THE ECOLOGY AND EVOLUTION OF AVIAN ALARM CALL SIGNALING SYSTEMS

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By

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       Communication is often set up as a simple dyadic exchange between one sender and one receiver. However, in reality, signaling systems have evolved and are used with many forms and types of information bombarding multiple senders, who in turn send multiple signals of different modalities, through various environmental spaces, finally reaching multiple receivers. In order to understand both the ecology and evolution of a signaling system, we must examine all the facets of the signaling system.

       My dissertation focused on the alarm call signaling system in birds. Alarm calls are acoustic signals given in response to danger or predators. My first two chapters examine how information about predators alters alarm calls. In chapter one I found that chickadees make distinctions between predators of different hunting strategies and appear to encode information about predators differently if they are heard instead of seen. In my second chapter, I test these findings more robustly in a non-model bird, the Steller's jay. I again found that predator species matters, but that how Steller's jays respond if they saw or heard the predator depends on the predator species. In my third chapter, I tested how habitat has influenced the evolution of mobbing call acoustic structure. I found that habitat is not a major contributor to the variation in acoustic structure seen across species and that other selective pressures such as body size may be more important. In my fourth chapter I present a new framework to understand the evolution of multimodal communication across species. I identify a unique constraint, the need for overlapping sensory systems, thresholds and cognitive abilities between sender and receiver in order for different forms of interspecific communication to evolve. Taken together, these chapters attempt to understand a signaling system from both an ecological and evolutionary perspective by examining each piece of the communication scheme.

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INTRODUCTION

Communication is the exchange of a signal between a sender and a receiver, which results in the behavior of the receiver changing to the advantage of the sender (Searcy & Nowicki, 2005). This sets up communication as a dyadic exchange between one sender and one receiver: a sender encodes and transmits information via a signal, which travels through environmental space where it is corrupted and degraded, and the signal is recognized and decoded by a receiver (Shannon, 1948). However, this is an extreme simplification because in reality there are multiple sources and types of information in multiple modalities bombarding multiple senders, who in turn encode that information into multiple signals of different modalities (i.e. multimodal) that are sent through different environments finally reaching multiple receivers, often of different species (Fig. 1). This is really how signaling systems have evolved and this is how signaling systems are used. Therefore, in order to understand the evolution and ecology of a particular signaling system, we need to understand, both individually and in tandem, each step of this complex communication process.

My dissertation has focused on the alarm call signaling system. Alarm calls are acoustic signals given by birds and mammals in response to predators or danger. Avian alarm calls are typically classified into two types: seet and mobbing calls (Marler, 1955; 1957). Seet calls are high frequency (typically 6 – 12 kHz), low-amplitude, relatively pure tone calls given to aerial or actively hunting predators. The acoustic structure of these calls make it very difficult for predators to locate the sender because the call is tonal with graded on/off and the frequencies are often above their optimal hearing (below 5 kHz) (Jones & Hill, 2001; Marler, 1955; Yamazaki et

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al., 2004). When a receiver hears a seet call they typically stop calling and freeze or dive for cover (Templeton et al. 2005).

In contrast, avian mobbing calls are loud signals covering a wide range of frequencies (i.e. broadband) given to stationary or not actively hunting predators. It is suggested that the acoustic structure aids the signal in travelling long distances and being easy to localize (Marler, 1955; 1957). When a mobbing call is given, receivers typically approach the caller, often to assist in mobbing and harassing the predator to force it from the area (Pettifor, 1990). Mobbing calls can be further split into referential and risk-graded mobbing calls. Referential calls are specific to a certain predator species (Seyfarth et al., 1980) whereas risk-graded mobbing calls are more dependent on the risk imposed from predator characteristics, such as predator size (Templeton et al., 2005), predator hunting strategies (Sherbrooke, 2008), predator distance (Stankowich & Coss, 2006), predator behavior (Caro, 2005; Lima & Dill, 1990), or even habitat (Eggers et al., 2006). However, some species can incorporate both referential and risk-based mobbing calls in their repertoires (Suzuki, 2014).

Avian alarm calls are a well-suited signaling system to examine all the steps of the communication process because they connect specific behaviors and vocalizations to a purpose and context, senders encode information about predators, urgency and risk level in their alarm calls (Caro, 2005; Lima & Dill, 1990) they are produced across variable habitats, and they are inherently social, offering insights into the use of signals across multiple senders and receivers (Zuberbühler, 2009).

My dissertation is focused on using the complex communication scheme (Fig. 1) to understand alarm call signaling systems in birds. I have focused my chapters to look at each

aspect of the communication scheme. Chapters 1 and 2 are focused on the sender portion of the communication scheme, specifically how senders encode different forms and types of information about predators in their alarm signals. Chapter 3 is focused on the environmental space, specifically on how habitat may have shaped the evolution of mobbing call acoustic structure. Finally, chapter 4 suggests a new framework for understanding multimodal communication across species with a focus on the relationship between sender and receiver. Taken together, these chapters address an important signaling system by understanding the individual components of the communication scheme as well as the interactions between them, which gives us a better understanding of the complexity in both the ecology and evolution of avian alarm call signaling systems.
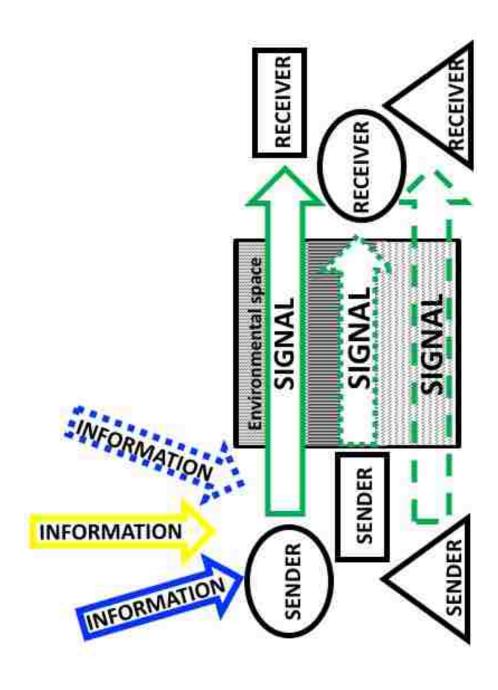
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FIGURE LEGEND

Figure 1: Communication scheme. The line type of the arrows indicates different communication modalities. Different colors indicate different information. Different shapes indicate different species. Different patterns of the environmental space indicate different habitat types with different transmission properties.

FIGURE 1

CHAPTER 1: Are chickadees good listeners? Antipredator responses to raptor vocalizations

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ABSTRACT

Many animals gather information about predators with a variety of cues, such as visual, acoustic, and olfactory. Several species of birds, including chickadees, are good at discriminating between species of raptors using visual cues, and they can encode information about the threat level in their alarm calls. Much less is known about how birds discriminate between the calls of different species of predators. We played back the calls of three species of raptors to black-capped chickadees (*Poecile atricapillus*), mountain chickadees (*Poecile gambeli*), and chestnut-backed chickadees (*Poecile rufescens*), to determine whether they can discriminate between them using acoustic cues. We played the calls of two species of small, high-threat raptors, northern pygmy-owl (*Glaucidium gnoma*), and sharp-shinned hawk (*Accipiter striatus*), which have very different hunting strategies (mainly sit-and-wait ambush predator versus very fast surprise attack flights). We also played a larger, lower-threat northern goshawk (*Accipiter gentilis*). Black-capped and mountain chickadees responded much more to the calls of the two small, more dangerous raptors than to the northern goshawk; they also acoustically responded very differently to the calls of the two small raptors. Chestnut-backed chickadees did not respond differently to the calls of the three raptors. These results indicate that black-capped and mountain chickadees can make specific discriminations between the calls of these three raptors and that they encode information in their alarm calls in sophisticated ways.

INTRODUCTION

For many animals, predators account for most mortality (Caro, 2005; Lima & Dill, 1990; Martin, 1995). Furthermore, predation can have large effects on the behavior of prey species. For example, the 'landscape of fear' (Laundre et al., 2001) that is created by the perception of risk can change species' foraging behavior, vigilance, movement patterns, habitat selection, densities and reproductive effort (Ohgushi et al., 2012; Preisser & Bolnick, 2008; Preisser et al., 2005; van der Merwe & Brown, 2008; Werner & Peacor, 2003). Thus, how prey species detect and avoid predators is of fundamental importance for understanding the ecology and evolution of predator–prey systems.

How prey species detect and avoid predators involves responses to many types of cues, and there are inherent differences in the information that prey species can gather about predators from different types of cues. For example, visual cues provide unambiguous information about the identity, direction, distance, movement and general behavior (actively hunting, preening, lounging, etc.) of predators. In contrast, information associated with acoustic or olfactory cues about predators is more ambiguous as there is less certainty about a predator's identity, location, movement and behavioral state. Since the information provided varies with the type of cue, antipredator behaviors may also vary across cue types. For example, male wolf spiders (*Schizocoas ocreata*) respond to a seismic cue (beak pecking on the substrate) and an acoustic cue (bird vocalization) by not moving. But, in response to a visual cue (bird shadow), wolf spiders seek cover, and they also take longer to resume to courtship behavior in response to the visual cue than they do in response to the other cues (Lohrey et al., 2009).

Birds primarily use visual and acoustic cues to gather information about predators. Birds

can discriminate between visual cues from different predator species and respond with species-specific antipredator behaviors (Baker & Becker, 2002; Bartmess-LeVasseur et al., 2010; Freeberg & Lucas, 2002; Soard & Ritchison, 2009; Sieving et al., 2010; Templeton et al., 2005). Much less is known about how birds discriminate between the sounds produced by potential predators (see review by Hettena et al., 2014), but recent studies suggest that birds may be remarkably sensitive to sounds produced by predators. For example, song sparrows (*Melospiza melodia*) exposed to the vocalizations of predators nested in denser vegetation, laid smaller clutches, spent less time on the nest during incubation and were more skittish, which led to a significant decrease in the number of offspring produced (Zanette et al., 2011).

Many bird species are known to produce antipredator alarm calls in response to visual cues. Two common types of alarm calls are 'seet' calls and 'mobbing' calls (Bradbury & Vehrencamp, 2011; Gyger et al., 1987; Griesser, 2009; Marler, 1955). Seet calls are typically produced in response to flying raptors or in high-threat situations. They tend to be relatively high-frequency (typically 6–12 kHz) tonal signals of short duration and low to medium amplitude. In contrast, mobbing calls are produced when birds detect a stationary or perched predator that is not actively hunting. They tend to be loud and harsh (broadband with complex overtone structure) with a high repetition cycle. Therefore, visual cues about a predator's specific behavior (flying versus perched) can completely alter antipredator responses. For example, Templeton et al. (2005) exposed black-capped chickadees (*Poecile atricapillus*) to models and live bird predators (visual cue) and found that black-capped chickadees altered their chick-a-dee mobbing call by adding more dee elements in response to predator species that posed a higher threat (Templeton et al., 2005). There are far fewer examples of birds altering their antipredator

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behavior in response to acoustic cues from predators (see review by Hettena et al., 2014).

Chickadees and their relatives (parids) are an ideal group to investigate acoustically based discrimination among predator species and their antipredator responses. Chickadees are highly vigilant, susceptible to several avian predator species, can discriminate different predator species by sight and can encode information to others about predator threat levels (Baker & Becker, 2002; Bartmess-LeVasseur et al., 2010; Courter & Ritchison, 2010; Freeberg & Lucas, 2002; Soard & Ritchison, 2009; Templeton et al., 2005). However, little is known about their ability to discriminate between predator species based on acoustic cues.

We designed this study to experimentally test whether three species of chickadees can discriminate between the vocalizations of different types of raptors and whether such discrimination influences their antipredator responses. We played back the calls of raptors that varied in threat level to black-capped chickadees, mountain chickadees (*Poecile gambeli*), and chestnut-backed chickadees (*Poecile rufescens*).

We assigned the threat level of the raptors a priori using size, hunting strategy and diet. The allometric risk hypothesis states that the risk that a raptor poses to another bird is strongly influenced by its relative size. This is a natural consequence of the aerodynamics of flight: small birds have smaller turning radii, accelerate faster and use more of the three-dimensional world than do larger birds (Dial et al., 2008). The allometric risk hypothesis predicts that raptors that are about the same size as their potential prey pose the greatest risk, whereas raptors that are either much larger or much smaller pose much less of a risk because the larger predators are not mobile enough to catch them and the smaller predators are not able to subdue them. We chose two small raptors that are highly threatening to chickadees, but that differ greatly in their hunting

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strategies. Northern pygmy-owls (*Glaucidium gnoma*), are small (ca. 50–70 g) and hunt mainly by using a sit-and-wait strategy. They are slow fliers and often plummet down on small chickadee-sized birds below them (Holt & Leroux, 1996; Holt & Peterson, 2000). Sharp-shinned hawks (*Accipiter striatus*) are mid-sized raptors (ca. 85–200 g), extremely fast and maneuverable in flight, and specialize on small- to medium-sized birds (Bildstein & Meyer, 2000). Northern goshawks (*Accipiter gentilis*) are large raptors (ca. 650–1400 g) that are a low threat to chickadees. They are also fast fliers and bird specialists, but they are less maneuverable than chickadees (Dial et al., 2008) and rarely attack birds as small as chickadees (Squires & Reynolds, 1997).

Following the allometric risk hypothesis, we predicted that chickadees would respond less to the large northern goshawk than to the smaller, more dangerous northern pygmy-owl and sharp-shinned hawk. We also predicted that the antipredator responses of chickadees would differ between the two small predators because of their different hunting strategies. And finally, we predicted that the encoding strategy would be similar across the three species of chickadees. Our specific research questions were (1) can chickadees discriminate between the vocalizations of these different raptor species and (2) if so, how is this encoded in their antipredator acoustic responses?

METHODS

Study Sites

We conducted this study on five mixed-species flocks in Missoula Valley, MT, U.S.A. (46°52´19´´N, 113°59´38´´W) and four flocks in Methow Valley, WA, U.S.A. (48°31´34´´N, 120°10´26´´W). During the winter in our study areas, mixed-species flocks tend to be very stable

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in composition and numbers of individuals (Morse, 1970; A. C. Billings, personal observation).

We have observed that flocks travel together in fairly tight groups, that they stay acoustically

connected (giving contact calls) and have fairly small home ranges. We conducted our playback

experiments near bird feeders, since these are useful hubs to reliably relocate flocks.

The feeders were located a minimum of 2 km from one another, so it is unlikely that the

same flock visited more than one feeder. The experiments were performed in the winter months

(December–March) of 2012–2014 when the mixed-species flocks regularly visit feeders. Four of

the nine feeders were replicated across consecutive years ($N = 52$ experiments; 13 experimental

blocks). All three chickadee species were not present at every feeder, so sample sizes varied

(black-capped chickadees, $N = 50$ experiments; mountain chickadees, $N = 46$ experiments;

chestnut-backed chickadees, $N = 32$ experiments).

Stimuli

The birds at each feeder were exposed to four acoustic stimulus treatments. We chose the

vocalizations of Townsend's solitaires (*Myadestes townsendi*), a common, nonpredatory

songbird, as a control and three common raptors: northern pygmy-owl, sharp-shinned hawk and

northern goshawk. These species differ in their seasonal production of vocalizations. Sharp-

shinned hawks and northern goshawks are mostly silent during the winter (when we conducted

our playback experiments) and call mainly during the breeding season (Bildstein & Meyer, 2000;

Squires & Reynolds, 1997). In contrast, northern pygmy-owls and Townsend's solitaires

vocalize throughout the year (Bowen, 1997; Holt & Peterson, 2000). However, like chickadees,

all of the stimulus species are year-round residents at our study sites, so it is probable that the

chickadees were exposed to the vocalizations of all the stimuli at some point during the year.

To make the playback stimuli, we chose the highest-quality recordings from the Macaulay Library of Natural Sounds at Cornell's Lab of Ornithology. The accession numbers and recording locations for the stimuli were as follows: Townsend's solitaire (ML 47553, California: Herr, 1990; ML 119411, California: Keller, 2001; ML 120266, California: Keller, 2002); northern pygmy-owl (ML 45192, Montana: Keller, 1987a; ML 40576, Arizona: Keller, 1987b); sharp-shinned hawk (ML 4153, New York: Kellogg, 1953; ML 139421, New York: D'Alessandro, 1996); and northern goshawk (ML 63118, Oregon: Herr, 1992; ML 40509, Arizona: Keller, 1987c; ML 105702, Oregon: Keller, 1995). Although most of the sounds we used were not recorded near our study sites, there is no evidence for geographical structure in the calls of these species (Bildstein & Meyer, 2000; Bowen, 1997; 1997 Holt & Peterson, 2000; Squires & Reynolds).

To avoid pseudoreplication, we created multiple playback samples (exemplars) for each stimulus (Hurlbert, 1984; Kroodsma, 1989, 1990). The exemplars were randomly assigned to each feeder. Vocalizations from the recordings were kept at their natural length to create the stimuli. To standardize across stimuli and exemplars, we used a 50% duty cycle (equal lengths of stimulus and silence alternating for the duration of the playback). We made the stimuli in Raven Pro 1.4 (Charif et al., 2008) and saved the audio files as 24-bit WAV files.

Playback Design

The calls were played from an Apple iPhone 4 (Model No. A1349, EMC No. 2422, frequency response curve is flat between 20 Hz and 20 000 Hz, Apple, Cupertino, CA, U.S.A.) connected to a PigNose Legendary 7-100 field speaker (frequency response curve is flat between 500 Hz and 17 000 Hz, PigNose Ind., Las Vegas, NV, U.S.A.). This equipment produces good

playback characteristics in the hearing range of chickadees (Henry & Lucas, 2010; Vélez et al., 2015) and is commonly used in playback experiments to birds (e.g. Greig & Webster, 2013). We hid the speaker in vegetation 10–20 m from the feeder and about 2 m off the ground. We calibrated the peak amplitude of each playback stimulus to 80 dB SPL A-weighting at 1 m using an Extech 407730 sound level meter (Extech Instruments, Nashua, NH, U.S.A.). The acoustic responses of the chickadees were recorded with Sennheiser 67 shotgun microphones (Sennheiser, Wedemark, Germany) into Marantz PMD 661 recorders at 48 kHz sampling rate and 24-bit depth (Marantz, Kanagawa, Japan).

We waited at least 10 min after hiding the speaker to allow the birds to return to natural activity. However, since all these experiments were performed near feeders, the birds were habituated to human activity and did not seem disturbed by our presence. There can be large variation in the numbers and species of birds active at bird feeders even during relative brief periods. However, we broadcast the playback stimuli into the woods around the feeders. We did this to maximize the chances that members of that flock would be able to hear and respond to the playback stimuli, not just birds that happened to be at the feeder during a particular minute of the experiments. Even if flock members were not actively feeding, they were still likely to be in the vicinity to be recorded during the pre-playback, to hear the playback, and to be recorded during the playback and post-playback periods. We designed our experiments to probe the acoustic responses of birds in each flock, rather than just the individual birds that happened to be at a feeder.

We were not able to measure the number of individuals of each species within a flock because the birds were not banded. In addition to short-term variation in the numbers of

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individual birds visiting a feeder, there could have been some changes within a flock due to mortality during the study periods. To control for these differences, each experiment was paired with a baseline period. Before each experiment, we recorded a 2 min pre-playback recording for a baseline level of acoustic activity of a particular flock. The playback stimulus lasted 2 min. Once the playback ended, we continued to record for 5 min (post-playback). We chose these times to ensure that we captured accurate activity levels during each playback time period. The order of the stimulus presentation was randomized for each feeder, and if multiple stimuli were presented at a feeder in one day, we waited at least 20 min between each presentation to allow the birds to return to normal activity.

Ethical Note

We simulated the presence of raptors by playing their calls to wild, free-living birds. Although in some cases the playbacks changed the vocal behavior of the birds (which is the focus of this study), we do not feel that these experiments were unduly stressful. Birds seemed to return to normal activity relatively quickly after our experiments. Our experiments conformed to the standards outlined in the ASAB/ABS Guidelines for the Use of Animals in Research and were approved by the University of Montana IACUC (AUP 049-14EGDBS-080814).

Acoustic Analysis

The three species of chickadees that we studied (black-capped, mountain and chestnut-backed chickadees) produce vocalizations that are acoustically similar (Dahlsten et al., 2002; McCallum et al., 1999; Smith, 1993). All three species produce chick-a-dee calls that consist of chicka elements followed by dee elements (Fig. 2a–c). For full chick-a-dee calls, we could distinguish the three species. All three species also produce independent chicka calls without any

following dee elements (Fig. 2d). We could not distinguish black-capped and mountain

chickadees using only chicka calls, but we could distinguish chestnut-backed chickadee chicka

calls from the two other species. Finally, all three species produce a wide variety of high-

frequency calls (seets, etc.; Fig. 2e). We could not distinguish species using these calls.

All recordings were analyzed using Raven Pro 1.4 (Charif et al., 2008). Spectrograms

were made of each recording using Hann window type with 50% overlap and a window size of

512–1150 samples. The analysts would visually and acoustically identify the various chickadee

calls. All the variables were tallied for each minute, so each recording had a count of each of the

variables broken into nine 1 min increments. We measured 11 acoustic variables: (1) total

number of complete black-capped chick-a-dee calls (Fig. 2a, one complete call); (2) number of

chicka element pairs per black-capped chick-a-dee call (Fig. 2a, one chicka element pair shown);

(3) number of dee elements per black-capped chick-a-dee call (Fig. 2a, three dee elements

shown); (4) total number of complete mountain chick-a-dee calls (Fig. 2b, one complete call

shown); (5) number of chicka element pairs per mountain chick-a-dee call (Fig. 2b, two chicka

element pairs shown); (6) number of dee elements per mountain chick-a-dee call (Fig. 2b, two

dee elements shown); (7) number of complete chestnut-backed chick-a-dee calls (Fig. 2c, one

complete call shown; we did not count the number of chestnut-backed chicka element pairs or

dee elements within the complete chick-a-dee call because sample sizes were small and there

was little variation in the make-up of the chestnut-backed chickadee call); (8) number of chicka

calls given without dees by black-capped or mountain chickadees (Fig. 2d, one chicka call

shown); (9) number of chicka element pairs within each chicka call (Fig. 2d, two chicka element

pairs shown); (10) number of chestnut-backed chicka calls without dees (Fig. 3d, one chickacall

shown; we did not analyse the number of chestnut-backed chickadee chicka element pairs because samples sizes were small and there was little variation in the number of elements); (11) number of high-frequency calls given (Fig. 2e, three high-frequency calls shown). We defined a high-frequency call as a tonal call between 6500 and 12 000 Hz.

Statistical Analysis

For each variable, we averaged the count across each playback period. Counts of each variable in the first and second minute of the pre-playback were added together and divided by two to give an average number of each variable per minute in the pre-playback. Counts of each variable in the third and fourth minute were added together and divided by two to give an average of each variable per minute in the playback. Counts of each variable in the fifth through ninth minute were added together and divided by five to give an average of each variable per minute in the post-playback.

