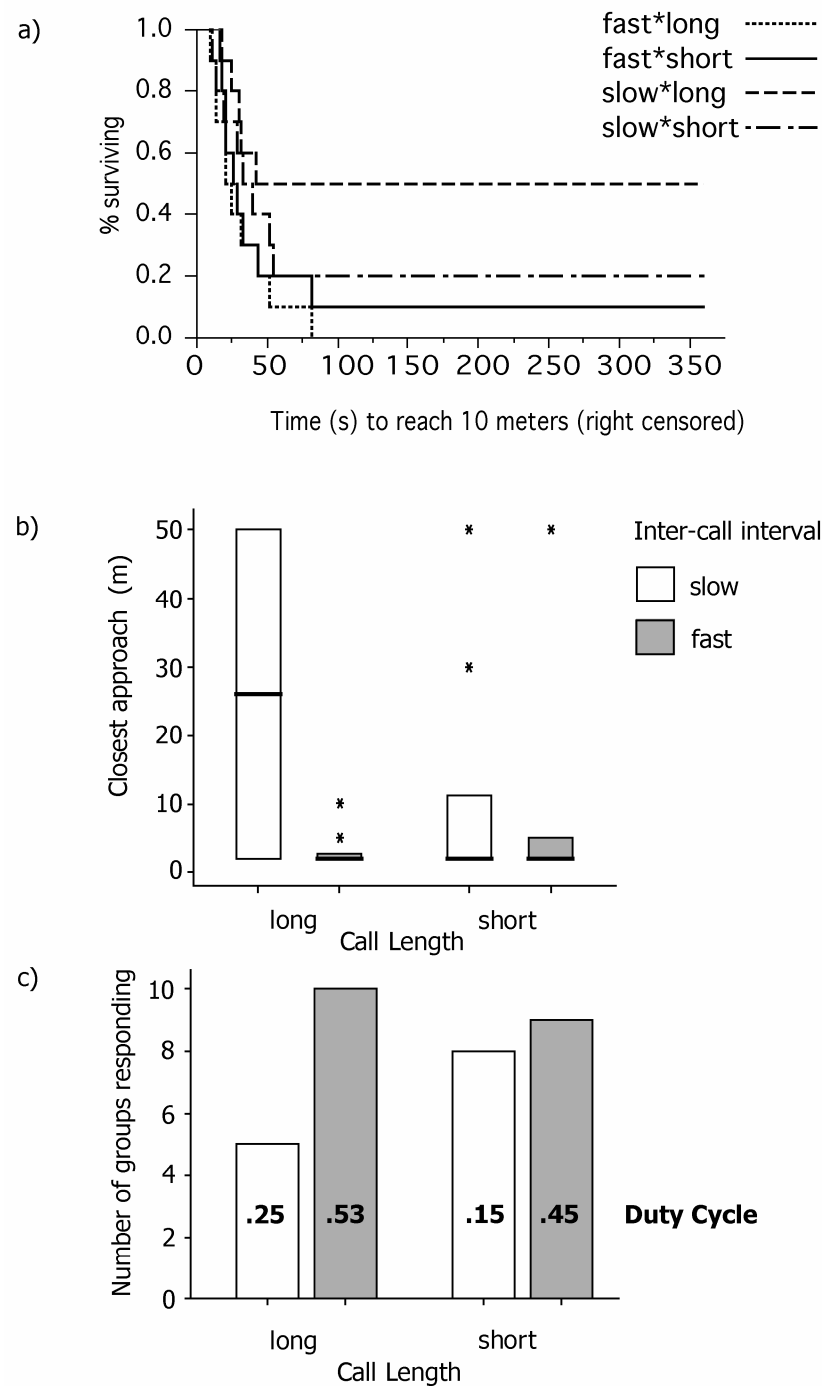
Time taken by a responder to approach within 10 m of the speaker was highest for long calls at long intervals (Figure 1.2a; call length:  $\chi^2_1 = 0.43$ ,  $P = 0.51$ , inter-call interval:  $\chi^2_1 = 6.64$ ,  $P = 0.010$ ; inter-call interval by call length interaction:  $\chi^2_1 = 6.93$ ,  $P = 0.009$ ). Group identity was also significant ( $\chi^2_9 = 34.28$ ,  $P < 0.0001$ ), and no order effects were detected ( $\chi^2_3 = 3.31$ ,  $P = 0.347$ ). Those magpie-jays that did respond almost always approached the speaker to within two meters (median 2 m, interquartile range 0 m). When non-responders (individuals that did not approach) were excluded, no factor except group was significant ( $F_{9,31} = 4.095$ ,  $P < 0.01$ ).

Probability of response, as measured by a close approach, was lowest for long calls at long intervals, and high for all other treatments (Figure 1.3b; call length:  $\chi^2_1 = 1.20$ ,  $P = 0.273$ ; inter-call interval:  $\chi^2_1 = 9.64$ ,  $P = 0.0019$ ; inter-call interval by call length interaction:  $\chi^2_1 = 8.66$ ,  $P = 0.0032$ ). Group had a significant effect ( $\chi^2_9 = 18.30$ ,  $P = 0.031$ ), but order did not ( $\chi^2_3 = 5.40$ ,  $P = 0.145$ ). In all cases, duty cycle as an explanatory variable was significant, but the models were weaker than those with both call length and inter-call interval (for close approach data: Duty cycle model:  $r^2 = 0.49$ , call length, inter-call interval and interaction model:  $r^2 = .74$ ). This probably



Figure 1.3. Playback experiment results. a) Survival plots for the four treatments. Key indicates the combinations of treatments. Inter-call interval is represented with “fast” (short inter-call intervals) and “slow” (long inter-call intervals) for clarity. Most responses occurred in the first 30 s, and time to approach did not differ between treatments if non-responders were excluded from analysis. b) Median closest approach to speaker, with interquartile ranges. Outliers are shown as asterisks. Call length is not significant, but the interaction between call length and inter-call interval is, as evident in the difference between long slow calling and long fast calling. c) Number of groups responding to each treatment. Two playback parameters were varied in a 2x2 design: call length (~0.21s and ~.35s) and inter-call interval (0.1s and 1.0s). Average duty cycle (total duration of all calls/playback duration [~1 minute]), a measure of time spent actually broadcasting calls, for treatments are plotted on each column and do not track number of groups responding (as defined where one individual approached within 10m of the speaker) or any other response.

Figure 3.



reflects the fact that duty cycle is associated with call rate because differences in inter-call interval treatments were greater than differences in call length treatments. However it fails to capture the true patterns of response (Figure 1.3c); the weakest response was associated with an intermediate duty cycle, and the lowest duty cycle was associated with an intermediate response

## **DISCUSSION**

In magpie-jays, call rate and call length were associated with the threat level of a situation, and conspecific receivers rapidly approached call variants that were associated with high threat. Such behavior is consistent with signaling perception of threat level to conspecifics or predators. However, unlike some alarm call systems, magpie-jays use a graded system, rather than multiple distinct calls. Mobbing call variants were not specific to a context, and low threat contexts elicited calls that spanned the range of call lengths and rates. Call parameters were unimodal and showed continuous variation across the parameter space. The stimuli near the nest was not one with which magpie-jays would have naturally had any experience, precluding a specific call type or set of calling parameters to indicate a mirror at the nest. The results are consistent with the few other studies that have examined signal variation during mobbing, which have generally concluded that variation is correlated to the threat associated with a predator, and not to any specific predator type (Naguib et al 1999; Baker & Becker 2002; Templeton et al 2005), but they also show that multiple parameters can transmit this information.

The experimental test of the effects of variation in multiple parameters suggest that both parameters contain information about threat level, but that they are not

independent and additive. This study is the first to my knowledge to independently test the salience of co-varying measures in mobbing calls by testing sender production and receiver response. In this communication system, both call length and call rate are salient to receivers. While call length was not significant alone, it interacted with inter-call interval; responses to one variable depend on the other. The significant interaction reflects the fact that magpie-jays did not respond more quickly or come closer in trials with short calls at fast rates. While this could be due to methodological issues, for instance if the parameters had an additive effect, the parameter values chosen caused responses at the maximum possible level of responses even before their addition. Indeed, stimuli parameters were near the extremes of their natural distributions. However it may also be that intermediate responses are simply not adaptive. A conspecific may not benefit if it does not approach the sender closely enough to localize predator.

If variation in mobbing is intended (in an evolutionary sense) to transmit threat level to conspecifics, then this communication system is redundant, because two parameters encode the same information (Green & Marler 1977). Using call length and inter-call interval to generate the same response reduces the amount of information that can be sent in a coding system, because two axes of variation that receivers could attend to are “spent” to encode the same information (Bradbury & Vehrencamp 1998). While inefficient in coding, redundancy probably increases the chances of signal detection in a noisy environment. Increased signal detection could be important in the tropical dry forests where magpie-jays live. In the dry season, Santa Rosa National Park is very windy, with wind speeds averaging 10-30 km/h and gusting to 90 km/h (Coen 1983). Such winds generate high levels of background noise in the same frequency band that mobbing calls occupy, and gusts do not seem predictable (Wiley & Richards 1982). Sending the same information using two axes of

variability may safeguard communication by assuring the signal is detected (Wiley 1983; Wiley 1994).

Another possibility is that the variation in mobbing is not intended to encode information for conspecifics, but is somehow functional with respect to potential predators. Signals given during mobbing have long been hypothesized to be directed at the predator (Klump & Shalter 1984). In my experiment, I was only able to compare responses to two novel stimuli. Perhaps variation in call rate and call length are independent, predator-directed signals, but both generally vary with the threat of the predator. Receivers could eavesdrop on both parameters to determine if a high-threat predator were present, and then react adaptively. A third interpretation is that the variation in both parameters is constrained by the production mechanism of this sound, and that it is non-adaptive. It may be difficult to produce long call rapidly, so rapid calling may be constrained to short calls. To test both of these alternatives, larger samples of predator encounters would be necessary to determine whether senders ever give combinations of short calls at long intervals or long calls at short intervals naturally.

While I was able to independently test calling rate and calls of varying lengths, and to show that the main frequency of calls did not differ between high and low threat contexts or between long and short stimuli, there may be some variables that I was unable to detect that vary with call length. Thus, a more exact interpretation may be that call length and call *structure* (a combination of call length and unmeasured parameters, but not including main frequency) have independent effects. However, this fact does not qualitatively change any interpretation of the results, because playback stimuli came from contexts where the recorded individual was mobbing an observer on the ground away from nests (i.e. threat was constant across recorded mobbing events).

The receiver responses to playback are an interesting example of how the encoding (message) and decoding (meaning) of a signal need not have a direct correspondence. Magpie-jays either approached the speaker closely or ignored the recording, with very few intermediate responses. In several treatments, some groups responded, and some did not, despite the fact that stimuli within treatments were consistent (Green & Marler 1979). This, in combination with the wide range of parameters elicited in the human encounters, suggests that magpie-jays use a threshold to decide when to respond, and then respond fully. Predator assessment prior to mobbing would require a receiver to approach the sender close enough to quickly find and detect the predator. Even if the signal corresponds to an intermediate level of threat, a magpie-jay should either respond or ignore the signal entirely, since an intermediate approach would give none of the potential benefits of approaching the sender, and presumably would incur some opportunity cost in time lost. As a coding scheme, this may not be particularly efficient, because a large range of variation in threat level encoded by continuous variation in the signal is decoded into a binary response (Bradbury & Vehrencamp 1998). However, if senders vary in their propensity to respond (for instance if breeding females are more likely to respond than non-breeding males because of investment in a nearby nest) then continuous variation may allow all possible receivers to respond adaptively. Conversely, if predator responses are the selective force creating continuous variation, then the sender's coding scheme would not be expected to match a conspecific eavesdropper's decoding scheme .

The data presented here represent one of the only experiments to independently test multiple signaling parameters in a predator-elicited signal. To better understand how these signals are used and to determine exactly what they mean to both senders

and receivers, we need more experiments examining exactly which components of anti-predator signals and displays are relevant to the potential receivers present.

**Chapter 2: Loud begging by reproductive female magpie-jays: signal of need or reproductive advertisement?**



**Abstract:** While begging is a common behavior in nestling birds, in several species the behavior has been co-opted by adults for functions that are poorly understood. Adult female magpie-jays (*Calocitta formosa*) beg loudly from their nest during each breeding attempt. Possible functions include solicitation of feeding by group members or advertisement of the female's current fertility. Because magpie-jays are cooperative breeders, begging also could act to suppress breeding by subordinate females or prepare group members for the subsequent need to help feed offspring. I found that magpie-jay begging peaks during the nest-building and pre-incubation phases while provisioning by group members is highest during the nestling phase. During all phases except the nestling phase, begging rates were positively correlated with provisioning rates. Females with helpers, helpers initiating secondary nests and females without any helpers all gave begging calls. Begging structure is highly variable, even within single bouts. Although many of these results are consistent with nutritional supplementation, they are also consistent with a fertility advertisement function of begging.

Keywords: female begging, courtship feeding, fertility, blackmail, dual function signal, food solicitation

Begging, the act of displaying to solicit feeding, is a widespread behavior in birds. Nestling begging is usually interpreted as a declaration of nutritional need. However, individual offspring prefer higher levels of resource allocation than their parents, who are selected to invest in all dependent offspring or retain resources for future reproductive efforts (Trivers 1971; Godfray 1991; Johnstone 1996). Begging in nestlings is thought to be both more conspicuous (Haskell 1994; Leech & Leonard 1997; Briskie et al. 1999; Haskell 1999) and more energetically costly than would be predicted if the interests of both parties were strictly aligned (Jurisevic et al. 1999; Rodriguez-Girones et al. 2001); but see (McCarty 1996; Bachman & Chappell 1998). The resultant conflict of interests may be mediated by parents adopting a strategically optimal allocation of food (Godfray 1991; Godfray 1995; Budden & Wright 2001). Offspring continue to beg after fledging, usually until nutritional independence (Edwards 1969; Redondo 1991; Langen 1996b). At fledging, begging displays often become more conspicuous and individually distinctive (Beecher et al. 1981a; Beecher et al. 1981b; Redondo & De Reyna 1988; Redondo 1991; Jurisevic 1999). These adaptations assist parents in locating and identifying specific offspring and allocating food accordingly. Even in a context as apparently simple as feeding nestlings, begging is viewed by some to be a complex negotiation between donor and recipient.

Behaviors homologous to nestling begging occur in some adult birds. Adult begging is pronounced in corvids (Cramp & Perrins 1994; Poole 2005). Interestingly, calls are often produced by the adult reproductive female in a group and can be loud enough to be audible at over 200 m (yellow-billed magpie [*Pica nuttalli*]: Verbeek 1972; Verbeek 1973; brown jay [*Psilorhinus morio*]: Lawton 1983; Lawton & Lawton 1985; black-billed magpie [*Pica pica*]: Buitron 1988; white-throated magpie-jay [*Calocitta formosa*]: Langen 1996a; American Crow [*Corvus brachyrhynchos*]: Verbeek & Caffrey 2002). While some species with adult female begging are

cooperative breeders with helpers, others (e.g., black-billed magpies *Pica hudsonia*) are not. Hence loud begging by adult females occurs across a wide spectrum of social and breeding systems in corvids.

The most obvious possible function of adult female begging is that it elicits feeding. Females, like nestlings, benefit from being fed, especially during breeding. If true, females should be most likely to beg during that phase of the nesting cycle when they experience the greatest nutritional need or the greatest benefit from being fed. Extra provisioning prior to incubation could increase a female's fecundity in the current nesting effort, improve current egg and nestling quality, or improve survival and fecundity in later nesting efforts, or all of these. Provisioning during incubation may enhance incubation efficiency and future fecundity and survival of the female. During the nestling phase, adult female begging may enhance nestling feeding or survival rates and future fecundity and survival of the female, if feeding nestlings is taxing for females. If groups renest, enhanced feeding rates could in turn allow groups to renest sooner. Whether females should beg during the nestling phase depends whether the mate and helpers first feed the female, who then transfers the food to the nestlings, or instead feed the nestlings themselves.

As with nestlings and their parents, adult female beggars and their mates or helper donors are likely to have some conflicts of interest. In corvids without helpers, the time a male mate expends feeding a female could be spent foraging for himself or securing matings with other nearby females. Foraging for females also increases predation risk for males. Female mates might not direct the additional resources to the offspring of the current social mate, but rather sequester them for their own survival, future reproductive efforts, or extra-pair mates. Where helpers are female, they are potential competitors with the dominant breeding female and this can generate

additional conflicts of interest. Given these possibilities, it would not be surprising to find that males and helpers do not feed a female every time she begs just as parents sometimes ignore begging nestlings.

While female provisioning is the most obvious and widely cited hypothesis for adult female begging in non-cooperative birds (Lack 1940), other intriguing functions of adult female begging might be considered. These include:

1. **Appeasement:** Subordinate Florida scrub-jays and several other crows and jays occasionally use begging to appease aggressive dominants (Goodwin 1986). While this strategy could potentially be a widespread function of begging in social corvids, it is not clear why begging is so often limited to reproductively active adult females.

2. **Suppression:** In group-living corvids where helpers are females, loud begging by the reproductive female might be a sufficient declaration of dominance that it reduces the chances of helper females starting their own nests. Again, this function would not explain loud female begging in species with male helpers or those with no helpers at all.

3. **Hormonal Synchronization:** It is possible that adult female begging early in the nesting cycle triggers hormonal changes in the male and helpers that in turn induce feeding and nest protection behaviors. Unlike suppression, this mechanism might work for both cooperative and non-cooperative breeders, but it is not clear why

female begging would be required to trigger male feeding behaviors in corvids when it is not necessary in other taxa.

**4. Fertility Advertisement:** In stable social pairs and groups, females cannot openly solicit matings with extra-pair males without concurrently attracting their mate. Begging when fertile could thus be a deceptive ruse by females to advertise their fertility while ostensibly seeking supplemental feeding by the mate or helpers. This function would explain the very high amplitude of female begging calls in many corvids and could apply to both cooperative and non-cooperative breeders. It would be an unlikely explanation if begging were most used during the later phases of the nesting cycle when the female is no longer fertile. As an example, begging by female black-billed magpies (*Pica hudsonia*, a non-cooperative breeder) can begin up to seven days before egg laying (Buitron 1988). These females beg despite the fact that male provisioning of females is largely associated with egg-laying date and occurs well into incubation after females have stopped begging. This mismatch between begging and feeding suggests that begging is not directly coupled to need and could be directed at possible extra-pair partners. Supporting this interpretation, begging in black-billed magpies is unusually loud, male magpies begin mate guarding when their females commence begging, and extra-pair copulations and neighbor male intrusions are common (Buitron 1983; Buitron 1988).

In this paper, I examine the evidence pertaining to several of the hypotheses for adult female begging in the White-throated Magpie-Jay (*Calocitta formosa*). Cooperative breeding groups of this species consist of a single breeding pair assisted by female daughters and sisters (Innes & Johnston 1996; Langen 1996a; Langen & Vehrencamp 1998; Langen & Vehrencamp 1999). Female helpers provision the paired

female and nestlings and aid in territory and nest defense. Female offspring stay on their natal territory as helpers, while males disperse at approximately one year to become floaters. Floaters play an unusual role in magpie-jay society: unlike many other bird species, floaters are not relegated to suboptimal habitat but are allowed to join groups and move easily among territories. While paired breeders have the highest reproductive success, several alternative breeding tactics exist for both sexes (Berg 2005). Helper females occasionally start secondary nests, but they are not attended by group members unless the primary nest fails. Helpers may also attempt to dump eggs in the primary nest. Floaters may mate with primary females (via extra-pair fertilizations, or EPFs), or with helpers attempting alternate breeding strategies. Breeding males may also mate with helpers, and with neighboring females. Given this complex social structure, all of the above hypotheses are relevant to this species.

Nesting female magpie-jays give distinctive begging calls from near their nest location during each breeding cycle (Skutch 1953; Innes 1992; Langen 1996a). Begging in adults is strongly homologous to that of juveniles (Figure 2.1). Juvenile magpie-jays give loud begging calls, and initially group members respond by feeding (Langen 1996b). However, as juveniles approach nutritional independence, begging increases and provisioning by group members decreases. Male magpie-jays may also occasionally beg, though much more rarely than females. Interestingly, begging is not strictly associated with allofeeding. Group members and floaters may feed members of all other classes without eliciting begging (pers. obs, Langen 1996a). Here, I assess the five hypotheses above using data on the phenology of begging and feeding relative to nesting cycle, group size, and begging in various social groups. I also examine the structure, relative amplitude and variability of begging. Each of the five hypotheses generates a combination of predictions about when females should beg, how begging call structure should vary, and the timing of begging

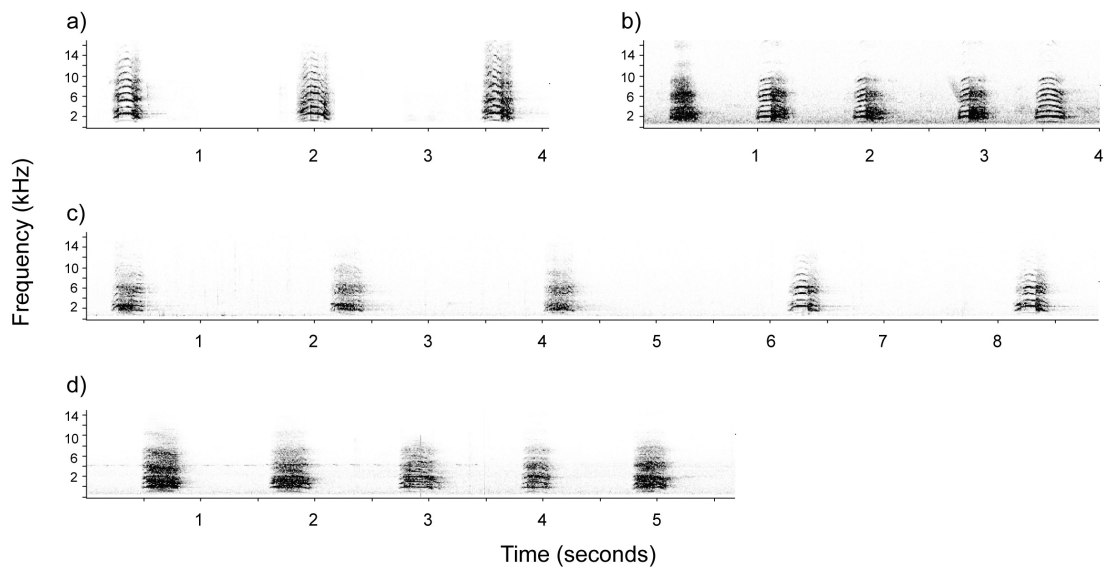


Figure 2.1: a: Beg calls of a fledgling white-throated magpie-jay. b, c, and d: sequences of beg calls from different female magpie-jays. Timing between calls was altered for comparison's sake.

relative to provisioning (Table 2.1). The **fertility** hypothesis predicts that females should beg most when fertile, begging should not be correlated with current need, and begging should attract potential extra-pair mates. Begging should be loud enough to reach potential partners. The **appeasement** hypothesis predicts that begging should occur primarily during dominance interactions, and should be produced by subordinates. Begging could vary with degree of appeasement. As a short-range signal, begging should be relatively quiet. The **suppression** hypothesis predicts that begging should occur when females are beginning the nesting cycle, and that females without helpers should not beg. Begging by helpers should elicit aggression by dominant breeding females. The **helping** hypothesis predicts that begging should occur when nestlings are present, and that females without helpers should not beg. The **need** hypothesis predicts that females should beg when their need for energy and nutrients is highest. Increasing provisioning should decrease begging, and begging structure could vary with need if it explicitly signals hunger. The latter three predict that begging should be a medium-range signal, primarily directed to group members.

## METHODS

### *Study site*

The study took place at the Santa Rosa unit of Area de Conservacion Guanacaste, Guanacaste, Costa Rica (10°50' N, 85°37' W), during two periods. In 1992 and 1993, between February and July, Tom Langen studied fourteen groups (Langen & Vehrencamp 1999), and I studied fourteen groups in 2003, 2004 and 2005, between February and May. Because of this time difference, group composition and territory boundaries differed substantially between the two study periods, although some



Table 2.1: Hypotheses and predictions for the function of female begging in white-throated magpie-jays.

Hypothesis	Predictions of timing, provisioning
1) Fertility	P1) Begging correlated with fertility P2) Begging not correlated to current need P3) Begging structured to maximize transmission and avoid habituation
2) Helping	P1) Begging occurs before nestlings present P2) Females without helpers do not beg
3) Appeasement	P1) Begging during dominance interactions or physical conflict P2) All individuals involved in conflicts should beg if context is appropriate P3) Low or medium amplitude for short-range communication
4) Suppression	P1) Begging during nest-building and preincubation period P2) Females without helpers do not beg P3) Helper females do not beg
5) Need	P1) Begging occurs at highest rates during period of highest need P2) Increased provisioning should reduce begging; larger group sizes (with higher provisioning rates [Langen 1998]) should reduce begging P3) Structure should differ before and after feeding if begging explicitly indicates hunger

individuals marked in the first period were still present in the second period.

Guanacaste is characterized by strongly seasonal climate, with a dry period lasting from December to mid-May (dry season). Abrupt heavy rains fall in late May and early June, immediately followed by leaf-out of deciduous trees, and accompanying explosions of insects (wet season). During the dry season, magpie-jays rely on acacia and other fruits, switching to insects and insect larvae in the wet season.

#### *Correlations between begging and provisioning across nest stages*

Basic methodological details for data collection are described by Langen & Vehrencamp (1999), but briefly, data on feeding and begging during nesting attempts were collected at least weekly for six primary groups. Eight other groups were studied less intensively. Tom Langen and field assistants performed multiple 90 minute observation during four nesting stages: 1) nest building, when nests were under sactive construction, 2) pre-incubation, when females were laying but not incubating, 3) incubation, when the female was brooding, and 4) the nestling period, after eggs had hatched. They quantified the number of begs given by the focal female and the number of provisioning events during each observation period. It was not possible to determine food quality.

#### *Begging and group composition*

In 2003, 2004 and 2005, I tracked breeding in fourteen groups. To test the suppression and helping hypotheses, I determined whether females in pairs and helper females ever begged. This sample included three helpers that bred as secondary females. In 16 of 36 breeding attempts group size was two, a single female and her mate. Because all individuals can occasionally give a few beg calls prior to

allofeeding, females were designated as begging if they were noted giving beg calls for prolonged periods without being immediately allofed (see Results).

### *Structure of begging vocalizations*

To better understand the function of begging I also examined the structure of begging. I recorded females during the pre-incubation phase. As suggested by the analysis of begging by nest stage (see Results), begging during the building and pre-incubation periods can often occur at high rates. Females may beg continuously for hours, barely stopping after being allofed (continuous begging). After these stages, begging primarily occurs just before being allofed (allofeed begging). Because in the latter study period group sizes were small, fewer allofeedings meant limited begging during incubation, resulting in small samples. I therefore limited my analysis of structure to continuous begging recorded during the nest-building and preincubation stages. Because the nest-building period can vary among females (Langen 1996), the number of days spent recording a female varied (1-7 days, 2-9 sessions each). Females were observed and followed with recording equipment for at least an hour on each day that they were recorded. Recording sessions lasted from 5 minutes to over an hour. I defined a session as a continuous recording event where all begs were recorded, all instances of allofeeding were noted, and all locations and identities of nearby group members and floater males were determined. Multiple sessions from one female were sometimes made on the same day but were separated by at least an hour. Recordings were made at distances from 5 to 15 meters from the subject on an hhB Portadat digital audiotape recorder with a Sennheiser MKH 815 long shotgun microphone (2004) or a Marantz PMD 690 digital recorder and Sennheiser MK67 shotgun microphone (2005). Both microphones have a 20Hz-20kHz flat response. Recordings

were made at 16 bits and 48 kHz, and the analog outputs were re-digitized at 16 bits and 48 kHz on a Macintosh Powerbook G4 for analysis.

### *Statistical analyses*

I analyzed relationships among nest stage, begging, and feeding rates with general linear models in SAS. Where necessary, I transformed variables to meet the requirements of the statistical tests used. A random intercept model controlled for the effect of groups. I tested whether group size, nest stage and season affected begging rates, and whether begging rates, nest stage and group size affected provisioning rates.

To analyze changes in beg call structure over bouts, among bouts and among years, I used subsets of recorded calls. Series of five sequential calls were selected from calling bouts available from each female, excluding calls given within 10 calls of an allofeeding event. If a bout was longer than 25 calls, I selected two calling series from that bout, separated by at least 10 calls, and if longer than 100 calls I selected three series. Sample sizes for each female in this analysis averaged 39 calls ( $\pm 20$ ), ranging from 15 to 85 calls. A new bout commenced if a female was allofed.

Similarity measures for each pair of calls from all of each female's series were generated using spectrogram cross-correlation (SPCC). Calls were cross-correlated using the Sound Xcorr Tool (Cortopassi 2006a; Cortopassi 2006b). Spectrograms were created using a frame size of 1024 points, and were filtered with a bandpass of 600Hz-5000Hz to exclude low-frequency noise and high-frequency insect sounds from analysis. SPCC generated a matrix of similarity values for each of the sampled calls of each female. I then classified the relationship of each pair of calls in time, creating a matrix of time relationships of the same dimensions as the similarity matrices for calls. Within each series, pairs of calls were labeled by the number of calls separating them: zero for comparisons with itself (which were not included in

analysis), four for the comparison of the first and last call in a series of 5. Call pairs from the same bout but different series were labeled 10; pairs from the same day but different bouts, 20, and any greater time span 30. To test whether differences among years were significant, I repeated the same procedure, but this time scored all pairs from different years as 40. Significance of association between call similarity and time difference matrices was assessed with a Mantel test in R (R-project for Statistical Computing, [www.r-project.org](http://www.r-project.org)), using a non-parametric Spearman rank correlation and 10000 permutations. A significant result indicates that calls grew more dissimilar in structure as time between them increased.

## RESULTS

### *Observations of female begging*

Begging was the loudest vocalization in the magpie-jay repertoire (Innes 1992; Ellis in prep). On at least three occasions begging females were audible when observers were at least 750m from the coordinates of the nest, while another observer placed the female within 5m of the nest. Average territory size is 17ha (Langen & Vehrencamp 1998) so average territory radius is approximately 230m. Beg calls were often audible two territories away. Females begged for long periods from exposed perches at the tops of trees, or from near their nest. During nest-building and preincubation, females usually begged from within 50m of the nest. During incubation and nestling phases, begging occurred on the nest, as helpers approached with food. When a female was fed, she often gave a distinctive swallowing call (allofeed gurgle) as she accepted food, hunching her body and quivering her wings.

### *Correlations among begging, provisioning and nest stage*

Female beg rate peaked during the nest-building and preincubation phases of nesting and dropped in the incubation phases and nestling phases (Figure 2.2;  $F_{3,46}=50.8$ ,  $P < 0.0001$ ). Provisioning rose significantly only in the nestling phase (Figure 2.3;  $F_{3,46}=18.4$ ,  $P < 0.0001$ ). However, this test included beg rate as a covariate, and begging decreased significantly during the incubation and nestling stages. When beg rate was removed from the model, provisioning decreased significantly during incubation as well; females begged less and were thus provisioned less during incubation. Group members responded to begging, increasing provisioning when begging rates increased in all stages except the nestling stage; little begging occurred during this stage but provisioning increased dramatically (Figure 2.4; Spearman's rank correlation: building:  $\rho = .486$ ,  $P = 0.008$ ; preincubation:  $\rho = 0.438$ ,  $P < 0.0001$ ; incubation:  $\rho = 0.476$ ,  $P < 0.0001$ ; nestlings:  $\rho = 0.154$ ,  $P = 0.19$ ). Group size did not affect either begging rates or provisioning rates after controlling for group identity. Season significantly affected begging rates, with females begging marginally more in the dry season ( $1.5 \pm 0.1$  begs/minute) than the wet ( $1.0 \pm 0.2$  begs/minute;  $F_{1,46} = 8.48$ ,  $P = 0.006$ ). The interaction between nest stage and season was significant as well ( $F_{3,46} = 3.45$ ,  $P = 0.024$ ); begging rates in the preincubation stage were higher in the dry season (post-hoc LS means tests,  $P > 0.013$ ). Season had no effect on provisioning rates.

### *Begging behavior and group composition*

Begging occurred regardless of group composition. All females that bred in the second study period were observed begging. Females lacking helpers begged in every breeding attempt, and four helpers were noted begging, three of which paired briefly with floater males and built secondary nests.

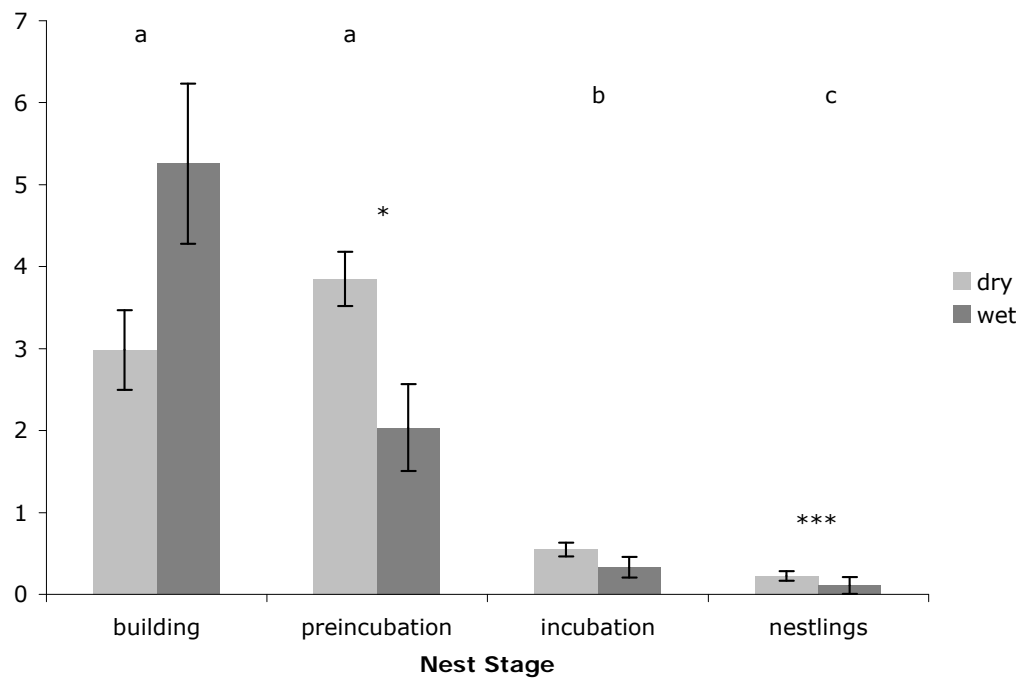


figure 2.2: Mean begging rate  $\pm$  SE for each nesting stage and season. \* =  $P < 0.05$ , \*\*\* =  $P < 0.0001$ , Least squares means tests of dry season vs. wet season for each stage. Nest stages with different letters were significantly different from each other.

F

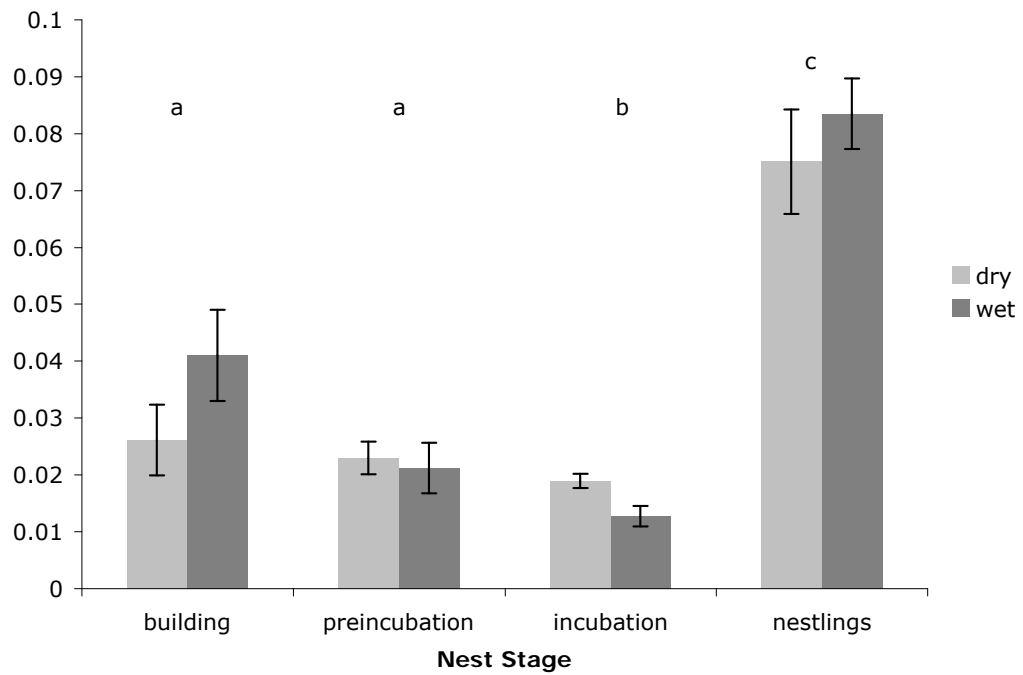


Figure 2.3: Mean provisioning rate  $\pm$  SE for each nesting stage. Least Squares means tests indicate no difference between dry and wet season provisioning rates at each stage (all  $P > 0.1$ ). Nest stage columns with different letters are significantly different.



### *Begging structure and variability*

Female begging is very similar to fledgling begging and is variable in structure (Figure 2.1). I could not make statistical comparisons of begging structure between juveniles and adults because of low nest survival rates. However, both female and fledgling begging have plaintive tones, an arched pattern of frequency modulation, and variability in the degree of noise present in the call. Within a single bout of begging, call structure can change from a harmonic stack to a combination of noise and harmonics, to noisy sound with little harmonic structure. The analysis of call similarity within females showed that begging calls given more closely in time are more likely to be similar in structure. Mantel tests for each of the 13 females were significant at the  $P = 0.05$  level. A simple Bonferroni correction ( $\alpha = 0.05/13 = 0.0038$ ) showed that only one female out of 14 had no significant correlation ( $P = 0.035$ ,  $r = 0.11$ ) of call structure and time between calls. All other females showed significant correlations at the  $\alpha = 0.0038$  level between call similarity and time between calls. Mantel statistics for the 14 tests ranged from  $r = 0.11$  to  $0.59$  ( $0.35 \pm 0.15$ ). The statistic was unrelated to sample size ( $r^2 = 0.05$ ,  $F_{1,13} = 0.62$ ,  $P = 0.44$ ). These results were stable when differences among years were scored as such, rather than treating them as differences among days. Of the six females that were recorded in two years, accounting for year led to higher correlations in three and decreased correlations in the other three, suggesting that differences among years are no greater than differences among days.

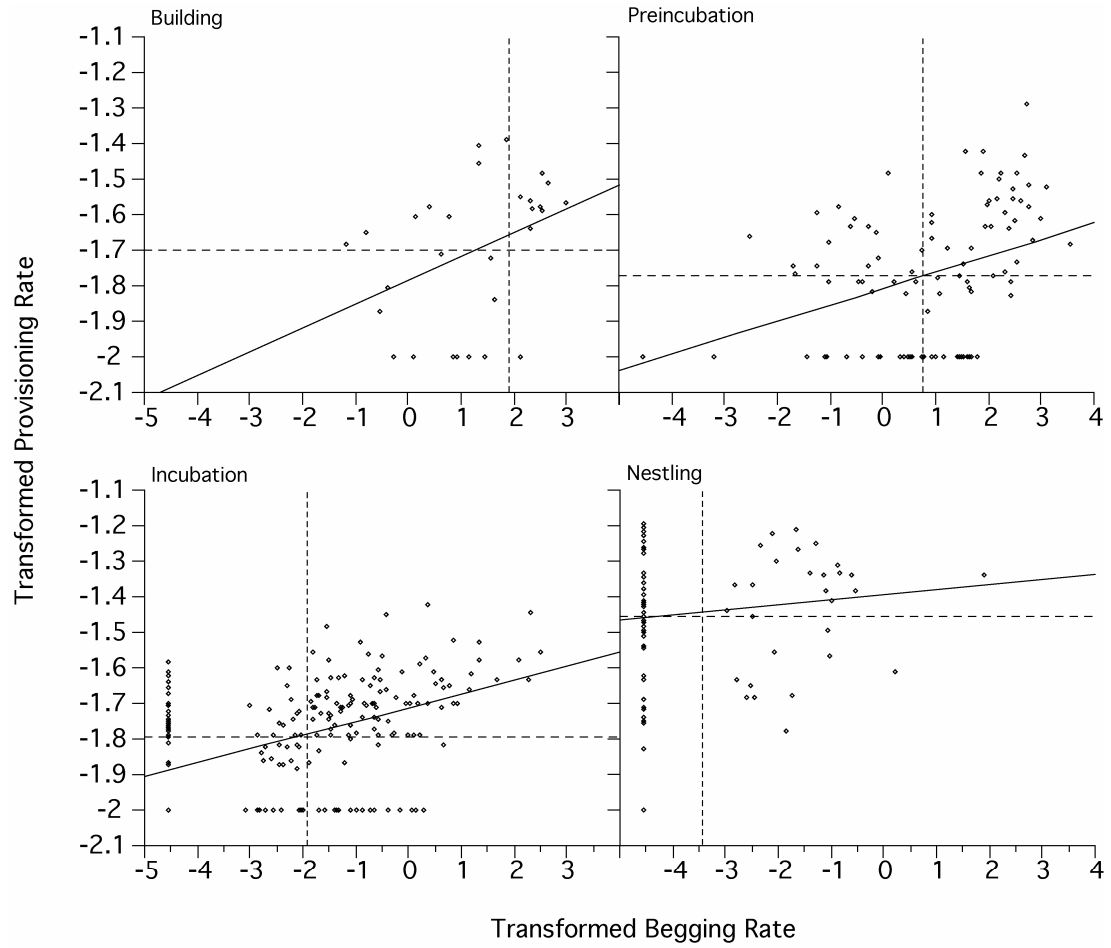


Figure 2.4: The relationships between begging rate and provisioning rate for different nest stages. Begging rate and provisioning rate are not significantly related in the nestling phase, when provisioning rates are high and begging rates are low. Linear regression represented by solid lines. Long dotted line is mean provisioning rate, short dotted line is mean begging rate, for each stage. Data were transformed using the following formula:  $\frac{(Rate^X - 1)}{X}$ , where X is a scaling factor, X for begging rates was 0.22, for provisioning rates, 0.5.

## DISCUSSION

Begging by female magpie-jays peaks during the nest-building and preincubation phases of nesting, dropping off steeply when incubation starts. Conversely, provisioning is low during nest-building and preincubation, lowest during incubation, and highest during the nestling phase. During phases where provisioning occurs at relatively low levels, the intensity of begging is more strongly correlated with consequent provisioning. Begging is also very loud, and shows characteristics of being a long range, easily localizable signal. It can vary substantially, even within a single begging bout, and abrupt changes are not unusual, although begs can be consistent over short periods of time.

If begging by female magpie-jays is strictly an advertisement of nutritional need, then the drop-off in high begging rates after the start of incubation implies that egg production is costlier to females than incubation and nestling care. While nestling feeding is generally regarded as the most energy-intensive period, egg production can be quite costly (e.g. Great Tits [*Parus major*]; Nilsson & Smith 1988). This is certainly possible since females begin their first nests of the season and egg production at the height of the dry season when protein is scarce (Innes & Johnston 1996; Langen 1996a; Langen & Vehrencamp 1998), and they can count on extensive help in feeding chicks by group members. The fact that high female begging rates prior to incubation elicit only low rates of provisioning could simply reflect the fact that there is less protein available to offer the begging female during this period. However, later nesting attempts that begin in the wet season when food is more abundant also show low levels of provisioning prior to incubation despite relatively high levels of begging. This suggests that more than simple nutritional pressures are at work.

A non-exclusive alternative is that begging advertises female fertility. Much like magpies (Buitron 1988), female magpie-jays beg well before they lay their clutch. Begging is correlated with the start of each nest attempt, so it would pay potential extra-pair copulation (EPC) partners, like neighbors and floater males, to pay attention to the onset of begging behavior. Begging is one of the loudest signals in the magpie-jay repertoire and easily carries outside of the territory, suggesting it is a long distance signal and may not be directed solely to group members. Male behavior and floater behavior are also suggestive of a fertility-signaling function in magpie-jays. Male magpie-jays mate guard intensely during the phases in which begging is most frequent. They were often observed within 10 m of their mate, not foraging or feeding her, despite the fact that she was begging loudly (Langen 1996a). Mated males also provision at lower rates than expected given their representation in groups (Langen & Vehrencamp 1999), probably because they are mate guarding. More data are necessary to examine whether floater males pay attention to these signals, but in an earlier study more floaters were seen near nests during periods when females were begging (Innes 1992). These data cannot readily be explained by the nutritional need hypothesis, suggesting that begging may have two overlapping functions.

The remaining hypotheses can be readily eliminated based on the data presented here. Appeasement is poorly supported; begging is not limited to social interactions and is associated with feeding interactions in the short term and the nesting cycle in the long term. It has no association with direct social conflict in magpie-jays, unlike several other corvids (Goodwin 1986). The suppression and hormonal synchronization hypotheses are also poorly supported. Females without helpers beg, despite the lack of competitors to suppress or helpers to stimulate. Begging females were unsuccessful at preventing secondary breeding attempts, as evidenced by multiple secondary nests during both study periods. It is possible that

begging could influence helpers to feed nestlings; examinations of hormonal profiles or experimental reductions in begging would be necessary to test whether begging stimulates expression of hormonal titers associated with helping (Schoech et al. 1996). Such a function seems unlikely, though; I would predict begging to peak during incubation or early in the nestling period if begging had such an effect on helpers. Unless some delayed effect stems from hormonal mechanisms, this hypothesis can be discounted. However, begging behavior by breeding females did not vary with the presence or absence of helpers. In short, no data exist to support the hypotheses that begging functions in appeasement, breeding suppression or hormonal synchronization.

Given these data, I propose that in some corvids, loud begging by females during preincubation serves two purposes: to elicit feeding and to signal fertility. Because begging occurs at the appropriate time of the nesting cycle, it is easily co-opted by females as an advertisement of their fertility. No doubt begging also retains its original function as a signal of hunger, as suggested by its similarity to fledgling begging and by the increase in provisioning during this period as intensity of begging increases. Paired males should still pay attention to this signal, since it may indicate both whether the female is hungry and whether she is fertile. Helpers may benefit from feeding the breeding female, for reasons similar to those in many cooperative breeders, while floaters clearly gain a unique advantage in this situation.

Because females beg persistently for periods longer than an hour, I hypothesize that structural variation in these calls is used to reduce habituation in potential receivers. Begging is surprisingly variable compared to other structurally distinct call types, and is much more variable than mob calling (Ellis in prep), which employs simple functional variation to signal threat level. In one other species in which adult begging has been studied, the European robin (*Erithacus rubecula*), begging is relatively invariant (Tobias & Seddon 2002). In magpie-jays, variation in

begging is not categorical; rather, begging varies such that begs from different bouts are different, which is most easily explained as a device to reduce habituation.

Another hypothesis for variability in begging is that changing beg structure prevents or reduces muscle fatigue. Given the intensity of begging (up to 16 begs per minute for 90 minutes) females could incur fatigue in the syrinx or other muscles modulating beg production. By shifting the structure, females might avoid taxing muscles repeatedly, allowing them to beg for longer. The fact that beg structure becomes more disparate in structure over time is consistent with this hypothesis.

Use of begging by females to advertise fertility could be adaptive in two ways. Tobias & Seddon (2002) suggested that females could blackmail their mates into feeding them, threatening to broadcast their fertility unless they are fed. If a male cannot feed his female enough, she will beg. Her begs will then be heard by marauding males and he will lose paternity. This neatly combines a signal of need with a signal of fertility. The blackmail mechanism predicts that courtship feeding should reduce begging, and better-fed females should produce larger clutches. Our study showed that begging is correlated with increased provisioning in magpie-jays, so the results do not strongly support the blackmail hypothesis. However, a response to blackmail could occur on a shorter time scale than I examined and therefore cannot be directly ruled out.

Another hypothesis for the function of fertility signaling is that females benefit from instigating competition among males, even if they do not actually copulate with a male other than their mate (Montgomerie & Thornhill 1989; Poston & Wiley 1996). High-quality males should be able to defend their female from interlopers, while low quality males might be less successful. This hypothesis predicts that females should beg regardless of the quality of their mate, and that extra-pair fertilization (EPF) rates should vary with male quality. A different hypothesis is that females mated to low

quality males beg to attract better males in general. Females with low-quality mates should beg more, and females that beg more should also have higher EPF rates. I cannot discriminate between these two derivative versions of the fertility hypothesis given current data, but either could explain the observed patterns of begging and consequent male guarding observed.

Why should females beg from the nest area to signal fertility instead of simply seeking out extra-pair mates off of the territory? Floater males are responsible for a significant amount of paternity in nests (~33%; Berg 2005) and are able to access territories readily, despite the fact that paired males mate-guard heavily during the nest-building and preincubation phases (Langen 1996a). A female magpie-jay may only be able to elude her mate to seek EPCs if multiple intruding males occupy her mate's attention. While her mate confronts one interloper, other floaters can solicit EPCs. Such events could be facilitated by female begging.

Another explanation for loud begging is nest-guarding. Helper females attempt to dump eggs in the nest of the dominant (Langen 1996a; Berg 2005). Breeding females vigorously defend access to the nest during the laying period, resulting in chases and occasionally fights. The requirements of nest defense may prevent a female from leaving the nest area to pursue EPCs. Begging may be an alternative solution to obtaining EPCs without exposing it to egg-dumping by opportunistic helpers. It is somewhat puzzling, however, that females beg so close to the nest, while eggs are present. Begging drastically simplifies nest-searching for human observers, so it would seem to pose a predation cost on females. Any predator that paid attention to female begging could locate both the female and a nest site, and in many cases eggs. Whether begging truly poses a cost remains to be tested.

Nest guarding could also explain the occurrence of loud female begging prior to incubation in other cooperative breeders. Several cooperative breeders noted for

begging loudly (above) have female helpers, although rates of egg-dumping are not known for these species. However, this hypothesis for signaling fertility does not explain why solitary breeders such as magpies should beg loudly. Two factors may influence loud begging: presence of helpers or nearby gravid females and unforced extra-pair copulations. Thus, I predict that colonial species, such as piñon jays (*Gymnorhinus cyanocephalus*), yellow-billed magpies (*Pica nuttalli*) and some crows, such as jackdaws (*Corvus monedula*) and possibly rooks (*Corvus frugilegus*) may have loud begging. Cooperative species with female helpers, such as brown jays (*Psilorhinus morio*) and probably many species of the genus *Cyanocorax*, should also beg loudly.

In summary, begging in adult females may have a dual function in the white-throated magpie-jay. Begging probably arose originally to signal nutritional need, but several other characteristics of begging behavior suggest it has been modified since for long-range communication to advertise the female's fertility. Experimental work in magpie-jays is now needed to clarify how receivers respond to these signals. While studies on magpies (Buitron 1983) and robins (Tobias & Seddon 2002) suggest that adult begging behavior may vary in details among species, a common factor may be that loud begging by female birds has an EPC facilitation function as well as functioning in fool solicitation.



**Chapter 3: Diverse loud calls in the white-throated magpie-jay: an enigmatic  
class of vocal signals**

**Abstract.** Determining signal function is critical for understanding how signals are adaptive and how they might evolve. Generally, information on context of production, sender identity, and the identities and responses of potential receivers is necessary to generate hypotheses for signal function. As part of a larger study of vocal repertoires, I gathered such data on a large class of structurally distinct signals that I term “loud calls” (LCs) in the white-throated magpie-jay (*Calocitta formosa*). Cataloging signal production revealed that male magpie-jays were far more likely to produce LCs than females. Calls were given primarily in response to low-threat predators (termed predator approach displays) and in sustained display performances at dawn. Consistent use of multiple call types and the results of a playback experiment suggest that LC calls are all equivalent in function. One male was recorded producing 51 call types during predator approach displays, and 134 call types classified as LCs were recorded over the course of the study. A second playback experiment showed that males were more likely to respond to LCs than were females, and more so when their mates were fertile. A predator presentation elicited some LCs, but with fewer calls and lower diversity than at dawn or in predator approach displays. Taken together, the male bias and high diversity suggest that LCs are an outcome of intersexual selection, while their elicitation by predators suggests an alarm function. I propose that male magpie-jays may use predator encounters as opportunities to advertise their presence and availability as mates. This co-option of alarm signals as male advertisement signals seems to have been favored by the unusual magpie-jay social system, where female groups defend territories and males have little opportunity to defend resources for mate attraction.

Keywords: secondary sexual trait, vocal communication, corvid, call repertoire, song repertoire size

A persistent and difficult problem facing behavioral biologists is why different species have vocal repertoires of different sizes (Smith 1965; Smith 1969; Moynihan 1970; Peters 1980; Kroodsma 1983; Hailman & Ficken 1996). A common approach is to identify specific vocal types within a given species' repertoire, characterize the levels of within-category variation, identify the social or environmental contexts in which specific types and any variants are given, and measure the responses of conspecifics. Contrasts in these characters between related species with different repertoire sizes should facilitate the development of testable hypotheses about why repertoire size varies.

I pursued this approach by characterizing and dissecting the vocal repertoire of a highly social corvid, the white-throated magpie-jay (*Calocitta formosa*), in Costa Rica. This species lives in territorial groups consisting of a dominant breeding pair, female offspring who stay and help, and male floaters who visit multiple territories within a day. Initial work showed that several call types, such as mobbing and begging, have clear functions easily defined by sender identity, context of production, and responses of receivers (Ellis in prep; Ellis 2008). Prior studies also have noted that magpie-jays give a wide variety of calls in response to disturbances or potential predators (Wetmore 1944; Skutch 1953; Slud 1964; Hardy 1967; Goodwin 1986). Observations of magpie-jays giving long strings of loud vocalizations while approaching and perching over observers corroborated these reports (Ellis, unpub). Because these vocalizations are louder than most other calls in the repertoire, I term them "loud calls" (LCs).

Calls given while approaching predators are usually thought to function as mobbing signals, which alert conspecifics to the location of the predator and/or inform the predator it has been discovered. The variety of LCs noted in the field suggests other potential functions, however. In some alarm systems, different predator types

elicit specific and distinct signals (Klump & Shalter 1983; Klump & Shalter 1984; Caro 2005). Another hypothesized function of predator approach behavior is self-advertisement (Slagsvold 1984; Dugatkin & Godin 1992; Maklakov 2002), and vocalizing could draw a conspecific receiver's attention to both predator and sender. In predator-defense contexts, signals are usually produced by both sexes, and are relatively invariant. Continuous and relatively limited variation in mobbing calls has been shown to communicate the level of threat a predator represents (Naguib et al. 1999; Templeton et al. 2005; Ellis 2008). Alarm signals denoting predator types are usually highly distinct but structurally simple, designed for rapid detection. Self-advertisement signals, in contrast, are often complex and diverse (Catchpole & Slater 1995). In mate-attraction contexts, male passerine birds can produce repertoires of over 1000 songs (i.e. brown thrashers; *Toxostoma rufum*: (Kroodsma & Parker 1977)). The diversity of signals reported in LCs could represent a graded alarm system, a diverse set of calls with different referents, or a single call category used in self-advertisement. Below, I describe the structural variation and context specificity of LCs, identify the senders and potential receivers of these signals, and assess their potential functions.

## **METHODS**

### **Site details and population**

I studied 14 social groups of White-throated Magpie-jays from early February to late May in 2003, 2004, and 2005, at Santa Rosa National Park, Guanacaste, Costa Rica. The park habitat consists of tropical dry forest and patches of secondary growth that

are recovering after use as a ranch. Approximately 50% of individuals in the population were marked, and group members that lacked bands were mostly identifiable by distinctive facial features. Individuals can be sexed by behavior and by sexually-distinctive facial patterns (Innes & Johnston 1996; Langen 1996). Group size averaged  $2.5 \pm 0.88$  individuals over the three years of my study. Magpie-jay social structure has been well described (Innes & Johnston 1996; Langen & Vehrencamp 1998; Langen & Vehrencamp 1999; Berg 2005). Briefly, groups consist of a breeding pair and a number of related females. Female offspring stay and help at the nest, occasionally build secondary nests, and sometimes dump eggs into the nests of dominant breeders. Females inherit breeding positions when the dominant female dies. Males disperse out of their natal neighborhood after about one year and become floaters in the population with home ranges of up to 6 group territories. Floaters may visit all the groups within their home range in a single day, and are not excluded from groups (Innes & Johnston 1996; Langen 1996). When male breeding vacancies open in groups, either through death or divorce, females usually pair with a local floater. Extra-pair fertilizations are common, representing ~33% of nestlings, and extra-pair fathers are both neighboring paired males and floaters (Berg 2005).

### **Observational recording**

As part of a larger study of the vocal repertoire of white-throated magpie-jays, I followed groups and focal individuals while recording the following data: any vocalizations uttered during the recording bout; the number, identity, and social status of all visible individuals; and all behaviors by the vocalizing individual or others nearby. I attempted to follow individuals for 10-minute periods, although recording times were variable. Most recording was conducted in the presence of breeding pairs,

and both sexes were usually present at my approach. While my recording methods were not directly experimental, I was occasionally able to elicit LCs by slowly approaching a focal individual for recording. In some cases my appearance would prompt a display approach by the focal bird, or by nearby individuals. Vocalizations and my narration were recorded on three different recording rigs: a Sennheiser 814 shotgun microphone with an hhB Portadat digital audio tape recorder; an Audiotecnica AT815b shotgun microphone and same digital audiotape recorder; and a Sennheiser ME67 shotgun microphone with a Marantz PMD 670. In all cases, recordings were made at sample rates of 48 kHz and 16-bit accuracy. Digital audiotapes were saved as .WAV files on a Macintosh Powerbook G4 with Raven (Bioacoustics Research Program, Cornell Lab of Ornithology) retaining 48 kHz sampling rates and 16-bit accuracy.

### **Classification criteria**

Several criteria were used to distinguish LCs from other categories of vocalizations. While songbird songs often can be classified as a single functional category with a common species-specific syntax despite their variability, the extreme structural diversity of magpie jay LCs made such an exercise difficult (Figure 3.1). Initially, two contextual criteria were used to classify calls as LCs: the presence of threatening environmental objects and the performance of a stereotyped “approach display” in the presence of predators and other animals. The display consists of a slow flight directly toward a threatening object with deep wing beats and emission of loud vocalizations. The sender may land nearby and continue calling. After such a display, individuals may call again when the object (often a human observer) moves. Once the regular association between LC calling and approach displays was recognized, I analyzed

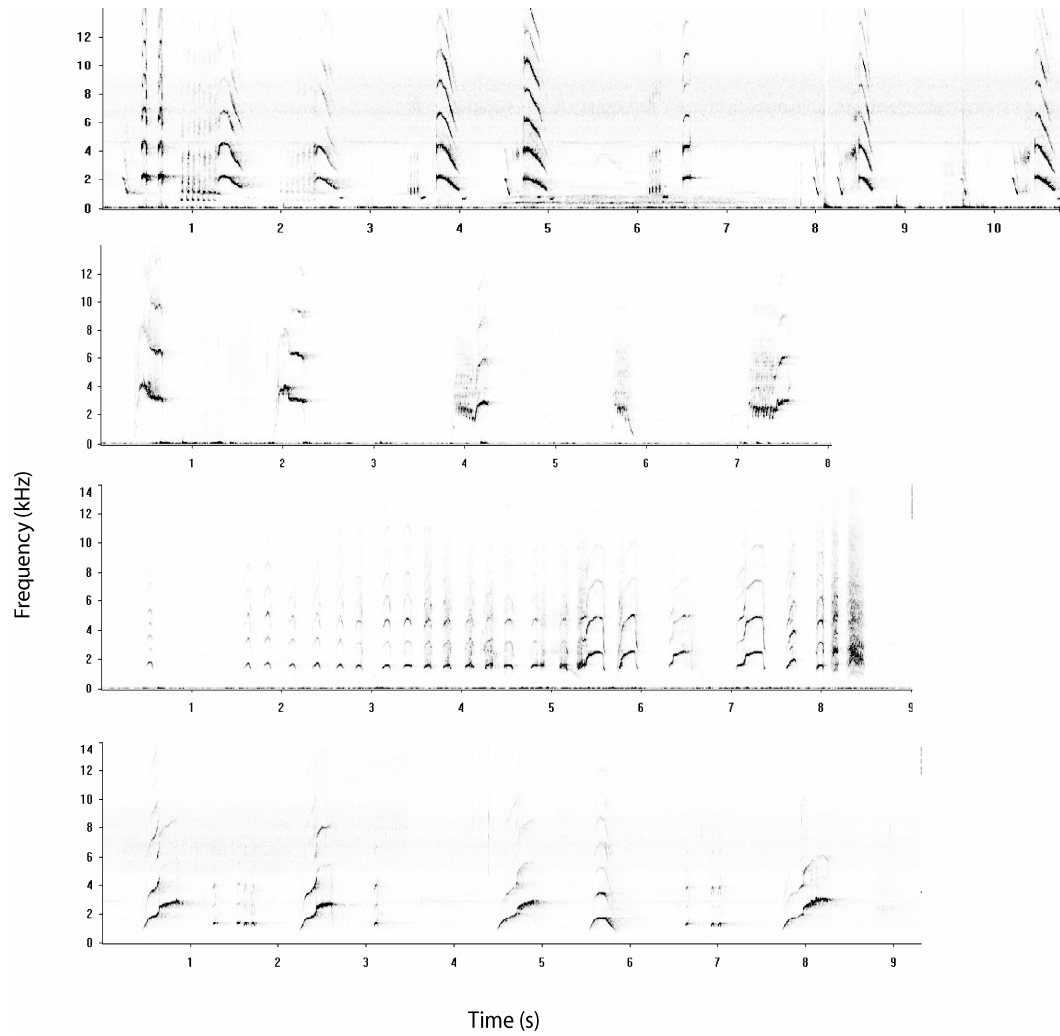


Figure 3.1: Within and between bout diversity of LCs. Each line is part of a separate calling bout. A single male produces all traces in each bout.

recordings for other instances of structurally identical call types. Such instances were generally classifiable into two other contexts, which I describe in the results.

### **Predator presentation**

I placed taxidermic mounts of an American Kestrel (*Falco sparverius*) and a Great-horned Owl (*Bubo virginianus*) in the territories of 12 groups to test whether both low-threat predators and high-threat predators elicited LCs. American Kestrels are rare but regular in the study area, and are only half the weight of magpie-jays. Although they probably do not represent a significant threat to magpie-jays, jays occasionally harass these small falcons. Great-horned Owls are native to Costa Rica, but are very rare in the study area. However, magpie-jays do encounter other large owls in the study site, especially Spectacled Owls (*Pulsatrix perspicillata*). Large owls are a significant threat to nestlings, fledglings, and adults. Each group was tested once with the kestrel and twice with the owl. The raptor was mounted on a pole approximately 2 m tall and tied upright in nearby vegetation. Subjects were attracted to the predator mount with one of three recordings of two white-throated magpie-jays mobbing a raptor. The speaker was placed at the bottom of the pole holding the raptor and was aimed in the direction of the group. I recorded each group as they approached, and identified those individuals calling. Each individual approaching was watched to determine if it had seen the mounted raptor; subjects were considered to have detected the owl if they oriented towards the mount and looked at it with both eyes, turning their head to do so. Calls given before detection were classified as being elicited by the lure or by other social circumstances.



## LC call classification and statistical comparison between contexts

Calls were classified primarily through patterns of frequency modulation. I took a conservative approach, in the sense that calls with different frequencies but similar shape (i.e., pattern of frequency modulation such as arched, rising, falling, tremolo, etc) were classified as the same call type. Calls with similar patterns of frequency modulation but different lengths were also classified as the same call type. Calls were sometimes combinatorial, with notes that are given independently also given in rapid sequence together. Calls more than 5 ms apart were defined as separate calls, and when calls were given in combination, I classified the call as the longer type. This scheme may underestimate some of the variation in the repertoire, but classifying combinatorial calls as structurally distinct call types could inflate repertoire size almost infinitely.

Several variables describe the patterning and nature of calling for each context in which magpie-jays produced LCs. *Number of calls* was simply the number of calls produced by each individual in a calling bout, which was defined as the beginning to end of a given recording or event. *Number of call types* was the number of distinct types, as defined above, in a bout. *Switching rate* was number of times an individual switched from one distinct type to another, divided by the number of calls in the bout minus 1. *Diversity* was number of call types produced divided by number of calls. *Versatility* was *diversity* multiplied by *switching rate*, which provides an index of how often an individual switches to unique types. Finally, I calculated the Simpson index  $D = 1 - \sum_{i=1}^s p_i^2$  for each bout, where  $s$  = number of call types,  $p_i$  = the proportion  $N_i/N$  of the  $i$ th call type,  $N_i$  = number of calls of the  $i$ th type, and  $N$  is the total number of calls in the bout. The index accounts for both number of types given and their relative representation in a bout. Indices were transformed to meet the requirements of

parametric statistics; the Simpson index was transformed by taking the log of the sum without subtracting it from 1 (that is, prior to the transformation needed to make low diversity 0 rather than 1). ANOVA and Tukey's HSD tests determined whether differences in such measures differed by context.

## **Playback Experiments**

I performed two playback experiments, and the following methods apply to both. I used Syrinx PC ([www.syrinxpc.com](http://www.syrinxpc.com)) to create treatment stimuli. All stimuli were filtered below 800 Hz to eliminate low-frequency noise. All playback exemplars had high signal to noise ratios and came from non-neighboring paired males to control for effects of familiarity. I amplified or attenuated each exemplar to the same standardized amplitude; exemplars were played back at 85dB SPL at one meter. Amplitude of complex calling sequences was difficult to determine accurately in the field, but 85dB is probably slightly lower than most calls given in this context. Stimuli were played on a Panasonic SL-SX320 portable CD player. Sound output was amplified with a HarmonKardon CA212 automotive amplifier and broadcast with a JBL Control 1Xtreme loudspeaker. The loudspeaker was hung at a height of 2 m in vegetation, 30 m from the focal individuals, along edges and open areas with short bushes. Magpie-jays could be observed for the duration of the approach and could approach intermediate distances to the speaker. I initially stood 25 m from the speaker, at an angle from the shortest distance between the speaker and the focal individuals. After playback began, I waited until the focal individuals had approached the speaker and then only moved as necessary to maintain visual contact with focal individuals and to note closest approach distances. This method assured that the observer was not the

stimulus of LCs. Treatment order was randomized. I measured the latency to approach within 10 m of the speaker and closest approach to the speaker, and recorded all vocalizations. Magpie-jays are individually distinctive, so once initially identified with binoculars, observers could track individuals by eye. To avoid habituation, trials on the same individual were separated by at least two days.

*Playback Experiment 1: Sex differences in response to loud calls.*

The first experiment compared responses to a heterospecific control, a conspecific control, and four different LC call types that occur commonly in the study area and are shared and used by most male magpie-jays: pow, oo-eer, peeoo, and rolling trills (Figure 3.2). Nine pairs received all six treatments. Stimuli consisted of three iterations of the same call type played 0.5 s apart, a 30 s period of silence, and the same three calls played again. Each of the three exemplars came from a single calling bout by a single male magpie-jay. The heterospecific control stimulus was a rattle call of Hoffman's Woodpecker (*Melanerpes hoffmani*), a common resident of the study area. This call falls in the general frequency band of loud calls. The conspecific control stimulus was female begging calls. Female magpie-jays give long bouts of begging calls during nesting. This treatment was not delivered in a natural pattern for begging calls, because this control was intended to test whether receivers were simply responding to conspecific vocalizations or to information in loud calls. Four stimuli of each experimental treatment were created, and each stimulus was used one to three times (initial intended sample size was 15 males, including floater males, but difficulties in broadcasting stimuli to floaters caused dropouts). Distance and vocalization response measures were analyzed with ANOVA. Latency measures were compared using survival analysis in JMP (SAS Institute Inc, Cary, NC).

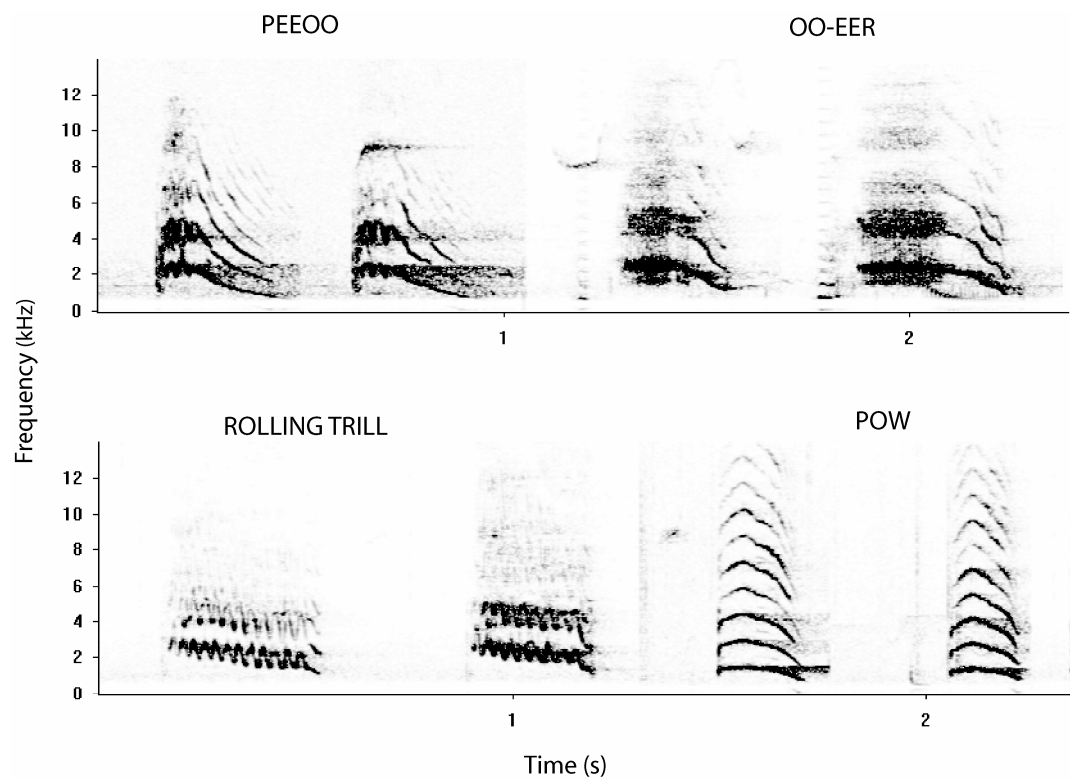


Figure 3.2: LC types used in playback.

### *Experiment 2: The effect of mate fertility on response to LCs*

To test whether female fertility affected a male's propensity to respond to LCs, I tested whether responses to LCs differed with female reproductive status. Thirteen paired males were exposed to two playback trials, differing only in his mate's reproductive status. One playback was performed when a male's mate was fertile, and the other while she was incubating a full clutch. I determined female fertility by checking nests twice per week. A female was assumed to be fertile if her nest contained 1 or 2 eggs, since average clutch size is 4 eggs (Berg 2006) and females are only known to lay one egg per day. Females were treated as incubating if their clutch size had not increased since the last nest check. I played back a single call type to each male when his mate was determined to be fertile or incubating. The stimuli consisted of a single loud call type, the oo-eer, played back as described above. I used a single call type because I was not attempting to analyze differences between LC call types in this experiment, and because it is a common call used by most males. Six exemplars were created, and each male received a different exemplar for each playback. Each exemplar was used four times. Variables analyzed were as noted above.

## **RESULTS**

Magpie-jays gave calls classified as LCs in three contexts: during approach displays, during dawn calling, and in response to high threat predators (e.g. raptor mounts). LCs given in response to raptor mounts lacked the visual component of approach displays. 134 different call types were identified from the combination of all three contexts.

## Observational recording

### *Approach displays*

Magpie-jays were observed performing approach displays to a variety of threatening and non-threatening objects (Table 3.1). From 235 hours of recording, I recorded 7097 calls from 49 known individuals during 272 approach displays; 251 approaches were made by 38 males and 22 approaches were made by 11 females. After excluding mobbing calls given during approaches, females gave only 2.8% of all recorded LCs. As might be expected, individuals used more call types when they produced more total calls (Figure 3.3a). Males gave more calls during approaches than females ( $F_{1,226} = 11.02$ ,  $P = 0.001$ ), and males uttered more call types per approach than females ( $F_{1,273} = 7.4$ ,  $P = 0.007$ ; Figure 3.3b). Because of the correlation between number of calls and number of call types, the between-sex effect of call diversity became non-significant after controlling for number of calls. There were no significant effects of group size or presence of males or females on the composition or number of LCs during approach displays.

### *Dawn calling*

Males occasionally give prolonged bouts of LCs at dawn using the same call types as were given during approach displays. Individuals began giving LCs and flying slowly from tree to tree well before dawn (~60 minutes before sunrise) in near darkness for approximately 20 minutes. As it became lighter, dawn calling ceased and individuals began to forage. No individuals identified giving LCs during dawn calling were female. Both paired males and floaters performed this display behavior.

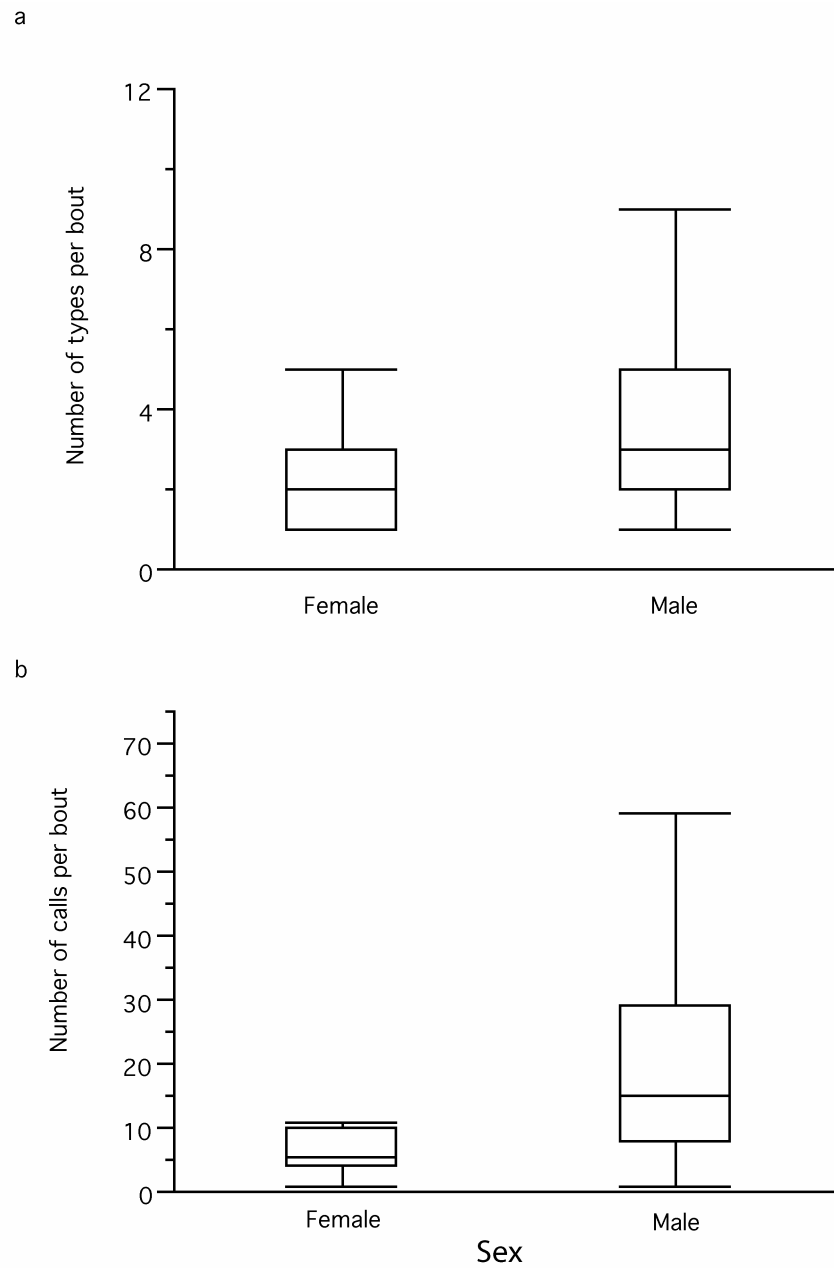


Figure 3.3: Sex differences in bout composition during predator approach displays (median, IQR, range). a) number of LC types per bout. b) number of calls per bout.

Table 3.1: Context of approach display production by magpie jays. Encounter rates with various target species are difficult to quantify, so observations do not represent rates of production per encounter with target species.

Target	Number of observations
Humans	>272
Coyote	2
Domestic dog	1
Vehicle	3
Guan ( <i>Penelope purpurescens</i> )	2
Caracara ( <i>Polyborus plancus</i> )	8
Other perched raptors	15
Capuchin monkeys ( <i>Cebus capucinus</i> )	7
White-nosed Coati ( <i>Nasua narica</i> )	2
White-tipped dove ( <i>Leptotila verreauxi</i> )	1



## **Responses to predator mounts**

Magpie-jays gave LCs in response to the owl in 7 of 22 (32%) trials and in response to the kestrel in 1 of 12 (8%) trials. In 16% of all raptor presentations, LCs were given in response to the playback of mobbing as the group approached the playback site, prior to discovering the predator mount. In this context the typical slow flight was not performed, and flight was not obviously directed at the speaker, the mount, or any observers. The call types were the same ones used in display approaches in low-threat contexts. Only one of fourteen individuals that gave LCs in response to raptor mounts was female.

## **Patterns of LC production**

Temporal patterns of production of loud calls differed in several ways among approach displays, dawn calling, and response to mobbing and predator mounts. Calling at dawn was often sustained for long periods, approach displays were highly variable in number of calls produced but averaged lower than at dawn, and raptor mounts elicited the fewest calls (Figure 3.4a). The number of types produced follows this same pattern, but diversity (number of types/number of calls) is far lower during dawn calling than during approach displays or raptor presentations (Figures 3.4b and 3.4c). Magpie-jays switched call types more often at dawn, and very rarely in response to predator mounts (Figure 3.4d). Versatility did not differ significantly among contexts (Figure 3.4e). In contrast to standard behavioral measures of call diversity, Simpson's index of diversity, which weights the evenness of occurrence of a call type, was highest during dawn calling (Figure 3.4f), probably because magpie-jays produce

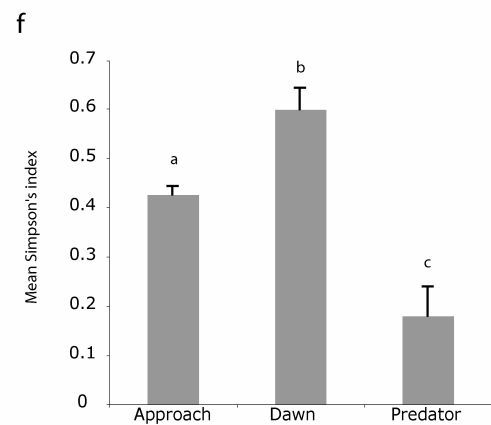
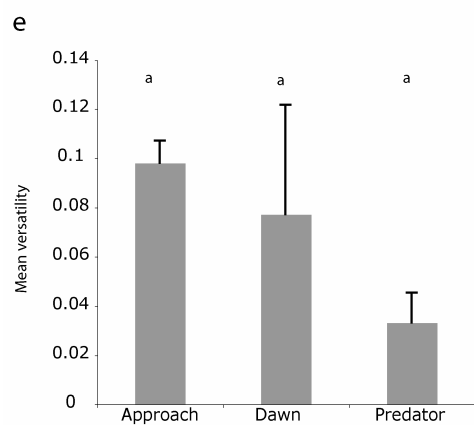
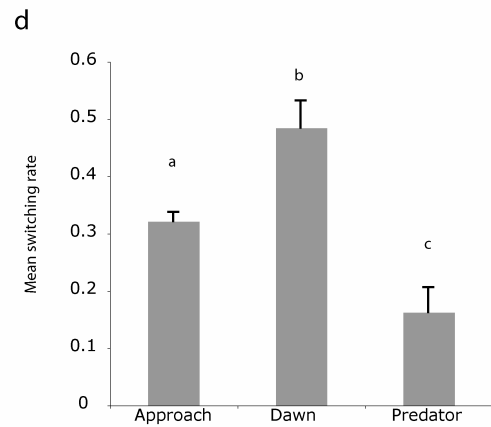
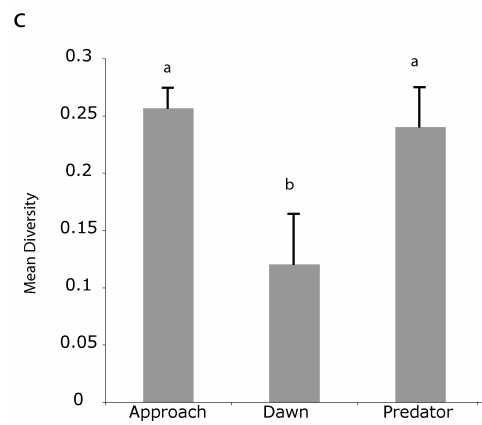
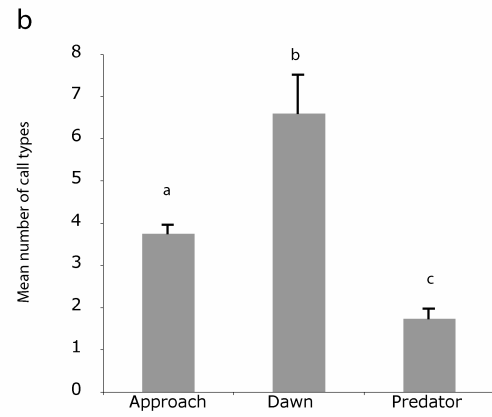
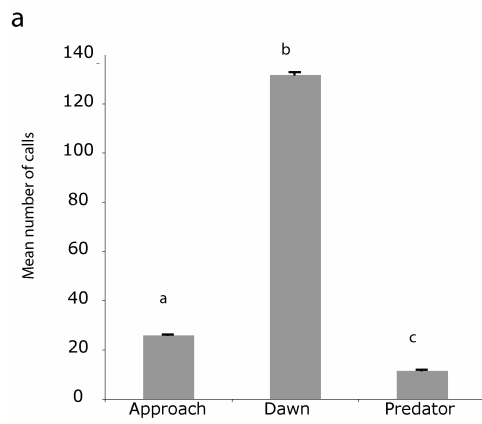
a large number of call types with relatively even distribution, often switching back and forth between two or three types for a long period.

Of the 134 call types recorded, most were given in approach displays. Only 15 (11%) were unique to dawn calling. Forty-two (31%) occurred in both contexts and 74 (56%) occurred only in approach displays. This result may reflect sample differences; 272 approach display bouts (7,096 calls) were recorded while only 22 dawn calling bouts (2,896 calls) could be analyzed. Twelve call types total were produced in response to raptor mounts, and all were also given in both approach display and dawn calling contexts.

### **Repertoire sizes**

The largest LC repertoire size for an individual male was 61 call types. Number of call types recorded per individual was significantly related to the number of recorded approach displays for that individual ( $R^2 = 0.86$ ,  $F_{1,46} = 292$ ,  $P < 0.0001$ ; number of call types =  $1.82 + 1.83 \times \text{number of recorded displays}$ ). Clearly, most individuals were not sampled adequately to determine their whole repertoire (Figure 3.5). The individual with the largest recorded repertoire was a floater male, but the second largest repertoire (44 call types) was obtained from a paired male who had been on territory for at least 4 years when he was last recorded. These two males did not differ in their acculumation rates. Accumulation curves for all males with more than 50 recorded calls were similar. Sample sizes were not large enough to estimate call-type sharing indices. However, males shared many calls.

Figure 3.4: Patterns of calling by context; columns with different letters are significantly different. Error bars are standard error. a) number of calls; b) number of call types; c) diversity (call types/total calls); d) switching rate (switches/call); e) versatility (switching rate\*diversity); f) Simpson's diversity index.



Context

### **Playback Experiment 1: Sex differences in response to LCs**

There were clear sex differences in the likelihood of responding to playback of LCs, but no differences in response to the four LC variant treatments. Females responded in significantly fewer trials (11%) than males (48%) after controlling for treatment (Figure 3.6). Males were more likely to approach to 10 meters ( $\chi^2_1 = 14.4$ ,  $P > 0.0001$ ) and moved closer to the speaker ( $F_{1,68} = 16.5$ ,  $P > 0.0001$ ). In each case where pair females approached, their mate approached first or at the same time, suggesting that their response was related to their mate's response. The type of LC played, however, had no effect on response in either sex, and each type was associated with at least one success and one failure of a male to reach 10 m from the speaker. Males sometimes vocalized in response to LCs by giving their own LCs. Matching occurred in 7 of 35 playbacks of LCs, but was not associated with call type. No individuals ever responded to the heterospecific control.

### **Playback 2 Experiment: Effect of mate's fertile status on responses to LCs**

When a male's mate was fertile, he was more likely to approach the speaker (Figure 3.7a  $F_{1,9} = 8.8$ ,  $P = 0.016$ ), did so faster ( $\chi^2_1 = 10.3$ ,  $P = 0.001$ ,  $n = 23$ ; Figure 3.7b), and approached more closely ( $\chi^2_1 = 6.3$ ,  $P = 0.01$ ,  $n = 23$ ) than when his mate was incubating. Female fertile status had no effect on vocal responses, and measures of vocal response were not associated with male approach behaviors. During this experiment, males gave a total of 27 different LCs, 4% of which were matches to the stimulus. Matches occurred in only 3 of 24 trials.

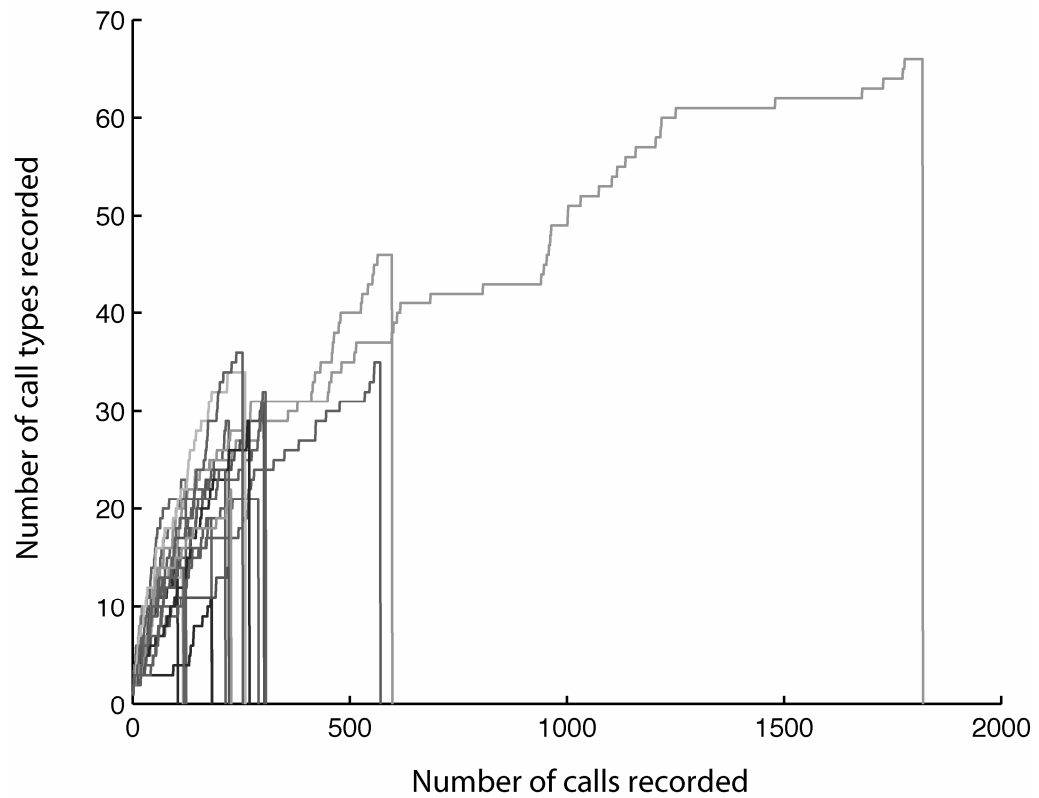
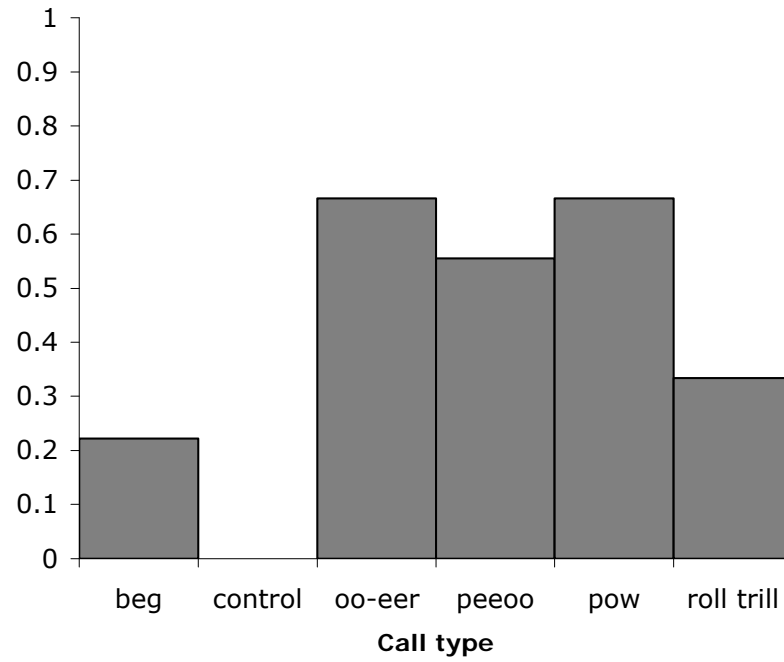


Figure 3.5: Repertoire accumulation plot for each individual for which more than 50 calls were sampled. X-axis is number of calls recorded, Y-axis is cumulative number of call types recorded.

a



b

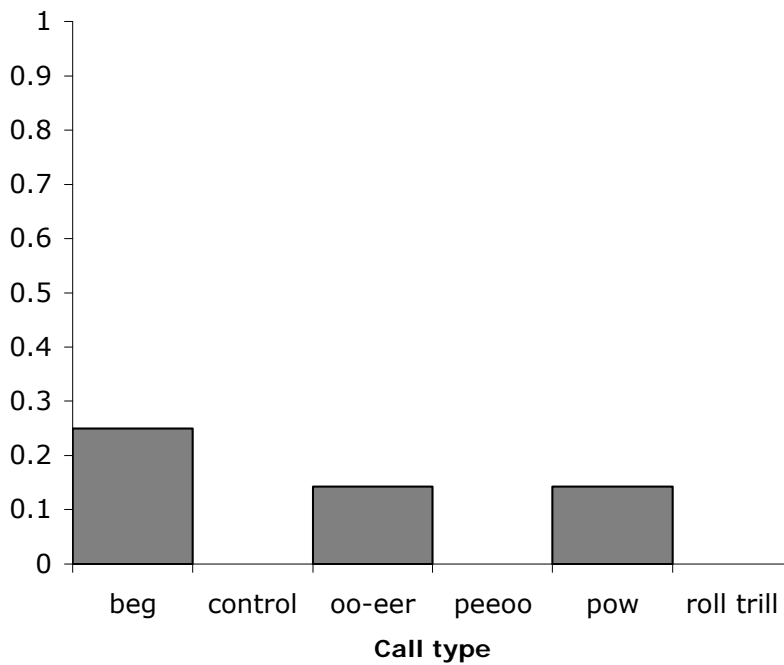
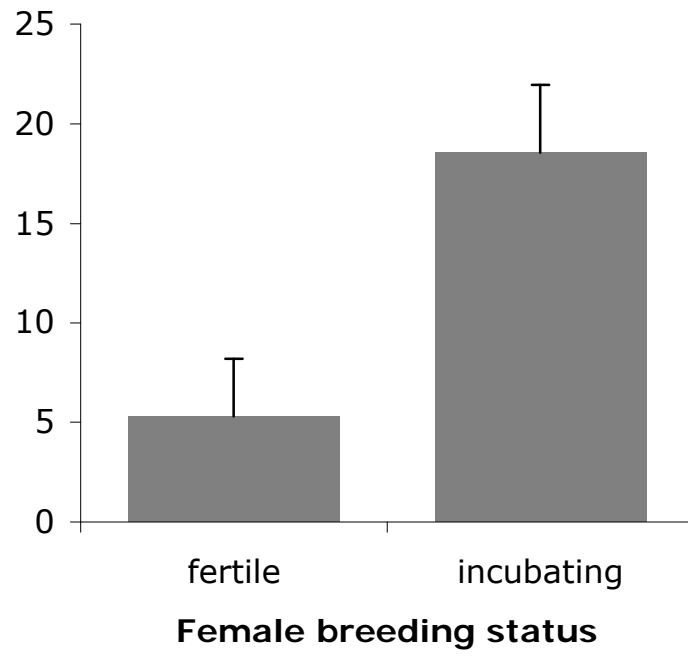


Figure 3.6: Male and female approach responses to four LC types and two controls, begging and a heterospecific call. a) Proportion of males approaching to 10m from playback speaker. b) Proportion of females approaching 10m from playback speaker.

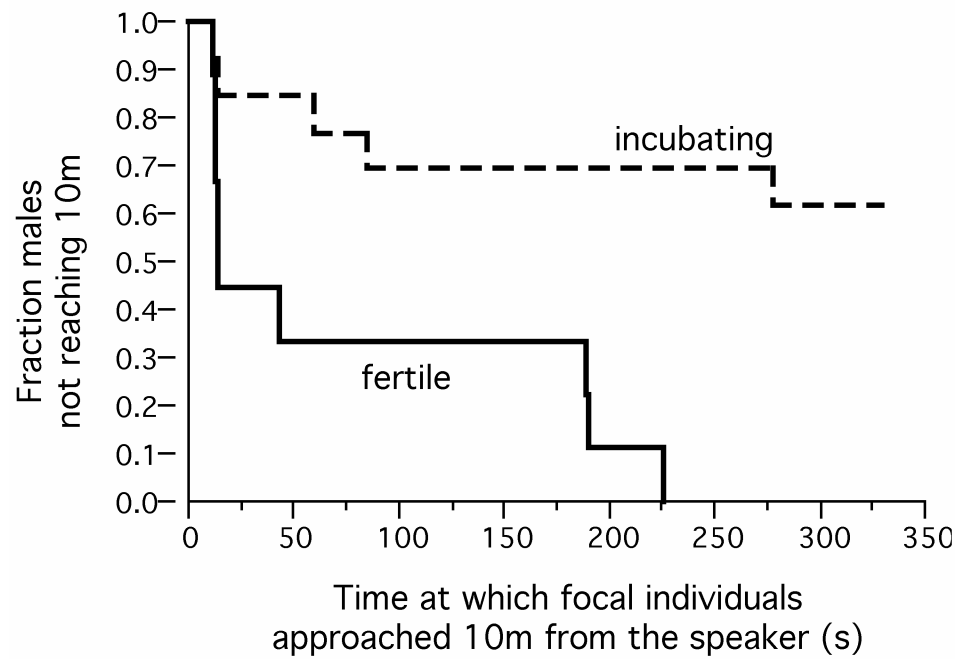
Figure 3.7: Effect of female fertility status on male approach responses to LC playback. a) Males with fertile mates approached the speaker more closely than males with incubating mates. Error bars are  $\pm$  SD. b) Failure curves for male response to playback.



a



b



## DISCUSSION

White-throated magpie jay loud calls represent an unusual level of vocal diversity, both in the Corvidae and among Passeriformes in general. The evidence suggests that call types are not fundamentally different in their function, but rather are either exactly equivalent or graded among closely related functions. Individuals responded similarly to several different but common LCs in playback experiments. Magpie-jays produce many call types in a single calling bout, and a large number of call types could be elicited by increasing proximity to a human observer. Individual males have large call repertoires. LCs appear to fall into a single functional category.

What is the function of loud calls? Two hypotheses best explain the data, alarm calling and mate attraction, but which one fits better is not easily resolved. LCs could be simple alarm calls, given by males to alert nearby conspecifics of the presence of predators. LCs are given in two predator-related contexts. In response to conspecific mobbing of an owl mount, magpie-jays give few calls and use significantly fewer call types in a calling bout. In contrast, terrestrial predators, some perched raptors, and even innocuous creatures such as conspecifics and frugivorous guans (*Penelope purpurescens*) can elicit an exaggerated visual display and a high diversity of LC call types. Given their use in the context of predator encounters, LCs could signal the presence of predators to nearby conspecifics or group members (Klump & Shalter 1984; Caro 2005). The different patterns of calling could function in signaling something about the nature of the discovered predator. In magpie-jays, mob calls signal the urgency of the context or the threat level of the predator (Ellis, in press). LCs may function similarly, though such redundancy would be puzzling. Several mammals (Blumstein & Armitage 1997a; Randall & Rogovin 2002) and birds (Evans et al 1993) use such urgency-based alarm systems. Unlike some sophisticated alarm

calling systems, specific calls of magpie jays were not associated with particular predator types; all were produced in response to human proximity. Alarm calling cannot explain several distinctive features of LCs, such as male sender bias, their production at dawn as well as in response to predators, and high diversity. Even if differences in calling patterns indicate urgency, signaling urgency cannot explain the number of call types each individual uses. Other urgency-signaling communication systems function without such high signal diversity.

A second hypothesis is that LCs function in mate attraction. Structurally diverse vocalizations, dawn calling in the absence of predators, and a strong male bias in production and response, are all characteristics of sexually-selected song in passerine birds (Kroodsma & Byers 1991; Catchpole & Slater 1995). Many male songbirds signal their availability with song, and in several songbirds, females prefer males with large song repertoires (Catchpole et al. 1984; Baker et al. 1986; Lambrechts & Dhondt 1986). Male magpie-jays, which otherwise lack the singing behaviors of non-corvid passerines, could be signaling their quality or availability with LCs. The experimental test of the effect of female breeding status on receiver responses showed that breeding males responded more aggressively to LC playbacks when their mate was fertile than when she was incubating, consistent with a mate attraction function. If LCs attract females, a paired male should defend against interlopers, since a substantial amount of social infidelity occurs (33% of offspring are extra-pair). However, mate attraction does little to explain the primary context in which these calls occur – as a response to potential predators.

A third hypothesis is that LCs, like mainstream passerine songs, mediate conflicts between males over territory and mates. Song often functions in territorial defense and conflict mediation among males (Collins 2004). Large song repertoires allow males of some species to interact vocally by switching, type matching,

repertoire matching, or avoiding matching (Dabelsteen et al. 1996; Vehrencamp 2001; Burt et al. 2002; Beecher & Campbell 2005; Vehrencamp et al. 2007). Only the higher rate of response to playback by males supports this hypothesis. Male magpie-jays are not territorial: paired males assist in group territorial defense against other female groups, but floater males roam at will. Floaters join groups regularly with no aggression and visit up to six groups a day (Innes & Johnston 1996; Langen 1996). I found little evidence of vocal interaction, and nothing suggested that males mediate conflicts with LCs. Indeed, while females have been observed in fierce fights at nests, male aggression involves little more than chases during mate guarding and occasional displacements among floater males (Innes & Johnston 1996; Langen 1996; Berg 2005). Males have not even been observed fighting. Conflict mediation does not appear to be a primary function of magpie-jay LCs.

I propose that the ancestral function of LCs is alarm signaling, but the call has not been co-opted by males for self-advertisement. It is clear that LCs can function as true alarms, and can be elicited from both sexes by predators. When females produce them, their patterns of delivery are similar to those used by males in response to the predator mounts. The mated female is often localized to the nest area during breeding, and her mate often guards her. As a result, neither is as likely to patrol the territory and detect potential threats. Floaters are not tied down in this manner, and often move throughout and among territories. By emitting LCs when they spot low risk threats, they provide a service to all group members within earshot. Higher predator detection rates by floaters could explain why they are permitted *carte blanche* access to territories in this species. Because it pays all group members to attend to LCs, floaters can concurrently advertise themselves to the breeding females in all groups that they visit. Varying the call types may be a mechanism to reduce habituation and thus allow the floaters to advertise themselves more often. Alternatively, floaters may be able to

signal quality or commitment by reliably signaling about threats, and LC repertoire size could indicate a male's quality. Large repertoires have been linked to quality in a number of other passerines (Catchpole et al. 1984; Searcy 1992). This interpretation would also explain dawn calling; males are taking an additional opportunity to signal their quality or availability during a low-activity period of the day. The co-opted alarm hypothesis accounts for male-biased signaling and the production of a diverse and complex signal in response to predators.

The co-opted alarm hypothesis generates several predictions. If repertoire diversity is related to quality, males with large repertoires should pair before males with smaller repertoires when a breeding position becomes available. Similarly, floaters with large repertoires should have higher EPC success than those with small repertoires. It is difficult to determine how females should respond to any single bout of calling. In the experiments I performed, females responded only rarely to LCs. In the cases where they did respond, they approached after their mate. Approach displays were not significantly associated with the presence of females. The data suggest that females do not attend to LCs, but because decisions about both EPC partners and long-term partners are probably not made quickly, responses may not be obvious. While males display in the apparent absence of females, this strategy may simply be a hedge in a low visibility environment. Females seeking mates, whether dominant breeding females who have lost a mate or helpers inheriting a breeding position, probably interact on a daily basis with most of the potential mates in the area. They have little need to respond rapidly to LCs, as they frequently observe males displaying. Female assessment of males could occur over a long period. If so, males could benefit from displaying as much as possible. Under this hypothesis, fertile females should pay more attention to signaling, suggesting that both dawn calling and LC display approaches would be more frequent in their territories.

An unusual suite of life-history traits and social structure suggest why male-biased signaling in magpie-jays is so strikingly different from that of other passerines. Sexual selection on male magpie-jays is presumably unusually high. Dominant females can breed multiple times in a single season; if nest failure rates are high, they can attempt as many as 6 nests in a season. Breeding becomes asynchronous as nests fail and pairs renest. Cooperative breeding behavior among females leads to female territory defense and an operational sex ratio highly skewed towards males because usually only the dominant female breeds. These factors generate high sexual selection (Schuster & Wade 2003). However, sexual selection is high in many species. Magpie-jays appear to be unusual because female territoriality limits male resource defense as a route to reproductive success, and requires that males visit females and advertise. Paired males actively mate guard, but the high level of extra-pair fertilizations and lack of direct conflict between males suggest that females have significant control over paternity. Males may be selected to advertise or trade assistance in group defense for matings. These strategies may be combined in male approach displays, with males drawing attention to their activities and the signals secondarily performing a self-advertising function. Interestingly, high longevity, repeated social interactions and alternative breeding strategies by *females* mean that a male could benefit from displaying to all females in his home-range, because any of them could inherit a territory and become a breeder, attempt to egg dump, or start a secondary nest. Female alternative mating strategies may explain why males seem to signal indiscriminately, without regard to audience identity, and why both floater males and paired males signal.

In other animals, most signals that show strong sex bias are used in purely mate-attraction contexts, and have no association with predator interactions. A few exceptions occur. In the Chaffinch (*Fringilla coelebs*), only males give a hawk alarm,

and then only in the breeding season (Marler 1956). Roosters (*Gallus domesticus*) give aerial predator alarms while hens do not. Males will produce this short-range signal even in the absence of hens, suggesting the hawk call does not function to attract females (Bayly & Evans; Gyger et al. 1987; Evans et al. 1993). In the chaffinch and the chicken, sex-biased production may reflect breeding ecology more than sexual selection. If alarm calls increase the chance of predator attack on the sender or the chances of nest detection, it may not pay females to call because of the risk of the loss of the whole brood. Such factors may not constrain males. In both chickens and chaffinches, the male-biased alarm fits the predicted structure of an aerial predator alarm, above the range of raptor hearing and with soft onset and offset (Marler 1955). A curious case is that of the splendid fairy-wren (*Malurus splendens*; Zelano et al. 2001). Young males sometimes give a song-like vocalization (the Type II vocalization) in response to vocalizations of avian predators, and are more likely to do so when their mother is present. The function of Type II vocalizations is unclear. The likelihood of calling does not appear to impact breeding success. Females do not respond differently to either Type I or II vocalizations. The former function as songs, so the association of Type II vocalizations and predator encounter contexts is confusing. While the sex-biased calls of the fairy-wrens are superficially similar to those of magpie-jays, they lack the extreme diversity of magpie-jay LCs. More data are necessary to predict when sex-biased predator alarms should occur, and exactly how they function.

Male-biased calling in response to predators appears to be a rare signaling behavior, and the diverse loud calls of magpie-jays constitute the most highly developed such system thus described. From the perspective of repertoire size, LCs are a single call category with a large number of variants, much like song repertoires in other birds. The rare combination of resource defense by cooperative female groups

and mobile males may have selected for advertisement by males. While corvid social systems vary greatly, from colonial pairs to solitary pairs to cooperatively breeding family groups, no other corvid has been described as having a complex repertoire of sex-biased signals. A better understanding of exactly when male magpie-jays use LCs and how females respond in both short term and long term time-frames is necessary to test the co-opted alarm hypothesis, and whether LC production reflects patterns of mate choice and social interaction among individuals.



**Chapter 4: Functional and structural analysis of the vocal signal repertoire of the magpie-jay, *Calocitta formosa*, in comparison to the repertoires of some other corvids**

**Abstract:** Understanding the factors that influence vocal repertoire size is a long-standing problem in animal communication. A useful approach is to distinguish between those factors increasing the potential for large repertoire size and those limiting actual repertoire size. Three main factors influence the selective pressure for large repertoire size: social complexity, sexual competition, and the diversity of environmental events. These factors influence which signal functions a species could benefit from using. Other factors may then influence the economics of signaling, reducing repertoire size from its potential given the level of sociality, sexual competition, and environmental events. To examine the factors that increase the potential for large repertoire size, I analyzed the vocal repertoire of the white-throated magpie-jay (*Calocitta formosa*), a species whose social structure is well described, and compared it those of other corvids. Corvids, the New World jays in particular, are ideal for such a comparison because they have a variety of social and mating systems and extra-pair paternity data are available for several species. Because phenomena such as graded signals and redundant signals make repertoires difficult to compare, I used a system for parsing repertoires in a way that facilitates comparisons of functional signal repertoire size across species. I assessed the function of each signal in a species' repertoire and grouped them into general signal classes. Structural variation was also described for each functional call type. Magpie-jays possessed fourteen functionally distinct signals, but produced well over 100 structurally distinct signals. The former measure is not usual for a corvid, but the latter is large and approaches the repertoire size of some wrens and mimids. Magpie-jays possessed a relatively large number of predator-related signals, two of which probably function in mate attraction, but relatively few territorial defense and conflict resolution vocalizations. Comparisons among New World jays and the European magpie

suggested that various aspects of sociality affect different signal classes. Magpies and piñon jays, both flocking species, possessed above average numbers of social integration signals. More territorial defense signals may be used by those species for which territory is highly important to fitness. Sexual competition appeared to have little effect on repertoire size in most corvids, except in the magpie-jay, whose unusual social system may enhance the degree of sexual selection. All corvids used at least two signals in predator defense contexts, usually a hawk alarm and a mob call. This study is one of the first to examine function in signal repertoires across multiple signal classes.

Keywords: scrub-jay, sexual selection, communicative complexity, brown jay

Understanding why each species possesses a particular repertoire of signals is a long-standing challenge in the study of animal communication. Moynihan (1970), Smith (1969, 1977) and Wilson & Hölldobler (1990) all independently proposed that the types of information a species could signal were limited to between 10 and 15 message categories. But their categories were quite general, and place no limit on the number of signals that may evolve within a category. Signal repertoire size varies greatly from species to species, presumably as a result of species differences in social systems, mating systems, life history strategies, ecological communities, and signaling environments. Few studies have compared whole signal repertoires among related species and evaluated the patterns of functional category elaboration in relation to social and ecological factors. A notable exception is Peters (1980), who descriptively compared signal repertoires across a range of mammalian species. However, we still lack a framework for parsing repertoires in a way that facilitates comparisons, and for testing alternative hypotheses of the selective factors favoring signal elaboration.

A first step is to note that hypothetical factors affecting repertoire size can be divided into those that affect the potential for communication and those that affect the economics of fulfilling that potential. Some conditions must be met for certain signal types to play a role in mediating interactions, but benefits of signaling must exceed the costs for signals to evolve, even when conditions for large repertoire size are met. This observation is analogous to the observation that the degree of polygyny establishes the potential for sexual selection, but the intensity of sexual selection is measured by the selection gradient on specific traits (Schuster & Wade 2003). Here, I discuss three main factors that may increase the potential for communication. I then propose a method for parsing repertoires to facilitate comparisons across species. This framework is then applied to the vocal signal repertoires of several corvid species.

Three main factors have been proposed to increase the potential for large communicative repertoires: social complexity, sexual competition, and the diversity of environmental events that may be salient to a species. The first, social complexity, has long been argued to affect repertoire size (Marler 1977; Hardy 1979; Waser 1982; Blumstein & Armitage 1997b). Communication is fundamentally a social behavior: the larger the number of potentially interacting individuals in a social group, the greater the potential for evolution of new signals will be (McComb & Semple 2005; Freeberg 2006). Different aspects of sociality potentially can affect communication to different degrees. Large groups often form dominance hierarchies and signals are required to establish and maintain such relationships. As a result, flock dwelling species of birds often have large repertoires of conflict resolution and social integration signals (Rohwer & Rohwer 1978; Popp 1987c; Popp 1987a). More demographic roles (adults, juveniles, etc.) and more social classes (for example soldiers, workers and nurses in eusocial insects) mean more pair-wise combinations of classes, each of which may require certain signals for interacting (Marler 1977; Blumstein & Armitage 1997b). As social stability and relatedness increase, cooperative interactions may emerge that favor the evolution of coordination signals (Hamilton 1963; Trivers 1971; Axelrod & Hamilton 1981). The nature of population-level social complexity can also affect repertoire size. Fission-fusion societies, while inherently unstable, may require group and individual identifiers (Janik 2000; Bradbury et al. 2001; Wright & Wilkinson 2001; Davidson & Wilkinson 2002). Migratory species may have distinctly different social systems at different periods, multiplying the number of signals they may require. All of these factors may increase the potential for more social species to have larger numbers of signals.

Sexual competition can also have profound consequences for communication.

Regardless of their level of sociality, species with a high degree of sexual selection often have large numbers of signals for attracting mates or dealing with competitors. These signals can take the form of courtship or mate attraction displays as in ducks (Johnson 2000), or conflict resolution displays and tactics as in crickets and some spiders (Hack 1997). A special case arises when repertoire size itself determines the likelihood of winning a contest for resources or mates, leading to arms races for large signal repertoires. I term this concept competitive diversity, where signal diversity exists for diversity's sake. Some songbirds exemplify this phenomenon. Females show preferences for males with higher song diversity, which selects for large song repertoire size (Catchpole et al. 1984; Hasselquist et al. 1996). In other species, males use multiple song types during countersinging interactions to negotiate territory boundaries (Krebs et al. 1978; Searcy et al. 2000; Molles 2006; Botero & Vehrencamp 2007).

A third factor that may increase the potential for communication is the diversity of environmental events. Human language is clearly the most evolved system encountered that deals with environmental events and objects, but many other species signal about predator encounters and food discoveries to conspecifics. When a species deals with a large number of predators, signaling about their nature may prove adaptive. Vervet monkeys give distinctive alarm calls to three qualitatively different predator types they commonly encounter; pythons, leopards and large raptors (Strusaker 1967; Cheney & Seyfarth 1990). Suricates signal about both the urgency of the situation and the nature of the predator (Manser 2001; Manser et al. 2001). Many bird species have hawk alarms that elicit specific evasive responses in conspecifics. While to date most food signals appear to alert conspecifics to divisible resources (Elgar 1986; Gyger & Marler 1988; Bugnyar et al. 2001) species that require a wide

variety of food types might be expected to signal their need for or the discovery of particular types to conspecifics.

Other factors constrain repertoire size below the potential circumscribed by the combined effects of sociality, sexual selection, and environmental events, because they affect the economics of signaling. The costs of communicating in particular environments (Morton 1975; Wiley & Richards 1982; Endler 1993) or the limitations of producing, transmitting, receiving, and processing signals obviously affect signal evolution (Endler 1993; Schluter & Price 1993). Two species with the same level of social complexity, similar degrees of sexual selection, and comparable environments could have markedly different repertoire sizes due to differences in the economics of signaling. For example, ground squirrels show some effect of sociality on the number of alarm calls they use (Blumstein & Armitage 1997b) but alarm calling systems may be more constrained by the economics of communicating predator type. If only one escape route for any predator type exists, only one alarm call should evolve, regardless of the number of predator types (environmental diversity) or social system (social complexity; (Macedonia & Evans 1993). Signal economics may also explain why habitat type also affects courtship repertoire size in ducks (Johnson 2000); those that court on land have fewer signals, despite the level of sexual selection. While we cannot assess the economics of every signal (or lack thereof) for every species' repertoire, we can start by comparing the potential for signal evolution in different species, and then see whether any additional economic arguments are necessary to explain observed patterns. This is my strategy here.

In this paper, I analyze the vocal repertoire of the white-throated magpie-jay (*Calocitta formosa*), a corvid with a previously undescribed vocal system, and compare it with the vocal repertoires of several New World jays (Corvidae) and two

other corvids with well-described repertoires. I examine vocal repertoire size because the acoustic signals are well described both structurally and functionally in many of these species, and because vocal signals are very important to birds that often live in groups but forage out of visual contact. Jays, and in fact all corvids, lack a song in the conventional sense of long, complex vocalizations used in both territory defense and mate attraction (Goodwin 1986; Catchpole & Slater 1995); they are instead known to give soft rambling vocalizations during courtship. Thus their vocal repertoires consist entirely of calls (Marler 2004).

As a taxon, New World jays have several other characteristics that make them ideal for testing the above three hypotheses (sociality, sexual competition, and environmental diversity) for potential increases in repertoire size (Figure 4.1; Bonaccorso & Peterson 2007). Indeed, Hardy (1979) initially compared provisional repertoires of several *Cyanocorax* species with regard to sociality, finding that those with larger repertoires produced more sounds. They vary greatly in group size and social systems, and some have mating systems that are otherwise rare among birds. In addition, the genetic mating systems are known for four species: the white-throated magpie-jay (Berg 2005), the brown jay (*Psilorhinus morio*; (Williams & Rabenold 2005), the Mexican jay (*Aphelocoma ultramarina*; (Li & Brown 2002), and the Florida scrub-jay (*Aphelocoma coerulescens*; (Quinn et al. 1999). These four have complex social structures and cooperative breeding. Here, I compare the vocal repertoires and social systems of these four species to each other, and to those of the piñon jay (*Gymnorhinus cyanocephalus*; (Marzluff & Balda 1992), a colonial breeder, and the western scrub-jay (*Aphelocoma californica*; Webber 1984; Carmen 2004), blue jay (*Cyanocitta cristata*; Hardy 1961; Edwards 1969; Cohen 1977), and Steller's jay (*Cyanocitta stelleri*; Brown 1963; Brown 1964b; Hope 1980), all pair-living, non-



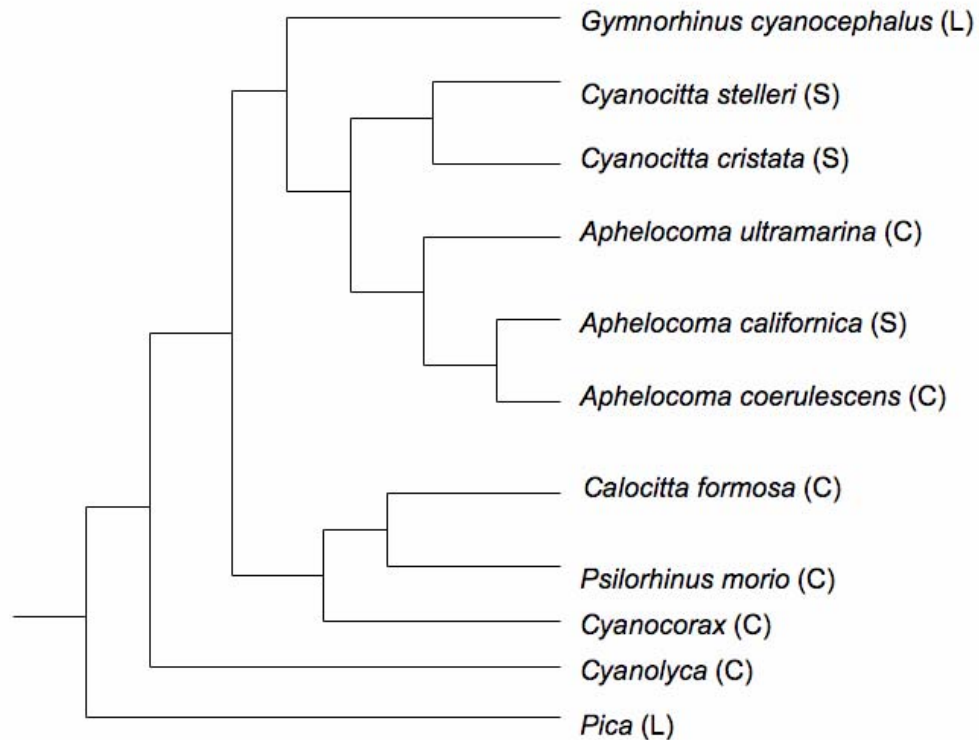


Figure 4.1: Relative relationships of the corvids in this study. Of the New World jay clade, all genera are included on the tree, though *Cyanolyca* and *Cyanocorax* (*sensu* Bonaccorso & Peterson 2007) are not represented in the study. Branch lengths are not representative of relative relatedness between sister pairs. Letters in parentheses represent the social system of each species; L = colonial or flocking, C = cooperative breeder, S = singular pair breeder. The relationship of *Gymnorhinus* to *Aphelocoma* and *Cyanocitta* has been difficult to determine (de los Monteros & Cracraft 1997; Saunders & Edwards 2000; Bonaccorso & Peterson 2007). This tree reflects the results of Bonaccorso & Peterson (2007).

cooperatively breeding species. The European magpie (*Pica pica*) and European jay (*Garrulus glandarius*), more distantly related corvids, are pair-breeding territorial species (Møller 1982; Andren 1990; Grahn 1990; Birkhead 1991; Rolando 1998). The European magpie roosts in groups during the non-breeding season (Møller 1985), while the European jay is non-territorial during the same period. Because their repertoires are also well described, I include them in my comparative analysis. While Hardy (1979) analyzed the repertoires of several Central American Cyanocorax species, I do not consider their repertoires well enough described for inclusion.

It can be difficult to compare repertoires between species because of coding differences between one signal and another, both within and between repertoires (Green & Marler 1979). Some signals may be graded, while others represent distinct structural variants. Such difficulties have stymied direct comparisons of repertoires. I deal with this problem in two ways. First, I characterize variation within the repertoire of the white-throated magpie-jays. Understanding variability in multiple signals could give us insight into whether signals are graded or not, and give us another potential measure of repertoire “complexity”, if not size. While such data are only rarely available for many species, providing such measures should facilitate future comparisons. Second, for comparative purposes I quantify repertoires at three levels. Initially, I assign specific functions to each signal, if such can be determined from signaling contexts and conditions, type of sender, subsequent sender behavior, and responses of potential receivers. Signals differing only in degree are considered to have the same function. The total number of specific functionally distinct signals is the functional repertoire size (Bradbury & Vehrencamp 1998). Functional types are assigned to widely recognized signal classes, such as mate attraction, conflict resolution and predator defense. The distributions of functional types across these

classes should reflect how important such general signal classes are to each species. Finally, the number of structurally distinct variants within the repertoire is the structural repertoire size. This number can increase when structurally distinct signals have the same function, such as the multiple songs of passerine birds. Given the diversity of social systems, life histories, foraging strategies, predators, and signaling environments among corvids, I hoped to determine which of the proposed factors for increasing repertoire potential actually affect vocal repertoire size in this group. By looking at the distributions of functional signal subtotals across general signal classes and assessing which functional signals appear to have a high degree of structural variation, it may be possible to determine which types of social interactions, sexual competition, or environmental factors have most influenced repertoire size and composition. While such categorizations cannot capture all of the variation of the communication systems of this group, this scheme represents a first step in the thorny issue of understanding repertoire evolution.

## **METHODS**

### **Field work: determining the repertoire of the white-throated magpie-jay**

*Study site.* I studied a banded population of white-throated magpie-jays at the Santa Rosa unit of the Area de Conservación Guanacaste (ACG), Guanacaste, Costa Rica (10°50' N, 85°37'W) during 2003, 2004 and 2005. Study periods lasted four months, from early February, the approximate start of the breeding season, to late May. The ACG is characterized by a mosaic of tropical dry deciduous forest and regenerating

pasture, creating a matrix of edge habitat that magpie-jays require (Langen & Vehrencamp 1998). Site details can be found in Langen & Vehrencamp (1998) and Berg (2004). Approximately 50% of subjects were individually color marked with metal leg-bands, either as nestlings or as adults, as described in Berg (2005). Most unbanded group members were recognizable by distinctive facial patterns, and could be sexed by face pattern and behavior (Langen 1996a). I studied 14 social groups over the three years of this study. Group sizes ranged from two to five (mean  $2.75 \pm \text{SE}$  0.88,  $n = 36$  group-years).

*Recordings.* To obtain recordings for analysis, I followed groups of magpie-jays from 0430 to 1100 hr and from 1400 to 1800 hr, periods when the birds were most active. When I encountered a group, I made ad lib observations and recordings of all activities associated with vocalizations. Group size and composition (males, females, floaters, breeders, etc.) were narrated whenever they changed. Specific activities noted included all affiliative and aggressive interactions between individuals, predator encounters, interactions with other heterospecifics, and breeding activities such as nest building and incubating. Magpie-jay vocalizations and my behavioral narrations were recorded on three different recording rigs: a Sennheiser MKH 816 shotgun microphone and hhB Portadat PDR 1000 digital audio tape recorder; an Audiotechnica AT815b shotgun microphone and same digital audiotape recorder; and a Sennheiser ME67 shotgun microphone and Marantz PMD 670 digital recorder. In all cases, recordings were made at sample rates of 48 kHz and 16-bit recording quality. Digital audiotapes were digitized to .WAV files on a Macintosh Powerbook G4 with Raven (Bioacoustics Research Program, Cornell Lab of Ornithology), also at 48 kHz sampling rate and 16-bit accuracy.

*Call analysis.* I used visual and aural methods for assigning calls to different structural categories. I took a conservative approach to this process, primarily using structural features such as call shape, noisiness, and sometimes duration. Some calls varied in frequency and duration between individuals and between calling bouts; I grouped these together in the absence of contextual information that indicated they were different. Vocalizations were generally temporally distinct, but in cases where they occurred in rapid succession I defined them as different if they were greater than 0.05 s apart. To visually classify calls, I used spectrograms generated in XBAT, with a FFT size = 512 samples, window size = 1, window function = Hanning, and FFT overlap = 0.5, giving 0.011 s time resolution and 93.75 Hz frequency resolution. To quantify the acoustic parameters of calls, I used the Energy Distribution tool in XBAT to automatically extract 21 measurement variables (Cortopassi 2006a; Cortopassi 2006b). Spectrogram settings in this case were: FFT = 1024 samples; window function = Hanning; FFT overlap = 0.75; and energy fraction = 0.95. A frequency window of 800 Hz to 5000 Hz excluded low-frequency wind noise and high-frequency insect noise from analysis. In no cases did this frequency band appear to exclude the frequencies of highest amplitude in magpie-jay calls.

Call variability was quantified by calculating coefficients of variation (CV). I computed the CV for each measurement variable within the four functional call categories for which I had large sample sizes, using the measures generated by the Energy Distribution tool (Table 4.1). Measures for which CVs were greater than one were excluded from analysis. Note that CVs greater than one occur when the standard deviation is larger than the mean. This situation occurs when measures can take both positive and negative values, placing the mean relatively near zero. CVs were log-transformed to meet parametric statistical requirements. To test for

differences in variability among call types, I used ANOVA while controlling for specific measures. Pair-wise differences were tested *post-hoc* with Tukey tests.

To assess the function of call types, I employed two criteria. First, I used the response of receivers to assess function, if such responses were noticeable. More often, the context of the call and behavior of the sender were used to assess the general functional properties of the call. Calls were named for their probable primary function. While behavioral ecologists often refrain from assigning functional names to signals (e.g., alarm call), I deviate from this convention precisely because I am attempting to assess function (Hailman & Ficken 1996). Calls were then assigned to general signal class categories (Table 4.2). These categories include mate attraction, courtship, conflict resolution, social integration, territory defense, food-related, and predator-related signal classes.

### **Comparison of corvid repertoires**

*Literature review.* Information on the communication systems of corvids were initially assessed using general species accounts (Cramp & Perrins 1994; Poole 2005). In most cases, repertoires were inadequately known for making comparisons. Repertoires were discarded for two primary reasons. In some, data on function are lacking (i.e. many South American *Cyanocorax* jays). In many others (i.e. the genus *Corvus*), communication systems are highly graded and the necessary work thus incomplete. Included in my initial comparisons are most North American jays (but not grey jay [*Perisoreus canadensis*], which is poorly known). The European magpie was included, but I excluded the North American species, black-billed (*Pica hudsonia*) and

Table 4.1. CVs for call measures used in analysis. Numbers in parentheses are sample sizes for each call type.

Measure	BEG	CHIRR	LOUDCALL	MOB	Description
asym_time	0.16	0.17	0.35	0.09	skew in frequency energy distribution
center_freq	0.14	0.27	0.44	0.04	center frequency
ipr_time	0.25	0.47	2.55	0.19	interpercentile time range
skew_time	0.16	0.16	0.35	0.10	skew in ordered time energy distribution
spread_time	0.26	0.50	2.73	0.20	time difference between upper and lower times
cfc_avgabsder	0.65	0.57	0.77	0.63	average absolute derivative of center frequency contour
cfc_cumabsder	0.70	1.10	3.01	0.67	cumulative absolute derivative of center frequency contour
cfc_inflex	0.71	0.66	3.92	0.48	number of inflection points on center frequency contour
pfc_avgabsder	0.69	0.59	0.83	0.89	average absolute derivative of peak frequency contour
pfc_inflex	0.74	0.67	3.80	0.49	number of inflection points on peak frequency contour
asym_freq	0.38	0.52	0.69	0.25	skew in time energy distribution
peak_freq	0.18	0.31	0.51	0.05	peak frequency
skew_freq	0.39	0.48	0.62	0.23	skew in ordered frequency energy distribution
ipr_freq	0.28	0.39	0.33	0.18	interpercentile frequency range
lower_freq	0.33	0.35	0.57	0.17	Lowest frequency in ordered frequency spectrum using specified energy percentage
p1_freq	0.28	0.32	0.50	0.14	frequency of initial percentile value of specified energy percentage
p2_freq	0.05	0.28	0.23	0.10	frequency of terminal percentile value of specified energy percentage
spread_freq	0.30	0.44	0.36	0.16	frequency difference between upper and lower frequencies
upper_freq	0.05	0.32	0.26	0.10	Highest frequency in ordered frequency spectrum using specified energy percentage

yellow-billed (*Pica nuttallii*) magpies, because descriptions of the former relied heavily on accounts of *Pica pica*, with which *P. hudsonia* was formerly lumped, and descriptions of the latter were incomplete and difficult to assess (Trost 1999). Of European corvids, *Garrulus glandarius* was well studied, but choughs (genus *Pyrrhocorax*), the genus *Corvus*, and siberian jay (*Perisoreus infaustus*) were inadequately understood vocally. The repertoire of the azure-winged magpie (*Cyanopica cyana*) was fairly well-described but difficult to categorize. Of other areas of corvid diversity, Asian and African species were obscure both vocally and socially; no corvids outside of the genus *Corvus* occur in Australia, and those suffered from the same limitations as in other areas (highly graded vocal systems). For the included species, I assessed repertoire size from the primary literature cited in general species accounts (Table 4.3). Data on the brown jay came from brief analysis of personal brown jay recordings from Monteverde, Costa Rica, existing literature and communication with D. Williams. Bonnie Bowen and John McCormack provided additional information on the context of begging and structural variation in Mexican jays. John Fitzpatrick provided additional information useful in discriminating between predator elicited and territorial signals in the Florida Scrub-jay.



Table 4.2: General signal classes in animal communication.

<b>General signal class</b>	<b>Functional call types encompassed</b>
Predator-related	Alarm, alert, distress,
Food-related	Begging, food location calls
Territory defense	Boundary location, owner interactions that are not direct conflicts
Conflict resolution	Submission, aggression
Social integration	Contact, coordination, flight calls, greeting, lost call, movement calls, maintenance of distance, group cohesion, assembly, recruitment
Mate attraction	Fertility signals, female attraction
Courtship	Signals associated with pair interactions (post-pairing): copulation coordination, nesting coordination, copulation rejection, post-copulation

Table 4.3: Functional and structural diversity of eight New and Old World corvids. Calls are partitioned into general signal classes. The left column of each signal class indicates the functional diversity (FD), and the right column the structural diversity (SD). Totals are on the right.

Table 4.3

Common Name	Species	Coop breed	Territorial	Group size: breeding (non-breeding)	Functional Categories														Ref
					Predator defense		Food related		Territory defense		Conflict resolution		Social integration		Courtship		Total FD	Total SD	
					FD	SD	FD	SD	FD	SD	FD	SD	FD	SD	FD	SD			
Florida Scrub-jay	Aphelocoma coerulescens	Yes	Yes	2-8 (same)	5	5	2	2	3	3	1	1	2	2	1	1	14 <sup>1</sup>	14	1 <sup>2</sup>
Mexican jay	Aphelocoma ultramarina	Yes	Yes	5-25 (same)	2	2	1	1	1	1	1	1	1	1	1	1	7	7	2
Brown Jay	Psilorhinus morio	Yes	Yes	6-20 (same)	2	3	2	2	1	2	1	3	1	1	1 <sup>b3</sup>	1	8	10	3
White-throated magpie-jay	Calocitta formosa	Yes	Yes	2-10 (same)	6	138	2	2	1	1	1	1	2	2	2	2	14	146	4
Pinyon jay	Gymnorhinus cyanocephalus	No	No	98-270 (1000+)	2	2	1	1	0	0	2	2	6	6	3	3	14	14	5

<sup>1</sup> Total structural diversity for *A. californica* does not equal the total over each general functional category, because several calls are used consistently in both territorial defense and in mobbing. The total structural diversity is the total number of structural variants produced as defined in the literature.

<sup>2</sup> References) 1: Barbour 1977; Francis et al. 1989; Hailman 1990; Barg & Mumme 1994 2: Cully & Ligon 1976; Brown 1994; Hopp et al. 2001 3: Lawton 1983; Hale et al. 2003 4: Innes 1992; Langen 1996a; Ellis in prep-b; Ellis in prep-a; Ellis 2008 5: Berger & Ligon 1977; Marzluff & Balda 1992; Balda 2002

<sup>3</sup> Brown jays, like many corvids, produce soft song. In this species soft song has only been noted in lone individuals, while in most other corvids it appears to function in courtship. I tentatively place it here.

Table 4.3 (Continued)

Common Name	Species	Coop. breeding	Territorial	Group size: breeding (non-breeding)	Functional Categories														Ref
Refs					Predator defense		Food related		Territory defense		Conflict resolution		Social integration		Courtship		Total FD	Total SD	
					FD	SD	FD	SD	FD	SD	FD	SD	FD	SD	FD	SD			
European Magpie	<i>Pica pica</i>	No	Yes	2 (roosts up to 300)	2	4	1	1	1	1	3	3	7	9	2	2	16	20	6 <sup>4</sup>
Blue jay	<i>Cyanocitta cristata</i>	No	No	2 (2+)	3 <sup>c5</sup>	3	3	3	0	0	0	0	2	≥2	1	1	9	>9	7
Steller's jay	<i>Cyanocitta stelleri</i>	No	No	2 (1-?)	4 <sup>c</sup>	4	0	0	0	0	3	3	2	3	1	1	12 <sup>d6</sup>	>12	8
Western Scrub-jay	<i>Aphelocoma californica</i>	No	Yes	2 (same)	3	6	1	1	2	6	2	2	3	3	1	1	12	16 <sup>a</sup>	9
European jay	<i>Garrulus glandarius</i>	No	Yes	2	6	6	1	1+	0	0	1	1	2	2+	2	2	12	12+	10

<sup>4</sup> 6: Baeyens 1979; Møller 1982; Redondo & Exposito 1990; Birkhead 1991; Redondo 1991; Stone & Trost 1991 7: Edwards 1969; Conant 1972; Cohen 1977; Kramer & Thompson 1979; Racine & Thompson 1983; Tarvin & Woolfenden 1999 8: Brown 1963; Hope 1980; Brown 1994; Greene et al. 1998 9: Webber 1984 10: Goodwin 1949; Goodwin 1951; Goodwin 1952

<sup>5</sup> Both blue jay and Steller's jay can mimic multiple raptor species, producing these calls as singular distinct utterances. Mimicry is treated as a single functional and structural call type, because the function of mimicry is unknown. Mimicry would also be expected to produce potentially large increases in structural diversity, depending on the number of species mimicked.

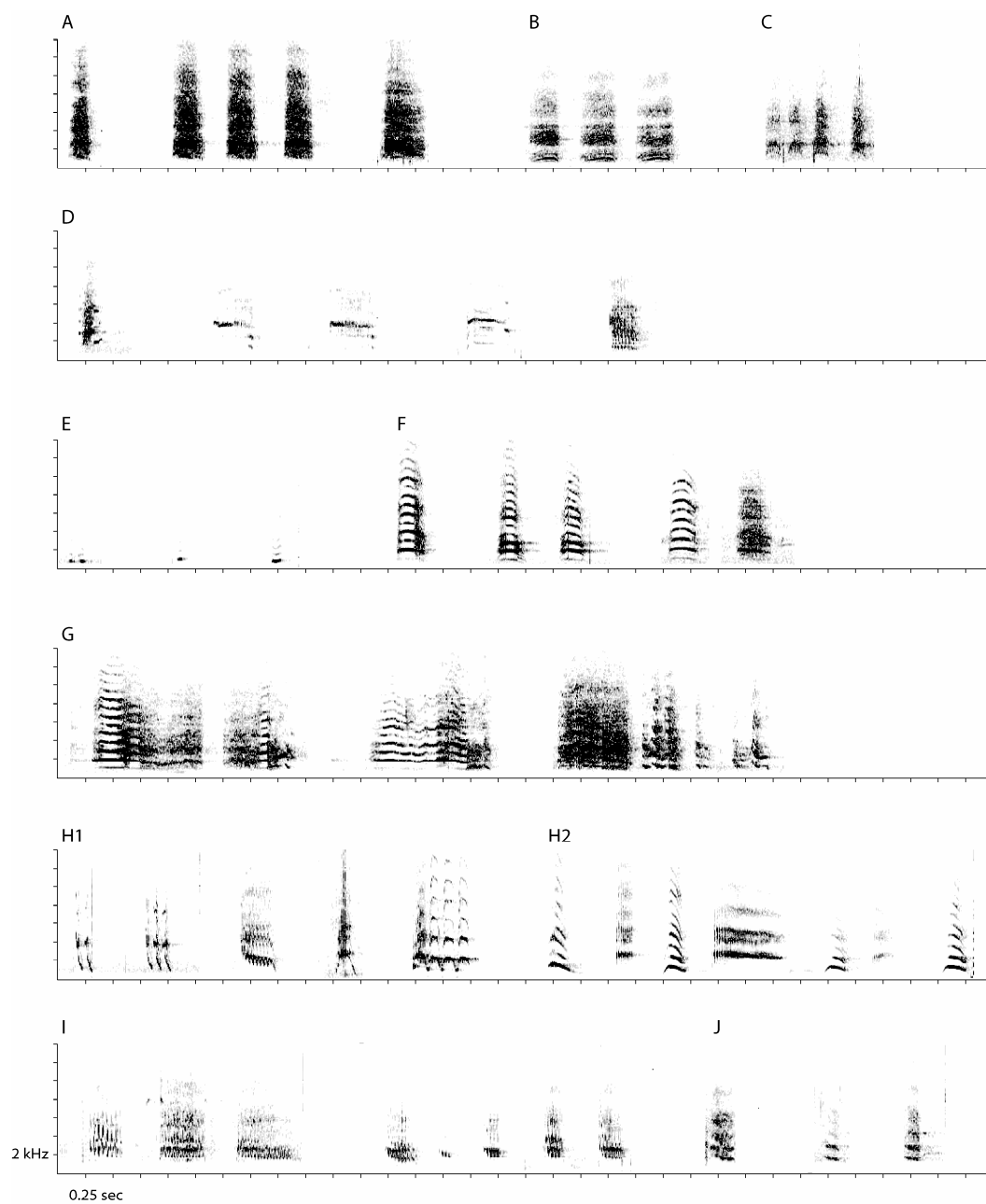
<sup>6</sup> The functions of two calls of the Steller's Jay are unknown, so totals across functional categories do not add to the total FD for this species.

