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Playing It By Ear: Can Wintering Sparrows Detect An Incoming Attack By Auditory Cues Alone?

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Playing it by ear: Can wintering sparrows detect an incoming attack by auditory cues alone?

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ABSTRACT

It is crucial for all prey species to possess the ability to precisely detect an incoming attack. For birds, vision is probably the main sensory mode in predator detection, but other senses are likely to be involved. In particular, auditory detection and recognition of predators in birds is largely unstudied. I thus evaluated the ability of wintering sparrows to detect attack based only on the non-vocal, “scary sounds” of predators, thus focusing on a single sensory modality. My study species were emberizid sparrows, focusing on dark-eyed juncos (*Junco hyemalis)* feeding in mixed flocks with American tree sparrow (*Spizella* arborea) and Whitethroated sparrow (*Zonotrichia albicollis)*. I exposed foraging flocks to non-vocal playbacks of departure wingbeats (flight sounds) of other passerines (juncos and chickadees), red-tailed hawks (*Buteo jamaicensis*), and sharp-shinned hawks (*Accipter striatus*). Playbacks of approaching footsteps of a potential terrestrial threat (dogs) were also used. All responses were video recorded for analysis. Behavioral responses were measured mainly in terms of the proportion of a given flock that flushed to cover, or became highly vigilant. Sparrows were responsive to all of the wingbeat stimuli, especially when played at a relatively loud volume. Hawk wingbeat sequences were, however, the most evocative stimuli in producing immediate flushes to cover or general alertness, especially when comparing stimuli that were played at low volume. The sparrows' response to an approaching terrestrial stimulus often involved an extended alert posture, or jumping up onto perches for a better view, reactions never seen to the wingbeat stimuli (and likely maladaptive during a hawk attack). Thus, the results of these experiments suggest that these wintering sparrows are able to distinguish wingbeats from smaller birds from those of hawks, and that they can differentiate the auditory approach of terrestrial threats from aerial threats. Other experiments were performed that examined the salient features of the most threatening stimulus, sharpshinned hawk wingbeats, to evaluate what these sparrows find most informational from the sounds of a predator. A single hawk wingbeat can elicit flushes to cover, but full reactions require 2 or 3 hawk wingbeats in their natural cadence. Removing the low-frequency portion of a hawk wingbeat, in a range presumably not heard well by these sparrows (under 2 kHz), rendered the hawk wingbeat stimuli much less salient to the sparrows; the full range of frequencies in a hawk wingbeat appears to be important. These emberizid sparrows clearly have the ability to sense incoming attacks, and make some assessment of the relative risks involved, using only their sense of hearing.

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INTRODUCTION

The degree of risk experienced by prey organisms can vary greatly on a daily, hourly, or even a minute-by-minute basis. Prey species must have the ability to accurately detect and recognize the current risk level at any given time, using different types of information, in order to employ appropriate and cost-effective anti-predator responses (Lima and Dill 1990). Any mistake in risk assessment may have obvious and negative fitness consequences. A key step in this process is predator detection and recognition, which may take place on a variety of spatial and temporal scales, and through several different sensory modalities (Caro 2005). The key strategic goal for prey is to gain any sort of advantage in detecting a predator before they themselves are detected, attacked, or captured.

At a relatively large spatial scale, predator detection is focused on the presence of predators within an animal's local surroundings or landscape. In principle, any sensory modality may come into play at this scale. Olfaction is a dominant sense for detecting the presence of predators by many vertebrates. Odors and other chemicals emitted by predators (skin, fur, urine, feces) leave unambiguous cues of predator presence in a given area, and can have a significant impact on prey behaviors, leading to predator avoidance or other antipredatory behaviors such as increasing vigilance (Kats and Dill 1998). Olfactory detection holds in both terrestrial systems and aquatic systems. Many cases are known in mammalian systems as well. Evidence suggests that mammals will respond to predatory, chemical cues with appropriate anti-predatory responses such as avoidance, freezing, alertness, etc. (Kats and Dill 1998, Apfelbach et al. 2005). Tongue flicking allows many reptiles to “taste/smell” chemicals emitted by nearby predators, and react accordingly (Lopez and Martin 2001, