SONG SPARROWS (*Melospiza melodia*; Emberizidae) RELIABLY BROADCAST INFORMATION ABOUT PERCEIVED THREATS USING ALARM CALLS

A thesis presented to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree of Masters of Science in Biology.

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ABSTRACT

SONG SPARROWS (*Melospiza melodia*; Emberizidae) RELIABLY BROADCAST INFORMATION ABOUT PERCIEVED THREATS USING ALARM CALLS.

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Expanding our understanding of signal complexity in animals could start with the very smallest songbirds. Black-capped Chickadees (*Poecile atricapillus*) can encode very specific details about a threat in their acoustically simple alarm calls. Can other small songbird species, such as the Song sparrow (*Melospiza melodia*), encode that same level of detail in their even simpler alarms? Furthermore, is it possible for them to interpret those details, and are those details reliable? I measured the response of Song sparrows to the suggestion of a threat (two recordings of Song sparrow alarms, one in which the call elements were played much faster than a normal call and one in which they were played much slower) then, separately, to the threat itself (a taxadermic mount of an Eastern screech owl, *Megascops asio*), and then to a non-threating control (a Northern bobwhite, *Colinus virginianus*). The Song sparrows consistently approached the speaker more closely when they heard a faster alarm call and also produced a faster alarm call in response to the more threatening screech owl mount. This suggests that there is specific data encoded in the alarms and that they will produce a different alarm according to the perceived threat level of what they are encountering.

INTRODUCTION

Animals make noises. Vocal and mechanical acoustic signals are extremely ubiquitous in the Animal Kingdom and they serve many purposes—attracting mates, keeping track of young, claiming and defending territories, communicating with flock- or herdmates. Those group communications span a wide array of signals for use in a multitude of situations, but perhaps the most important sound an animal makes is to alert to danger. Without those alarm signals and the ability to understand them, the animal becomes another's prey.

Alarm calls are signals produced to warn conspecifics of danger and are prevalent in most species of social animals. First and foremost, they act as a general warning for anyone listening but in certain animals they can also provide information specific to the situation that caused the alarm. For instance, Vervet monkeys have separate, distinct signals for aerial, arboreal, and ground predators, and the troop will react appropriately to each signal. When the signal for an eagle is sounded, the members of the troop climb to the middle of the trees and look to the sky for the threat. When the snake signal is sounded the monkeys all stand on their hind legs and look around and to the ground, and for a leopard signal they climb to the ends of the tree branches where the heavier predator would not be able to follow. The specificity of their separate alarms allows the troop to communicate clearly and quickly because each member of the troop knows the correct action to take in response to each alarm (Seyfarth et al. 1980).

Other species can use variations of a single signal to indicate different kinds of dangers, such as the "chick-a-dee" call systems used by chickadees (Poecile spp.) and other small members of family Paridae (Freeburg et al. 2012). This is a very complex call system that can be used to communicate a wide range of information to flockmates. There are call types which are broadcast when a new food source has been found (Freeburg et al. 2012b) and Black-capped chickadees (*Poecile atricapillus*) in particular can successfully communicate the size and relative threat of a predator via their alarms—more "dee" notes on the end of the call signals a smaller predator and therefore, to a small bird, a higher perceived threat (Freeburg et al. 2012; Templeton et al. 2005; Templeton and Greene 2007).

Signaling a higher perceived threat is only useful if recipients can distinguish it from other messages and respond appropriately to that particular, meaningful signal (Macedonia and Evans 1993). Black-capped chickadees and other small "backyard" birds tend to congregate into large flocks over the winter months while they are not maintaining a breeding territory and the chickadees still make these calls while in those flocks. The question then is whether or not other songbirds are capable of detecting the different calls and whether they are able to discriminate between them. Wilson and Mennill (2011) showed that if the duty cycle (i.e. the rate at which the elements of the call are produced) in a Black capped chickadee call is experimentally increased with all other aspects of that call held constant, the birds have a much greater mobbing reaction to a call with a higher duty cycle than to one with a lower duty cycle. It wasn't that there were simply more "dee" notes, but that they were produced comparably faster than calls with fewer "dee" notes.

Our study species, the Song sparrow (*Melospiza melodia*; Emberizidae), has a much simpler signaling system. These small, sexually monomorphic songbirds nest and roost in hedgerow habitats along the open fields that they use for foraging. The males are territorial and broadcast their song primarily during the mating season to defend their territories and to attract mates. Although only the males sing during the breeding season, both sexes of this species give calls (Elekonich 1998), but unlike the "chick-a-dee" call system, the Song sparrow's call is only a repeated *chip* and offers little variation (Nice and Pelkwyk 1941).

Song sparrows readily respond to heterospecific alarms (i.e. Carolina wren [*Thryothorus ludovicianus*], Tufted titmouse [*Baeolophus bicolor*]) but heterospecifics do not, in turn, reliably respond to Song sparrow alarms (personal communication with J Hyman 2012; personal observation by J Carman 2012). These sparrows understand the cross-species alarms and do not alarm heavily when in the mixed-species winter flocks but they produce their own species-specific alarm, nonetheless. If those alarms are primarily for their conspecifics, such as mates or fledgling offspring, can the Song sparrow extract the same sort of information from their own species-specific alarms as other species can from the alarms of heterospecifics which are more predominantly utilized while in mixed-species winter flocks?

In this study, we examine whether a Song sparrow alarm call is capable of transmitting information about the relative danger of a perceived threat. On the receiving side, the birds were played two recordings of conspecific alarms with drastically different duty cycles and we tested for differences in the strength of the birds' mobbing reaction to each call. For the signaler's side, taxadermic mounts were used to present each bird with a threatening, “predator present” scenario and a non-threatening, “non-predator present” scenario. We tested for differences in the signals the birds produced when confronted with each of the two stimuli.

METHODS

This study was conducted on the campus of Western Carolina University in Cullowhee, Jackson County, North Carolina (35.3097° N, 83.1836° W). This location includes both high and low traffic areas in the center of a densely developed campus surrounded by less intensively used open areas such as athletics fields. The experiments were conducted from June to August 2012 during the Song sparrow's breeding season to ensure that the males had territories, mates, and offspring to defend and would more reliably respond to our playback stimuli.

This study consisted of two experiments. In the first experiment, we tested whether the same predator warning information that was seen in studies on chickadees is contained in a Song sparrow's alarm (Wilson and Mennill 2011). This would mean that an alarm made in response to a "high-danger" stimulus is not only a longer call, but a call made more quickly than those made in response to a "low-danger" stimulus. This duty cycle evaluation was conducted by administering a nine-minute playback experiment to 10 male Song sparrows on their territories using recordings of Song sparrow alarm calls. The playback consisted of six minutes of the alarm followed by three minutes of silence. During these nine minutes the position of the bird was recorded every five seconds using a 16 meter scale. The speaker was placed at the zero mark and the scale extended eight meters on either side marked off at two meter increments. After the position data points were collected, I calculated the bird's average distance to the speaker over the nine minutes. The lower the average distance over the nine minutes, the more time the bird spent nearer to the zero mark (the source of the alarm calls), demonstrating a higher perceived threat (Searcy et al. 2006).

This willingness to approach what the sparrow perceives as danger is called its "boldness," and varies among individuals (Evans et al. 2010; Hyman et al. 2013). I accounted for that variation in boldness among the birds by using a repeated measures approach. The effect of duty cycle on a bird receiving an alarm signal was evaluated by playing two artificially created tracks made from the same pre-recorded instance of Song sparrow alarm. The first track was made to simulate an alarm consisting of 20 calls per minute. The second track was made to simulate an alarm consisting of 80 calls per minute. Each individual received two playback trials performed at least one day apart to reduce any residual effects that might transfer from one test to another and the order in which the tracks were presented was randomized from bird to bird. I compared the resulting "average distance to speaker" data from each bird's set of encounters to its pair to look for a difference in the mobbing intensity of each sparrow during the two trials.

In the second experiment I looked for differences in a sparrow's reaction to finding a threatening stimulus versus finding a non-threatening stimulus after they have responded to a heterospecific's alarm. This "threat versus non-threat" evaluation consisted of two six minute trials the presence of a taxadermic mount of a Northern bobwhite (*Colinus virginianus*), a small, non-predatory game-bird, or in the presence of a taxadrmic mount of an Eastern screech owl (*Megascops asio*), a predator species that is similar in size to the bobwhite. Thirteen male Song sparrows were played one minute of a Carolina wren alarm call to attract them to the site of the mount, followed by five minutes of silence. I counted the number of *chip* calls that the responding sparrow made during each of those six minutes and compared the resulting “chips per min” data from each bird’s set of encounters to its pair to try to detect a difference in the duty cycle of each sparrow’s response calls during the two trials. Only one experiment was performed per day at each site so as to reduce the chance of the experience from one playback affecting the bird’s response to the next trial and the order of the trials (predator first, non-predator second or vice versa) was randomized from bird to bird.

For each experiment, (slow vs. fast duty cycle and threat vs. non-threat) we compared responses using a paired two-tailed T-test.

RESULTS

Of the ten sparrows tested for the duty cycle trials, eight demonstrated a higher boldness score, approaching the speaker more closely during the fast duty cycle playback than they did during the slow duty cycle playback (paired T-test: t=3.2966, df=9, p=0.0092; Figs. 1 & 2).