*Comparative analysis:* To analyze call repertoires for comparative analysis, I assigned calls to functional categories using descriptions of context and receiver responses and each author's assessment of function, and used descriptions and spectrograms of call structure to determine the structural diversity. In cases where the functions of structurally distinct calls differed only in degree (i.e. low-threat mobbing vs. high-threat mobbing or degree of willingness to attack) I classified them as a single function with multiple structural variants. While I presume most full accounts of repertoire size to be fundamentally correct, especially if the work treats the repertoire as a whole, one caveat must be made. Signal types can differ in their detectability and in the obviousness of their function and context. For example, signals elicited by predators clearly have an external stimulus and clear context, and are often adapted to be detected at long range. Thus, such signals should be relatively well understood. However, it may be difficult to detect or assign a context to soft, short-range signals. Many accounts contain references to such soft, undetermined signals, so estimations of social integration and conflict resolution signals may be low for all accounts. For instance, the two species of the genus *Cyanocitta*, blue jay and Steller's jay, are both poorly understood vocally. Consequently, I made no attempts to enumerate the structural diversity for each signal type. Both species probably use several graded signals, and beyond this may generate new distinct structural types on a rare but regular basis (Tarvin & Woolfenden 1999). Structural diversity for both of these species is higher than functional diversity. I did not assess call variation for any of these species beyond the descriptions of the authors. Little quantitative work exists on the vocalizations of most corvids, so comparisons of within-function structural variation could not be undertaken.

I determined total functional and structural diversity (wherever possible) for each species, and categorized them by general function. Territoriality, social system, and

maximum group sizes in the breeding and non-breeding seasons were collated from the available literature. I compared total functional repertoire sizes and structural repertoire sizes for each group. Although chi-square tests are not valid because expected cell totals are low, I assessed which species had relatively high or low numbers of call types in particular signal class categories. For those species that obviously had larger numbers of certain functional signal types, I assessed how that signal class and the functions of those signals reflected their social system.

Figure 4.2: Spectrograms of the repertoire of the white-throated magpie-jay, showing variation within functional call types. Time between calls is not natural except in H2. A) Mobs B) Distress calls C) Hawk alarms D) Hawk alerts E) Approach vocalizations F) Adult female begs G) Allofeed gurgles H1) Loud calls H2) Loud call approach display I) Social chirrs J) Flight buzzes.





## RESULTS

### *Repertoire of the white-throated magpie-jay*

The total functional repertoire size of white-throated magpie-jays is at least 14 call categories (Figure 4.2). Below, I group them by general signal class. For each functional call type, I indicate sender, probable receivers, the contexts in which they occurred and their proposed specific function, and describe the structural variation within each functional type.

#### **Predator-associated calls**

*Mob call*: Loud, harsh vocalizations given in response to terrestrial and arboreal predators and perched raptors (Ellis 2008). Mob calls attracted conspecifics in some contexts, and both context and structure defined them as classic mob calls (Marler 1955; Curio 1978; Caro 2005). Call rate and call duration were associated with threat level and determined the likelihood of conspecific approach. However, such variation was continuous and did not appear to represent discrete structural variants (Ellis 2008).

*Raptor alarm*: A short, harsh, call vocalization very similar to the mob call. When a raptor stooped on a group, magpie-jays often gave a short series (2-4) of calls. Receivers would dive into nearby underbrush immediately. I was not able to record

this call frequently enough to determine the structural differences between this call and mob calls, but calls were probably shorter on average than mob calls. This call was primarily noted when roadside hawks, *Buteo magnirostris*, stooped on magpie-jays. Roadside hawks do not appear to be significant predators on adults, even though they regularly stoop on magpie-jays. No successful attempts were observed, and magpie-jays never mob roadside hawks even after stoops. This category will be treated as one variant.

*Raptor alert:* High-pitched, variable vocalizations given when a high-flying, potentially dangerous raptor is detected. Magpie-jays appeared to be able to differentiate between non-threatening turkey vultures (*Cathartes aura*) and potentially dangerous *Buteo* hawks (Swainson's hawk, *B. swainsonii*; white-tailed hawk, *B. albicaudatus*; and short-tailed hawk, *B. brachyurus*; and even the zone-tailed hawk, *B. albonotatus*) which mimics the flight and plumage of turkey vultures (Willis 1963). Other non-threatening hawks such as the roadside hawk (*B. magnirostris*) and crane hawk (*Geranospiza caerulescens*) were ignored, even when circling above the canopy. The responses of conspecifics were difficult to determine, but alerting conspecifics to any dangerous raptor may be important, because of the ability of aerial predators to approach swiftly and silently. At least four variants of this call were recorded. Several conformed to the structure predicted for hawk alarms, with long, even notes produced at high pitch, which should be difficult for hawks to detect (Marler 1955).

*Distress call:* A loud, harsh, high-pitched whine given when a predator or conspecific grabbed a magpie-jay. The two contexts in which this call was recorded were during banding activities, and once when a helper female was caught at an active nest by the breeding female; the helper gave this call while hanging by her wing in the beak of the breeding female beneath the nest. 12 playbacks of this call attracted nearby magpie-jays and in all cases they began giving mobbing calls. Only one variant was noted.

*Approach vocalizations:* Soft, low-pitched notes given by resting or foraging magpie-jays when an observer approached or shifted position after being still. Both sexes gave these soft vocalizations, and they were also incorporated into loud calling sequences (below). They appeared to indicate movement by potentially threatening objects. All recordings were made in response to recordists/observers, so it was difficult to determine the range of potential threats that might elicit this call. Magpie-jays produced a wide variety of structural variants of this functional call type, though all variants were similar in their short duration and low frequency and amplitude.

*Loud calling sequences:* One distinct context accounted for a large number of structural call types in the repertoire. Magpie-jays, usually males but occasionally females, performed a distinct display in the presence of terrestrial predators, perched raptors, and other animals. They would slowly fly directly toward a threatening object with deep wing beats, give loud vocalizations (loud calls or LCs), land nearby, and often continue calling. After such a display, they sometimes called again when the object (often a human observer) moved. LCs were also given during a brief period before dawn before it was light enough to forage. 134 call types were recorded in these two contexts (Ellis in prep-a). While these calls probably have some alarm function, their disproportionate production by males and high diversity suggest that

they have a mate attraction function as well. I have proposed that these low-level alarm calls have been co-opted by males for advertisement purposes (Ellis in prep-a).

### **Conflict resolution**

*Grunt*: A soft, short call, given occasionally by individuals during chases. In such cases it was not clear which individual uttered the calls. The occurrence of this call while being mobbed by small birds (*Polioptila albiloris*) suggests that it is given in annoyance or before being physically struck during a chase. Only recorded from males, but this call is so rarely given that this may be an artifact of circumstance.

### **Territory defense**

*Territorial chirr*: Given by groups of females during border skirmishes, when two groups encounter each other at the border of a territory. Such border skirmishes were marked by forays into the neighboring territory, upon which the neighbors would chase the intruder back over the border. I was unable to obtain recordings of this call. For the duration, all individuals involved give rolling “chirr” calls. Similar calls were sometimes given when a magpie-jay discovers a food resource that may require help to acquire, or in cases where resources are high quality or abundant, such as over army ant swarms. Five bouts of chirring were recorded when one or both individuals were feeding, two bouts occurred when an individual had caught a large arthropod, one bout was observed while a group fed on the back of a resting deer, and two bouts were associated with approach towards baited traps. Langen (pers. comm.) also reports that magpie-jays gave chirrs when foraging for large arthropods, especially over army ant swarms. Thus, this vocalization

may function to recruit group members to the location, with the greatest urgency occurring during territorial interactions.

### **Social group/pair integration**

*Flight buzz:* When in groups, magpie-jays sometimes gave a short trill just prior to or during flight, or as a group member flew. I most often recorded this call when following pairs, but members of all social classes gave it. This call appeared to be a movement coordination call between pairs and within groups.

*Social chirr:* Given primarily by paired individuals in interactions with mates, and occasionally in small choruses by group members, or by a helper and floater. Chirrs were almost always given repeatedly, and individuals both alternate and overlap with each other. Long chirring interactions between paired individuals were reliable indicators of intent to nest. Of 75 chirring bouts, 76% were associated with a known nest attempt or nesting behavior, that is, during periods when an individual was gathering nest material, actively building a nest, or laying eggs. In 71% of chirring bouts, two individuals vocalized, always a male and a female. Of those, 83% involved mated pairs. The remainder of two-individual chirring events occurred between floater males and helper females or in a few cases between paired males and helper females. Chirring, then, seemed to coordinate mating efforts between pairs. Floaters and helpers may give this signal to assess whether the other is willing to start a secondary nest.

## **Food-associated signals**

*Adult begging:* Loud, broadband calls given by female magpie-jays in two contexts. Females begged loudly (audible over 750 m in still conditions) and at times constantly during their fertile periods, just prior to and during egg-laying. Once eggs were laid, frequency of begging decreased, and females gave begs only when they saw group members approach the nest with food. These calls were homologous to those of fledglings (Ellis in prep-b), and elicited feeding by group members, primarily helpers. In some cases, paired males stationed themselves near begging females, begged when a group-member approached with food, and often managed to be fed (similar behaviors noted in Langen 1996a; Berg 2005). While begging probably signals a female's need for food to her group, the timing and amplitude mean that floaters and neighboring males could use this signal as a cue to a female's fertility (Ellis in prep-a).

*Allofeed gurgle:* A soft, short-range whine given as an individual is fed by another magpie-jay. Most often recorded when a begging female was allofed. However, it was not dependent on begging vocalizations, nor was every allofeeding accompanied by this call. Magpie-jays are somewhat unusual in that allofeeding can occur between any dyadic pair of individuals within a group, including visiting floaters. Allofeed gurgles were occasionally produced in these interactions. The gurgling quality of this call may be due to individuals beginning swallowing actions prior to being fed, obstructing the vocal tract. In other jay species with analogous calls, allofeeding calls have been presumed to be beg calls that are obstructed by swallowing actions (Conant 1972; Cohen 1977; Tarvin & Woolfenden 1999). Several observations suggest that in magpie-jays the allofeed gurgle is distinct from begging as a vocalization. They were usually much longer than beg calls, and individuals receiving food sometimes gurgled

even though they were not begging. The exact function and intended receivers of this call were not clear. It did not appear to elicit feeding; usually a food-carrying individual was already approaching the target. It was strongly associated with actual feeding events, but why this information should be broadcast is uncertain.

### **Mate attraction**

While there is no evidence for vocalizations functioning uniquely on mate attraction in white-throated magpie-jays, both begging and loud calls may function in part in mate attraction. Both these signals probably have a dual function, primarily acting as food-solicitation signals and alarm calls, respectively, but also serving in self-advertisement (Ellis in prep-b; Ellis in prep-a).

### **Courtship**

*Soft song/sotto voce song*: Streams of very low-amplitude notes of highly variable structure, ranging from whirrs and whines to rattles and pops (Figure 4.3). Some notes appeared to be biphonations, in which sounds are produced simultaneously by two independent sound sources (Wilden et al. 1998; Fitch et al. 2002). Magpie-jays most consistently gave sotto voce song during courtship, often in association with a courtship dance. A male would approach a female and either dance or lean forward while erecting his crest; during these displays he would vocalize softly. Sotto voce song also occurred when male dancing was directed at another male. Solo magpie-jays also produced sotto voce song unpredictably, often such as in response to the approach of a low-threat predator or observer.

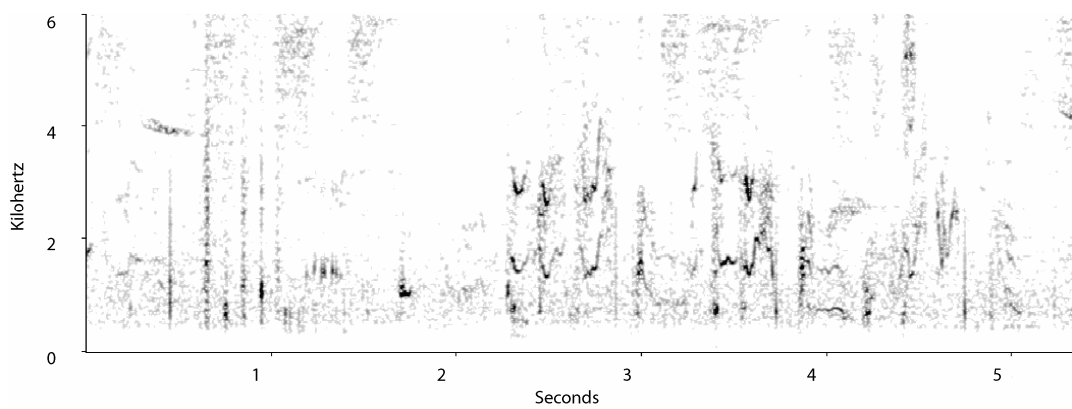


Figure 4.3. A section of a bout of sotto voce song in the white-throated magpie-jay. Tonal ticking occurs early, followed by a several discrete notes and high-pitched twittering.



*Copulation call:* A medium amplitude call given in one case just prior to copulation. An unpaired female solicited a paired male in the presence of his mate, fluttering her wings at her sides and quivering her tail. As the male mounted, the female gave a single vocalization. This call was given during only one of the three copulations that I observed in 12 months of observation over three breeding seasons.

### **Call variability**

Magpie-jay calls differ in their overall levels of variability within a functional call type. I had large enough samples to measure coefficients of variation for four functional call types: social chirrs, mob calls, begging, and loud calls. These four calls differed significantly from each other in level of variation, after controlling for differences in the means of measures (whole model:  $F_{3,47} = 27.5$ ,  $P < 0.0001$ ; Figure 4.4). Mobbing calls were least variable on average, followed by beg calls; chirrs and loud calls were most variable. Loud calls were most variable because many structurally distinct variants were grouped together functionally. Social chirrs were the next most variable, due to high levels of variability within a single structural variant: chirrs were always a frequency modulated trill or quaver, but were otherwise quite variable in temporal, frequency and bandwidth parameters (Figure 4.2). The structural variability of social chirrs produced several exceptions to the general result of the ANOVA. Chirrs were most variable in bandwidth, because they may rise in frequency, fall, or be relatively flat, while most other magpie-jays calls are less variable. Measures of call duration were also most variable for social chirring.

Generally over the repertoire, measures of frequency modulation within a call were most variable (Table 4.1). The CVs for several of these measures were not included in the analysis because the standard deviation (SD) was larger than the mean.

When the mean is relatively small compared to the SD, CV takes a value greater than one and assessing CV is suspect. Means for many of the frequency modulation measures were close to zero, implying that although calls were quite variable, they were not consistent in the direction of frequency modulation, and ascending calls were balanced by descending calls.

### **Call Amplitude**

Calls generally fell into three amplitude categories. While direct sound pressure measures were not made, they were easily classified by general range (Table 4.4). Begging calls and mobbing calls are sometimes detectible from two territories away. Loud calls and raptor alarms can be audible in neighboring territories. Most other signals are not easily heard beyond territory boundaries when calling individuals are near the center of their territories.

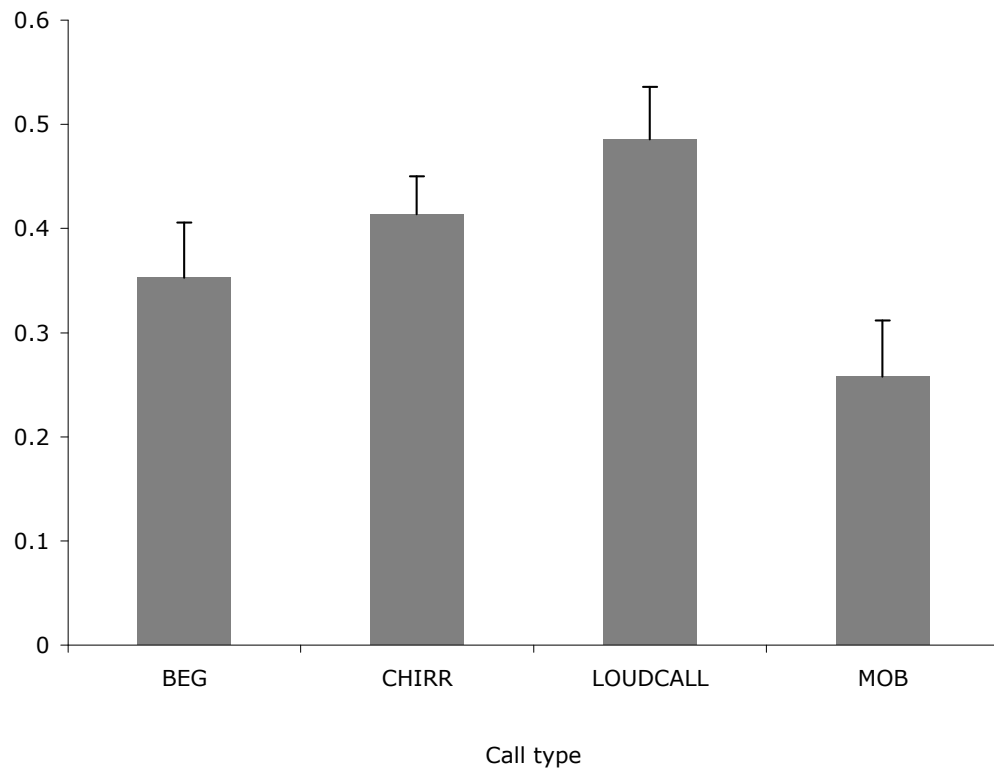


Figure 4.4: Mean $\pm$ SE coefficient of variation of four common call types: begging, mobbing, social chirring, and loud calls. The means for all call types are significantly different ( $\alpha = 0.05$ , post-hoc Tukey test) after controlling for specific measure.

### **Comparison of New World jays**

The vocal diversity of the corvids analyzed here ranges from 7 to 16 (Table 4.3). Structural diversity ranges from 7 in the Mexican jay to approximately 150 in the white-throated magpie-jay. White-throated magpie-jays are a significant outlier, however; magpies' structural diversity, the second highest, comprises 20 variants. There is little obvious effect of cooperative or colonial species to have larger functional repertoire sizes overall. However, several signal classes may reflect specific aspects of each species social structure. Maximum group size has no obvious effects on any one signal class category, but both species with large numbers of social integration signals, the piñon jay and the European magpie, have large maximum non-breeding group sizes.

Predator-related signals: All the species examined here possess at least two functionally distinct predator-related signals, a mobbing call and a hawk alarm. Neither Mexican jays nor brown jays were reported to use distress signals when caught by predators or handled during banding. Only white-throated magpie-jays have a high-pitched hawk alert and a broad-band hawk alarm. They were also distinguished by having several low-threat alerts distinct from mobbing. Both Florida scrub-jays and blue jays use specific calls in response to predator at nests.

Food-related signals: Almost all corvids produce begging calls as adults. Of the species examined here, only Steller's Jays lack such calls. Begging is usually produced by females, but in Florida Scrub-jays and Mexican jays, begging can be used

Table 4.4: Amplitude categories of magpie-jay vocalizations. Within categories call types are also ordered by relative amplitude, from loudest to softest.

<b>Range</b>	<b>Call types</b>
Long range, often audible over 100 m	Begging, mobbing, raptor alarm, loud calling sequences
Medium range, often audible over 50 m	Distress call, raptor alert, territorial chirr, social chirr, allofeed gurgle
Soft, often only audible less than 50 m	Flight chirr, approach vocalizations, grunt, sotto voce song, copulation call

by subordinates of either sex to signal submission. Beyond this, some species have allofeeding calls (blue jay and white-throated magpie-jay), and several have calls specifically to elicit begging by offspring.

**Territory defense signals:** The Florida scrub-jay has the largest number of functionally distinct territory defense signals. Its sister species, the western scrub-jay, uses two functionally distinct signals for territory defense, but is notable for having relatively large structural diversity in this category. While not well understood, western scrub-jays engage in matching interactions at territorial boundaries (Webber 1984). Both members of *Cyanocitta* and the piñon jay lack territorial defense signals.

**Conflict resolution signals:** All species but the blue jay possess at least one conflict resolution signal: usually conflict resolution repertoires consisted of a submissive signal and in some cases a signal given when physically attacking conspecifics.

**Social integration signals:** Both the communal piñon jay and the communally-roosting European magpie are notable for the number of functionally distinct social integration signals they use. In piñon jays, three calls maintain contact among flock members at different ranges (long, short, and between pairs), one call is given when an individual finds itself alone, and a fifth is individually distinctive and used during greeting and other contexts where such distinctiveness may be useful. A sixth social integration call coordinates flock movement. In piñon jays the large number of social integration signals clearly reflects the need for integrating flock movements and interacting with large numbers of individuals repeatedly and amicably. The same may be true for European magpies, due to their communal roosting habits (Møller 1985), although

social integration signals are evenly split between those given between pair members and those given in flocks or gatherings.

Mate attraction signals: None of the species here have signals that function primarily to attract mates. The LCs of magpie-jays may have such a function, but because of their elicitation by predators I include them as predator defense signals. Female white-throated magpie-jays and all species of magpies (genus *Pica*) may attract extra-pair males by begging loudly, but these calls are not used to attract potential mates when a female is unpaired.

Courtship signals: While numbers of courtship signals are low for all species (usually soft song is the only vocalization used in courtship), piñon jays again have the most. These include a pair-interaction signal, a male precopulatory signal and a female copulation call.

## **DISCUSSION**

### *The repertoire of the white-throated magpie-jay*

The repertoire of the white-throated magpie-jay is quite typical for corvids in some respects, and exceptional in others (Figures 4.2 and 4.5). The distribution of these calls across signaling classes generally reflects the social structure of white-throated magpie-jays.

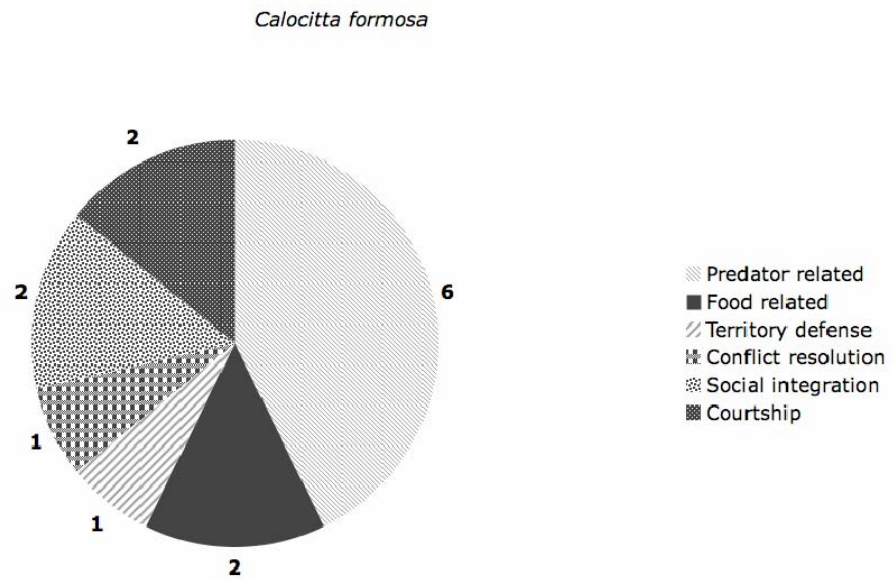
Predator-related calls are best represented functionally. Relatedness among group members could account for the large number of predator-related signals, (Sherman

1977; Sherman 1980; Berg 2005) but many other jay species have high relatedness and fewer such calls. High rates of nest predation (Berg 2004) and juvenile mortality (Langen 1996b) may offer a better explanation. While levels of predation and numbers of predators are difficult to compare among species, lowland tropical forests are often noted for high biodiversity, including predators, and tropical dry forest is no exception. Known predators on magpie-jays and their nests include snakes, iguanas, procyonids, primates, mustelids, rodents, and both resident and migrant raptors. More data from other tropical jays are needed. Conflict resolution signals and territory defense signals are poorly represented in the magpie-jay repertoire. Magpie-jays rarely vocalize in conflicts and instead simply chase or displace competitors. Unlike flocking species such as finches, icterids, and emberizid sparrows, which have complex conflict resolution behaviors and dominance hierarchies (Rohwer & Ewald 1981; Popp 1987b; Popp 1987a; Popp 1988), magpie-jays rarely compete for food but clash over relatively high-value resources such as territories and breeding opportunities. Conflict resolution signals are selected for when the value of the resource is low enough that the relative cost of aggressive escalation outweighs the benefits gained from the resource (Enquist & Leimar 1987; Hurd & Enquist 2001). More interesting is the relative paucity of territory defense signals in magpie-jays compared to other territorial passerines. The single vocalization given by magpie-jays in territorial defense may simply function to recruit other group members to the border, rather than to advertise the territory or signal to other groups.

In a separate preliminary study, T. Langen (unpub. data) noted many of the same functional call types, primarily those produced in predator-related contexts, contact, and food related signals. He classifies several types that I designate as loud calls or approach vocalizations as separate call types. He also noted three types of calls given in low aggression or annoyance, whereas I only noted one call in this context.



a



b

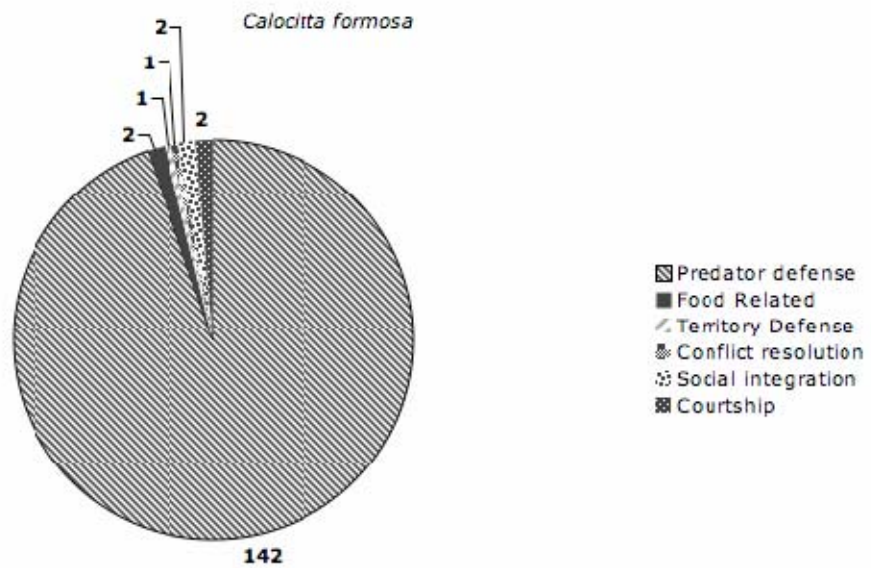


Figure 4.5. Repertoire of the white-throated magpie-jay *Calocitta formosa*. a) Functional repertoire b) Structural repertoire

Such differences could be attributed to differences in methodology and the focus or recording efforts. Langen observed social interactions near the nest, and had more opportunities to see low-level aggression within groups (1996). Group sizes were also larger when he collected data (1991-1993; Langen & Vehrencamp 1998), so magpie-jays may have been producing more social interaction vocalizations. He notes another type, that he terms loud song, that I did not identify as such. Occasionally I observed magpie-jays slowly producing a wide variety of vocalizations while perched, as described by Langen, but this was not as common in my population. My interpretation of this behavior was that young birds, probably young males, were practicing their learned vocalizations.

Magpie-jays distinguish themselves from other jays in the structural diversity of their repertoire (Figure 4.2). With 134 calls recorded in a single functional category, the structural diversity of the repertoire exceeds that of all other corvids. Individual repertoire sizes of LCs were probably under-sampled even at 51 calls (Ellis in prep-a), and probably approach song repertoire sizes of mimids and *Cistothorus* wrens (Wildenthal 1965; Kroodsma & Parker 1977; Boughey & Thompson 1981; Kroodsma et al. 1999). Most South American *Cyanocorax* and *Cyanolyca* are poorly known vocally (Hardy 1967a; Hardy 1967b; Hardy 1979), but no other corvid has as large a repertoire of structurally distinct signals. Most of the magpie-jay's structural diversity occurs in a predator-defense signal, but its sex-biased production suggests an additional mate-attraction or self-advertisement function (Ellis in prep-a). Mate attraction is handled unusually by corvids when compared to other passerines: little is known about how many corvids pair, but they generally choose mates through association as non-breeders, rather than by advertising like many passerines. Male magpie-jays may have evolved mate attraction signals in the context of predator defense due to a combination of their unusual social system and high intensity of

sexual selection. I discuss this issue in comparison with other species below.

On a basic level, the structure of most magpie-jay call types reflects their function (Marler 1955). Wide frequency bandwidth and sharp on- and offset make long distance signals such as mobbing and begging easily detected. Aerial predator alarms are extremely short, while some aerial predator alerts are high-pitched, much like those of smaller passerines. Marler's (1955) theory can also be extended to signal variation, as demonstrated by the measurements of coefficients of variation on four call types. Variation in mobbing is limited, yet two variable measures convey information about threat or urgency level (Ellis 2008). High stereotypy and reliable variation are probably useful in a signal that may require a rapid response from receivers. Begging is intermediate in variation. It is a long-distance signal, so detectability is important, but some variation may prevent habituation during long signaling bouts. High stereotypy may be difficult or costly to maintain. It may pay off more in contexts where the cost of mistakes is high, such as mobbing, compared with low-urgency calls like begging. Far more variable are social chirring and LCs, but the two signals are variable for different reasons. Social chirring is primarily produced between pairs at short range, and calls are extremely variable in length, frequency, and frequency over time within a call. Stereotypy is probably not selected for, messages may be redundant with visual signals, and variation may allow signaling of degree or emphasis at short distances that would be useless or undetectable at long range. LCs are medium to long distance signals, but the variation in this functional class arises primarily because multiple structurally distinct signals occur in the same functional class. The variation in this class of signals probably does aid in its function, but as diversity for diversity's sake.

One notable aspect of the repertoire of this species is the apparent subversion of the conflict of interest between sender and different classes of receiver in both

begging and LCs. Beg calls signal female hunger level to their group members, but signal fertility to extra-pair males. LCs probably signal the presence of potential predators, but may also signal the availability and potentially the quality of the males producing them. LCs are often given by floaters, who are allowed to enter territories and associate with social groups with no apparent consequences. In both cases, paired males may benefit from receiving the information, but have a conflict of interest with the receivers of the secondary message. If such information were sent outside of the context of the primary message, paired males might be selected to disrupt or jam communication. By coupling these messages with others that benefit the paired males, senders (females and floater males, respectively) preclude paired males from acting on the conflict of interest. Indeed, the value of receiving information about predators from floater males could be one reason that paired males do not exclude floaters from territories and why such high structural diversity is associated with a predator-defense signal.

### **Vocal repertoire size in corvids**

Functional diversity and structural diversity varied widely among the corvids examined here, from seven to sixteen functionally distinct call types and from seven to over 100 structurally distinct call types. I was able to assess three general aspects of sociality that could affect the potential for repertoire size in corvids: territoriality, mating system, and maximum group size. In contrast to both theory and several empirical studies, none of these variables appear obviously related to total functional repertoire size or structural repertoire size (McComb & Semple 2005, Blumstein & Armitage 1997b, Marler 1977). This result is not unanticipated, however, because corvid repertoires have diverse functions, and not every signal class is relevant to

social interactions common in groups with high social complexity. It does contrast, however, with the results of Hardy (1979) and dos Anjos & Vielliard (1993), who noted that in the genus *Cyanocorax*, a South American group, repertoire size reflects a greater degree of sociality. I did not include these species because the functions and variation of each signal type were not well known for any of the species described, so it is unclear how much variation is functional and how much is not. Given that within the sister taxa of *Cyanocorax*, the *Psilorhinus/Calocitta* group, variation runs from minimal to enormous, it is difficult to make inferences about how variation might function in the vocal repertoire of any *Cyanocorax*.

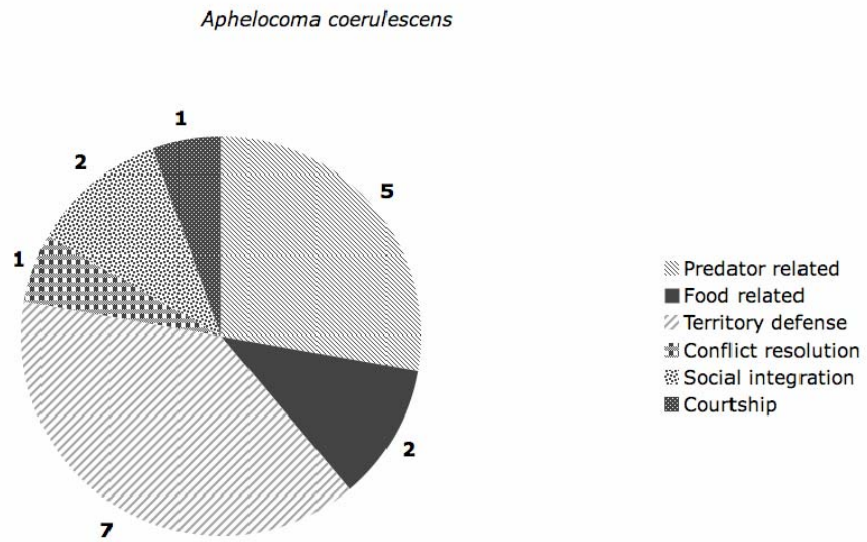
Partitioning functional diversity into general signal class categories should allow one to understand which factors affect the evolution of repertoire size. Among prior studies, Blumstein & Armitage (1997b) examined alarm signaling in sciurids, and Ord & Blumstein (2002) and Ord et al. (2002) examined a suite of signals that are used in territory defense and courtship in lizards. Both studies found links to characteristics of social system. Comparing the distributions of whole repertoires reveals similarly interesting patterns in the Corvidae. For example, the white-throated magpie-jay, piñon jay and Florida scrub-jay all have the same functional repertoire size, but piñon jays have proportionately more social integration signals, magpie-jays more predator-defense signals, and Florida Scrub-jays more predator-defense and territorial signals (Figures 4.5 and 4.6).

Group size may be related to functional diversity of social integration signals. Both the piñon jay and the European magpie have at least six of these signals, while no other species has more than two functionally distinct social integration signals. Piñon jays breed communally in large flocks, which can swell in winter to over 1000 individuals (Marzluff & Balda 1992). European magpies defend territories as a pair but roost communally during the non-breeding season, commuting each day to their territories

(Møller 1985). Dealing with social interactions in such large groups appears to necessitate large numbers of signals. Territoriality clearly affects the number of functionally distinct territory defense signals. Piñon jays, blue jays and Steller's jays lack territories and thus have no need for such signals (Brown 1963; Brown 1964a; Cohen 1977; Racine & Thompson 1983; Oberski & Wilson 1991; Marzluff & Balda 1992; Tarvin & Woolfenden 1999). Among the species that are territorial, both functional and structural repertoire sizes in this signal class vary. Florida scrub-jays have the largest number of functionally distinct territory-defense calls. In this species, the only route to fitness for males appears to be the acquisition and defense of a territory. Young males must inherit territories, bud off a portion of their family territory, or establish a new territory on their own (Woolfenden & Fitzpatrick 1978; Woolfenden & Fitzpatrick 1984). Clearly, territory maintenance and acquisition are of extreme importance in this species. Western scrub-jays have fewer functionally distinct territorial signals, but mediate territorial conflicts with vocal matching interactions. Matching interactions represent an unusual instance of competitive diversity in corvids. Selection may be strong in both scrub-jay species for clear communication during territorial disputes (Woolfenden & Fitzpatrick 1984; Carmen 2004). Why other territorial corvids do not have more territorial defense signals is not obvious. Territory size and frequency of interactions with neighbors could be responsible; if groups interact relatively rarely over territory boundaries there may not be strong selection for evolving signals that resolve such conflicts.

Sexual competition, which has been shown to influence repertoire size in other taxa, plays little obvious role in most corvid repertoires. Corvids only rarely show sexual plumage dimorphism (Goodwin 1986; Madge & Burn 1994). Their generalist habits may select for pair or group resource defense, precluding male territory advertisement for mate attraction. Pair formation usually takes place over time in non-

a



b

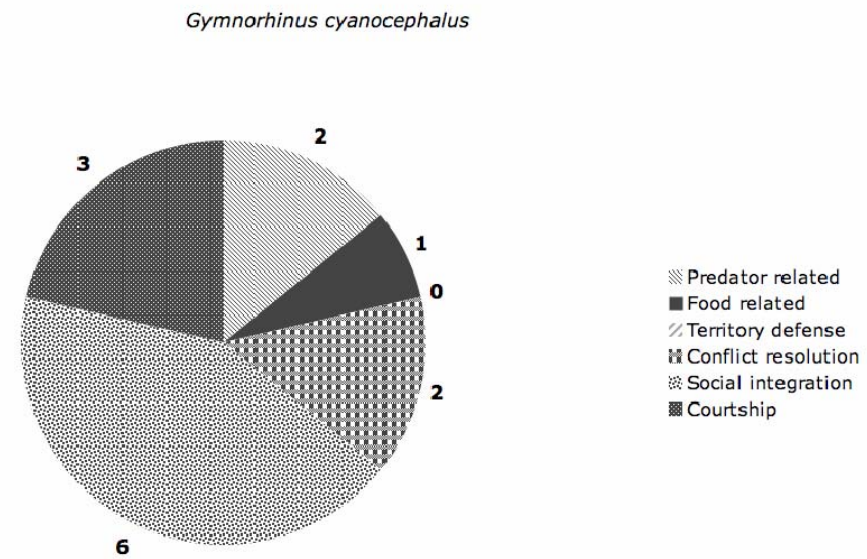


Figure 4.6: General functional distribution of the repertoires of a) Florida scrub-jay (*Aphelocoma coerulescens*) and b) piñon jay (*Gymnorhinus cyanocephalus*).

breeding aggregations. Given that structurally diverse, complex songs are usually used for male mate attraction and territory defense, they are not predicted in corvids.

However, in at least one species, the white-throated magpie-jay, an unusual combination of traits has led to an explosion of structural diversity that strongly suggests sexual selection. The loud call system of this species parallels that of many other passerines but no other corvid, with large numbers of male-biased calls used as advertisement displays.

Several unique aspects of magpie-jay social structure and life history probably account for the evolution of a complex advertising signal in magpie-jays. Brown jays (*Psilorhinus morio*) are the closest relatives of the genus *Calocitta* (Bonaccorso & Peterson 2007), and have a similar social structure (Lawton & Lawton 1985; Hale et al. 2003; Williams 2004; Williams & Rabenold 2005), yet their repertoire shows no sign of sexual selection. Both species are cooperative breeders in which the breeding unit consists of related females who help a primary breeding pair. Females remain on their natal territories while males disperse. Differing patterns of male dispersal may lead to differences in reproductive skew among males. In brown jays, all males integrate into groups, meaning each group can have multiple males. Of these males, one becomes a “consort” to the breeding female. Though consorts on average obtain more paternity than other males, such a role is not a particularly good route to fitness. Consort members only achieve 20% of paternity on average (Williams & Rabenold 2005). In contrast, only a single male magpie-jay is permanently associated with any group, and the remainder float. To become a paired male is a relatively good route to fitness in magpie-jays; such males achieve ~67% of paternity, more than floaters on average (Berg 2005). Reproductive skew is reduced among male brown jays and sexual selection must be as well (Schuster & Wade 2003). Two other differences between brown jays and magpie-jays reflect these species differences as well. Magpie-



jays show a larger absolute degree of ornamentation, with blue, black and white plumage and an obvious forehead plume compared to the brown jay's dull brown plumage and white tail-tips. White-throated magpie-jays in Costa Rica (*C. f. pompata*) are also sexually dimorphic (Langen 1996a), with older females having blacker faces than males.

Florida scrub-jays have a social system similar to magpie-jays except that males help and females disperse and float. Like brown jays, they lack complex mate attraction signals, but conversely, skew among males is probably higher than in magpie-jays. However, EPC rates are functionally 0% and male fitness depends on inheriting or budding a territory. Thus, there is likely less selection for mate attraction (Woolfenden & Fitzpatrick 1984; Quinn et al. 1999) and more on territory defense.

The potential for corvids to signal about environmental events is probably high, but the limited benefits of signaling in most cases may reduce functional diversity within this class. As medium-sized generalists, they encounter a variety of predators and a large range of food resources about which they could signal. Signals about the nature of food should only evolve when both the receiver and sender benefit from the receiver acquiring information about different food types. However, because corvids handle most foods individually, signaling about the presence or nature of food resources is probably limited. One well-documented exception is the yell call of the raven, which recruits non-breeders to carcasses to drive off defending breeders and allows discoverers to access these resources (Heinrich & Marzluff 1991; Bugnyar et al. 2001). Food-related calls in this study pertain more to need; nearly all species use a loud beg call, homologous to that of juvenile begging, to signal need to group members or mates.

All corvids use at least two functionally distinct call types in response to predators: either an alarm or alert in response to aerial predators, and mob calls.

Despite a wide range of predators, corvids do not signal more than general information about predator types, threat level, or movement patterns. This is probably a reflection of the economy of communication; if all predators require a similar response, there is no need to differentiate between them (Macedonia & Evans 1993). Predator defense calling in corvids needs more study. Repertoires of such signals differ considerably between species: magpie-jays and Florida scrub-jays, both subtropical lowland species, have relatively high numbers of predator-related signals. This could be related to heavy predation in this habitat, but brown jays also occur in tropical lowland (Madge & Burn 1994), and do not have large numbers of these signals. While many corvids can mimic, both Steller's jays and blue jays have been documented specifically mimicking a variety of avian predators (Hailman 1990; Greene et al. 1998; Tarvin & Woolfenden 1999; pers. obs). The function of such mimicry is not clear, but from the perspective of repertoire size *does* inflate structural repertoire size. Such mimicry could also represent an instance of true representational signaling in bird alarms (Marler et al. 1992; Evans & Evans 1999; Zuberbuhler 2001). Among birds, only chickens have been shown to produce functionally representational signals (Evans & Evans 2007). Mimicry would be a simple way to designate the object represented.

Understanding the functional and structural repertoire of the white-throated magpie-jay, relative to related species, has given us a better sense of how different factors promote large repertoire size. Parsing repertoires by both function and structure may prove fruitful for examine the effects of sociality, sexual selection, and environmental events in other taxa as well, and could be extended to other media of communication. This study is one of the first to compare whole repertoires, and the results will hopefully encourage more documentation of the functional and structural repertoires of other species.

## EPILOGUE

The goal of my dissertation was to examine the repertoire of a single species, the white-throated magpie-jay, to understand how it reflects the biology of that species, and to understand how it compares to relatives with different social structures, life histories and external environments. Several important results arose from this work. Some are specific to magpie-jays but shed light on how repertoire size may be affected in other species, and one, the discovery of dual-function signals in the repertoire, is an important conceptual issue in animal communication.

Magpie-jays use a huge variety of structurally distinct vocal signals, far more than other corvids described. These do not all have distinct and separate functions, however. Magpie-jays use fourteen functionally distinct signals. The structural diversity of the repertoire is primarily the result of the use of a large number of vocalizations in a single context, when male magpie-jays approach predators or call at dawn. Specific loud call types within this functional category do not appear to have different functions, and individual males have large repertoires of loud calls. Such a vocal signaling system is unlike that of any other corvid, and is similar to standard passerine song systems.

Magpie-jay loud calls represent a secondary evolution of song in the passerine line. The nearest relatives of corvids, the birds of paradise, not only sing but also perform extremely complex displays for mate attraction, so song is certainly an ancestral trait. But no other corvids are known to have a loud song (Goodwin 1986), possibly because cooperative breeding, which is also an ancestral trait in corvids (Cockburn 1998), altered social structure and the mechanics of mate attraction, and selected against song. The unusual social structure of magpie-jays, where groups of females defend territories, means that males cannot defend resources. The

reproductive skew in both sexes selects for alternative mating tactics, and floater males can roam and advertise, selecting for the secondary evolution of song.

A greater conceptual issue uncovered by my analysis of both male loud calling behavior and adult female begging is that of dual-function signaling. In both these call types, some level of elaboration within the signal appears to have a secondary function in self-advertisement or mate attraction. In loud calling, both sexes call in response to low-threat predators, but males take these opportunities to produce the huge structural diversity upon which so many ornithologists have commented. They elaborate upon a simple alarm call to advertise their presence and actions. Females produce begging calls that function to indicate need, but they too have “elaborated” these calls by increasing the amplitude and possibly the detectability of their calls to extend beyond their territory boundaries. Given that these calls are produced when females are fertile, and that levels of extra-pair copulation are high, they may function to indicate fertility to floater and neighbor males.

In both loud calling and begging, senders of these secondary self-advertisements may have some level of conflict of interest with other individuals in the population. Floater males advertise to females in the population and paired females signal fertility to floater males, both in conflict with the interests of paired males. Perhaps the use of dual function signals in these cases is driven by the conflict of interest with the paired male. Paired males would be selected to jam or attack senders producing signals directly against their self interests, such as floaters courting their mates or mates soliciting EPCs. By coupling or disguising the signal with one that does benefit the paired male, senders may be able to structure the benefits of the signal to the conflicted party, the paired male, such that he does not interrupt signaling. The contexts in which dual function signals occur, in predator encounters and food

solicitation, allow for elaboration and modification of the primary signal to send an entirely different message, while still benefiting the primary receivers.

My close analysis of mob calls showed that even within a single uniform, stereotyped signal, continuous variation can function to influence receivers. I was not able to analyze such subtle variation within other signal types in the white-throated magpie-jay repertoire, but variation in other signals could function similarly. The highly variable social chirr is one prime candidate, but any signal could conceivably work this way. From the perspective of repertoires and repertoire size, this result suggests that simple assessments of repertoire size probably do not come close to capturing all of the information transmitted in a repertoire. While I was not attempting to perform such an analysis for every signal, questions about information processing capabilities as they relate to various aspects of a species life may have to account for such complex yet subtle communication systems.

A final point is that all of these adaptations in signaling may be driven by relatively high predation rates. High rates of nest turnover result in asynchronous breeding within a neighborhood, setting the stage for high levels of sexual selection on males, since a single male could have multiple mates. The need to locate and respond to predators may select for the unusual floater system in the species. Paired males allow floaters into their territories because they are effective predator-detectors. These two factors set the stage for the loud calls given by floater males to display to potential mates in the context of predator encounters.

Hopefully, my close and systematic analysis of the repertoire of the white-throated magpie-jay will pioneer the study of repertoires and communication systems as a whole. I have produced a method for tabulating and comparing repertoires at various levels, which was lacking. As noted above, several important results have come from studying the repertoire as a whole, rather than focusing on a single signal

type. To better understand the factors affecting repertoire size and the evolution of communication systems, we need more studies analyzing whole repertoires.

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