The pre-playback was a paired measure of the baseline acoustic activity for a particular experiment at a particular feeder. To standardize both within and across feeders and to remove confounding effects such as differences in flock size and activity, differences across days or differences due to weather, we subtracted the average of each variable in the pre-playback from the average of that variable in the playback and in the post-playback. This provided an average change in each of the 11 variables given during the playback and the post-playback relative to the baseline or pre-playback period. Thus, a positive number indicates more calls were given than baseline, a negative number indicates fewer calls were given than baseline and zero means no difference in the number of calls given from baseline.

We constructed linear mixed-effects models using maximum likelihood for each of the 11

variables. Stimuli (four levels: Townsend's solitaire, northern pygmy-owl, sharp-shinned hawk, northern goshawk) and playback period (two levels: playback, post-playback) were assigned as fixed effects and the feeder location (nine levels) and the time in the season (two levels: winter = December, January and February; late winter = March) were assigned as random effects. Although we controlled for differences within and between flocks using the pre-playback baseline, we also included the feeder location in all the statistical models to account for any variation that was not taken care of by the pre-playback control. All fixed and random effects were tested for significance using likelihood ratio tests. Residuals from the models failed a Shapiro–Francia test for normality, so following Faraway (2004) and Galecki and Burzykowski (2013), we used parametric bootstraps on each variable. To identify how responses differed between all stimuli and all playback categories, any models that were significant from the bootstraps were run with a Tukey–Kramer post hoc test. This is a conservative correction and is the best available when doing all pairwise comparisons when sample sizes are small and unequal. Because Tukey–Kramer tests also assume a normal distribution, we ran parametric bootstraps on all pairwise comparisons. All statistical analyses were done in R using the lme4 package with an alpha of 0.05 (Bates et al., 2010).

RESULTS

Chickadees were able to distinguish the different predators by their vocalizations. In response to the experimental stimuli, chickadees produced vocalizations that differed across multiple acoustic variables. We did not find the random effects of feeder location or season to be significant in any of the models ($P < 0.05$). Also, how chickadees encoded information about the different predators varied by acoustic variable, chickadee species and playback period.

Chick-a-dee Calls

Black-capped chickadees altered the number of full chick-a-dee calls given in response to different stimuli ($\chi^2_3 = 17.48$, $P < 0.001$; Fig. 3a). Specifically, black-capped chickadees marginally increased the number of chick-a-dee calls in response to northern pygmy-owls during the playback period (control versus pygmy-owl: $P = 0.082$; goshawk versus pygmy-owl: $P = 0.184$; sharp-shinned versus pygmy-owl: $P = 0.380$) and significantly increased the number of full chick-a-dee calls in response to northern pygmy-owls during the post-playback period (control versus pygmy-owl: $P < 0.001$; goshawk versus pygmy-owl: $P < 0.001$; sharp-shinned versus pygmy-owl: $P < 0.001$). However, they only showed a marginal increase in the number of chicka elements and dee elements within their chick-a-dee calls (chicka: $\chi^2_3 = 3.9753$, $P = 0.069$; dee: $\chi^2_3 = 6.2286$, $P = 0.07$; graphs not shown), and post hoc pairwise comparisons did not reveal any significant differences among stimuli within a playback period.

Mountain chickadees also altered the number of full chick-a-dee calls given in response to different stimuli ($\chi^2_3 = 36.572$, $P < 0.001$; Fig. 3b). They also gave significantly more full chick-a-dee calls in response to northern pygmy-owls than in response to the other stimuli during the playback period (control versus pygmy-owl: $P = 0.003$; goshawk versus pygmy-owl: $P = 0.007$; sharp-shinned versus pygmy-owl: $P = 0.005$) and post-playback period (control versus pygmy-owl: $P < 0.001$; goshawk versus pygmy-owl: $P < 0.001$; sharp-shinned versus pygmy-owl: $P < 0.001$). Within the chick-a-dee call, mountain chickadees did not alter the number of chicka elements ($\chi^2_3 = 3.4047$, $P = 0.144$; graph not shown), but they did alter the number of dee elements ($\chi^2_3 = 14.776$, $P < 0.001$; graph not shown). Mountain chickadees added significantly more dee elements to their chick-a-dee calls in response to the northern goshawk stimulus than in

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response to the other stimuli during the playback period (control versus goshawk: $P = 0.009$; sharp-shinned versus goshawk: $P = 0.014$; pygmy-owl versus goshawk: $P = 0.046$) but not during the post-playback period.

Chestnut-backed chickadees marginally increased the number of full chick-a-dee calls given in response to the stimuli ($\chi^2_3 = 6.0311$, $P = 0.081$; graph not shown), but post hoc pairwise comparisons did not reveal any significant differences among stimuli within a playback period.

Chicka Calls and Chicka Element Pairs

Black-capped and mountain chickadees altered the number of independent chicka calls given in response to the different stimuli ($\chi^2_3 = 26.56$, $P < 0.001$; Fig. 4a). Specifically, they significantly increased the number of independent chicka calls they gave to northern pygmy-owls during the playback period (control versus pygmy-owl: $P < 0.001$; goshawk versus pygmy-owl: $P = 0.022$; sharp-shinned versus pygmy-owl: $P = 0.004$) and post-playback period (control versus pygmy-owl: $P = 0.003$; goshawk versus pygmy-owl: $P = 0.015$; sharp-shinned versus pygmy-owl: $P = 0.033$).

Black-capped and mountain chickadees also altered the number of chicka element pairs within their independent chicka calls ($\chi^2_3 = 6.606$, $P = 0.004$; Fig. 4b). During the playback period, they marginally increased the number of chicka element pairs per chicka call to northern pygmy-owls (control versus pygmy-owl: $P = 0.066$; goshawk versus pygmy-owl: $P = 0.103$; sharp-shinned versus pygmy-owl: $P = 0.009$). But, there was no difference in their responses to stimuli during the post-playback period (control versus pygmy-owl: $P = 0.608$; goshawk versus pygmy-owl: $P = 0.436$; sharp-shinned versus pygmy-owl: $P = 0.532$).

Chestnut-backed chickadees did not alter the number of independent chicka calls given to stimuli ($\chi^2_3 = 3.4322$, $P = 0.375$; graph not shown).

High-frequency Calls

Black-capped, mountain and chestnut-backed chickadees altered the number of high-frequency calls given in response to the different stimuli ($\chi^2_3 = 9.6091$, $P = 0.023$; Fig. 5). Specifically, they significantly increased the number of high-frequency calls to the sharp-shinned hawk stimulus during the post-playback period (control versus sharp-shinned: $P = 0.062$; goshawk versus sharp-shinned: $P = 0.117$; pygmy-owl versus sharp-shinned: $P = 0.012$) but not during the playback period (control versus pygmy-owl: $P = 0.550$; goshawk versus pygmy-owl: $P = 0.134$; sharp-shinned versus pygmy-owl: $P = 0.159$).

DISCUSSION

Can Chickadees Discriminate Vocalizations of Different Raptors?

Our playback experiments showed that black-capped and mountain chickadees distinguish between the vocalizations of different species of sympatric raptors. On the basis of the allometric risk hypothesis and diet and hunting behavior, we predicted that chickadees would respond differently to the smaller raptors (northern pygmy-owl and sharp-shinned hawk) than to the larger northern goshawk. This prediction was generally supported, since both black-capped and mountain chickadees responded by changing call elements in response to the vocalizations of both northern pygmy-owls and sharp-shinned hawks but they responded very little to northern goshawks.

Do Chickadees Alter Their Acoustic Responses to Vocalizations of Different Raptors?

We found that black-capped and mountain chickadees responded differently to the two

small, high-threat raptors. In response to northern pygmy-owls, both black-capped chickadees and mountain chickadees gave more complete chick-a-dee calls, more chicka calls and more chicka elements. They produced more chick-a-dee calls and more chicka calls during both the playback and the post-playback periods, but they produced more chicka elements only during the playback period. Templeton et al. (2005) presented visual cues about predators (i.e. models and live birds) to black-capped chickadees and found that the chickadees added more dee elements in response to smaller predators. This indicates that, at least, black-capped chickadees respond differently to a visual predator cue versus an acoustic predator cue. They also seem to encode this information differently by altering different characteristics of their mobbing calls.

We found that mountain chickadees increased the number of dee elements in their chick-a-dee calls to the northern goshawk stimulus. This may be because mountain chickadees have a different encoding strategy for high- and low-threat predators than black-capped chickadees. And it raises questions of how mountain chickadees respond and encode information to visual predator cues, but this remains to be tested.

A striking difference in the responses of chickadees to northern pygmy-owls and sharp-shinned hawks was detected only after the acoustic cue stopped (i.e. the post-playback period). After the calls of sharp-shinned hawks stopped, chickadees produced significantly more high-frequency calls. The difference in antipredator response between these two raptors may be related to their very different hunting tactics. Northern pygmy-owls are relatively slow fliers and they rely mainly on perch-and-pounce ambush tactics (Holt & Leroux, 1996; Holt & Peterson, 2000). In contrast, sharp-shinned hawks are very maneuverable and stealthy, and they capture prey mainly by flying very fast (Bildstein & Meyer, 2000). When chickadees see a northern

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pygmy-owl calling, they tend to approach and engage in vigorous mobbing behaviors (Templeton et al., 2005). This mobbing behavior is generally effective at driving a northern pygmy-owl out of the area. But once a sharp-shinned hawk stops calling, the information giving rough distance and direction is gone. The high-frequency calls produced by chickadees might signal that the sharp-shinned hawk is flying and hunting, which would be very dangerous for chickadees. While these ideas are speculative, the results show that black-capped and mountain chickadees respond to two different species of small and dangerous raptors very differently.

Black-capped chickadees and mountain chickadees responded to the sounds of potential predators in similar ways. However, chestnut-backed chickadees showed no significant variation in any call characteristics we measured. Although we could not distinguish among species in the high-frequency calls, the overall difference in high-frequency calls seems to be driven by black-capped and mountain chickadees (A. C. Billings, personal observation during playback experiments). In fact, we observed that chestnut-backed chickadees made up a very small number of the individuals in the mixed-species flocks. The similar responses of black-capped and mountain chickadees and the lack of response of chestnut-backed chickadees suggest that chestnut-backed chickadees may encode predator information in different ways. Black-capped and mountain chickadees are sister species, while chestnut-backed chickadees are more distantly related (Johansson et al., 2013). Carolina chickadees (*Poecile carolinensis*), which are closely related to black-capped and mountain chickadees (Johansson et al., 2013), also give more chick-a-dee calls in response to higher-threat predators (Bartmess-LeVasseur et al., 2010; Courter & Ritchison, 2010). Therefore, chestnut-backed chickadees may differ simply due to a lack of shared phylogeny.

We did not anticipate that chickadees would respond to the control songs of Townsend's solitaires. Townsend's solitaires defend berry and fruit trees and bushes during the winter, and they often sing throughout the winter from tall, exposed perches (Bowen, 1997), especially when predators are not around (A. C. Billings, personal observation). Townsend's solitaires also give harsh alarm calls when they detect a raptor (Bowen, 1997; A. C. Billings, personal observation). Thus, Townsend's solitaires may serve as vigilant sentinel species: when they are singing, it may signal to other species that no predators are nearby. We found that black-capped and mountain chickadees gave fewer chicka calls during the playbacks of Townsend's solitaire songs than during the baseline period. This implies that the calls of Townsend's solitaires may not be a completely neutral control, but may be interpreted as an 'all clear' signal.

Overall, our study demonstrates that black-capped and mountain chickadees are good listeners. Most studies examine whether species can discriminate between different classes of predators such as terrestrial versus aerial. Our study is one of the few that examines the subtle differences in antipredator responses within a predator class (Hettena et al., 2014). Our results also suggest that the classification of predators is not as simple as threatening versus nonthreatening raptors, or small versus large raptors. We found that the responses of chickadees were more nuanced, subtle and complex than we had predicted: both black-capped and mountain chickadees responded differently to the two small and dangerous raptors. Alarm call systems are complex, and a lot of information about the size, hunting strategy and behavior of the predator as well as the modality of the predator cue (e.g. visual versus acoustic) may influence the structure and use of alarm calls.

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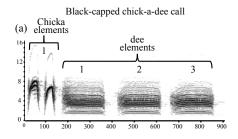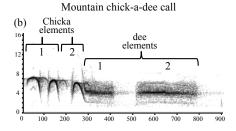
FIGURE LEGENDS

Figure 2. Spectrograms of (a) one full black-capped chick-a-dee call, (b) one full mountain chick-a-dee call, (c) one full chestnut-backed chick-a-dee call, (d) independent chicka calls from black-capped/mountain chickadees and chestnut-backed chickadees and (e) high-frequency calls from black-capped/mountain/chestnut-backed chickadees. All acoustic elements used for analysis are indicated with brackets, labelled and numbered. Spectrograms made with Raven Pro 1.4.
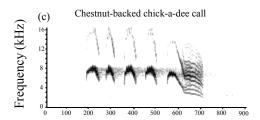
Figure 3. Mean ± SE number of full chick-a-dee calls given by (a) black-capped chickadees and (b) mountain chickadees during the playback period (closed circles) and the post-playback period (open circles). Lowercase letters indicate differences significant at $P < 0.1$. Note that the Y-axis scales differ between (a) and (b).
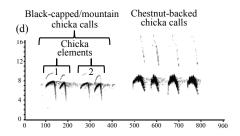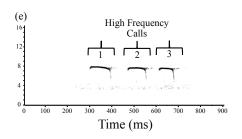
Figure 4. Mean ± SE number of (a) independent chicka calls and (b) chicka element pairs per chicka call given by black-capped and/or mountain chickadees during the playback period (closed circles) and the post-playback period (open circles). Lowercase letters indicate differences significant at $P < 0.1$.
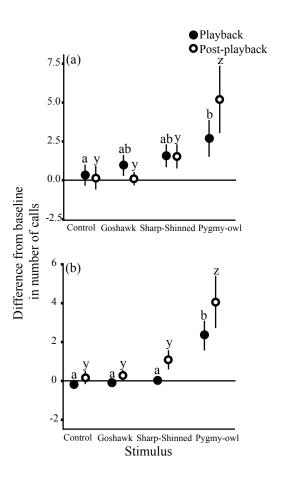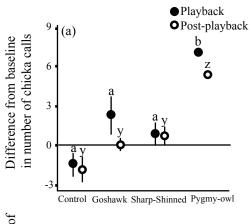
Figure 5. Mean ± SE number of high-frequency calls given by black-capped, mountain and chestnut-backed chickadees during the playback period (closed circles) and the post-playback period (open circles). Lowercase letters indicate differences significant at $P < 0.1$.
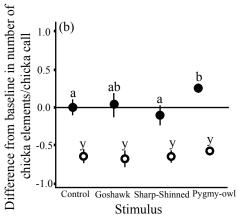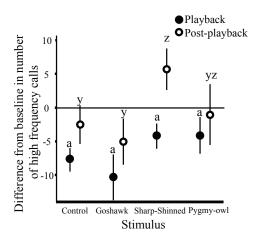
FIGURE 2

Black-capped chick-a-dee call

(a)

Mountain chick-a-dee call

(b)

Chestnut-backed chick-a-dee call

(c)

Black-capped/mountain chicka calls   Chestnut-backed chicka calls

(d)

(e)

High Frequency Calls

Frequency (kHz)

Time (ms)

30

FIGURE 3

FIGURE 4

FIGURE 5

CHAPTER 2: Steller's jays assess and communicate about predator risk using detection cues and identity

Alexis C. Billings, Erick Greene, & Dylan MacArthur-Waltz

KEYWORDS: Communication; Anti-predator behavior; Alarm calls; Steller's jay; Mobbing; Predator cues

ABSTRACT

Predators can vary in the risk they pose, depending upon factors such as body size, maneuverability, hunting strategy and diet. Prey can also detect predators with different senses, such as seeing, hearing or smelling them. We presented wild Steller's jays (*Cyanocitta stelleri annectens*) with visual cues (robotic raptors) or acoustic cues (call playbacks) of four different raptors to test how they assess risk and how this influences their alarm calls. The assessment of risk from different predator cues varied with different species of raptors: jays responded to sharp-shinned hawks (*Accipiter striatus*) with an increase in latency to resume foraging regardless of whether they were seen or heard, whereas latency responses to northern goshawks (*Accipiter gentilis*) were longer if they were seen versus if they were heard. Furthermore, Steller's jays altered the acoustic structure of their alarm calls depending on the species of raptor, and whether they saw or heard them. These results demonstrate that Steller's jay's assessment of risk involves an interaction between predator identity and predator detection cue, and in response, they alter their acoustically-simple alarm calls in surprisingly nuanced ways.

INTRODUCTION

Predation is a pervasive source of selection, often accounting for a large part of the mortality for many species (Caro, 2005; Lima, 1998; Lima & Dill, 1990). The risk posed to an

animal by a given predator can vary depending upon many factors, such as type of predator (Seyfarth et al., 1980), body size (Templeton et al., 2005), hunting strategy (Sherbrooke, 2008), behavior (Bradbury & Vehrencamp, 2011; Caro, 2005; Lima & Dill, 1990; Marler, 1955), distance (Stankowich & Coss, 2006) or habitat (Eggers et al., 2006). Furthermore, different kinds of predator cues might also influence a prey's perception of risk. For example, visual cues provide unambiguous information about the identity, direction, distance, movement and general behavior of a predator. In contrast, acoustic cues about predators are more ambiguous, as there is less certainty about the predator's identity, location, movement and behavior (Billings et al., 2015). Yet, it is not clear if animals differentially use various cue types to assess risk, nor how they incorporate this information into their antipredator behaviors.

Many animals give alarm calls in response to a predator. Studies of how animals respond to different types of predators have been instrumental in our understanding of cognitive and perceptual abilities (Blumstein & Armitage, 1997; Seyfarth & Cheney, 2003; 2010). Alarm calls can have simple or complicated acoustic structures (Marler, 1955), and that structure can vary in systematic ways depending on risk (Blumstein & Armitage, 1997; Courter & Ritchison, 2010; Sieving et al., 2010; Templeton et al., 2005). For example, in response to seeing predators of different body size, black-capped chickadees (*Poecile atricapillus*) alter the number of "dee" elements in their chick-a-dee call (Templeton et al., 2005): small predators receive significantly more "dee" elements than larger predators. However, recent work has shown that the chickadee alarm calling system is more complex: when chickadees hear rather than see a predator, they respond differently to two small predators with different hunting strategies. Although the number of "dee notes given to the two small raptors did not differ, chickadees gave more chick-a-dee

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calls, more "chicka" elements, and more high frequency calls in response to acoustic cues from

northern pygmy-owls (an ambush predator_ compared to acoustic cues from sharp-shinned

hawks (a quick attack, aerial predator) (Billings et al., 2015); also see (Suzuki, 2014). Taken

together, these studies suggest that black-capped chickadees assess risk based on predator

identity as well as how they perceive the predator (e.g. seeing versus hearing the predator).

However, more direct tests are needed of how the perceptual use of predator cues across different

predators influences assessment of risk and alarm call behaviors.

We studied the assessment of risk and alarm calls of Steller's jays (*Cyanocitta stelleri*) –

a species with a vocal repertoire that includes two alarm calls, the wah (Fig. 5a) and wek (Fig.

5b) call, as well as mimicking calls of predators (Fig. 5c) (Walker et al., 2016). Steller's jays are

a good species to explore discrimination and communication about predator risk. First, their

vocal repertoire includes two different alarm calls that are acoustically simple and only contain

one note or element type per call (Greene et al., 1998). In contrast, other well-studied parids

(Billings et al., 2015; Sieving et al., 2010; Soard & Ritchison, 2009; Templeton et al., 2005) and

Siberian jays (Griesser, 2009) have many different note types that they can use in their alarm

calls. Secondly, Steller's jays have a wide variety of natural predators that vary in the risk they

pose.

We presented free-living, stable flocks of Steller's jays with predator stimuli at feeding

stations during the winter months. We chose raptors that differed in possible threat level based

on size and hunting strategy (Fig. 6), and we experimentally manipulated whether the predator

was heard or seen. Size is one factor that may be important in the risk a predator poses to prey.

The allometric risk hypothesis refers to the predator-prey size ratio, and it predicts that avian

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raptors that are about the same size or slightly larger than their prey will be the most dangerous to the prey (Templeton et al., 2005). This is because of how size affects the aerodynamics of flight (Dial et al., 2008; Templeton et al., 2005): small birds have higher power-to-mass ratios and can turn and accelerate faster than larger birds.

Hunting strategy is another factor that may be important in determining how risky a predator is to prey (Stankowich & Blumstein, 2005). Some predators hunt by stealth and require the element of surprise, whereas others chase down their prey (Fig 2). These different hunting strategies present different threats and animals should respond to these differences. For example, Texas horned lizards (*Phrynosoma cornutum*) adopt different anti-predator behaviors in response to two snake predators that vary in their hunting strategies (Sherbrooke, 2008).

Finally, the type of cue that prey use to detect predators (e.g. hearing versus seeing a predator) is another factor that may be important to the risk a predator poses to prey. Since the information provided about a potential predator can vary depending upon how it was detected, antipredator behaviors may also vary with cue type. For example, male wolf spiders (*Schizocosa ocreata*) respond to seismic and acoustic cues of an avian predator by not moving, but seek cover in response to visual cues of that same predator (Lohrey et al., 2009).

We investigated two important questions: (1) how do Steller's jays assess risk using different predator detection cues across different predators; and (2) how do these factors influence their alarm calls? To test how Steller's jays assess risk, we measured the amount of time it took Steller's jays to resume feeding as a proxy for perceived risk because reduced feeding is a common response to increased perceived risk (Brown et al., 1999). To test whether

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the difference in assessment is reflected in their alarm calls, we recorded the alarm calls given by Steller's jays to determine if and how they alter them in response to different stimuli.

METHODS

Raptor stimuli

We presented flocks of Steller's Jays with stimuli of four species of raptors – northern pygmy owl (*Glaucidium gnoma*), sharp-shinned hawk (*Accipiter striatus*), red-tailed hawk (*Buteo jamaicensis*) and northern goshawk (*Accipiter gentilis*). We chose these species since they vary in body size, hunting strategy and diet, and thus pose different threats to Steller's Jays. All four species are common breeders at all of our study sites.

Northern pygmy-owls are small owls (approx. 52 g, Holt & Peterson, 2000) about half the size of Steller's jays (approx. 106 g; Walker et al. 2016). They are often active during the day, are generalist hunters that kill both mammals and birds, and use a perch-and-pounce hunting strategy (Holt & Leroux, 1996; Holt & Peterson, 2000). Most or their prey is 30 g or less, but they will occasionally attack birds much larger (such as bobwhite quail, American robins and northern flickers; (Holt & Peterson, 2000). Based on size, hunting strategy and diet, northern pygmy-owls probably pose the smallest threat to Steller's Jays.

Sharp-shinned hawks are fast and stealthy forest-dwelling hunters. Although male sharp-shinned hawks are about the same size as Steller's jays (approx. 100 g vs. 106 g), females can be much larger (approx. 175 g). Sharp-shinned hawks eat mainly small birds, with the mean prey size less than 50 g. However, they can eat larger birds such as American robins, and have been recorded killing birds as large as ruffed grouse (>550 g; Bildstein & Meyer, 2000). Thus, although sharp-shinned hawks are about the same size as Steller's Jays, because of their stealthy

hunting strategy and diet comprised mainly of birds, they likely pose a moderate to high threat to Steller's jays.

Red-tailed hawks are about 10 times as large (approx. 1,000 g) as Steller's jays. They often soar and then dive on their prey from above. They eat a wide variety of vertebrates but take more mammals than birds (Preston & Beane, 2009). However, they will eat jay-sized birds and are abundant at all of our study sites. Red-tailed hawks probably pose a moderate threat to Steller's jays because although they are appropriately sized to take Steller's jays, their hunting strategy and diet make them less threatening.

Northern goshawks are large forest hawks (males approx. 700-925 g; females approx. 980-1,150 g; Squires & Reynolds, 1997) that are fast and maneuverable hunters in dense forests. They appear to be fairly common at our study sites, and we have seen or heard them at our study sites in Montana and Washington. Northern goshawks eat a wide variety of medium to large mammals and birds (Squires & Reynolds, 1997). Where they co-occur, Steller's jays are one of the most common bird species in their diet (Drennen, 2006; Reynolds & Meslow, 1984; Watson et al., 1998). Northern Goshawks probably pose the highest risk to Steller's Jays because of their size, hunting strategy and diet.

Study sites

We conducted experiments at bird feeders in the Missoula Valley, MT, USA (46°52'19" N, 114°59'38" W) and the Methow Valley, WA, USA (48°31'34" N, 120°10'26" W). This work was done with IACUC approval from the University of Montana AUP 049-14EGDBS-080814.

Social behavior of Steller's jays

The same subspecies of Steller's jay, *Cyanocitta stelleri annectens,* occurs at both of these sites (Walker et al., 2016). The experiments were performed between 8:00 AM and 3:00 PM in the winter months (November – March) when Steller's jays form flocks and regularly visit feeders. There is little known about the social behavior of Steller's jays during the winter (Walker et al., 2016), but in some places, they form large flocks. At our study sites in Montana and Washington, Steller's jays came to feeders in groups, ranging in size between 2 to approx. 15 birds. There is no information on home ranges for winter flocks of Steller's jays. Although we did not have birds individually-banded, each flock appeared to be consistently associated with a particular feeder, and remained stable in size during the winter. To minimize the chance that we tested the same jays at different feeders, we chose feeders that were far apart: the average distance between feeders was 15 km, and the closest feeders were 3 km apart. It is thus very unlikely that we recorded the same individual jays at different feeders.

Hearing raptors - playback experiments

We conducted playback experiments at 18 feeders during the winters of 2012-2015. Seven of the feeders were located in Montana and 11 in Washington. Steller's jays at the feeders were exposed to five acoustic stimuli. We chose the song of Townsend's solitaires (*Myadestes townsendi*) as a control. Townsend's solitaires are common winter residents at our study sites that sing and defend patches of berries and fruit throughout the winter. We also played the territorial vocalizations of four raptors: northern pygmy-owl, sharp-shinned hawk, red-tailed hawk, and northern goshawk.

Because of the variability in weather from year to year not all feeders were visited every year so the sample sizes of each stimulus varied ($N_{\text{Townsend's solitaire}}$=28; $N_{\text{northern pygmy-owl}}$=28; $N_{\text{sharp-}}$

shinned hawk=30; $N_{red-tailed\ hawk}$=29; $N_{northern\ goshawk}$=28). However, when a feeder was used all stimuli were presented at that feeder during the field season. To make the playback stimuli and avoid pseudoreplication, we created multiple exemplars from high quality recordings from the Macaulay Library of Natural Sounds at Cornell's Lab of Ornithology (Kroodsma, 1989; 1990). The accession numbers and recording locations for the stimuli were: Townsend's solitaire (ML47553, California; ML119411, California; ML120266, California), northern pygmy-owl (ML45192, Montana; ML40576, Arizona), sharp-shinned hawk (ML4153, New York; ML139421, New York), red-tailed hawk (ML164412, California; ML105680, California) and northern goshawk (ML63118, Oregon; ML40509, Arizona, ML105702, Oregon). Exemplars were randomly assigned to each feeder. To standardize across stimuli and exemplars we used a 50% duty cycle and peak amplitude was set to 80 dB SPL A-weighting at 1m using an Extech 407730 sound level meter (Extech Instruments, Nashua, NH, U.S.A) We made the stimuli in Raven Pro 1.4 (Charif et al., 2008) and saved the audio files as 24-bit WAV files.

Seeing raptors - robotic raptors

We conducted experiments at eight feeders during the winter of 2014-2015 (*N*=8 for each stimulus). Six of the eight feeders used for the visual experiments were used for the acoustic experiments as well, but the experiments were done several months apart.

We presented Steller's jays with four robotic birds matched to the acoustic stimuli: Townsend's solitaire (adult), northern pygmy-owl (adult male), sharp-shinned hawk (adult female), and a northern goshawk (yearling female). We did not have a robotic red-tailed hawk. These robotic birds were taxidermied birds with small servo motors to move their heads. Head movements were controlled by an Arduino computer (Arduino, Torino, Italy). We videotaped

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perched, alert (i.e., non-preening) birds of these species and programmed the head movements (e.g., angles of head movements, rate of head movements, and intervals between head movements) of the robotic raptors so they moved in realistic ways. In order to minimize disturbance to Steller's jays before each experiment, the robotic birds were concealed by a tube of cloth painted to resemble a tree trunk. We slowly lowered and raised the false tree trunk from a distance (approx. 15-20 m) using a modified radio-controlled garage door opener.

Experimental design

The speaker for the playbacks was hidden in natural vegetation and placed between 15 m and 20 m from the feeder approximately 2 m off the ground. The variation in the speaker distance from the feeder was due to the variation in distance of the vegetation available to hide the speaker. The robotic birds were placed between 15 m and 20 m from the feeder and approximately 2 m off the ground. An acoustic stimulus and a visual stimulus were never presented on the same day. After placing the speaker or robotic bird near the feeder we waited until the birds returned to normal foraging activity before starting an experiment. Since all these experiments were performed at feeders, the birds were habituated to human activity and did not seem disturbed by our presence and quickly returned to normal foraging.

For the playback experiments, the calls were played from an Apple iPhone 4 (Model No. A1349, EMC No. 2422, frequency response curve is flat between 20 Hz and 20,000 Hz, Apple, Cupertino, CA, U.S.A) connected to a PigNose Legendary 7-100 field speaker (frequency response curve is flat between 500 Hz and 17,000 Hz, PigNose, Las Vegas, NV, U.S.A). When the birds returned to feeding regularly and at least one jay was perched on the feeder we began the two-minute playback (exposure). We recorded the vocalizations with a Sennheiser 67

shotgun microphone (Sennheiser, Wedemark, Germany) into a Marantz PMD 661 (Marantz, Kanagawa, Japan) recorder at 48 kHz sampling rate and 24-bit depth.

For the visual cue experiments, we recorded vocalizations with a Sennheiser omnidirectional microphone (Sennheiser, Wedemark, Germany) and a Roland R-26 recorder (Roland, Hamamatsu, Japan) at 48 kHz sampling rate and 24-bit depth.

When at least one jay was perched on the feeder, we remotely lowered the tree trunk to reveal the robotic bird for a four-minute exposure period. At the end of the exposure, we remotely raised the tree trunk concealing the robotic bird. We chose a longer exposure period for the visual than the acoustic experiments to ensure that Steller's jays would have time to notice the robotic bird before it was concealed.

Behavioral analysis

We measured the latency to resume foraging of the flock as a proxy for threat level. If the Steller's jays fled in response to a stimulus, we measured how long it took for any Steller's jay flock member to return to the feeder. Since we were unable to identify individuals within the flocks, this was meant as a measurement of the flock response to the stimuli. We assumed that the perceived threat level of a predator stimulus was correlated with the length of time that Steller's jays stayed away from the feeder.

Acoustic Analysis

Although Steller's jays have a complex vocal repertoire, the most common calls given in the winter months at our field sites are wah, wek and red-tailed hawk mimetic calls. We analyzed all recordings using Raven Pro 1.4 (Charif et al., 2008). Spectrograms were made of each recording using Hann window type with a 50% overlap and a window size between 512 – 1150

samples. We measured 11 acoustic variables (Fig. 6): 1) The average number of wah calls during the exposure period, 2) the average number of elements per wah calls, 3) the average duration of each wah element, and 4) the average duration of the interval between each wah element within a wah call, 5) the ratio of wah element duration to interval duration between the wahs (i.e., wah duty cycle), 6) the average number of wek calls during the exposure period, 7) the average number of elements per wek calls, 8) the average duration of each wek element, 9) the average duration of the interval between each wek element, 10) the ratio of wek element duration to interval duration between weks (i.e., wek duty cycle), and 11) the average number of red-tailed hawk mimetic calls during the exposure period. For the average number of call variables (wah, wek and red-tailed hawk mimics), we counted the number of each call type for the exposure period then averaged by the exposure period (2 min for acoustic playbacks, 4 min for robo-raptor presentations) and analyzed as an average per exposure period (e.g. for a given experiment the number of wah calls were added and divided by the duration of the exposure period). For the element variables, we added the number of elements together and divided by the number of calls to get an average number of elements per call per exposure period. For the element duration and element interval duration, we added the durations for the exposure period and divided by the number of elements or element intervals to give an average duration or interval duration for the exposure period. Finally, for the ratio of element duration to interval duration (i.e. duty cycle) we took the ratio of the average element duration per stimulus and divided by the average element interval duration per stimulus. Because we did not have a robotic red-tailed hawk, we only analyzed the number of red-tailed mimetic calls for the acoustic stimuli. There were very few

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red-tailed hawk mimetic calls to any of the visual stimuli and they were not significantly different from one another nor the matched acoustic stimuli ($P < 0.05$).

Statistical Analysis

We constructed linear mixed effects models using maximum likelihood for each of the 9 variables. For all the wah and wek variables we assigned stimuli (four levels: Townsend's solitaire, northern pygmy-owl, sharp-shinned hawk, northern goshawk), exposure period (two levels: exposure, post-exposure) and cue (two levels: acoustic, visual) as fixed effects. Since there were differences in flock size and behavior and the possibility that individuality of alarm calls within a flock may result in some of the differences in calling behavior, feeder location (20 levels) was assigned as a random effect to account for these differences before testing the fixed effects for significance. All fixed and random effects were tested for significance using likelihood-ratio tests. The random effect of feeder location was significant in all models ($P < 0.05$) and so was kept it in each model to account for those differences while testing the fixed effects. We ran the red-tailed hawk mimetic calls with only acoustic stimuli (five levels: Townsend's solitaire, northern pygmy-owl, sharp-shinned hawk, red-tailed hawk, northern goshawk) and exposure period (two levels: exposure, post-exposure) as fixed effects and with feeder location (18 levels) as a random effect.

Residuals from the models failed a Shapiro-Francia test for normality, so following Faraway (2004) and Galecki and Burzykowski (2013), we used parametric bootstraps on each variable run 999 times (Faraway, 2004; Galecki & Burzykowski, 2013). To identify how the responses differed between all stimuli, playback and cue categories, any models that were significant from the fixed effect bootstraps were run with a Tukey−Kramer post hoc test. This is

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a conservative correction and is the best available when doing all pairwise comparisons when sample sizes are unequal. Because Tukey−Kramer tests also assume a normal distribution, we ran parametric bootstraps on all pairwise comparisons. All statistical analyses were done in R using the lme4 package with an alpha of 0.05 (Bates et al., 2015).

RESULTS

(1) Do Steller's jays assess risk using different predator detection cues for different predators?

Steller's jays differed in their latency to resume foraging depending on the cue and predator identity (Fig. 8; Stimuli*Cue: $\chi^2 = 80.49$, df = 4, p < 0.001). They took longer to return to foraging after exposure to a sharp-shinned hawk or northern goshawk than after exposure to the control (sharp-shinned versus control: p < 0.001; goshawk versus control: p < 0.001; Fig. 8). They did not distinguish between seeing or hearing a sharp-shinned hawk (visual sharp-shinned versus acoustic sharp-shinned: p = 0.391; Fig. 8), but they took longer to return to foraging when they saw a goshawk than when they heard a goshawk (visual goshawk versus acoustic goshawk: p = 0.013; Fig 8). In response to hearing a red-tailed hawk, they stayed away significantly longer than when exposed to a hearing a northern pygmy-owl or hearing or seeing the control (acoustic red-tailed versus acoustic pygmy-owl: p = 0.026; acoustic red-tailed versus visual pygmy-owl: p = 0.280; acoustic red-tail versus acoustic control: p = 0.004; acoustic red-tail versus visual control: p = 0.077; Fig. 8).

(2) How risk factors influence jay alarm calls?

Steller's jays varied a number of features of their alarm calls depending on the interaction between predator identity and cue type. Consistent with their foraging behavior, Steller's jays produced different alarm calls depending on whether they saw or heard a northern goshawk.

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When Steller's jay's saw a northern goshawk, they gave more wah calls (Stimuli*Exposure*Cue: $\chi^2 = 33.88$, df = 10, p < 0.001) in comparison to all the other stimuli (Fig. 9a; visual goshawk versus visual sharp-shinned: p = 0.017; visual goshawk versus visual pygmy-owl: p < 0.001; visual goshawk versus visual control: p < 0.001; visual goshawk versus acoustic sharp-shinned: p < 0.001 ; visual goshawk versus acoustic pygmy-owl: p < 0.001; visual goshawk versus acoustic control: p < 0.001) with more wah elements (Stimuli*Exposure*Cue: $\chi^2 = 16.99$, df = 10, p = 0.075) than to all the other stimuli except seeing a sharp-shinned hawk (Fig. 9b; visual goshawk versus visual sharp-shinned: p = 0.937; visual goshawk versus visual pygmy-owl: p = 0.004; visual goshawk versus visual control: p = 0.010; visual goshawk versus acoustic sharp-shinned: p = 0.010; visual goshawk versus acoustic pygmy-owl: p = 0.037; visual goshawk versus acoustic control: p = 0.002). Steller's jays also increased the duty cycle of their wek call, meaning the wek elements were longer than the intervals between the wek elements (Stimuli*Exposure*Cue: $\chi^2 = 20.716$, df = 10, p = 0.023) in comparison to hearing a northern goshawk (Fig. 9c; visual goshawk versus acoustic goshawk: p = 0.023). There was no effect of stimuli on just the duration of the wek elements (p = 0.908) or the intervals between the wek elements (p = 0.607), but only the ratio of wek element duration to wek interval duration (p = 0.023). When they heard a northern goshawk, they increased the number of wek elements per wek call in comparison to seeing a northern goshawk (Fig. 9d; acoustic goshawk versus visual goshawk: p = 0.004).

Although Steller's jays did not differ in their latency to resume feeding behavior in response to seeing versus hearing a sharp-shinned hawk (Fig. 8), there were differences in their calling behavior. When Steller's jays saw a sharp-shinned hawk they gave more wah calls than

the control and northern pygmy-owl (Fig. 9a; visual sharp-shinned versus visual pygmy-owl: p = 0.010; visual sharp-shinned versus visual control: p < 0.001; visual sharp-shinned versus acoustic pygmy-owl: p = 0.002; visual sharp-shinned versus acoustic control: p < 0 .001) with more wah elements than the other stimuli except seeing the northern goshawk (Fig. 9b; visual sharp-shinned versus acoustic sharp-shinned: p = 0.017; visual sharp-shinned versus visual goshawk: p = 0.936; visual sharp-shinned versus visual pygmy-owl: p = 0.006; visual sharp-shinned versus visual control: p = 0.009; visual sharp-shinned versus acoustic goshawk: p = 0.051; visual sharp-shinned versus acoustic pygmy-owl: p = 0.37; visual sharp-shinned versus acoustic control: p = 0.001) and increased the duty cycle of their wek calls in comparison to hearing a sharp-shinned hawk (Fig. 9c; visual sharp-shinned versus acoustic sharp-shinned: p = 0.027). And when they heard a sharp-shinned hawk they gave more wah calls than the control and northern pygmy-owl (Fig. 9a; acoustic sharp-shinned versus visual sharp-shinned: p = 0.396; acoustic sharp-shinned versus acoustic pygmy-owl: p = 0.002; acoustic sharp-shinned versus acoustic control: p < 0.001; acoustic sharp-shinned versus visual pygmy-owl: p = 0.018; acoustic sharp-shinned versus visual control: p < 0.001), but they did not alter the number of wah elements per wah call or wek duty cycle like they did when they saw a sharp-shinned hawk. Instead, they decreased the duty cycle of their wah call in comparison to northern pygmy owl (Fig. 9e; acoustic sharp-shinned versus acoustic pygmy-owl: p = 0.028). Again, there were no differences between stimuli in the duration of the wah elements (p = 0.396) or the duration of the intervals between the wahs (p = 0.144), only in the ratio of wah element duration to interval duration. Unexpectedly, when Steller's jays saw a northern pygmy owl they also increased the duty cycle of their wek call similar to seeing a sharp-shinned hawk or a northern goshawk (Fig.

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9c; visual pygmy-owl versus visual sharp-shinned: p = 0.678; visual pygmy-owl versus visual goshawk: p = 0.972). Finally, when they heard a red-tailed hawk they gave more red-tailed hawk mimetic calls than to the other acoustic stimuli (Fig. 9f; acoustic red-tailed versus acoustic goshawk: p < 0.001; acoustic red-tailed versus acoustic sharp-shinned: p < 0.001; acoustic red-tailed versus acoustic pygmy-owl: p = 0.002; acoustic red-tailed versus acoustic control: p < 0.001).

DISCUSSION

We tested whether Steller's jays respond differentially to various levels of risk by presenting four species of raptors that varied in likely level of threat to jays, and we also experimentally altered the detection cue (visual versus acoustic). Previous studies have shown that different aspects of predators and their behavior influence both behavior and acoustic responses of prey (Blumstein, 2000; Griesser, 2009; Marler, 1955; Seyfarth et al., 1980; Templeton et al., 2005). However, few studies have examined how predator detection cue type influences risk assessment or acoustic responses across different predators. Our results showed that Steller's jays integrate information about predator species identity with predator detection cue type to assess risk, and this is reflected in their alarm calls.

(1) Do Steller's jays assess risk using different predator detection cues across different predators?

Steller's jays responded differently depending on whether they saw or heard different predators: sharp-shinned hawks were responded to with a longer latency to resume foraging regardless of being heard or seen; northern goshawks were responded to with a longer latency to resume feeding if they were seen rather than heard. Townsend's solitaires (control) and northern

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pygmy-owls were responded to as low threat regardless of being seen or heard. And when red-tailed hawks were heard they were deemed more threatening than the control and northern pygmy owl, but less threatening than sharp-shinned hawks and northern goshawks. This shows that there is an interaction between predator detection cue and predator species used in assessment of risk. It is not as simples as one predator being more threating than another but instead Steller's jays are combining multiple sources of information to assess risk. Predators differ in the information they provide to prey. And because predation is such a strong selective force, it is not surprising that prey use information from several sources to assess risk.

(2) How does this influence alarm calls?

Previous studies have shown that information about predators can be encoded in different ways. Acoustically different calls can be produced for different types of predators (i.e. referential) (Griesser, 2009; Seyfarth et al., 1980). Within a call type, there can be graded variation in acoustic characteristics such as elements per call (Fallow & Magrath, 2010; Sieving et al., 2010; Soard & Ritchison, 2009; Templeton et al., 2005), calling rate (Colombelli-Négrel et al., 2010; Griesser, 2009) and call length (Ellis, 2008; Wilson & Evans, 2012; Yorzinski & Vehrencamp, 2009). Animals can also combine different note types in different orders and sequences to convey information about predators (Blumstein, 1999; Griesser, 2009; Suzuki, 2014; 2016). Steller's jays change the number of calls, the number of elements and the duty cycle of the elements in response to the interaction between predator species and detection cues. Steller's jays' responses to predators appear to be complex, and differ between their foraging behavior versus their alarm calling behavior. For example, Steller's jays did not distinguish between seeing or hearing a sharp-shinned hawk in how long it took them to resume feeding

behavior (Fig. 8), but they did alter their alarm calls differently depending on whether they saw or heard the sharp-shinned hawk (Fig. 9a-c, e).

Many species of jays and their allies are known to mimic the sounds of other animals, including predators. Steller's jays produced mimetic red-tailed hawk calls mainly in response to hearing the calls of red-tailed hawks. We conclude that their production of these mimetic calls is not random, nor associated with sexual selection since they mimic red-tailed hawks all year. We also never observed Steller's jays give mimetic red-tailed hawk calls that scared others from feeding sites so that they could feed (Flower et al., 2014). Thus, it does not seem that Steller's jays mimic raptor calls to deceive other jays so they can steal food (Flower et al., 2014). Finally, in all of our red-tailed hawk presentations we never observed a predator come to the area in response to the playback or the mimetic calls as predicted if the mimetic calls function as fear screams (Curio, 1976), so it does not seem that they mimic red-tailed hawks to bring in other raptors to try and escape. Since Steller's jays produce mimetic red-tailed hawk calls almost exclusively in response to hearing real red-tailed hawk calls, we suggest that they function as alarm calls (Goodale & Kotagama, 2006). We did not have a robotic red-tailed hawk, but it would be very interesting to test whether Steller's jays mimicked red-tailed hawk calls when they see (but not hear) a red-tailed hawk.

We cannot say whether these subtle changes in the alarm calls of Steller's jays are relevant to conspecifics or used to deter predators. The differences in alarm calls could be due to arousal levels alone and may not encode information about predator species, detection cue or threat level to receivers. Future research with playback studies would be fascinating to test if

these changes are to communicate information about threat level to conspecifics, or to deter predators.

Cues differ in their information content. When jays see a predator, they know its exact location, and when and where it moves. In contrast, when jays hear a predator, they know its general location, but not much else about it. Thus, hearing a predator might be fundamentally more dangerous than seeing it (Billings et al., 2015; Blumstein, 2000). However, contrary to this, Steller's jays had a longer latency to resume foraging and gave more wah calls with more elements and a higher wek duty cycle when they saw rather than heard a northern goshawk. This may have been since the robotic raptors were all presented fairly close to the feeders (approx. 15-20 m away).

In our experimental design, we did our best to control for as many characteristics of predators as we could: type of predator (we used all raptors), distance (acoustic and visual stimuli were all presented at 15-20 m from feeder), predator behavior (all the robo-raptors were perched and had heads that moved), and habitat (all feeders were surrounded by coniferous forests). We also attempted to control for body size and hunting strategy by selecting predators that either shared or differed in these attributes (Fig. 7). However, we could not control for the experience of the free-living Steller's jays. Experience plays a large part in how prey species will respond to particular predators because cognitive properties and perception of risk can be closely linked to previous experience (Chivers et al., 2016; Stankowich & Blumstein, 2005). It is very probable that Steller's jays are eaten more often by northern goshawks and sharp-shinned hawks than red-tailed hawks and northern pygmy owls. Thus, Steller's jays may have more experience

with goshawks and sharp-shined hawks, and that could be why they respond to them as higher threat.

Conclusions

Steller's jays varied the production of their wah, wek, and mimetic red-tailed hawk calls in response to different raptors and different detection cues. They did this by varying the number of wah calls, the number of wah and wek elements per call and the wah and wek duty cycle. This is similar to the graded variation in alarm calls of species with more complex alarm calls, such as Siberian jays, tufted titmice (*Baeolophus bicolor*), and Japanese great tits (*Parus major minor*) (Griesser, 2009; Sieving et al., 2010; Suzuki, 2014). These results show that the assessment of risk from different detection cues depends on the species of predator, and that even alarm calls that are relatively simple in acoustic structure can contain potentially large amounts of information about predators, which suggests unexplored frontiers of communication among animals.

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FIGURE LEGENDS

Figure 6: Spectrograms of Steller's jay alarm calls. (a) A wah call, (b) a wek call, and (c) a red-tailed hawk call followed by a Steller's jay red-tailed hawk mimetic call. All acoustic elements used for analysis are indicated with brackets, labeled and numbered. Spectrograms made with Raven Pro 1.4.
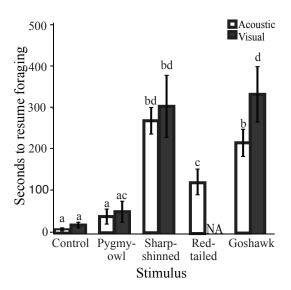
Figure 7: Stimuli used for experiments. Predator stimuli chosen for the differences in size (small versus large) and hunting strategy (pounce versus chase). The bracket next to the predator indicates the relative size of an average Steller's jay in comparison to the predator. The arrows indicate their most common hunting strategy.

Figure 8: Seconds to resume foraging. Mean ± SE of the amount of time it took the Steller's jays to resume foraging to the five acoustic predator stimuli and the four visual predator stimuli. The white bars indicate response to the acoustic stimuli and the gray bars indicate response to the visual stimuli. The lowercase letters indicate differences at $p < 0.05$.

Figure 9: Alarm Call Response. Mean ± SE of (a) the average number of wah calls given, (b) the average number of wah elements per wah call, (c) the average wek duty cycle (duty cycle is the ratio of sound versus silence), (d) the average wek elements per wek call, (e) the average wah duty cycle, and (f) the average number of red-tailed hawk mimetic calls. The white bars indicate response to the acoustic stimuli and the gray bars indicate response to the visual stimuli. The lowercase letters indicate differences at $p < 0.05$.

FIGURE 6

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FIGURE 7

FIGURE 8

FIGURE 9

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CHAPTER 3: The effect of body size, habitat and phylogeny on the acoustic structure of mobbing calls in three passerine families

Alexis C. Billings

ABSTRACT

The acoustic adaption hypothesis predicts that animals should adaptively respond to the transmission properties of the habitat in which they communicate. Although there have been many tests of the acoustic adaptation hypothesis with bird song, there have been very few tests with different types of bird vocalizations. Here I tested the predictions of the acoustic adaption hypothesis with avian mobbing calls produced in closed, open and urban habitats in three families of passerine birds. I also controlled for body size and phylogeny since these are known to influence acoustic characteristics of vocalizations. I found that body size was important in duration and frequency measurements of mobbing call acoustic structure. Phylogeny was not very predictive of acoustic structure of mobbing calls. And finally, habitat did not explain the variation in acoustic structure between species classified as occurring in predominately open or closed habitats. However, I did find that species classified as urban had a lower minimum frequency. This is in direct opposition to previous findings for bird song, where species appear to shift lower minimum frequencies upward, likely to avoid masking by anthropogenic noise. I conclude that there may be alternative strategies for different vocalization types and that species in urban habitats may be able to increase communication distance by having a lower minimum frequency.

INTRODUCTION

Successful transmission and reception of communication signals are crucial for mate attraction, territory defense, parent-offspring relationships, behavior synchronization and warnings about danger (Bradbury & Vehrencamp, 2011). One major challenge faced by communicating animals is that signals are corrupted and degraded as they travel through the environment (Bradbury & Vehrencamp, 2011). Therefore, the environment in which a signal is produced may have important effects on its transmission and detection.

For acoustic signals produced in terrestrial environments, there are many forms of degradation (e.g. spreading loss/acoustic impedance, reflection, refraction) and interference (e.g. masking from other sound sources) (Bradbury & Vehrencamp, 2011). How signals degrade can vary with the properties of different habitats (Blumenrath & Dabelsteen, 2004). Therefore, the habitats in which acoustic signals evolve may select for particular signal design features. This idea was formalized by Morton (1975) as the acoustic adaptation hypothesis, which states that acoustic signals are adaptively structured to the habitat in which they are produced in order to maximize their propagation. The acoustic adaptation hypothesis was traditionally explored in natural habitats focusing on the physics of sound propagation and the transmission properties of a habitat. More recently it has also been applied to urban habitats with anthropogenic noise (Potvin et al., 2014). The acoustic adaptation hypothesis provides testable predictions of how habitat (natural or anthropogenic) may influence the structure of acoustic signals (Ey & Fischer, 2009; Roca et al., 2016).

Tests of the acoustic adaptation hypothesis have focused primarily on learned oscine bird song (Boncoraglio & Saino, 2007; Ey & Fischer, 2009). In natural habitats, these tests have

yielded mixed results: some studies have found differences in frequency, amplitude or temporal features between open and closed habitats, whereas others found no differences between habitats (reviewed in Ey & Fischer, 2009). In urban environments, some songbirds shift to longer duration (Montague et al., 2013; Potvin & Mulder, 2013), higher amplitude (Lowry et al., 2012) or higher frequency (reviewed in Roca et al., 2016) of their songs. These acoustic changes are hypothesized to increase propagation and detection in the presence of low-frequency urban noise.

Other types of bird vocalizations besides song have been less studied, but are well-suited signals to test the predictions of the acoustic adaptation hypothesis because many are also used for long-distance communication and rely on effective transmission with little degradation (Marler, 1955; 1957). In particular, mobbing calls are acoustic signals given by birds in response to danger. Generally, although not ubiquitously, they have a broadband acoustic structure with a loud, harsh sound (Marler, 1957). Like song, each species has a specific mobbing call, which functions to attract other individuals, both conspecific and heterospecific, to the location of the caller to assist in harassing and mobbing to drive the predator from the area (Pettifor, 1990). They are a relevant signal to test the predictions of the acoustic adaptation hypothesis for both natural and urban habitats because their structure differs widely across habitats and species (Fig. 10a-b), they are considered innate (Benedict & Krakauer, 2013; Marler, 2004; Potvin et al., 2014), they are important for survival and thus likely experience consistent selection for optimal transmission (Potvin et al., 2014), and very few studies have explored the role of habitat in the shaping the acoustic structure of mobbing calls (Potvin et al., 2014; Proppe et al., 2010).

I tested predictions of the acoustic adaptation hypothesis for open, closed and urban habitats in mobbing calls across three families of passerine birds using a phylogenetic comparative approach (Felsenstein, 1988). I also included body size as a covariate, because body size is often found to be an important factor in acoustic vocalizations (Ryan & Brenowitz, 1985) because larger species are able to produce lower frequencies (Fletcher, 2005).

The predictions between open and closed habitats are based on attenuation (inverse square law + excess attenuation; Marten & Marler, 1977) and environment-related variations, such as closed habitats may have more stable acoustic conditions than open habitats (Ey & Fischer, 2009; Morton, 1975). Vocalizations produced in closed habitats are predicted to have a longer duration and lower frequencies than those produced in open habitats. Lengthening the signal may increase the likelihood of detection in closed habitats where in open habitats shorter signals may be less susceptible to influences from the fluctuating transmission conditions (e.g. wind). Lower frequencies transmit further than high frequencies, especially in closed habitats (Ey & Fischer, 2009; Marten & Marler, 1977; Marten et al., 1977).

I tested six predictions of the acoustic adaptation hypothesis for open versus closed and one prediction relating to urban habitats while controlling for both body size and phylogenetic relatedness. I predicted that mobbing calls produced by species from closed habitats will have (1) longer duration, (2) lower highest frequency, (3) lower minimum frequency, (4) lower mean frequency, (5) lower dominant frequency, and (6) a narrower frequency range than mobbing calls produced by species from open habitats (from Ey & Fischer, 2009). And for urban habitats, I predicted that mobbing calls produced by species from urban habitats will have (7) a higher low

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frequency to avoid masking from low frequency (0-3 kHz) anthropogenic noise (from Roca et al., 2016).

METHODS

Species selection

I selected species from the Corvidae, Icteridae, and Turdidae families from the order Passeriformes, because these three families because they include species that vary in body size and are found in a wide range of habitat types. In order for a species to be included in the analysis it had to meet four requirements: (1) at least two 3-star or above recordings of mobbing calls available from the Macaulay Library at Cornell's Lab of Ornithology, (2) habitat information available for the species, (3) mass measurements available for the species, and (4) the species must be included in the Jetz et al. phylogenetic tree (Jetz et al., 2012; Jetz et al., 2014). A total of 84 species met these four requirements: 22 species from the Corvidae, 35 from the Icteridae and 27 from the Turdidae.

Acoustic recordings

In order to identify the mobbing call for a species, I first examined all recordings of that species and looked for notes associated with the recording pertaining to a mobbing event (e.g. "calls given in response to predator", "calls given in response to approach at nest"). If notes by the recordist indicated a mobbing call, all other recordings for that species were examined for calls that sounded and looked the same. If no metadata notes existed for a recording, I assessed field guides for descriptions of a species' mobbing call, followed by searching the collection at the Macaulay Library for calls that fit the description from the field guide. About 25% of the species had more than one described mobbing call, for example Steller's jays (*Cyanocitta*

stelleri) have a "wah" and "wek". These calls are both used in the mobbing of predators and therefore have may same function. I chose the mobbing call with the most high-quality recordings available.

Acoustic measurements

All acoustic measurements were made in Raven Pro 1.4. All recordings were set to the same spectrogram parameters (Window Size = 15.9 ms, Overlap = 75%, Hop Size = 3.97 ms, DFT = 4096, and Grid Spacing = 10.8). I used ms instead of samples for the Size and Hop Size because the recordings had different sampling rates and using ms adjusts for these differences. I chose six acoustic measurements available in Raven Pro 1.4 to test the predictions of the acoustic adaptation hypothesis (Fig 10a). (1) Delta time, the duration of the selection. (2) High frequency, the highest frequency in the selection. (3) Low frequency (also known as minimum frequency), the lowest frequency in the selection. (4) Center frequency (also known as mean frequency), the frequency that divides the selection into two frequency intervals of equal energy (5) Maximum/Peak frequency (also known as dominant frequency), the frequency that contains the maximum energy in the selection. And (6) Delta frequency (also known as frequency range), the difference between the upper (high frequency) and lower frequency (low frequency) limits of the selection.

Selection of mobbing call characteristics

Individual call elements were selected from the mobbing call. Ten random elements were selected per recording unless there were fewer elements available for selection; in the latter case all the elements in the recording were selected. All measurements were averaged to get a mean per species per acoustic measurement.

Habitat classification

I used field guides and online species sources (e.g. Birds of North America) to classify the habitat type of each species (see Appendix). I then condensed the habitats into three habitat categories: open (e.g. meadows, grassland, scrub), closed (e.g. deciduous forest, rainforest, coniferous forest) and urban (Mason & Burns, 2015). A species was classified as urban if it's habitat description mentioned human-built structures or human-altered landscapes (e.g. cities, suburbs, parks, gardens, etc.; after Hu & Cardoso, 2009; Fig. 11). The number of habitat classifications were limited by the relatively low sample size (84 species) and the array of habitat types (12+). Thus, each of the three broad habitat types likely included substantial diversity in habitat structure.

Body size classification

I used The Handbook of Avian Body Mass (Dunning, 2007) and appropriate field and online guides to gather average body mass for each species (see Appendix). If both male and female masses were given, I averaged the two because mobbing calls are given by both males and females (as in Mason & Burns, 2015).

Phylogeny

I conducted phylogenetic generalized least squares (PGLS; Grafen, 1989; Paradis, 2012) analysis, which required a phylogenetic tree (Fig. 11). I used the species-level tree from Jetz et al. (2012).

Statistical Analyses

All analyses were conducted in R using *ape* and *nlme* (Paradis et al., 2004; Pinheiro et al., 2012; R Core Team, 2012) following methods from Paradis (2012) and Wright et al. (2016).

Using PGLS, I identified the best-fit model of character evolution using AIC criterion (Paradis, 2012) for each of the 6 acoustic variables. I considered three models of character evolution: (1) a null model where character changes are completely random with respect to the phylogeny so that there is no phylogenetic constraint or inertia, (2) Brownian motion, which assumes a character evolves randomly in any direction along the phylogeny, and (3) Pagel's, which is a stochastic evolution model where internal branches are multiplied by parameter λ that indicates the level of phylogenetic signal present for a given character (Mason & Burns, 2015; Pagel, 1999; Paradis, 2012).

I analyzed a continuous variable (log mass) and a categorical variable (habitat), with three levels (open, closed, urban). Both with and without the phylogenetic correlation structure, I tested for the effect of log-mass and then for the effect of habitat while controlling for log mass. With the phylogenetic correlation structure, I used *gls* with REML and a Pagel's phylogenetic correlation structure (Paradis, 2012). This used a likelihood ratio test to look for effects of log mass and then for habitat while controlling for log mass. Without the phylogenetic correlation structure, I used *glm* to test for the effects of log mass and then for habitat while controlling for log mass. I also obtained the correlation among the estimated parameters (e.g. habitat categories) both with and without the phylogenetic correlation structure by getting the summary of the models with both habitat and log mass (Paradis, 2012).

RESULTS

Model of character evolution

All variables supported either a null model or Pagel's model; none supported a Brownian motion model. The variables that supported a Pagel's model were: delta time (Pagel's $\lambda = 0.207$),

high frequency (Pagel's $\lambda = 0$), maximum frequency (Pagel's $\lambda = 0.572$) and delta frequency (Pagel's $\lambda = 0$). The variables that supported a null model were: low frequency (Pagel's $\lambda = 0.050$) and center frequency (Pagel's $\lambda = 0.215$).

Effect of body size

When controlling for phylogeny, delta time was positively correlated with log mass (Likelihood ratio = 3.717, df = 4,3, $P = 0.030$; Fig. 12a); whereas the other five frequency variables were negatively correlated with log mass: high frequency (Likelihood ratio = 12.31, df = 4,3, $P < 0.0001$; Fig. 12b), low frequency (Likelihood ratio = 11.36, df = 4,3, $P < 0.0001$; Fig. 12c), center frequency (Likelihood ratio = 21.61, df = 4,3, $P < 0.0001$; Fig. 12d), maximum frequency (Likelihood ratio = 28.44, df = 4,3, $P < 0.0001$; Fig. 12e) and delta frequency (Likelihood ratio = 14.65, df = 4,3, $P < 0.0001$; Fig. 12f).

Without controlling for phylogeny, species' log mass was still positively correlated with delta time (t-value = 2.488, $P = 0.015$; Fig. 12a), and negatively correlated with maximum frequency (t-value = -4.916, $P < 0.0001$; Fig. 12e) and center frequency (t-value = -4.25, $P < 0.0001$; Fig. 12d). However, log mass was not significantly correlated with high frequency (t-value = -1.336, $P = 0.185$; Fig. 12b), low frequency (t-value = -1.182, $P = 0.241$; Fig.12c) or delta frequency (t-value = -1.181, $P = 0.241$; Fig. 12f).

Effect of habitat

Regardless of whether I controlled for phylogeny, there were no differences between habitat categories for any of the tested variables (all $P > 0.05$; Fig 13a-b, d-f), with the exception of low frequency (controlling for phylogeny: closed-open: t-value = 0.663, $P = 0.509$, closed-urban: t-value = -2.03, $P = 0.0462$, open-urban: t-value = -2.55, $P = 0.0128$; without controlling

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for phylogeny: closed-open: t-value = 1.751, *P* = 0.084, closed-urban: t-value = -1.36, *P* = 0.177, open-urban: t-value = -2.45, *P* = 0.016; Fig 13c).

DISCUSSION

This comparative study examined the role of phylogeny, body size, and broad habitat characteristics (open, closed, urban) in the evolution of mobbing call acoustic structure. Overall, our results suggest that body size and, to a lesser extent, phylogeny may play a role in shaping variation in acoustic structure of mobbing calls, but that habitat does not appear to have been an important factor in the evolution of the acoustic structure of these calls.

Effect of body size

As predicted, body size was a significant factor in explaining some of the diversity in acoustic structure, although this was stronger when phylogeny was included than when not. Larger species had longer mobbing calls than smaller species (Fig 13a). The pattern for duration (i.e. delta time) was consistent with previous studies focused on avian song that examined temporal features such as note duration (Jurisevic & Sanderson, 1998; Mason & Burns, 2015; Ryan & Brenowitz, 1985). However, the reasons for this pattern are not completely clear. Morphological characteristics that are also related to body size such as bill length and size (Podos & Nowicki, 2004) or metabolic rate (Gillooly & Ophir, 2010) may be responsible for this pattern.

Larger species also had lower low, high, center, and maximum frequencies and a smaller frequency range (i.e. bandwidth or delta frequency) than smaller species (Fig. 13b-f). Correlations between the five frequency variables and body size are also consistent with previous research, which found that body size was correlated with various measures of frequency, such as

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low frequency, high frequency and maximum frequency (Jurisevic & Sanderson, 1998; Mason & Burns, 2015; Ryan & Brenowitz, 1985). The relationship between body size and the various measures of frequency are generally explained by the functional relationship between syrinx size and body size. As body size increases, syrinx size increases, and larger syrinx sizes can produce lower frequencies (Bowman, 1979; Wallschläger, 1980).

Effect of phylogeny

There was a low phylogenetic signal for most of the call components (indicated by relatively low Pagel's λ: 0 - 0.572). This suggests that phylogeny is not a strong predictor of acoustic structure in general, but that some of the acoustic features (e.g. maximum frequency) may be linked to phylogeny. Tobias et al. (2010) also found limited phylogenetic signal when testing the predictions of the acoustic adaption hypothesis in non-passerine Amazonian birds (Tobias et al., 2010). Phylogeny appears to be a factor in tests of the acoustic adaptation hypothesis in song of birds from different orders because of differences in syrinx morphology across orders (Ryan & Brenowitz, 1985). Therefore, it is not overly surprising that there is low phylogenetic signal since the three families are all within the same order of birds and share similar syrinx morphology.

Effect of habitat

I tested six predictions of the acoustic adaptation hypothesis by comparing species occurring in closed, open and urban habitats. I found no support for any of the predictions of the acoustic adaptation hypothesis for closed versus open habitats; there were no significant differences between the acoustic variables of species classified as living in closed versus species classified as living in open (Fig 13a-f). This suggests that habitat structure in the broadest sense

(i.e. open versus closed) does not seem to be a strong selective force on the acoustic structure of mobbing calls.

I found that species classified as urban had a lower minimum acoustic frequency than species classified as non-urban (i.e. open or closed). This is in direct opposition of the findings for the effects of urbanization on bird song, where species in urban habitats seem to shift their minimum frequencies up. Since anthropogenic noise is low frequency (below 3 kHz) (Hu & Cardoso, 2009; Potvin et al., 2014), it is thought that species will increase the frequencies of their vocalizations above anthropogenic noise frequencies to avoid masking (Barber et al., 2010; Bradbury & Vehrencamp, 2011; Roca et al., 2016). This has been shown extensively in bird song using comparisons between urban and non-urban populations within species to test for divergence across populations and playback experiments of anthropogenic noise to test for real-time shifts to exposure of anthropogenic noise (reviewed in Roca et al., 2016).

However, this opposite pattern was also found for silvereye (*Zosterops lateralis*) mobbing calls (Potvin et al., 2014). Silvereyes residing in urban habitats had lower minimum, peak and maximum acoustic frequencies compared to silvereyes residing in rural habitats. Furthermore, silvereyes also appear to shift the frequency of their song and contact calls in the presence of anthropogenic noise (Potvin et al., 2011). Potvin et al. (2013) suggested that there may be divergent selection on different vocalizations such as song and mobbing calls. There may be a tradeoff with shifting minimum frequencies upward to avoid masking anthropogenic noise. Low frequencies transmit further and are degraded less than higher frequencies, so when shifts to higher frequencies are made, the active space of the vocalization is reduced (Parris & McCarthy, 2013). Since mobbing calls may be a longer distance signal than song, it may be advantageous to

decrease the frequency of a vocalization to increase the active space. Further evidence for the increase in communication distance in urban habitats comes from noisy miners (*Manorina melanocephala*), which increase the amplitude of their alarm calls in noisier habitats to increase the signal-to-noise ratio effectively increasing the active space of their vocalizations (Lowry et al., 2012). Species studied here might also increase the amplitude of their mobbing calls to further increase the active space of their vocalization. However, this could not be tested with the current dataset because there was no calibration of the recording equipment to make unbiased amplitude measurements.

Another possibility is that mobbing calls are not susceptible to masking. Mobbing calls tend to be broadband (i.e. larger frequency range). Perhaps this acoustic structure makes calls resilient to masking because even if the lower frequencies are masked, the higher frequencies transmit. However, recent research shows that receivers show reduced response when mobbing calls are given in the presence of anthropogenic noise suggesting mobbing calls are masked by anthropogenic noise (Grade & Sieving, 2016; Kern & Radford, 2016). However, these studies cannot distinguish between receivers being distracted by the noise, versus receivers being unable to detect the signal. Future studies could attempt to test for this distinction by playing mobbing calls with removed lower frequencies in the absence of noise to see if the lack of response is due to the birds missing lower frequencies of the calls.

Mobbing calls may be masked by anthropogenic noise and there is no evidence of frequency shifting to avoid this masking as there is for song. Instead urban species may increase the communication distance of their vocalization to combat anthropogenic noise. However, more studies are needed to test if this increase of active space is common among a larger number of

urban dwelling species. For example, Carolina chickadees (*Poecile carolinensis*) showed no shift in the frequency of the "dee" note of the chick-a-dee call in response to increased anthropogenic noise (Grace & Anderson, 2014). Also, there was considerable variation in means of the species included in this study, which also suggests that this may not be true for all urban species. However, future studies should continue to look at mobbing calls and the potential for a different strategy in dealing with anthropogenic noise.

Are species in urban habitats shifting or pre-adapted to urban living?

This study raises the question of whether there is active shifting occurring (where species are making real-time adjustments in their mobbing call frequency) or if this is a feature of some species mobbing call acoustic structure that pre-adapts them to urban living. This has been debated for bird songs, where the degree of plasticity in songs may pre-adapt species to live in urban habitats (Hu & Cardoso, 2009; Slabbekoorn, 2013). For example, birds that learn their songs show a tighter adjustment of their song in noisier habitats than species whose songs are considered innate (Ríos Chelén, Salaberria, Barbosa, Macías Garcia, & Gil, 2012). Silvereyes appear to undergo a real-time shift, as evidence by differences between populations (Potvin et al., 2014). Although this study only tested for broad patterns in acoustic structure between urban and non-urban birds, the recordings used for the urban species were not recorded in urban habitats (see Appendix). This suggests that the species classified as urban for this study were not actively shifting since they were not in noisy habitats when recorded. This lends some support that this difference in acoustic structure may be another characteristic that pre-adapts them for urban living.

Assuming that all closed habitats have the same transmission properties and therefore impose the same selective pressures on signal propagation is limiting. Furthermore, habitats classified as the same (e.g. deciduous) are not the same over seasons. For example, temperate deciduous forests have different transmission properties when leafed out versus bare and this influences the propagation of great tit (*Parus major*) song (Blumenrath & Dabelsteen, 2004). By classifying habitats into broad categories, I may have missed important selective pressures imposed by the very specific habitat a species resides in. Furthermore, many species reside in multiple habitat types (e.g. breed in closed, forage in open) and the category they were assigned in may not best represent the habitat that may impose selection pressure on their vocalizations. Future studies could incorporate more fine-scale habitat classifications.

CONCLUSIONS

I explored components of the acoustic adaptation hypothesis in the context of how habitat has influenced the evolution of acoustic structure of mobbing calls. Body size explained some of the variation in mobbing call acoustic structure, phylogenetic relatedness to a lesser degree, and habitat explained very little. I found that species that are classified as urban have a lower minimum frequency than species classified as occurring in non-urban habitats. This finding, along with those of Potvin et al., (2014), suggests that mobbing calls may be under different selection pressures from anthropogenic noise and instead of shifting out of the noise to avoid masking, species in urban habitats may be increasing the active space of their mobbing calls. Research into the effects of anthropogenic noise on vocalizations has focused almost exclusively on song. However, other vocalizations, such as mobbing calls, are essential for survival and under selection to propagate and be detected. As anthropogenic noise is likely to continue to

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increase, more studies on the strategies species use for vocalizations, other than song, would be

of substantial value.

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FIGURE LEGENDS

Figure 10: a. Spectrogram samples of mobbing calls from two Corvidae (American crow and red-billed chough), Icteridae (brown-headed cowbird and Baltimore oriole) and Turdidae (black-billed nightingale thrush and Eurasian blackbird) species to show acoustic variation across mobbing calls. b. Spectrogram of Setller's jay (Family: Corvidae) "wah" call with six acoustic variables labelled. See text for explanation of acoustic variables. All spectrograms made in Raven Pro 1.4 with Window Size = 8 - 11 ms, Overlap = 50%, Hop Size = 525 ms, DFT = 1024 – 2048 samples, and Grid Spacing = 46.9 – 93.8 Hz).

Figure 11: Phylogenetic tree with Icetridae, Turdudae and Corvidae species used for analysis. Species classified as occupying closed habitats are in purple, species classified as open inhabitants are in green and species classified as urban dwellers are in yellow.

Figure 12: Scatterplot of acoustic variables by log mass with Corvidae in red squares, Icteridae in blue circle and Turdidae in black triangles. a. Delta time by log mass. b. High frequency by log mass. c. Low frequency by log mass. d. Center frequency by log mass. e. Maximum frequency by log mass. f. Delta frequency by log mass.

Figure 13: Boxplot of acoustic variables by habitat type. a. Delta time by habitat. b. High frequency by habitat. c. Low frequency by habitat. d. Center frequency by habitat. e. Maximum frequency by habitat. f. Delta frequency by habitat. Star indicates difference between habitat categories ($P < 0.05$).

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FIGURE 10

a

Steller's jay (*Cyanocitta stelleri*)

b

American crow (*Corvus brachyrhynchos*)

Red-billed chough (*Pyrrocorax pyrrhocorax*)

Brown-headed cowbird (*Molothrus ater*)

Baltimore oriole (*Icterus galbula*)

Black-billed nightengale thrush (*Catharus gracilitostris*)

Eurasian blackbird (*Turdus merula*)

FIGURE 11

FIGURE 12

FIGURE 13

CHAPTER 4: A framework to understand interspecific multimodal signaling systems

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ABSTRACT

Continued interest in multimodal signaling systems has resulted in new frameworks to understand the evolution and use of multimodal signals. Most of these studies have focused on multimodal communication within a species (sexual and agonistic signaling), but members of different species also benefit by communicating through both eavesdropping and evolved signals. Here we develop a framework to understand interspecific multimodal signaling systems that asks three questions: (1) is there an ecological incentive to communicate? (2) Is interspecific communication mechanistically possible? And (3) is there a fitness consequence to this communication? Many aspects of multimodal signaling systems are expected to be similar within and across species, and signal reliability underlies all signaling. However, we identify a unique constraint that applies to interspecific signaling systems: the need for overlapping sensory systems between the two species. This new framework should help explain the conditions under which multimodal signaling has evolved in interspecific signaling systems.

INTRODUCTION

Multimodal signaling occurs when signals consist of components from two or more sensory modalities (Table 1). Multimodal signals are common within most animal signaling systems, and perhaps the norm (Hebets & Papaj, 2004; Partan & Marler, 2005). For instance, the black-tailed prairie dog's (*Cynomys ludovicianus*) multi-function, contagious jump-yip contains a visual component (the jump) and an acoustic component (the yip) (Hare et al. 2014). However,

given the inherent costs of producing and receiving signals, a fundamental question is why have these complex signals evolved (Bro-Jørgensen, 2010)? Previous research has focused on trying to understand the benefits of multimodal communication; however, prior research has focused predominantly on intraspecific signaling systems, specifically sexual and agonistic signals (Bro-Jørgensen, 2010; Bro-Jørgensen & Dabelsteen, 2008; Candolin, 2003). Here we present a framework to explain the conditions under which multimodal signaling has evolved in *inter*specific signaling systems.

A number of hypotheses have been developed to explain the evolution of multimodal signals (reviewed in Bro-Jørgensen, 2010). Many of the adaptive explanations for multimodal signaling in intraspecific signaling systems are likely to apply to interspecific signaling systems because there will be similar selection for increased robustness, content and/or reliability. However, there are likely notable differences between intra- and interspecific multimodal signaling systems because of differences in ecology, sensory systems and cognition that exist between different species.

A BRIEF BACKGROUND OF MULTIMODAL SIGNALING

Multimodal signals are often classified as redundant or non-redundant depending on the information contained in the components of the signal (Partan & Marler, 2005; Table 1). Furthermore, the evolution of multimodal signals can be explained using two main mechanisms: content-driven selection for increased information (i.e., the multiple messages hypothesis; Johnstone, 1996) and efficacy-driven selection for increased robustness (i.e., the backup signals hypothesis; Johnstone, 1996) (Hebets & Papaj, 2004; Table 1). To study receiver responses, each component of a multimodal signal is tested separately and then together to understand how the

combination of the components alters response (Partan & Marler, 2005). For example, fruit flies (*Drosophila melanogaster*) that use both an acoustic and a chemical component in their female courtship display have more successful matings than males that use only acoustic or chemical components (Rybak et al. 2002). This illustrates redundant enhancement (Partan & Marler, 2005), where both components provide information to assess male suitability (redundant), but when combined males have significantly more matings than from either component presented alone (enhancement).

Prior work and existing frameworks fail to distinguish between intraspecific and interspecific signaling systems. The majority of empirical examples of multimodal signaling have focused on intraspecific signaling systems (Bro-Jørgensen & Dabelsteen, 2008; Candolin, 2003; Partan & Marler, 2005; Wilkins et al., 2015). Recently, however, frameworks and hypotheses that enable the analysis of a signaling system as a whole have been proposed (Bro-Jørgensen, 2010; Hebets et al., 2016; Wilkins et al., 2015). These frameworks use network and systems approaches that account for dynamic selection and consider the possibility of interactions between components across contexts (i.e., inter-signal interaction; Table 1; Hebets & Papaj, 2004). Although, these new frameworks and hypotheses aim to better understand a signaling system as a whole, again no distinction has been formally made between intraspecific and interspecific signaling systems.

INTERSPECIFIC SIGNALING AND COMMUNICATION

Kostan (2002) developed stage-based a framework for the evolution of interspecific communication (Table 1) that acknowledges the progression from eavesdropping (Table 1) by one species, to both species eavesdropping on one another, to asymmetrical communication

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where one species is intentionally signaling to the other, which leads to mutualistic communication where both species produce signals that alter the behavior of the other (Kostan 2002). Interspecific communicative interactions can occur across all of these stages and in a variety of contexts that include (but are not limited to) predator-prey interactions, habitat selection, resource acquisition and species recognition.

Regardless of the stage of communication, it is important to understand the costs and benefits of the exchange from both a signaler's and a receiver's perspective (Westrip & Bell, 2015) In eavesdropping situations, the receiver benefits from the information in the signal and the sender can either be negatively affected (sender -, receiver +; as seen when a predator eavesdrops on prey; Rhebergen et al., 2015) or not affected at all (sender 0, receiver +; as seen when one species eavesdrops on the alarm calls of another species; Fallow & Magrath, 2010). In mutualistic asymmetrical communication, both the sender and the receiver benefit (sender +, receiver +; as seen when flowers signal to their pollinators). The fitness benefits of both the sender and the receiver are important in order to understand the stage of the signaling system and the mechanisms that maintain it.

We develop an integrative framework that specifies the conditions under which we expect to find multimodal signaling systems across species that is based on three broad questions: (1) is there an ecological incentive to communicate? (2) Is interspecific communication mechanistically possible? And (3) is there a fitness consequence to this communication?

AN INTERSPECIFIC MULTIMODAL FRAMEWORK (FIG. 14)

1. Is there an ecological incentive to communicate?

First, there needs to be an ecological incentive for communication (e.g., two species share predators, share food, or there is a predator-prey relationship; Murray & Magrath 2015). Some species have more opportunities for interactions that others. For instance, there may be relatively more ecological overlap between two species leading to more opportunities for interactions and perhaps stronger selection for communication to evolve. If there is an ecological incentive to communicate, then are there aspects of each species' ecology that favor multimodal signals over unimodal or multicomponent signals (Table 1)? In intraspecific systems, it is hypothesized that selection for increased content, reliability or robustness (i.e., content- and efficacy-driven selection) leads to multimodal signals over unimodal or multicomponent signals, and similar selection may exist for interspecific signaling systems. For example, aposematic signals are often multimodal and combine visual, acoustic and often olfactory components to deter predators. One hypothesis for the use of multimodal signals rather than unimodal or multicomponent signals is that the multimodal signals aid in learning and associating a defended prey with unpalatability (Rowe & Halpin, 2013).

2. Is interspecific multimodal communication mechanistically possible?

Sensory drive (Table 1) suggests that the relationship between the environmental conditions signals are produced in, sensory systems, and signals together drive the evolution of signaling systems (Endler, 1992). Following this, we ask three main questions to identify the mechanisms behind interspecific multimodal signaling: (1) do the environmental conditions support multimodal signals? (2) Do the sensory systems overlap? And (3) do the sensory thresholds and cognitive abilities overlap? The answers to these questions highlight the main differences between intraspecific and interspecific communication.

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Do the environmental conditions support multimodal signals? Environments influence communication signals in two ways: the environment can influence the transmission and diffusion properties of a potential signal, and the environment can influence the ability of the receiver to detect the signal above the background noise (Bradbury & Vehrencamp, 2011; Endler, 1992). Environmental influences differ across signal modalities because of inherently different transmission and diffusion rates. For example, both acoustic and chemical signals can be used for short and long distance communication, but acoustic signals are generally short term signals, while chemical signals can persist for a longer time (Weissburg et al., 2014). However, the environment can influence transmission and diffusion rates even further. For example, an acoustic signal travels further in water than in air (Bradbury & Vehrencamp, 2011). Furthermore, habitats are not always stable (Bro-Jørgensen, 2010). For example, there may be seasonal variation in the transmission properties of a habitat type. Great tit (*Parus major*) song transmits differently in a deciduous forest habitat before and after foliation (Blumenrath & Dabelsteen, 2004). Finally, within a habitat type, variation in background noise from other species and abiotic features will further modify signal transmission. For example, the backup signal hypothesis (Johnstone, 1996) predicts that the multimodal signal components will be redundant in information in case one of the channels/modalities is blocked by environmental influence. Thus, signals—multimodal or not—will be selected to function under a set of environmental conditions (e.g., the acoustic adaption hypothesis, Morton, 1975).

Do the sensory modalities overlap? Receivers can influence signal evolution through how they perceive and process signals (Rowe, 1999). Therefore, the receiver's sensory system can be a selective force on the evolution of signals, including multimodal signals. In interspecific

signaling systems, this means that the species must have overlapping sensory modalities: the sender needs to produce signal components in modalities the receiver possesses. This can be accomplished through the co-evolution of sender and receiver (e.g., sensory drive; Endler, 1992) or through sensory exploitation (Table 1) of sensory systems evolved for another purpose (e.g., conspecific communication, predator or prey detection; Ryan, 1998).

Do the sensory thresholds and cognitive abilities overlap? Beyond possessing overlapping signaling systems, the signals must also be within the receiver's detection thresholds (Murray & Magrath 2015). For example, plants may vary their signals to be within the spectrum of some receivers (i.e., pollinators) and outside the spectrum of others (i.e., herbivories) (Endler, 1992; Schaefer et al., 2004).

The opportunity for overlapping sensory systems, sensory thresholds and cognitive abilities is the key difference between intraspecific and interspecific communication systems. In general, conspecifics share similar sensory systems and thresholds (but see Gall & Lucas 2010). However, different species may not necessarily have the same sensory systems, the same sensory sensitivity or thresholds within a given sensory system, the same cognitive abilities, or the same information processing abilities.

It is the interaction between the environmental conditions the signal is produced in, the sensory systems and the signal itself that drive the evolution of signaling systems (Endler, 1992). We can explore this further with interspecific multimodal signals. First, the components within a multimodal signal can interact depending on environmental conditions or receiver psychology (i.e., inter-signal interaction; Hebets & Papaj, 2004). For example, Uy and Safran (2013) found that the habitat density influences the use of the components of a multimodal signal used for

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species recognition. A subspecies of *Monarcha* flycatcher found in dense habitats used the acoustic and visual components sequentially, with the acoustic signal acting as a long-range signal and the visual signal acting as a close-range signal. Whereas another subspecies found in more open habitats used both acoustic and visual signals simultaneously (Uy & Safran, 2013). Second, there is also the possibility that the different components have evolved to maximize communication with different receivers (i.e., audience effects; Higham & Hebets, 2013). For example, aposematic prey may use multimodal signals to communicate their defenses to multiple predators. Arctiid moths may have evolved different display components depending on whether their predators are diurnal or nocturnal (Ratcliffe & Nydam, 2008; Rowe & Halpin, 2013). Third, independent of sensory abilities, there are cognitive and information processing constraints. For example, Murray & Magrath (2015) found different responses to conspecific and heterospecific mobbing calls in two passerine birds. They concluded that there may be constraints on eavesdropping, which includes the lack of perceptual specializations (Murray & Magrath, 2015). Thus, there will be sensory and cognitive limitations on interspecific multimodal communication that will prevent effective communication or eavesdropping.

Asking whether multimodal communication is mechanistically possible between species reveals important and unique constraints on the evolution of such communication because of the need for overlapping sensory modalities, sensory thresholds and cognitive abilities between species. Although receiver psychology (including sensory thresholds and cognitive abilities) has been acknowledged as important in intraspecific signaling systems (Rowe, 1999), it may be even more crucial in interspecific signaling systems because of the greater chance of a mismatch between sensory modalities, sensory thresholds or cognitive/processing abilities.

3. Is there a fitness consequence to interspecific multimodal communication?

Like intraspecific signaling systems, the fitness consequences of signaling are dictated by the costs and benefits of signaling for both senders and receivers: both sender and receiver benefit (sender +, receiver +), sender benefits (sender +, receiver -) or receiver benefits (sender -, receiver +). These costs and benefits may also be driven by selection for increased robustness (efficacy-driven selection) or increased information or reliability (content-driven selection). Furthermore, there may be an adaptive reason to signal or the signaling system may be a by-product of another process (e.g. sensory exploitation). Finally, the costs and benefits of signaling between a sender and receiver can act as an ecological incentive to interact. Below, we present an example of for each of the cost/benefit situations between sender and receiver using the presented framework.

Signaler +, Receiver +: Plant-pollinator signaling systems

Most plant-pollinator signaling systems are asymmetrical communication systems (Kostan, 2002) that involve an olfactory component and a visual component. The ecological incentive to communicate is the mutual benefit to both sender and receiver: plants get pollinated (sender +) and pollinators get an energy reward (receiver +). Selection for increased information and reliability about the nutritional reward (content-driven selection; Leonard et al., 2011) and robustness against a noisy background with multiple olfactory and visual signals bombarding pollinators (efficacy-driven selection; Leonard & Masek, 2014) may drive the need for multimodal signals over unimodal signals. Communication is mechanistically possible because these systems are thought to coevolve, with plant multimodal signals coevolving with the sensory and perceptual systems of their pollinators (Haverkamp et al., 2016; Leonard & Masek,

2014). For example, the evening primrose (*Oenthera neomexicana*) and hawkmoth (*Manduca sexta*) plant-pollinator system uses both olfactory and visual signals (Raguso & Willis, 2002). Hawkmoths require both a visual component and an olfactory component from evening primrose in order to elicit feeding behavior (i.e., proboscis extension). Decoupling the visual and olfactory stimulus will elicit approach but not feeding.

Signaler +, Receiver -: Predators manipulating their prey

Some asymmetrical signaling systems (Kostan, 2002) are deceptive or manipulative where the signaler benefits and the receiver does not. For example, painted redstarts (*Myioborus pictus*) are flush-pursuing birds that elicit escape responses in insects so they can pursue them until capture (Jabłoński & Lee, 2006). The use visual signals accompanied by substrate vibrations to exploit their insect prey escape responses so they can pursue them in aerial chases. The ecological incentive to signal is a benefit to the sender in a predator-prey context. The use of a multimodal signal over a unimodal signal may result from sensory exploitation where the two components together flush prey more often or successfully than a unimodal signal. Another possibility is the signals are linked through morphology and one cannot be produced without the other. If sensory exploitation is involved in this system, then the signal will be in the modalities, thresholds and cognitive abilities that the prey evolved for other purposes. This is conjecture because the necessary experiments have not been completed. Yet, sensory exploitation seems reasonable to expect since the visual stimulus alone has been linked to sensory exploitation (Jablonski, 2001).

Signaler -, Receiver +: Predators eavesdropping on their prey

Some signaling systems are characterized by eavesdropping receivers that benefit at the cost to the sender. Predators often eavesdrop on their prey's signals to locate them (Halfwerk et al., 2014; Rhebergen et al., 2015; Roberts et al., 2007). For example, Túngara frogs (*Physalaemus pustulosus*) produce acoustic signals to attract females and compete with other males. A by-product of these acoustic signals is the visual signal of the inflating vocal sac. Females in this system prefer males with a linked acoustic and visual signal (Taylor et al., 2011; Taylor & Ryan, 2013). Fringe-lipped bats (*Trachops cirrhosus*) also prefer the acoustic and visual components to aid in localizing their prey (Halfwerk et al., 2014; Rhebergen et al., 2015). Therefore, in this system, the multimodal signal evolved as a sexual signal, but is being eavesdropped on by predators. The ecological incentive to use the multimodal signal is a predator-prey relationship. Male frogs use a multimodal signal over a unimodal signal because of intraspecific sexual selection (Taylor et al., 2011; Taylor & Ryan, 2013). For the predators, the multimodal signal improves prey localization under various acoustic environmental conditions, suggesting the environment that these signals are produced in favors multimodal over unimodal because Túngara frogs call in choruses (Rhebergen et al., 2015). Finally, the bats have the capacity to hear the acoustic signals and use echolocation on the vocal sac to aid in localizing prey (Rhebergen et al., 2015), which is interesting because the bats are not using their visual sensory system for the visual component, but instead are using their unique sensory system (echolocation).

CONCLUSIONS

The literature on intraspecific multimodal signaling and communication is rapidly expanding. This rapid expansion has been driven by clearly articulated frameworks for

understanding the signaling system as a whole. We hope that by developing a similar framework for interspecific multimodal signaling systems researchers will have a better understanding of the costs and benefits that shape interspecific multimodal signaling systems. Potential information is everywhere and for many species, particularly those with overlapping sensory and cognitive systems, there may be clear benefits from acquiring and using information produced by other species. The proposed framework should give structure empirical examples and provide predictions that can be empirically tested for future work. Finally, understanding interspecific multimodal signaling puts us in a better position to assess and understand how anthropogenic changes that effect multimodal signaling systems will influence these important interspecific relationships (Halfwerk & Slabbekoorn, 2015).

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FIGURE LEGENDS

Figure 14: Conceptual framework for understanding how and why multimodal signaling systems evolve in interspecific signaling systems. Black arrows indicate a "yes" response to the question posed in the boxes, where a gray arrow indicates a "no" response.

TABLE 1: Key definitions used within the text.

Communication: The exchange of signals between a sender and a receiver, which results in the behavior of the receiver changing to the advantage of the sender (Bradbury & Vehrencamp, 2011; Searcy & Nowicki, 2005).

Content-driven selection: Selection to increase the information content of the signal to the recipient (Hebets & Papaj, 2004).

Eavesdropping: When individuals are not directly involved in a signaling interaction, but are able to gather information from it (Searcy & Nowicki, 2005).

Efficacy-driven selection: Selection to increase signal propagation from the signaler, through the environment, to the recipient (Hebets & Papaj, 2004).

Inter-signal interaction: "Occurs when the presence of one signal or component alters the receiver's respond to a second signal or component" (Hebets & Papaj, 2004 p. 207).

Multicomponent signal: Signals composed of more than one component within a sensory modality (Kikuchi et al., 2016).

Multimodal signal: Complex signals composed of more than one component in more than one sensory modality (Hebets & Papaj, 2004).

Non-redundant signals: Information content is different in each component of the multimodal signal (Partan & Marler, 2005).

Redundant signals: Information content is the same in each component of the multimodal signal (Partan & Marler, 2005).

Sensory drive: Sensory systems and sensory conditions drive the evolution of signaling systems to decrease degradation and increase conspicuousness against background noise (Endler, 1992; Tobias et al., 2010).

Sensory exploitation: Signals that have evolved to exploit preexisting receiver biases (Ryan 1998).

Signal: "Behavioural, physiological, or morphological characteristics fashioned or maintained by natural selection because they convey information to other organisms" (Searcy & Nowicki, 2005, p. 2).

Unimodal signal: A single signal produced in one modality.

FIGURE 14

3. What are the fitness consequences of communication?

Sender +, Receiver +

Sender +, Receiver -

Sender -, Receiver +

2. Is communication mechanistically possible?

Do sensory thresholds/ cognitive abilities overlap?

If no sensory threshold/cognitive overlap = no communication

Do sensory systems overlap?

If no sensory systems overlap = no communication If one sensory system overlaps = unimodal communication in that modality

Is the environment conducive to multiple modalities?

Unimodal or multicomponent communication

1. Is there ecological incentive to communicate?

Are there aspects of both species' ecology that make multimodal communication beneficial?

Unimodal or multicomponent communication

No communication

APPENDIX

Family	Scientific name	Common name	Described habitat	Habitat classification	Mass	ML number	Recordist	Location	Year	Recording habitat	References
Corvidae	Aphelocoma californica	California Scrub-Jay	Scrub	Open	87.5	ML13025	Allen, Arthur A.	California, USA	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Curry, R. L., A. T. Peterson and T. A. Langen. 2002. California Scrub-Jay (Aphelocoma californica), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/cowscj1
Corvidae	Aphelocoma californica	California Scrub-Jay	Scrub	Open	87.5	ML21245	Zimmerman, Dale A.	New Mexico, USA	1980		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Curry, R. L., A. T. Peterson and T. A. Langen. 2002. California Scrub-Jay (Aphelocoma californica), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/cowscj1
Corvidae	Aphelocoma californica	California Scrub-Jay	Scrub	Open	87.5	ML118848	Keller, Geoffrey A.	California, USA	2001		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Curry, R. L., A. T. Peterson and T. A. Langen. 2002. California Scrub-Jay (Aphelocoma californica), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/cowscj1
Corvidae	Aphelocoma coerulescens	Florida Scrub-Jay	Scrub	Open	77.15	ML13034	Worden, K. W.	Florida, USA	1972		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Woolfenden, G. E. and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (Aphelocoma coerulescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/flsjay
Corvidae	Aphelocoma coerulescens	Florida Scrub-Jay	Scrub	Open	77.15	ML13035	Worden, K. W.	Florida, USA	1972		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Woolfenden, G. E. and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (Aphelocoma coerulescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/flsjay
Corvidae	Aphelocoma coerulescens	Florida Scrub-Jay	Scrub	Open	77.15	ML13036	Worden, K. W.	Florida, USA	1972		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Woolfenden, G. E. and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (Aphelocoma coerulescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/flsjay
Corvidae	Aphelocoma coerulescens	Florida Scrub-Jay	Scrub	Open	77.15	ML105382	Keller, Geoffrey A.	Florida, USA	1994		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Woolfenden, G. E. and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (Aphelocoma coerulescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/flsjay
Corvidae	Aphelocoma coerulescens	Florida Scrub-Jay	Scrub	Open	77.15	ML105735	Keller, Geoffrey A.	Florida, USA	1996		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Woolfenden, G. E. and J. W. Fitzpatrick. 1996. Florida Scrub-Jay (Aphelocoma coerulescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/flsjay
Corvidae	Calocitta formosa	White-throated Magpie-Jay	Deciduous dry tropical forest	Closed	201	ML13064	Davis, L. Irby	Nicaragua	1962		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jesse M. S. Ellis. 2010. White-throated Magpie-Jay (Calocitta formosa), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=514796 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Corvidae	Calocitta formosa	White-throated Magpie-Jay	Deciduous dry tropical forest	Closed	201	ML13065	Thurber, Walter A.	El Salvador	1972		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jesse M. S. Ellis. 2010. White-throated Magpie-Jay (Calocitta formosa), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=514796 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Corvidae	Calocitta formosa	White-throated Magpie-Jay	Deciduous dry tropical forest	Closed	201	ML13067	Thurber, Walter A.	El Salvador	1972		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jesse M. S. Ellis. 2010. White-throated Magpie-Jay (Calocitta formosa), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=514796 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Corvidae	Calocitta formosa	White-throated Magpie-Jay	Deciduous dry tropical forest	Closed	201	ML20747	Thurber, Walter A.	Morazan, El Salvador	1975		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jesse M. S. Ellis. 2010. White-throated Magpie-Jay (Calocitta formosa), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=514796 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.

Family	Scientific name	Common name	Habitat	Nest	Mass	ML#	Recordist	Location	Year	Habitat notes	References
Corvidae	Calocitta formosa	White-throated Magpie-Jay	Deciduous dry tropical forest	Closed	201	ML145889	Robbins, Mark B.	La Paz, El Salvador	2004		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jesse M. S. Ellis. 2010. White-throated Magpie-Jay (Calocitta formosa), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=514796 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Corvidae	Corvus corax	Common Raven	Coniferous/Urban	Urban	1000	ML18731	Hewitt, Oliver H.	Alberta, Canada	1980	Forest, coniferous forest, park/ campus/ cemetery, montane grassland	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Boarman, W. I. and B. Heinrich. 1999. Common Raven (Corvus corax), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/476
Corvidae	Corvus corax	Common Raven	Coniferous/Urban	Urban	1000	ML96245	Macaulay, Linda R.	Morocco	1995	Forest, coniferous forest	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Boarman, W. I. and B. Heinrich. 1999. Common Raven (Corvus corax), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/476
Corvidae	Corvus corax	Common Raven	Coniferous/Urban	Urban	1000	ML132203	Andersen, Michael J.	Alaska, USA	2006	Arctic tundra, tundra	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Boarman, W. I. and B. Heinrich. 1999. Common Raven (Corvus corax), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/476
Corvidae	Corvus corax	Common Raven	Coniferous/Urban	Urban	1000	ML137570	Vyn, Gerrit	Alaska, USA	2007	Bay/Habor	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Boarman, W. I. and B. Heinrich. 1999. Common Raven (Corvus corax), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/476
Corvidae	Corvus coronoides	Australian Raven	Varied/Urban	Urban	680	ML13167	Leotscher, Jr., Fred W.	New South Wales, Australia	1968	Rainforest/Royal National Park	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pizzey, G. 1980. A Field Guide to the Birds of Australia. Princeton University Press. Princeton, NJ.
Corvidae	Corvus coronoides	Australian Raven	Varied/Urban	Urban	680	ML78589	Robbins, Mark B.	New South Wales, Australia	1992	Forest, Evergreen forest	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pizzey, G. 1980. A Field Guide to the Birds of Australia. Princeton University Press. Princeton, NJ.
Corvidae	Corvus coronoides	Australian Raven	Varied/Urban	Urban	680	ML125981	Macaulay, Linda R.	Victoria, Australia	2005	Hattah-kulkyne Park- no habitat data	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pizzey, G. 1980. A Field Guide to the Birds of Australia. Princeton University Press. Princeton, NJ.
Corvidae	Corvus coronoides	Australian Raven	Varied/Urban	Urban	680	ML128305	Macaulay, Linda R.	New South Wales, Australia	2005	Deniliquin - no habitat data	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pizzey, G. 1980. A Field Guide to the Birds of Australia. Princeton University Press. Princeton, NJ.
Corvidae	Covus brachyrhynchos	American crow	Varied/Urban	Urban	520	ML13118	McChesney, Donald S.	South Carolina, USA	1958	Forest, coniferous forest	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Verbeek, N. A. and C. Caffrey. 2002. American Crow (Corvus brachyrhynchos), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/amecro
Corvidae	Covus brachyrhynchos	American crow	Varied/Urban	Urban	520	ML86384	van den Berg, Arnoud B.	New Jersey, USA	1995	Forest, deciduous forest	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Verbeek, N. A. and C. Caffrey. 2002. American Crow (Corvus brachyrhynchos), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/amecro
Corvidae	Covus brachyrhynchos	American crow	Varied/Urban	Urban	520	ML105346	Keller, Geoffrey A.	Florida, USA	1994	Freswater, Everglades National Park	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Verbeek, N. A. and C. Caffrey. 2002. American Crow (Corvus brachyrhynchos), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/amecro
Corvidae	Cyanocitta cristata	Blue Jay	Mixed forest/Urban	Urban	71	ML49715	Evans, William R.	New York, USA	1989	Grassland, forest, coniferous forest, active agriculture, field	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Smith, K. G., K. A. Tarvin and G. E. Woolfenden. 2013. Blue Jay (Cyanocitta cristata), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/blujay
Corvidae	Cyanocitta cristata	Blue Jay	Varied/Urban	Urban	71	ML105259	Keller Geoffrey A.	Texas, USA	1993	Mixed coniferous/deciduous forest; Sam Houston National Forest	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Smith, K. G., K. A. Tarvin and G. E. Woolfenden. 2013. Blue Jay (Cyanocitta cristata), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/blujay
Corvidae	Cyanocitta cristata	Blue Jay	Varied/Urban	Urban	71	ML120468	Fischer, Martha J.	New York, USA	2004	Deciduous forest, pasture	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Smith, K. G., K. A. Tarvin and G. E. Woolfenden. 2013. Blue Jay (Cyanocitta cristata), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/blujay

Corvidae	Cyanocitta cristata	Blue Jay	Varied/ Urban	Urban	71	ML13451	Stein, Robert C.	Florida, USA	1963	Orchard edge	1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Smith, K. G., K. A. Tarvin and G. E. Woolfenden. 2013. Blue Jay (Cyanocitta cristata), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/blujay
Corvidae	Cyanocitta stelleri	Steller's Jay	Coniferous forest	Closed	120	ML56865	Keller, Geoffrey A.	Arizona, USA	1991		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Walker, L. E., P. Pyle, M. A. Patten, E. Greene, W. Davison and V. R. Muehter. 2016. Steller's Jay (Cyanocitta stelleri), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/stejay
Corvidae	Cyanocitta stelleri	Steller's Jay	Coniferous forest	Closed	120	ML56865	Keller, Geoffrey A.	Arizona, USA	1991		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Walker, L. E., P. Pyle, M. A. Patten, E. Greene, W. Davison and V. R. Muehter. 2016. Steller's Jay (Cyanocitta stelleri), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/stejay
Corvidae	Dendrocitta formosae	Gray Treepie	Broadleaf secondary evergreen forest	Closed	103.75	ML13496	Severinghaus, Sheldon R.	Pingtung, Taiwan	1966		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) King, B.F. & E.C. Dickinson. 1975. The field guide to the birds of south-east Asia. Houghton Mifflin Company, Boston, MA.
Corvidae	Dendrocitta formosae	Gray Treepie	Broadleaf secondary evergreen forest	Closed	103.75	ML13497	Severinghaus, Sheldon R.	Pingtung, Taiwan	1966		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) King, B.F. & E.C. Dickinson. 1975. The field guide to the birds of south-east Asia. Houghton Mifflin Company, Boston, MA.
Corvidae	Dendrocitta formosae	Gray Treepie	Broadleaf secondary evergreen forest	Closed	103.75	ML111648	Macaulay, Linda R.	Nepal	1999		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) King, B.F. & E.C. Dickinson. 1975. The field guide to the birds of south-east Asia. Houghton Mifflin Company, Boston, MA.
Corvidae	Gymnorhinus cyanocephalus	Pinyon Jay	Pinyon/ juniper forests	Closed	105	ML21254	Zimmerman, Dale A.	New Mexico, USA	1980		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Balda, R. P. 2002. Pinyon Jay (Gymnorhinus cyanocephalus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/pinjay
Corvidae	Gymnorhinus cyanocephalus	Pinyon Jay	Pinyon/ juniper forests	Closed	105	ML47589	Herr, David S.	California, USA	1990		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Balda, R. P. 2002. Pinyon Jay (Gymnorhinus cyanocephalus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/pinjay
Corvidae	Gymnorhinus cyanocephalus	Pinyon Jay	Pinyon/ juniper forests	Closed	105	ML147569	Budney, Gregory F.	Nevada, USA	1991		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Balda, R. P. 2002. Pinyon Jay (Gymnorhinus cyanocephalus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/pinjay
Corvidae	Nucifraga caryocatactes	Eurasian (spotted) Nutcracker	Coniferous forest	Closed	120	ML53560	Connop, Scott	Nepal	1990		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flint, V.E., Boehme, R.L., Kostin, Y.V., Kuznetsov, A.A. 1984. A Field Guide to Birds of the USSR. Princeton University Press. Princeton, NJ. 3) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Nucifraga caryocatactes	Eurasian (spotted) Nutcracker	Coniferous forest	Closed	120	ML69054	Connop, Scott	Wangdue Phodrang, Bhutan	1994		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flint, V.E., Boehme, R.L., Kostin, Y.V., Kuznetsov, A.A. 1984. A Field Guide to Birds of the USSR. Princeton University Press. Princeton, NJ. 3) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Nucifraga caryocatactes	Eurasian (spotted) Nutcracker	Coniferous forest	Closed	120	ML145774	Robbins, Mark B.	Wangdue Phodrang, Bhutan	2003		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flint, V.E., Boehme, R.L., Kostin, Y.V., Kuznetsov, A.A. 1984. A Field Guide to Birds of the USSR. Princeton University Press. Princeton, NJ. 3) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Nucifraga columbiana	Clark's Nutcracker	Coniferous forest	Closed	130	ML50141	Keller, Geoffrey A.	Oregon, USA	1990		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Tomback, D. F. 1998. Clark's Nutcracker (Nucifraga columbiana), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/clanut
Corvidae	Nucifraga columbiana	Clark's Nutcracker	Coniferous forest	Closed	130	ML111175	Sander, Thomas G.	Oregon, USA	1991		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Tomback, D. F. 1998. Clark's Nutcracker (Nucifraga columbiana), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/clanut
Corvidae	Nucifraga columbiana	Clark's Nutcracker	Coniferous forest	Closed	130	ML120231	Keller, Geoffrey A.	California, USA	2002		1) Dunning, J.B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Tomback, D. F. 1998. Clark's Nutcracker (Nucifraga columbiana), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/clanut

Corvidae	Platysmurus leucopterus	Black Magpie	Rainforest	Closed	180	ML33178	van den Berg, Arnoud B.	Pahang, Malaysia	1984		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY. 3) Robson, C. 2000. A Guide to the Birds of Southeast Asia. Princeton University Press. Princeton, NJ. 4) Wells, D. R. 2007. The Birds of the Thai-Malay Penninsula. Volume 2. Christopher Helm. London, UK.
Corvidae	Platysmurus leucopterus	Black Magpie	Rainforest	Closed	180	ML36556	van den Berg, Arnoud B.	Pahang, Malaysia	1985		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY. 3) Robson, C. 2000. A Guide to the Birds of Southeast Asia. Princeton University Press. Princeton, NJ. 4) Wells, D. R. 2007. The Birds of the Thai-Malay Penninsula. Volume 2. Christopher Helm. London, UK.
Corvidae	Platysmurus leucopterus	Black Magpie	Rainforest	Closed	180	ML36680	van den Berg, Arnoud B.	Negeri Sembilan, Malaysia	1985		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY. 3) Robson, C. 2000. A Guide to the Birds of Southeast Asia. Princeton University Press. Princeton, NJ. 4) Wells, D. R. 2007. The Birds of the Thai-Malay Penninsula. Volume 2. Christopher Helm. London, UK.
Corvidae	Platysmurus leucopterus	Black Magpie	Rainforest	Closed	180	ML76932	Marantz, Curtis A.	Malaysia	1993		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY. 3) Robson, C. 2000. A Guide to the Birds of Southeast Asia. Princeton University Press. Princeton, NJ. 4) Wells, D. R. 2007. The Birds of the Thai-Malay Penninsula. Volume 2. Christopher Helm. London, UK.
Corvidae	Pyrrhocorax pyrrhocorax	Red-billed Chough	Rocky outcrops	Open	137.5	ML58083	Coopmans, Paul	Spain	1992		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flint, V.E., Boehme, R.L., Kostin, Y.V., Kuznetsov, A.A. 1984. A Field Guide to Birds of the USSR. Princeton University Press. Princeton, NJ. 3) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Pyrrhocorax pyrrhocorax	Red-billed Chough	Rocky outcrops	Open	137.5	ML60495	Carey, Geoff J.	Qinghai, China	1997		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flint, V.E., Boehme, R.L., Kostin, Y.V., Kuznetsov, A.A. 1984. A Field Guide to Birds of the USSR. Princeton University Press. Princeton, NJ. 3) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Pyrrhocorax pyrrhocorax	Red-billed Chough	Rocky outcrops	Open	137.5	ML60497	Carey, Geoff J.	Qinghai, China	1997		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flint, V.E., Boehme, R.L., Kostin, Y.V., Kuznetsov, A.A. 1984. A Field Guide to Birds of the USSR. Princeton University Press. Princeton, NJ. 3) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Pyrrhocorax pyrrhocorax	Red-billed Chough	Rocky outcrops	Open	137.5	ML96251	Macaulay, Linda R.	Morocco	1995		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flint, V.E., Boehme, R.L., Kostin, Y.V., Kuznetsov, A.A. 1984. A Field Guide to Birds of the USSR. Princeton University Press. Princeton, NJ. 3) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Urocissa erythrorhyncha	Red-billed Blue Magpie	Mountainous jungle	Closed	214	ML23508	King, Ben F.	Mandalay, Myanmar	1979		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Urocissa erythrorhyncha	Red-billed Blue Magpie	Mountainous jungle	Closed	214	ML41542	King, Ben F.	Madhyamanchal, Nepal	1982		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Urocissa erythrorhyncha	Red-billed Blue Magpie	Mountainous jungle	Closed	214	ML175651	King, Ben F.	Sichaun, China	1982		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press. Ithaca, NY.
Corvidae	Zavattariornis stresemanni	Stresemann's Bush Crow	Thorn-acacia forest	Closed	130	ML100202	Macaulay, Linda R.	Ethiopia	1996		1) Collar, N. 2005. Handbook of the birds of the world. Volume 10. Lynx Edicions. Barcelona, Spain. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press . Ithaca, NY.
Corvidae	Zavattariornis stresemanni	Stresemann's Bush Crow	Thorn-acacia forest	Closed	130	ML96331	Macaulay, Linda R.	Ethiopia	1996		1) Collar, N. 2005. Handbook of the birds of the world. Volume 10. Lynx Edicions. Barcelona, Spain. 2) Goodwin, D. 1976. Crows of the World. Cornell University Press . Ithaca, NY.
Icteridae	Agelaioides badius	Baywinged Cowbird	Semi-open scrub	Closed	45	ML20180	Belton, William	Rio Grande do Sul, Brazil	1977		Lowther, P. E. 2013. Bay-winged Cowbird (Agelaioides badius), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=34598
Icteridae	Agelaioides badius	Baywinged Cowbird	Semi-open scrub	Closed	45	ML20183	Belton, William	Rio Grande do Sul, Brazil	1978		Lowther, P. E. 2013. Bay-winged Cowbird (Agelaioides badius), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=34598
Icteridae	Agelaioides badius	Baywinged Cowbird	Semi-open scrub	Closed	45	ML80792	Parker, III, Theodore A.	Santa Cruz, Bolivia	1991		Lowther, P. E. 2013. Bay-winged Cowbird (Agelaioides badius), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=34598

Family	Species	Common Name	Habitat		Mass	Catalog	Recordist	Location	Year		Reference
Icteridae	Agelaioides badius	Baywinged Cowbird	Semi-open scrub	Closed	45	ML132382	Andersen, Michael J.	Entre Rios, Argentina	2006		Lowther, P. E. 2013. Bay-winged Cowbird (Agelaioides badius), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=34598
Icteridae	Agelaioides badius	Baywinged Cowbird	Semi-open scrub	Closed	45	ML143446	Zyskowski, Krzysztof	Presidente Hayes, Paraguay	1995		Lowther, P. E. 2013. Bay-winged Cowbird (Agelaioides badius), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=34598
Icteridae	Agelaius humeralis	Tawny-shouldered Blackbird	Semi-open forest edge	Closed	33.1	ML34502	Morton, Eugene S.	Matanzas, Cuba	1978		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Tawny-shouldered Blackbird (Agelaius humeralis). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=666476
Icteridae	Agelaius humeralis	Tawny-shouldered Blackbird	Semi-open forest edge	Closed	33.1	ML34504	Morton, Eugene S.	Matanzas, Cuba	1978		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Tawny-shouldered Blackbird (Agelaius humeralis). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=666476
Icteridae	Agelaius phoeniceus	Red-winged Blackbird	Marsh	Open	57.1	ML94447	Hershberger, Wilbur L.	Maryland, USA	1998		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Yasukawa, K. and W. A. Searcy. 1995. Red-winged Blackbird (Agelaius phoeniceus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/rewbla
Icteridae	Agelaius phoeniceus	Red-winged Blackbird	Marsh	Open	58.1	ML168307	Hershberger, Wilbur L.	West Virginia, USA	2011		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Yasukawa, K. and W. A. Searcy. 1995. Red-winged Blackbird (Agelaius phoeniceus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/rewbla
Icteridae	Alegaius tricolor	Tricolored Blackbird	Marsh	Open	55	ML22900	Fish, William R.	California, USA	1951		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meese, R. J., E. C. Beedy and W. J. Hamilton, III. 2014. Tricolored Blackbird (Agelaius tricolor), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/tribla
Icteridae	Alegaius tricolor	Tricolored Blackbird	Marsh	Open	55	ML56922	Keller, Geoffrey A.	California, USA	1991		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meese, R. J., E. C. Beedy and W. J. Hamilton, III. 2014. Tricolored Blackbird (Agelaius tricolor), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/tribla
Icteridae	Amblycercus holosericeus	Yellow-billed Cacique	Second growth thickets	Closed	65	ML21646	Parker, III, Theodore A.	Cajamarca, Peru	1980		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Amblycercus holosericeus	Yellow-billed Cacique	Second growth thickets	Closed	65	ML57013	Robbins, Mark B.	Loja, Ecuador	1992		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Amblycercus holosericeus	Yellow-billed Cacique	Second growth thickets	Closed	65	ML60755	Schwartz, Paul A.	Tachira, Venezuela	1963		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Amblycercus holosericeus	Yellow-billed Cacique	Second growth thickets	Closed	65	ML144879	Robbins, Mark B.	Campeche, Mexico	1998		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Amblycercus holosericeus	Yellow-billed Cacique	Second growth thickets	Closed	65	ML173906	Robbins, Mark B.	Ayacucho, Peru	2012		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Cacicus cela	Yellow-rumped Cacique	Varied forest	Closed	94	ML60747	Schwartz, Paul A.	Zulia, Venezuela	1970		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jaramillo, A. and P. Burke. 1999. New World Blackbirds: The Icterids. Princeton University Press. Princeton, NJ. 3) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Cacicus cela	Yellow-rumped Cacique	Varied forest	Closed	94	ML75245	Marantz, Curtis A.	Madre de Dios, Peru	1994		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jaramillo, A. and P. Burke. 1999. New World Blackbirds: The Icterids. Princeton University Press. Princeton, NJ. 3) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Cacicus cela	Yellow-rumped Cacique	Varied forest	Closed	94	ML127501	Marantz, Curtis A.	Amazonas, Brazil	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jaramillo, A. and P. Burke. 1999. New World Blackbirds: The Icterids. Princeton University Press. Princeton, NJ. 3) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.