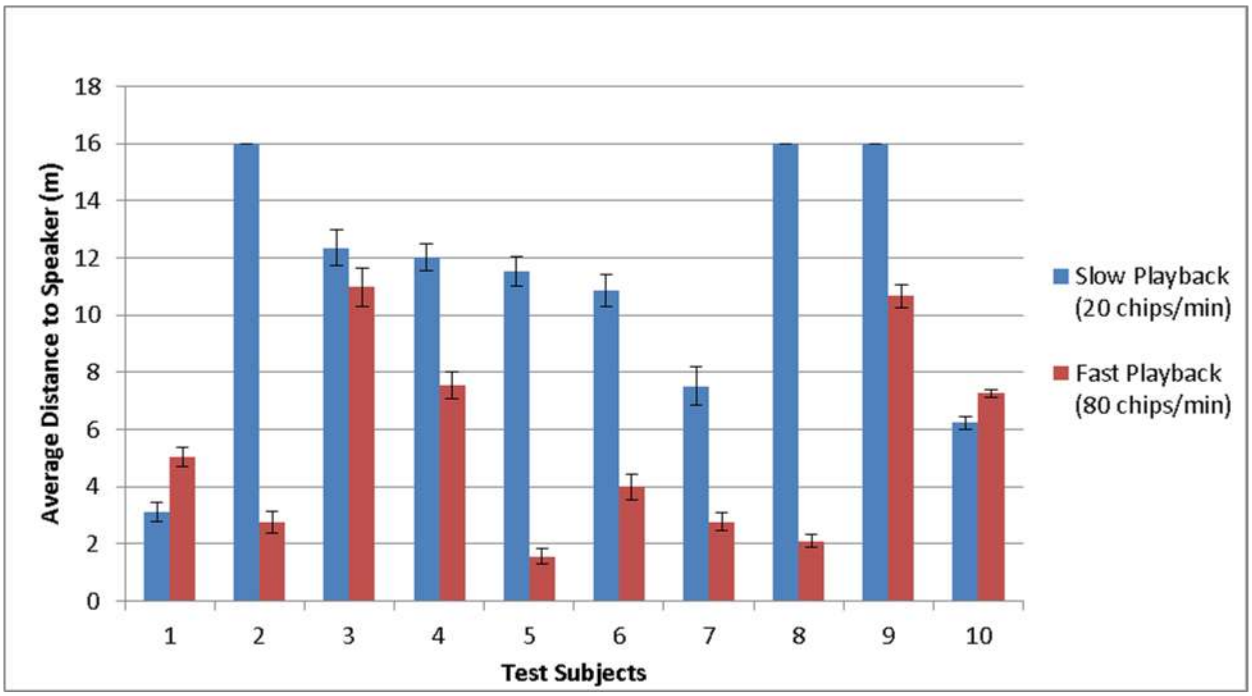

Figure 1: Average distance from speaker in response to slow (20 chips/min; mean distance from speaker: 11.16 m) or fast playback (80 chips/min; mean distance from speaker: 5.47 m) of conspecific alarm calls (N=10; +/- 1 SE; paired T-test: t=3.2966; df=9; p=0.0092).

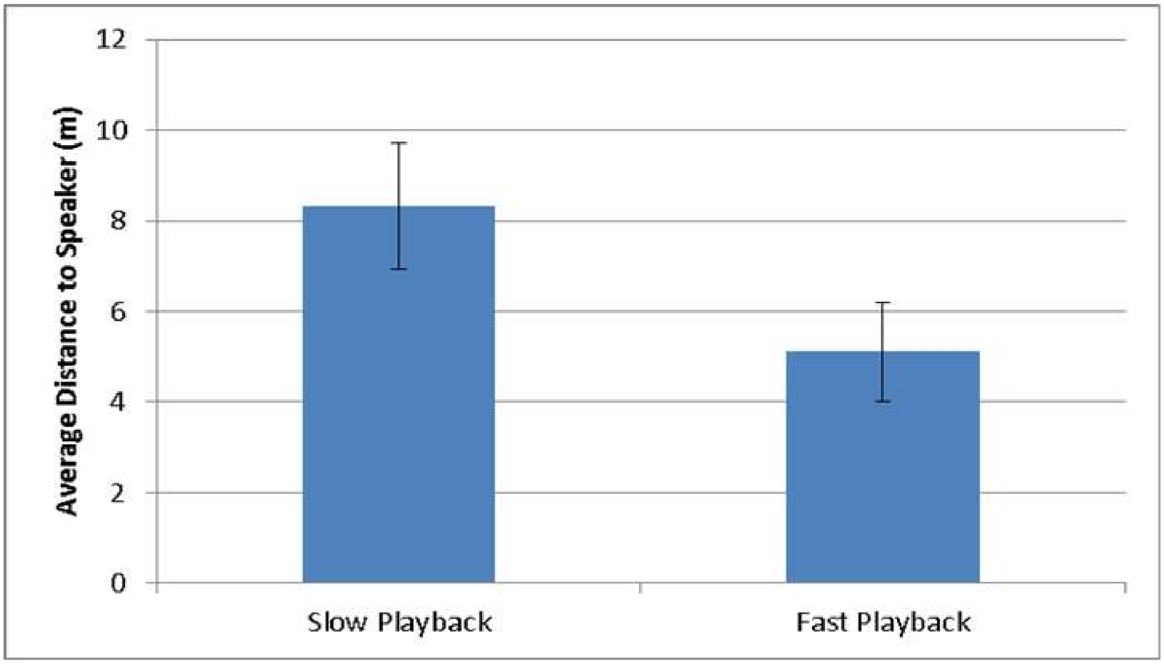

Figure 2: Average distance from speaker for each playback test group (N=10; +/- 1 SE).

Slow = 20 chips/min; Fast = 80 chips/min.

For the threat versus non-threat trials, nine of thirteen birds produced a higher number of chip notes during a five minute playback trial in response to the presence of a taxadermic mount of a Screech owl than to that of a Northern bobwhite (paired T-Test: $t=2.6875$; $df=12$; $p=0.0197$; Figure 3).

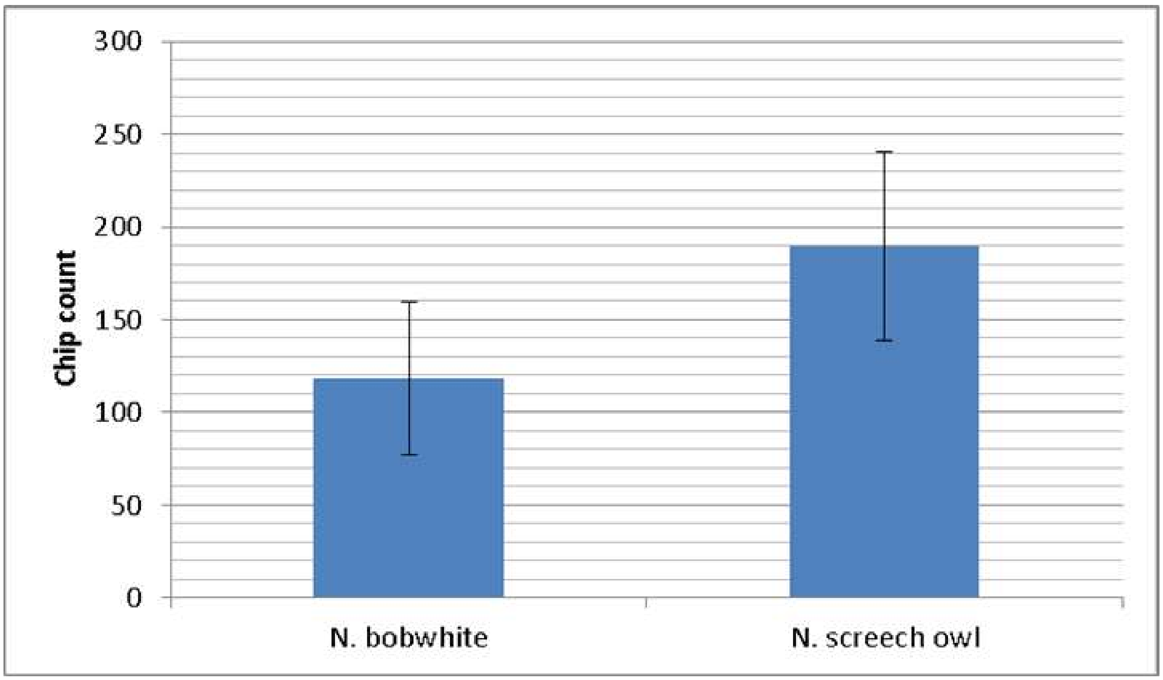

Figure 3: Average number of alarm calls counted during playbacks of one minute of wren alarm followed by 4 minutes of silence while displaying either the Northern screech owl mount “threat” stimulus or the Northern bobwhite mount “non-threat” stimulus (N=13; +/- 1 SE).

DISCUSSION

Previous work with Black-capped chickadees, Vervet monkeys and other groups of animals has shown that individuals receive much more detailed information from alarm calls than simply an indication that there is danger present (Templeton et al. 2005; Macedonia and Evans 1993; Seyfarth et al. 1980). Our results provide evidence that Song sparrows can decode the same types of useful details (i.e. size of predator, relative level of threat) from their own acoustically simple alarm calls.

In the duty cycle playback trials, I demonstrated that Song sparrows can distinguish between a slow chip note duty cycle (20 chips/min) and a fast chip note duty cycle (80 chips/min) and will respond more strongly to the faster duty cycle. This behavior was consistent among most of our subjects and suggests that the sparrows, like the chickadees, are interpreting the faster cycle as a signal that a greater threat to the sparrow is likely present.

In the "threat versus non-threat" trials I established that Song sparrows will react appropriately to threats presented to them by producing the high duty cycle alarm when a greater threat is present, and the low duty cycle alarm in less threatening situations. This way they can correctly inform conspecifics of the potential danger nearby. This supports the idea that Song sparrows can recognize high- and low-threat situations, signal accordingly, and that other Song sparrows who hear the signal can then reliably interpret it and respond correctly.

Hatch (1997) also observed differential responses to "threat versus non-threat" in female Song sparrows defending a nest. Female Song sparrows stayed much longer and perched much closer to a mount of a crow (more dangerous) than to a mount of a junco (less dangerous). The female staying closer to the crow for longer periods demonstrates that the female interprets the crow as a bigger threat. A close approach to a dangerous predator may sound counterintuitive, but such behavior, often termed mobbing, is widespread among vertebrates such as fish, birds, and mammals, though the benefits of this behavior are poorly understood (Curio 1978; Curio and Regelmann 1985). By approaching closely, a female may be keeping the crow's attention on herself and away from her nest as well as ensuring that any conspecifics nearby who are receiving her signal know exactly where the threat is located. This parallels our results. Maintaining a smaller average distance to the speaker indicates that the bird perceived that something threatening should have been present at that spot and the alarm call in response demonstrates that it wanted others to know where that danger was. This connection reinforces our argument for the importance of the alarm within a conspecific group. When a nest or fledgling is threatened and one parent begins to produce the alarm call, the first individual to respond will probably be their mate because that individual is most likely the closest and has the greatest interest in deterring predators from that location. In the Hatch (1997) study mentioned above, the female sparrow alarming to the mount of the crow is going to get the attention of at least her mate and any of her young adult offspring in the area.

These reactions also mirror observations made by other researchers as far back as Nice and Pelkwyk (1941). Their paper describes Song sparrows' reactions to a wide array of perceived enemies, most of which involve the birds giving different types of alarms as the situations escalated. However, if the threat was definitely a predator, such as an American kestrel, or “Sparrow hawk” (*Falco sparverius*), or a Sharp-shinned hawk (*Accipiter striatus*, Nice and Pelkwyk [1941] specify the subspecies *velox*), the Song sparrows were more likely to alarm quietly and stay hidden. This cryptic behavior was consistent unless a nest or young fledglings were involved. In that case the birds reacted noisily, attempting to attract the predator’s attention and lead them from the nest site.

Several other studies of alarm calling behavior have found that when alarm calls contain reliable information on threats, not only will conspecifics respond to the calls, but heterospecifics will as well (Fallow and Magrath 2010; Magrath et al. 2007; Templeton and Greene 2007). Despite the fact that Song sparrow alarm calls appear to provide correct information on threats present in the environment, other song bird species do not seem to eavesdrop on the Song sparrow (personal observation by J Carman 2012). Why might this be? First, consider the Song sparrow’s position in mixed-species flocks. A Song sparrow’s winter flockmates tend to be larger (cardinals, catbirds, towhees) or louder birds (chickadees, titmice) that, due to social, environmental, and predatory pressures, have developed a louder and longer call that overpower the comparatively softer chips of the Song sparrow. Freeburg et al. (2012a) argue that social complexity is an important driver of signal complexity in communication. These authors describe a few pressures on signal development, the first of which is the animal’s social standing. Does it live in a group or primarily only with its mate? Are there multiple generations living together or is it only parents and their most recent offspring? Are pairs mainly monogamous or is it a polygamous or polyandrous society? Any one of these situations changes the individual social interactions or creates them where they might not exist in other social systems. Birds such as chickadees live in large, complex social groups during the non-breeding season, and presumably, their complex alarm calls have evolved in order to convey information to their flockmates in such a setting. When the Song sparrows are in their (mostly) monogamous pairs on their defended territories with their mate and offspring, their alarm calls are very important signals. But when they are interacting with a mixture of larger and perhaps more aggressive species, the importance of their specific signal is lost in the cacophony of the others.

Environmental factors also affect signal development (Freeburg et al. 2012a). For the most part, Song sparrows live in short hedge rows along open fields and that lends to being easily seen. A wild, loud, sweeping alarm signal would be deleterious in that environment because with nothing in the way to break up the sound propagation the signaler would be easily pinpointed. Short, high, sharp chips on the other hand make it difficult for predators to find the signaler because of the brevity of the noise (Richards and Wiley 1978).

Relying on the alarms of others seems like a risky way to ensure one's safety, especially if those "others" aren't even a member of your own species, let alone invested in your particular genetic longevity. Animals that live in mixed-species groups do their best to avoid that problem by establishing a standard for their eavesdropping. Magrath et al. (2009) identified criteria for successful eavesdropping and outlined three main attributes that make a stranger's alarm call a reliable one: Relevance – alarms to stimuli that are mutually threatening; Discrimination – alarms to stimuli that are actually dangerous and not just anything that moves; and Deception – alarms that signal true danger and are not ploys to clear a feeding ground, for example.

Along with social complexity and environmental factors, the third pressure that drives signal development is predation. If everything is a potential predator then one all-encompassing alarm signal might be all that is needed to keep conspecifics safe. Song sparrows and chickadees, however, live alongside some species that are threats and some species that are not. This means if a signal is to be reliable it has to tell the listeners something specific about the subject it is being broadcast about. Each species learns which other species are most likely to alarm to shared threats. The signal is deemed "reliable" if the alarm from the sender also indicates danger to the listener (Searcy and Nowicki 2005). In our experiment, broadcasting the danger about the presence of the Northern screech owl was more important than broadcasting the presence of the Northern bobwhite. Alone on their spring/summer territories Song sparrows need to be able to do this for themselves which, according to my results, they can, but if they are living in mixed-species flocks alongside species with very reliable alarms they simply may not need to contribute.

So, if the standards for reliable eavesdropping are learned and Song sparrows have other species that are reliable enough to eavesdrop upon, then they do not have to make the primary alarms in their mixed-species winter flocks and those heterospecific flockmates may not have learned to acknowledge a Song sparrow alarm like they have a Black-capped chickadee's or a Tufted titmouse's. That being said, some species such as Northern cardinals (Cardinalidae), Gray catbirds, and Northern mockingbirds (Mimidae) do seem to react to Song sparrow alarms if they live near a Song sparrow territory (personal observation by J Carman 2011-12), but it does not appear to be a universal behavior. This is possibly due to the Song sparrow's relative silence when other species are most exposed to them (ie: in mixed-species flocks).

Then again, perhaps the requirement that a signal be reliable to others is the problem. From both personal observations and as reported in Nice and Palkwyk (1941), it is clear that in general Song sparrows as a species tend to be easily excitable. There are very few novel stimuli that they do not immediately alarm to, only realizing, after harassing it for a number of minutes, that the new object might not actually be a danger. If anything will set the resident Song sparrows of a mixed-species flock alarming, (for instance a child on a bike) then they may fail the "Discrimination" requirement of being a reliable signaler.

Although Song sparrows are not a strongly mobbing or alarming species and although other conspecifics may not consider a Song sparrow's alarm to be reliable, this signal must be important within family groups and between Song sparrows whose territories are near one another. The results from my duty cycle experiment (Fig. 1) demonstrate that the Song sparrows' seemingly simple *chip* notes can communicate the level of a nearby threat and, therefore, illustrate the importance of that signal to their conspecifics.

The primary comparison species in this research was the chickadee and its recently discovered ability to encode information in its *chicka-dee-dee* call (Templeton et al. 2005; Templeton and Greene 2007). My research has uncovered a species whose signal sounds much simpler than the chickadee's but also contains very detailed information about its surroundings. I have pinpointed aspects within a Song sparrow's alarm call that reliably translate to very specific messages that can consistently be correctly interpreted by conspecifics around them.

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