Family	Species	Common Name	Habitat	Nest	Mass	ML#	Recordist	Location	Year	References
Icteridae	Cacicus cela	Yellow-rumped Cacique	Varied forest	Closed	94	ML138749	Seeholzer, Glenn F.	Ucayali, Peru	2008	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jaramillo, A. and P. Burke. 1999. New World Blackbirds: The Icterids. Princeton University Press. Princeton, NJ. 3) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Chrysomus ruficapillus	Chestnut-capped Blackbird	Marsh	Open	44	ML22513	Kane, Stephanie	Minas Gerais, Brazil	1980	1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Chestnut-capped Blackbird (Chrysomus ruficapillus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=671756
Icteridae	Chrysomus ruficapillus	Chestnut-capped Blackbird	Marsh	Open	44	ML110774	Hennessey, A. Bennett	Santa Cruz, Bolivia	2001	1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Chestnut-capped Blackbird (Chrysomus ruficapillus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=671756
Icteridae	Chrysomus ruficapillus	Chestnut-capped Blackbird	Marsh	Open	44	ML110775	Hennessey, A. Bennett	Santa Cruz, Bolivia	2001	1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Chestnut-capped Blackbird (Chrysomus ruficapillus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=671756
Icteridae	Chrysomus ruficapillus	Chestnut-capped Blackbird	Marsh	Open	44	ML132377	Andersen, Michael J.	Entre Rios, Argentina	2006	1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Chestnut-capped Blackbird (Chrysomus ruficapillus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=671756
Icteridae	Chrysomus ruficapillus	Chestnut-capped Blackbird	Marsh	Open	44	ML177473	Areta, Juan I.	Entre Rios, Argentina	2006	1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Chestnut-capped Blackbird (Chrysomus ruficapillus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=671756
Icteridae	Curaeus curaeus	Austral Blackbird	Semi-open forest edge	Closed	90	ML42276	Parker, III, Theodore A.	Region Metropolitana de Santiago, Chile	1988	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Curaeus curaeus	Austral Blackbird	Semi-open forest edge	Closed	91	ML135820	Areta, Juan I.	Neuquen, Argentina	2005	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Gnorimopsar chopi	Chopi Blackbird	Marsh	Open	79.5	ML17723	Parker, III, Theodore A.	Mato Grosso, Brazil	1977	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jaramillo, A. and P. Burke. 1999. New World Blackbirds: The Icterids. Princeton University Press. Princeton, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Gnorimopsar chopi	Chopi Blackbird	Marsh	Open	79.5	ML81512	Donahue, Paul K.	Mato Grosso, Brazil	1988	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Jaramillo, A. and P. Burke. 1999. New World Blackbirds: The Icterids. Princeton University Press. Princeton, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Gymnomystax mexicanus	Oriole Blackbird	Marsh	Open	93	ML45571	Parker, III, Theodore A.	Loreto, Peru	1987	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Gymnomystax mexicanus	Oriole Blackbird	Marsh	Open	93	ML61040	Schwartz, Paul A.	Miranda, Venezuela	1961	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Icterus bullockii	Bullock's Oriole	Riparian	Closed	37.7	ML22790	Fish, William R.	California, USA	1953	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flood, N. J., C. L. Schlueter, M. W. Reudink, P. Pyle, M. A. Patten, J. D. Rising and P. L. Williams. 2016. Bullock's Oriole (Icterus bullockii), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bulori
Icteridae	Icterus bullockii	Bullock's Oriole	Riparian	Closed	37.7	ML50152	Keller, Geoffrey A.	California, USA	1990	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flood, N. J., C. L. Schlueter, M. W. Reudink, P. Pyle, M. A. Patten, J. D. Rising and P. L. Williams. 2016. Bullock's Oriole (Icterus bullockii), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bulori
Icteridae	Icterus bullockii	Bullock's Oriole	Riparian	Closed	37.7	ML50153	Keller, Geoffrey A.	California, USA	1990	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flood, N. J., C. L. Schlueter, M. W. Reudink, P. Pyle, M. A. Patten, J. D. Rising and P. L. Williams. 2016. Bullock's Oriole (Icterus bullockii), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bulori

Family	Species	Common Name	Habitat		Mass	Catalog	Recordist	Location	Year		References
Icteridae	Icterus croconotus	Orange-backed Troupial	Second growth rainforest	Closed	48	ML28554	van den Berg, Arnoud B.	Napo, Ecuador		1981	1) Fraga, R. 2016. Orange-backed Troupial (Icterus croconotus). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona, Spain. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Icteridae	Icterus croconotus	Orange-backed Troupial	Second growth rainforest	Closed	48	ML43152	Parker, III, Theodore A.	Mato Grosso, Brazil	1985		1) Fraga, R. 2016. Orange-backed Troupial (Icterus croconotus). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.). Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona, Spain. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Icteridae	Icterus cucullatus	Hooded Oriole	Riparian	Closed	24.3	ML12448	Davis, L. Irby	Baja California Sur, Mexico	1958		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pleasants, B. Y. and D. J. Albano. 2001. Hooded Oriole (Icterus cucullatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/hooori
Icteridae	Icterus cucullatus	Hooded Oriole	Riparian	Closed	24.3	ML12449	Allen, Arthur A.	California, USA	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pleasants, B. Y. and D. J. Albano. 2001. Hooded Oriole (Icterus cucullatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/hooori
Icteridae	Icterus cucullatus	Hooded Oriole	Riparian	Closed	24.3	ML12469	Allen, Arthur A.	California, USA	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pleasants, B. Y. and D. J. Albano. 2001. Hooded Oriole (Icterus cucullatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/hooori
Icteridae	Icterus cucullatus	Hooded Oriole	Riparian	Closed	24.3	ML12470	Allen, Arthur A.	California, USA	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pleasants, B. Y. and D. J. Albano. 2001. Hooded Oriole (Icterus cucullatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/hooori
Icteridae	Icterus cucullatus	Hooded Oriole	Riparian	Closed	24.3	ML45173	Keller, Geoffrey A.	Arizona, USA	1987		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pleasants, B. Y. and D. J. Albano. 2001. Hooded Oriole (Icterus cucullatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/hooori
Icteridae	Icterus cucullatus	Hooded Oriole	Riparian	Closed	24.3	ML61616	Gunn, William W.H.	Arizona, USA	1979		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Pleasants, B. Y. and D. J. Albano. 2001. Hooded Oriole (Icterus cucullatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/hooori
Icteridae	Icterus galbula	Baltimore Oriole	Open forest	Closed	34	ML12493	Stein, Robert C.	New York, USA	1964		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Rising, J. D. and N. J. Flood. 1998. Baltimore Oriole (Icterus galbula), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/balori
Icteridae	Icterus galbula	Baltimore Oriole	Open forest	Closed	35	ML125217	Andersen, Michael J.	New York, USA	2005		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Rising, J. D. and N. J. Flood. 1998. Baltimore Oriole (Icterus galbula), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/balori
Icteridae	Icterus galbula	Baltimore Oriole	Open forest	Closed	36	ML135768	Little, Randolph S.	New Jersey, USA	2003		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Rising, J. D. and N. J. Flood. 1998. Baltimore Oriole (Icterus galbula), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/balori
Icteridae	Icterus icterus	Venezuelan Troupial	Semi-open forest edge	Closed	72.35	ML61021	Schwartz, Paul A.	Guarico, Venezuela	1961		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Icterus icterus	Venezuelan Troupial	Semi-open forest edge	Closed	72.35	ML163498	Wells, Jeffrey V.	Aruba	1998		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Icterus icterus	Venezuelan Troupial	Semi-open forest edge	Closed	72.35	ML177311	Areta, Juan I.	Lara, Venezuela	2005		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.

Family	Species	Common Name	Habitat	Type	Value	Catalog	Recordist	Location	Year	Notes	References
Icteridae	Icterus mesomelas	Yellow-tailed Oriole	Dense thickets	Closed	70	ML45866	Plymire, Margery R.	Belize, Belize			1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus mesomelas	Yellow-tailed Oriole	Dense thickets	Closed	70	ML60779	Schwartz, Paul A.	Zulia, Venezuela	1970		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus nigrogularis	Yellow Oriole	Open woodland/gardens	Urban	40.5	ML84923	Finch, Davis W.	Upper Takutu-Upper Essequibo, Guyana	1995	Riparian, river	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Icterus nigrogularis	Yellow Oriole	Open woodland/gardens	Urban	40.5	ML163484	Wells, Jeffrey V.	Aruba	1997	Mangrove	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Icterus nigrogularis	Yellow Oriole	Open woodland/gardens	Urban	40.5	ML171338	McGowan, Jay W.	Guarico, Venezuela	2012	No habitat information; Forest based on lat/long	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Icterus nigrogularis	Yellow Oriole	Open woodland/gardens	Urban	40.5	ML61006	Schwartz, Paul A.	Distrito Capital, Venezuela	1960	No habitat information; Forest based on lat/long	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Icterus parisorum	Scott's Oriole	Open woodland	Closed	35.7	ML61660	Gunn, William W.H.	Arizona, USA	1979		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flood, N. J. 2002. Scott's Oriole (Icterus parisorum), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/scoori
Icteridae	Icterus parisorum	Scott's Oriole	Open woodland	Closed	35.7	ML61663	Gunn, William W.H.	Arizona, USA	1980		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flood, N. J. 2002. Scott's Oriole (Icterus parisorum), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/scoori
Icteridae	Icterus parisorum	Scott's Oriole	Open woodland	Closed	35.7	ML74286	Macaulay, Linda R.	Baja California Sur, Mexico	1997		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Flood, N. J. 2002. Scott's Oriole (Icterus parisorum), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/scoori
Icteridae	Icterus pectoralis	Spot-breasted Oriole	Open woodland	Closed	50	ML12551	Davis, L. Irby	Chiapas, Mexico	1961		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus pectoralis	Spot-breasted Oriole	Open woodland	Closed	50	ML105972	Hanks, Cullen K.	Sonsonate, El Salvador	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus pustulatus	Streak-backed Oriole	Open woodland	Closed	45	ML12554	Davis, L. Irby	Morelos, Mexico	1957		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus pustulatus	Streak-backed Oriole	Open woodland	Closed	45	ML20710	Thurber, Walter A.	La Libertad, El Salvador	1979		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus pustulatus	Streak-backed Oriole	Open woodland	Closed	45	ML109157	Keller, Geoffrey A.	Sonora, Mexico	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus pustulatus	Streak-backed Oriole	Open woodland	Closed	45	ML165036	Ross, Jr., David L.	Guanacaste, Costa Rica	1996		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus pustulatus	Streak-backed Oriole	Open woodland	Closed	45	ML165062	Ross, Jr., David L.	Guanacaste, Costa Rica	1996		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus spurius	Orchard Oriole	Second growth scrub/gardens	Urban	20	ML25626	Parker, III, Theodore A.	Panama, Panama	1982	Forest; thicket/brush	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus spurius	Orchard Oriole	Second growth scrub/gardens	Urban	20	ML40813	Budney, Gregory F.	Maryland, USA	1988	Pond; Blackwater National Wildlife Refuge	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Icterus spurius	Orchard Oriole	Second growth scrub/gardens	Urban	20	ML105529	Keller, Geoffrey A.	Texas, USA	1995	Riparian; Big Bend National Park	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.

Icteridae	Icterus spurius	Orchard Oriole	Second growth scrub/gardens	Urban	20	ML176197	Keller, Geoffrey A.	Indiana, USA	2009	No habitat information; Forest based on lat/long	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Lampropsar tanagrinus	Velvet-fronted Grackle	Rainforest edge	Closed	57.3	ML29251	Parker, III, Theodore A.	Loreto, Peru	1982		1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3. Velvet-fronted Grackle (Lampropsar tanagrinus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=670476
Icteridae	Lampropsar tanagrinus	Velvet-fronted Grackle	Rainforest edge	Closed	57.3	ML31718	Parker, III, Theodore A.	Loreto, Peru	1983		1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3. Velvet-fronted Grackle (Lampropsar tanagrinus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=670476
Icteridae	Lampropsar tanagrinus	Velvet-fronted Grackle	Rainforest edge	Closed	57.3	ML101777	Hennessey, A. Bennett	El Beni, Bolivia	1998		1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3. Velvet-fronted Grackle (Lampropsar tanagrinus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=670476
Icteridae	Macroagelaius imthurni	Golden-tufted Grackle	Slopes of tepuis/rocky outcrops	Open	79.5	ML134910	O'Shea, Brian J.	Guyana	2001		1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3. Golden-tufted Grackle (Macroagelaius imthurni). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=669996
Icteridae	Macroagelaius imthurni	Golden-tufted Grackle	Slopes of tepuis/rocky outcrops	Open	79.5	ML145257	Robbins, Mark B.	Guyana	2001		1) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3. Golden-tufted Grackle (Macroagelaius imthurni). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=669996
Icteridae	Molothrus ater	Brown-headed Cowbird	Riparian	Closed	40.45	ML12579	Stein, Robert C.	British Columbia, Canada	1958		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Lowther, P. E. 1993. Brown-headed Cowbird (Molothrus ater), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bnhcow
Icteridae	Molothrus ater	Brown-headed Cowbird	Riparian	Closed	40.45	ML12580	Allen, Arthur A.	Texas, USA	1958		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Lowther, P. E. 1993. Brown-headed Cowbird (Molothrus ater), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bnhcow
Icteridae	Molothrus ater	Brown-headed Cowbird	Riparian	Closed	40.45	ML126422	Sander, Thomas G.	California, USA	1988		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Lowther, P. E. 1993. Brown-headed Cowbird (Molothrus ater), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/bnhcow
Icteridae	Molothrus oryzivorus	Giant Cowbird	Open clearings	Open	170	ML52902	Hilty, Steven L.	Venezuela	1990		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY. 2) Lowther, P. E. 2010. Giant Cowbird (Molothrus oryzivorus), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=34934
Icteridae	Molothrus oryzivorus	Giant Cowbird	Open clearings	Open	170	ML104270	Budney, Gregory F.	Potaro-Siparuni, Guyana	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY. 2) Lowther, P. E. 2010. Giant Cowbird (Molothrus oryzivorus), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=34934

Family	Species	Common name	Habitat	Open/Closed	Mass	ML #	Recordist	Location	Year	Notes	References
Icteridae	Oreopsar bolivianus	Bolivian Blackbird	Scrub	Open	70	ML132510	Hosner, Peter A.	Cochabamba, Bolivia	2006		1) Bolivian Blackbird (Oreopsar bolivianus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=672556 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Oreopsar bolivianus	Bolivian Blackbird	Scrub	Open	70	ML168169	Vidoz, Julian Quillen	Cochabamba, Bolivia	2010		1) Bolivian Blackbird (Oreopsar bolivianus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=672556 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Psarocolius angustifrons	Russet-backed Oropendola	Cloud rainforest	Closed	222.5	ML12600	Schwartz, Paul A.	Aragua, Venezuela	1956		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Psarocolius angustifrons	Russet-backed Oropendola	Cloud rainforest	Closed	222.5	ML68244	Coopmans, Paul	Pichincha, Ecuador	1994		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Psarocolius angustifrons	Russet-backed Oropendola	Cloud rainforest	Closed	222.5	ML78336	Robbins, Mark B.	Pichincha, Ecuador	1991		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Psarocolius angustifrons	Russet-backed Oropendola	Cloud rainforest	Closed	222.5	ML80848	Alvarez, Mauricio	Cundinamarca, Colombia	1997		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Psarocolius angustifrons	Russet-backed Oropendola	Cloud rainforest	Closed	222.5	ML80911	Alvarez, Mauricio	Cundinamarca, Colombia	1997		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Psarocolius angustifrons	Russet-backed Oropendola	Cloud rainforest	Closed	222.5	ML165269	Sarver, Matthew J.	Antioquia, Colombia	2009		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Icteridae	Psarocolius atrovirens	Dusky-green Oropendola	Rainforest edge	Closed	152	ML17168	Parker, III, Theodore A.	La Paz, Bolivia	1979		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Psarocolius atrovirens	Dusky-green Oropendola	Rainforest edge	Closed	152	ML120853	Hennessey, A. Bennett	La Paz, Bolivia			1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Psarocolius atrovirens	Dusky-green Oropendola	Rainforest edge	Closed	152	ML120888	Hennessey, A. Bennett	La Paz, Bolivia			1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Psarocolius atrovirens	Dusky-green Oropendola	Rainforest edge	Closed	152	ML120959	Hennessey, A. Bennett	La Paz, Bolivia			1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Pseudoleistes guirahuro	Yellow-rumped Marshbird	Marsh	Open	98	ML39153	Parker, III, Theodore A.	Minas Gerais, Brazil	1986		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Pseudoleistes guirahuro	Yellow-rumped Marshbird	Marsh	Open	98	ML101404	Madroño, Alberto	Canindeyu, Paraguay	1995		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Pseudoleistes virescens	Brown-and-yellow Marshbird	Marsh	Open	76	ML20169	Belton, William	Rio Grande do Sul, Brazil	1973		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Pseudoleistes virescens	Brown-and-yellow Marshbird	Marsh	Open	76	ML179230	Depino, Emiliano A.	Buenos Aires, Argentina	2012		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Pseudoleistes virescens	Brown-and-yellow Marshbird	Marsh	Open	76	ML179234	Depino, Emiliano A.	Buenos Aires, Argentina	2012		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Quiscalus lugubris	Carib Grackle	Open woodland/Urban	Urban	64.5	ML12624	Worden, K. W.	Saint Vincent and the Grenadines	1965	No habitat information; no lat/long	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Icteridae	Quiscalus lugubris	Carib Grackle	Open woodland/Urban	Urban	64.5	ML60769	Schwartz, Paul A.	Aragua, Venezuela	1961	No habitat information; Urban based on lat/long information (40+ years since recording)	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Icteridae	Quiscalus major	Boat-tailed Grackle	Marsh	Open	158.6	ML12644	Little, Randolph S.	Florida, USA	1962		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Post, W., J. P. Poston and G. T. Bancroft. 2014. Boat-tailed Grackle (Quiscalus major), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/botgra

Family	Species	Common name	Habitat		Mass	Catalog	Recordist	Location	Year	Habitat notes	References
Icteridae	Quiscalus major	Boat-tailed Grackle	Marsh	Open	158.6	ML12648	Stein, Robert C.	Florida, USA	1963		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Post, W., J. P. Poston and G. T. Bancroft. 2014. Boat-tailed Grackle (Quiscalus major), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/botgra
Icteridae	Quiscalus major	Boat-tailed Grackle	Marsh	Open	158.6	ML12649	Stein, Robert C.	Florida, USA	1963		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Post, W., J. P. Poston and G. T. Bancroft. 2014. Boat-tailed Grackle (Quiscalus major), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/botgra
Icteridae	Quiscalus major	Boat-tailed Grackle	Marsh	Open	158.6	ML105348	Keller, Geoffrey A.	Florida, USA	1994		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Post, W., J. P. Poston and G. T. Bancroft. 2014. Boat-tailed Grackle (Quiscalus major), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/botgra
Icteridae	Quiscalus major	Boat-tailed Grackle	Marsh	Open	158.6	ML135404	Andersen, Michael J.	Florida, USA	2007		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Post, W., J. P. Poston and G. T. Bancroft. 2014. Boat-tailed Grackle (Quiscalus major), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/botgra
Icteridae	Quiscalus major	Boat-tailed Grackle	Marsh	Open	158.6	ML135406	Andersen, Michael J.	Florida, USA	2007		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Post, W., J. P. Poston and G. T. Bancroft. 2014. Boat-tailed Grackle (Quiscalus major), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/botgra
Icteridae	Quiscalus mexicanus	Great-tailed Grackle	Marsh/Urban	Urban	168.7	ML12636	Davis, L. Irby	Tabasco, Mexico	1958	Active agricultural	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Johnson, K. and B. D. Peer. 2001. Great-tailed Grackle (Quiscalus mexicanus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/grtgra 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Quiscalus mexicanus	Great-tailed Grackle	Marsh/Urban	Urban	168.7	ML115826	Macaulay, Linda R.	Texas, USA	2000	No habitat information; no lat/long	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Johnson, K. and B. D. Peer. 2001. Great-tailed Grackle (Quiscalus mexicanus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/grtgra 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Quiscalus mexicanus	Great-tailed Grackle	Marsh/Urban	Urban	168.7	ML45015	Keller, Geoffrey A.	Texas, USA	1986	Deciduous forest, riparian, river; thicket/brush	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Johnson, K. and B. D. Peer. 2001. Great-tailed Grackle (Quiscalus mexicanus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/grtgra 3) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Sturnella magna	Eastern Meadowlark	Meadow	Open	85	ML12699	Stein, Robert C.	Florida, USA	1963		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Sturnella magna	Eastern Meadowlark	Meadow	Open	85	ML105327	Keller, Geoffrey A.	Florida, USA	1994		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Sturnella magna	Eastern Meadowlark	Meadow	Open	85	ML105634	Keller, Geoffrey A.	Indiana, USA	1995		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Sturnella magna	Eastern Meadowlark	Meadow	Open	85	ML105637	Keller, Geoffrey A.	Indiana, USA	1995		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Icteridae	Xanthopsar flavus	Saffron-cowled Blackbird	Marsh	Open	50	ML20160	Belton, William	Rio Grande do Sul, Brazil	1971		1) Saffron-cowled Blackbird (Xanthopsar flavus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=672076 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Xanthopsar flavus	Saffron-cowled Blackbird	Marsh	Open	50	ML32164	Parker, III, Theodore A.	Rio Grande do Sul, Brazil	1982		1) Saffron-cowled Blackbird (Xanthopsar flavus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=672076 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.

Family	Species	Common name	Habitat		Mass	Catalog	Recordist	Location	Year		References
Icteridae	Xanthopsar flavus	Saffron-cowled Blackbird	Marsh	Open	50	ML132483	Andersen, Michael J.	Corrientes, Argentina	2006		1) Saffron-cowled Blackbird (Xanthopsar flavus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=672076 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Xanthopsar flavus	Saffron-cowled Blackbird	Marsh	Open	50	ML132890	Hosner, Peter A.	Corrientes, Argentina	2006		1) Saffron-cowled Blackbird (Xanthopsar flavus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=672076 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Icteridae	Xanthopsar flavus	Saffron-cowled Blackbird	Marsh	Open	50	ML178298	Areta, Juan I.	Rocha, Uruguay	2007		1) Saffron-cowled Blackbird (Xanthopsar flavus). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=672076 2) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Catharus dryas	Spotted Nightingale-Thrush	Cloud rainforest	Closed	21	ML66345	Schwartz, Paul A.	Tachira, Venezuela	1969		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Catharus dryas	Spotted Nightingale-Thrush	Cloud rainforest	Closed	21	ML80996	Ross, Jr., David L.	Pichincha, Ecuador	1992		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Catharus dryas	Spotted Nightingale-Thrush	Cloud rainforest	Closed	21	ML120876	Hennessey, A. Bennett	La Paz, Bolivia			1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Catharus fuscescens	Veery	Deciduous forest	Closed	32.4	ML27061	Plymire, Margery R.	Maine, USA	1981		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Bevier, L. R., A. F. Poole and W. Moskoff. 2005. Veery (Catharus fuscescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/veery
Turdidae	Catharus fuscescens	Veery	Deciduous forest	Closed	32.4	ML27069	Plymire, Margery R.	Maine, USA	1981		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Bevier, L. R., A. F. Poole and W. Moskoff. 2005. Veery (Catharus fuscescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/veery
Turdidae	Catharus fuscescens	Veery	Deciduous forest	Closed	32.4	ML135730	Heckscher, Christopher M.	Delaware, USA	2003		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Bevier, L. R., A. F. Poole and W. Moskoff. 2005. Veery (Catharus fuscescens), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/veery
Turdidae	Catharus gracilirostris	Black-billed Nightingale-Thrush	Second growth oak forest	Closed	21	ML28115	van den Berg, Arnoud B.	Costa Rica	1981		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Catharus gracilirostris	Black-billed Nightingale-Thrush	Second growth oak forest	Closed	21	ML74207	Ross, Jr., David L.	Costa Rica	1988		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Catharus gracilirostris	Black-billed Nightingale-Thrush	Second growth oak forest	Closed	21	ML165816	Ross, Jr., David L.	Cartago, Costa Rica	1996		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Catharus gracilirostris	Black-billed Nightingale-Thrush	Second growth oak forest	Closed	21	ML28188	van den Berg, Arnoud B.	Costa Rica	1981		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Catharus guttatus	Hermit Thrush	Mixed coniferous/deciduous forest	Closed	31.2	ML49714	Evans, William R.	New York, USA	1989		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Dellinger, R., P. B. Wood, P. W. Jones and T. M. Donovan. 2012. Hermit Thrush (Catharus guttatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/herthr
Turdidae	Catharus guttatus	Hermit Thrush	Mixed coniferous/deciduous forest	Closed	31.2	ML107506	Hershberger, Wilbur L.	West Virginia, USA	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Dellinger, R., P. B. Wood, P. W. Jones and T. M. Donovan. 2012. Hermit Thrush (Catharus guttatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/herthr
Turdidae	Catharus guttatus	Hermit Thrush	Mixed coniferous/deciduous forest	Closed	31.2	ML107510	Hershberger, Wilbur L.	West Virginia, USA	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Dellinger, R., P. B. Wood, P. W. Jones and T. M. Donovan. 2012. Hermit Thrush (Catharus guttatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/herthr

Turdidae	Catharus guttatus	Hermit Thrush	Mixed coniferous/deciduous forest	Closed	31.2	ML110376	Hershberger, Wilbur L.	West Virginia, USA	2001	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Dellinger, R., P. B. Wood, P. W. Jones and T. M. Donovan. 2012. Hermit Thrush (Catharus guttatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/herthr
Turdidae	Catharus guttatus	Hermit Thrush	Mixed coniferous/deciduous forest	Closed	31.2	ML126456	Sander, Thomas G.	California, USA	1988	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Dellinger, R., P. B. Wood, P. W. Jones and T. M. Donovan. 2012. Hermit Thrush (Catharus guttatus), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/herthr
Turdidae	Hylocichla mustelina	Wood Thrush	Moist thickets	Closed	48	ML11317	Allen, Arthur A.	New York, USA	1951	1) Austin, O.L. 1961. Birds of the World. Golden Press Inc., New York, NY. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY. 3) Evans, M., E. Gow, R. R. Roth, M. S. Johnson and T. J. Underwood. 2011. Wood Thrush (Hylocichla mustelina), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/woothr
Turdidae	Hylocichla mustelina	Wood Thrush	Moist thickets	Closed	48	ML22464	Davis, William E., Jr. E.	Massachusetts, USA		1) Austin, O.L. 1961. Birds of the World. Golden Press Inc., New York, NY. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY. 3) Evans, M., E. Gow, R. R. Roth, M. S. Johnson and T. J. Underwood. 2011. Wood Thrush (Hylocichla mustelina), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/woothr
Turdidae	Hylocichla mustelina	Wood Thrush	Moist thickets	Closed	48	ML26240	Little, Randolph S.	Ohio, USA	1975	1) Austin, O.L. 1961. Birds of the World. Golden Press Inc., New York, NY. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY. 3) Evans, M., E. Gow, R. R. Roth, M. S. Johnson and T. J. Underwood. 2011. Wood Thrush (Hylocichla mustelina), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/woothr
Turdidae	Hylocichla mustelina	Wood Thrush	Moist thickets	Closed	48	ML41325	Minis, Dolly	New Jersey, USA	1981	1) Austin, O.L. 1961. Birds of the World. Golden Press Inc., New York, NY. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY. 3) Evans, M., E. Gow, R. R. Roth, M. S. Johnson and T. J. Underwood. 2011. Wood Thrush (Hylocichla mustelina), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/woothr
Turdidae	Hylocichla mustelina	Wood Thrush	Moist thickets	Closed	48	ML85131	Hershberger, Wilbur L.	Maryland, USA	1997	1) Austin, O.L. 1961. Birds of the World. Golden Press Inc., New York, NY. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY. 3) Evans, M., E. Gow, R. R. Roth, M. S. Johnson and T. J. Underwood. 2011. Wood Thrush (Hylocichla mustelina), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/woothr
Turdidae	Myadestes ralloides	Andean Solitaire	Second growth rainforest	Closed	27.7	ML66330	Schwartz, Paul A.	Aragua, Venezuela	1965	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Andean Solitaire (Myadestes ralloides). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=545996 3) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Myadestes ralloides	Andean Solitaire	Second growth rainforest	Closed	27.7	ML87683	Hennessey, A. Bennett	La Paz, Bolivia	1997	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Andean Solitaire (Myadestes ralloides). 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=545996 3) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Sialia currucoides	Mountain Bluebird	Meadow	Open	29.6	ML47578	Herr, David S.	California, USA	1990	Power, H.W. and M. P. Lombardo. 1996. Mountain Bluebird (Sialia currucoides), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/moublu
Turdidae	Sialia currucoides	Mountain Bluebird	Meadow	Open	29.6	ML50745	Little, Randolph S.	California, USA	1990	Power, H.W. and M. P. Lombardo. 1996. Mountain Bluebird (Sialia currucoides), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/moublu
Turdidae	Sialia currucoides	Mountain Bluebird	Meadow	Open	29.6	ML56947	Keller, Geoffrey A.	California, USA	1991	Power, H.W. and M. P. Lombardo. 1996. Mountain Bluebird (Sialia currucoides), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/moublu
Turdidae	Sialia mexicana	Western Bluebird	Open woodland	Closed	28.44	ML13551	Stein, Robert C.	Oregon, USA	1961	Guinan, J.A., P.A. Gowaty and E.K. Eltzroth. 2008. Western Bluebird (Sialia mexicana), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/wesblu

Family	Species	Common name	Habitat		Value	Catalog	Recordist	Location	Year		Reference
Turdidae	Sialia mexicana	Western Bluebird	Open woodland	Closed	28.44	ML42246	Keller, Geoffrey A.	California, USA	1988		Guinan, J.A., P.A. Gowaty and E.K. Eltzroth. 2008. Western Bluebird (Sialia mexicana), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/wesblu
Turdidae	Sialia mexicana	Western Bluebird	Open woodland	Closed	28.44	ML57539	Gunn, William W.H.	Arizona, USA	1979		Guinan, J.A., P.A. Gowaty and E.K. Eltzroth. 2008. Western Bluebird (Sialia mexicana), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/wesblu
Turdidae	Sialia sialis	Eastern Bluebird	Open woodland	Closed	29.5	ML13553	Allen, Arthur A.	Ohio, USA	1954		Gowaty, P.A. and J.H. Plissner. 2015. Eastern Bluebird (Sialia sialis), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/easblu
Turdidae	Sialia sialis	Eastern Bluebird	Open woodland	Closed	29.5	ML13561	Little, Randolph S.	Michigan, USA	1964		Gowaty, P.A. and J.H. Plissner. 2015. Eastern Bluebird (Sialia sialis), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/easblu
Turdidae	Sialia sialis	Eastern Bluebird	Open woodland	Closed	29.5	ML44105	Gunn, William W.H.	Ontario, Canada	1952		Gowaty, P.A. and J.H. Plissner. 2015. Eastern Bluebird (Sialia sialis), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/easblu
Turdidae	Turdus albicollis	White-necked Thrush	Second growth rainforest	Closed	53.75	ML32437	Bierregaard, Richard O.	Amazonas, Brazil	1984		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus albicollis	White-necked Thrush	Second growth rainforest	Closed	53.75	ML113103	Marantz, Curtis A.	Para, Brazil	1998		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus albicollis	White-necked Thrush	Second growth rainforest	Closed	53.75	ML117192	Marantz, Curtis A.	Amazonas, Brazil	1997		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus albicollis	White-necked Thrush	Second growth rainforest	Closed	53.75	ML120877	Hennessey, A. Bennett	La Paz, Bolivia			1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus albicollis	White-necked Thrush	Second growth rainforest	Closed	53.75	ML127550	Marantz, Curtis A.	Amazonas, Brazil	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus albicollis	White-necked Thrush	Second growth rainforest	Closed	53.75	ML135028	O'Shea, Brian J.	Pando, Bolivia	2002		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus albicollis	White-necked Thrush	Second growth rainforest	Closed	53.75	ML139260	Macaulay, Linda R.	Argentina	2004		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus assimilis	White-throated Thrush	Open rainforest	Closed	72	ML13592	Davis, L. Irby	Morelos, Mexico	1957		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus assimilis	White-throated Thrush	Open rainforest	Closed	72	ML39270	Parker, III, Theodore A.	Costa Rica	1983		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus assimilis	White-throated Thrush	Open rainforest	Closed	72	ML71845	Parker, III, Theodore A.	Costa Rica	1992		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus assimilis	White-throated Thrush	Open rainforest	Closed	72	ML71847	Parker, III, Theodore A.	Costa Rica	1992		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus assimilis	White-throated Thrush	Open rainforest	Closed	72	ML72800	Parker, III, Theodore A.	Costa Rica	1991		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML13721	Snow, David W.	Trinidad and Tobago	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.

Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML13722	Ward, Rodman	Espirito Santo, Brazil	1962		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML48309	Isler, Phyllis R.	Espirito Santo, Brazil	1988		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML66280	Schwartz, Paul A.	Distrito Capital, Venezuela	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML66281	Schwartz, Paul A.	Distrito Capital, Venezuela	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML66295	Schwartz, Paul A.	Aragua, Venezuela	1968		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML70005	Parker, III, Theodore A.	Upper Takutu-Upper Essequibo, Guyana	1993		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus fumigatus	Cocoa Thrush	Varied forest	Closed	69.75	ML113365	Marantz, Curtis A.	Espirito Santo, Brazil	1999		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus fuscater	Great Thrush	Semi-open forest edge	Closed	141	ML35910	Schulenberg, Thomas S.	Pasco, Peru	1982		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus fuscater	Great Thrush	Semi-open forest edge	Closed	142	ML69615	Schwartz, Paul A.	Tachira, Venezuela	1963		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus fuscater	Great Thrush	Semi-open forest edge	Closed	143	ML86026	Wall, John W.	Ecuador	1992		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus fuscater	Great Thrush	Semi-open forest edge	Closed	144	ML135311	O'Shea, Brian J.	Cuzco, Peru	2001		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus fuscater	Great Thrush	Semi-open forest edge	Closed	145	ML167236	Sarver, Matthew J.	Colombia, Magdalena	2012		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ. 3) Ridgely, R. S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus grayi	Clay-colored Thrush	Varied/Urban	Urban	76	ML13735	Davis, L. Irby	Chiapas, Mexico	1957	Cloudforest	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2. Clay-colored Thrush (Turdus grayi),. 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell. edu/portal/species/overview?p_p_spp=550476 3. Howell, S.N.G. and Webb, S. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford & New York: Oxford University Press. ISBN 0-19-854012-4.

Family	Species	Common name	Habitat	Type	#	ML #	Recorder	Location	Year	Habitat detail	References
Turdidae	Turdus grayi	Clay-colored Thrush	Varied/Urban	Urban	76	ML13754	Morton, Eugene S.	Panama, Panama	1966	Forest edge	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2. Clay-colored Thrush (Turdus grayi),. 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=550476 3. Howell, S.N.G. and Webb, S. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford & New York: Oxford University Press. ISBN 0-19-854012-4.
Turdidae	Turdus grayi	Clay-colored Thrush	Varied/Urban	Urban	76	ML13761	Thurber, Walter A.	Alta Verapaz, Guatemala	1972	Forest	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2. Clay-colored Thrush (Turdus grayi),. 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=550476 3. Howell, S.N.G. and Webb, S. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford & New York: Oxford University Press. ISBN 0-19-854012-4.
Turdidae	Turdus grayi	Clay-colored Thrush	Varied/Urban	Urban	76	ML46283	Minis, Dolly	Puntarenas, Costa Rica	1988	Rainforest, evergreen forest	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2. Clay-colored Thrush (Turdus grayi),. 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=550476 3. Howell, S.N.G. and Webb, S. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford & New York: Oxford University Press. ISBN 0-19-854012-4.
Turdidae	Turdus grayi	Clay-colored Thrush	Varied/Urban	Urban	76	ML103190	Medler, Matthew D.	Guanacaste, Costa Rica	1999	No habitat information; Forest based on lat/long; Santa Rosa National Park	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2. Clay-colored Thrush (Turdus grayi),. 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=550476 3. Howell, S.N.G. and Webb, S. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford & New York: Oxford University Press. ISBN 0-19-854012-4.
Turdidae	Turdus grayi	Clay-colored Thrush	Varied/Urban	Urban	76	ML164035	Medler, Matthew D.	Guanacaste, Costa Rica	1999	No habitat information; no lat/long	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2. Clay-colored Thrush (Turdus grayi),. 2010. Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=550476 3. Howell, S.N.G. and Webb, S. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford & New York: Oxford University Press. ISBN 0-19-854012-4.
Turdidae	Turdus hauxwelli	Hauxwell's Thrush	Rainforest	Closed	69	ML29815	Parker, III, Theodore A.	Madre de Dios, Peru	1982		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Johnson, T. 2010. Hauxwell's Thrush (Turdus hauxwelli), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=549996
Turdidae	Turdus hauxwelli	Hauxwell's Thrush	Rainforest	Closed	69	ML136650	Barry, Jessie H.	Madre de Dios, Peru	2007		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Johnson, T. 2010. Hauxwell's Thrush (Turdus hauxwelli), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=549996
Turdidae	Turdus infuscatus	Black Thrush	Rainforest edge	Closed	76.25	ML95051	Hanks, Cullen K.	Chiapas, Mexico	1999		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Soberanes-González, C., C. Rodríguez-Flores & M.C. Arizmendi. 2010. Black Thrush (Turdus infuscatus), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=548716
Turdidae	Turdus infuscatus	Black Thrush	Rainforest edge	Closed	76.25	ML172608	de León Lux, Josué Odías	Suchitepéquez, Guatemala	2010		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Soberanes-González, C., C. Rodríguez-Flores & M.C. Arizmendi. 2010. Black Thrush (Turdus infuscatus), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=548716
Turdidae	Turdus lawrencii	Lawrence's Thrush	Rainforest	Closed	72.6	ML28539	van den Berg, Arnoud B.	Napo, Ecuador	1981		1) Dunning, John B. Jr. CRC Handbook of Avian Body Masses, CRC Press, 1992. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. (1978).
Turdidae	Turdus lawrencii	Lawrence's Thrush	Rainforest	Closed	72.6	ML110522	Hennessey, A. Bennett	La Paz, Bolivia	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus leucomelas	Pale-breasted Thrush	Varied forest	Closed	69.6	ML128081	Marantz, Curtis A.	Sergipe, Brazil	2001		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.

Family	Species	Common Name	Habitat	Type	Mass	ML#	Recorder	Location	Year	Habitat notes	References
Turdidae	Turdus leucomelas	Pale-breasted Thrush	Varied forest	Closed	69.6	ML69498	Schwartz, Paul A.	Aragua, Venezuela	1973		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus leucomelas	Pale-breasted Thrush	Varied forest	Closed	69.6	ML94917	Aleixo, Alexandre Luis Padovan	Sao Paulo, Brazil	1996		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ. 3) Restall, R. 2007. Birds of Northern South America: An Identification Guide. Vol. 1. Yale University Press. New Haven, NJ.
Turdidae	Turdus merula	Common (Eurasian) Blackbird	Open woodland	Closed	115.5	ML13785	Ward, William V.	New Zealand	1966		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Heather, B.D. and Robertson, H.A. 1996. The field guide to the birds of New Zealand. Viking, Auckland, NZ.
Turdidae	Turdus merula	Common (Eurasian) Blackbird	Open woodland	Closed	115.5	ML13787	Ward, William V.	New Zealand	1969		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Heather, B.D. and Robertson, H.A. 1996. The field guide to the birds of New Zealand. Viking, Auckland, NZ.
Turdidae	Turdus merula	Common (Eurasian) Blackbird	Open woodland	Closed	115.5	ML36168	van den Berg, Arnoud B.	Noord-Holland, Netherlands	1984		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Heather, B.D. and Robertson, H.A. 1996. The field guide to the birds of New Zealand. Viking, Auckland, NZ.
Turdidae	Turdus merula	Common (Eurasian) Blackbird	Open woodland	Closed	115.5	ML162883	Budney, Gregory F.	England, United Kingdom	1991		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Heather, B.D. and Robertson, H.A. 1996. The field guide to the birds of New Zealand. Viking, Auckland, NZ.
Turdidae	Turdus migratorius	American Robin	Varied/Urban	Urban	81.5	ML63026	Herr, David S.	California, USA	1991	Forest, coniferous forest, montane grassland, stream; thicket/brush	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Vanderhoff, N., P. Pyle, M.A. Patten, R. Sallabanks and F.C. James. 2016. American Robin (Turdus migratorius), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/amerob
Turdidae	Turdus migratorius	American Robin	Varied/Urban	Urban	81.5	ML105301	Keller, Geoffrey A.	Colorado, USA	1993	Forest, coniferous forest, montane grassland; Rocky Mountain National Park	1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Vanderhoff, N., P. Pyle, M.A. Patten, R. Sallabanks and F.C. James. 2016. American Robin (Turdus migratorius), The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://birdsna.org/Species-Account/bna/species/amerob
Turdidae	Turdus nigrescens	Sooty Thrush	Scrub	Open	96	ML28195	van den Berg, Arnoud B.	Costa Rica	1981		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus nigrescens	Sooty Thrush	Scrub	Open	96	ML74169	Ross, Jr., David L.	Heredia, Costa Rica	1988		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus nigrescens	Sooty Thrush	Scrub	Open	96	ML76568	Marantz, Curtis A.	Heredia, Costa Rica	1991		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus nigrescens	Sooty Thrush	Scrub	Open	96	ML165399	Ross, Jr., David L.	Cartago, Costa Rica	1996		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus nudigenis	Spectacled Thrush	Open rainforest	Closed	64.75	ML14062	Schwartz, Paul A.	Distrito Capital, Venezuela	1958		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus nudigenis	Spectacled Thrush	Open rainforest	Closed	64.75	ML14071	Ward, Rodman	Trinidad and Tobago	1965		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus nudigenis	Spectacled Thrush	Open rainforest	Closed	64.75	ML66258	Schwartz, Paul A.	Miranda, Venezuela	1959		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus nudigenis	Spectacled Thrush	Open rainforest	Closed	64.75	ML77955	Finch, Davis W.	Upper Takutu-Upper Essequibo, Guyana	1994		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus nudigenis	Spectacled Thrush	Open rainforest	Closed	64.75	ML145129	Robbins, Mark B.	Guyana	2000		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus olivater	Black-hooded Thrush	Second growth rainforest	Closed	77.5	ML134915	O'Shea, Brian J.	Guyana	2001		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus olivater	Black-hooded Thrush	Second growth rainforest	Closed	77.5	ML145313	Robbins, Mark B.	Guyana	2001		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus olivater	Black-hooded Thrush	Second growth rainforest	Closed	77.5	ML69605	Schwartz, Paul A.	Aragua, Venezuela	1970		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.

Family	Species	Common name	Habitat	Closed	Mass	ML#	Recordist	Location	Year		References
Turdidae	Turdus olivater	Black-hooded Thrush	Second growth rainforest	Closed	77.5	ML69609	Schwartz, Paul A.	Aragua, Venezuela	1974		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus olivater	Black-hooded Thrush	Second growth rainforest	Closed	77.5	ML69610	Schwartz, Paul A.	Aragua, Venezuela	1974		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Meyer de Schauensee, R. and W.H. Phelps Jr. 1978. A Guide to the Birds of Venezuela. Princeton University Press, Princeton, NJ.
Turdidae	Turdus plebejus	Mountain Thrush	Rainforest edge	Closed	86	ML14101	Thurber, Walter A.	El Salvador	1973		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus plebejus	Mountain Thrush	Rainforest edge	Closed	86	ML72828	Ross, Jr., David L.	Puntarenas, Costa Rica	1991		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus plebejus	Mountain Thrush	Rainforest edge	Closed	86	ML74173	Ross, Jr., David L.	Heredia, Costa Rica	1988		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus plebejus	Mountain Thrush	Rainforest edge	Closed	86	ML74208	Ross, Jr., David L.	Heredia, Costa Rica	1988		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Stiles, F.G. and A.F. Skutch. 1989. A Guide to the birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY.
Turdidae	Turdus plumbeus	Red-legged Thrush	Rainforest edge	Closed	68.98	ML14108	Dean, Paul A.	New Providence, Bahamas	1971		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Larsen, N. 2011. Red-legged Thrush (Turdus plumbeus), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=553996
Turdidae	Turdus plumbeus	Red-legged Thrush	Rainforest edge	Closed	68.98	ML35342	Parker, III, Theodore A.	Dominican Republic	1985		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Larsen, N. 2011. Red-legged Thrush (Turdus plumbeus), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=553996
Turdidae	Turdus plumbeus	Red-legged Thrush	Rainforest edge	Closed	68.98	ML115837	Macaulay, Linda R.	Freeport and West Grand Bahama, Bahamas	2002		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Larsen, N. 2011. Red-legged Thrush (Turdus plumbeus), Neotropical Birds Online (T. S. Schulenberg, Editor). Ithaca: Cornell Lab of Ornithology; retrieved from Neotropical Birds Online: http://neotropical.birds.cornell.edu/portal/species/overview?p_p_spp=553996
Turdidae	Turdus poliocephalus	Island Thrush	Rainforest	Closed	63	ML38636	Kennedy, Robert S.	Philippines	1981		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Brazil, M. 2009. Birds of East Asia: China, Taiwan, Korea, Japan and Russia. Princeton University Press. Princeton, NJ.
Turdidae	Turdus poliocephalus	Island Thrush	Rainforest	Closed	63	ML64497	Pratt, H. Douglas	Fiji	1992		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Brazil, M. 2009. Birds of East Asia: China, Taiwan, Korea, Japan and Russia. Princeton University Press. Princeton, NJ.
Turdidae	Turdus poliocephalus	Island Thrush	Rainforest	Closed	63	ML114802	Hsu, Wayne W.	Nantou, Taiwan	2001		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Brazil, M. 2009. Birds of East Asia: China, Taiwan, Korea, Japan and Russia. Princeton University Press. Princeton, NJ.
Turdidae	Turdus poliocephalus	Island Thrush	Rainforest	Closed	63	ML139694	Pratt, H. Douglas	Northern Fiji	2005		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Brazil, M. 2009. Birds of East Asia: China, Taiwan, Korea, Japan and Russia. Princeton University Press. Princeton, NJ.
Turdidae	Turdus poliocephalus	Island Thrush	Rainforest	Closed	63	ML139923	Pratt, H. Douglas	Samoa	2006		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Brazil, M. 2009. Birds of East Asia: China, Taiwan, Korea, Japan and Russia. Princeton University Press. Princeton, NJ.
Turdidae	Turdus poliocephalus	Island Thrush	Rainforest	Closed	63	ML140733	Mittermeier, John C.	Samoa	2005		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Brazil, M. 2009. Birds of East Asia: China, Taiwan, Korea, Japan and Russia. Princeton University Press. Princeton, NJ.
Turdidae	Turdus rufiventris	Rufous-bellied Thrush	Open woodland	Closed	69.5	ML30170	Parker, III, Theodore A.	Rio de Janeiro, Brazil	1982		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R.S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus rufiventris	Rufous-bellied Thrush	Open woodland	Closed	69.5	ML50376	Macaulay, Linda R.	Brazil	1990		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R.S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus rufiventris	Rufous-bellied Thrush	Open woodland	Closed	69.5	ML129765	Andersen, Michael J.	Jujuy, Argentina	2005		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R.S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.
Turdidae	Turdus rufiventris	Rufous-bellied Thrush	Open woodland	Closed	69.5	ML165125	Lammertink, Martjan	Misiones, Argentina	2008		1) Dunning, J. B. Jr. 1992. CRC Handbook of Avian Body Masses. CRC Press. Boca Raton, FL. 2) Ridgely, R.S. and G. Tudor. 1989. The Birds of South America: Volume I. University of Texas Press. Austin, TX.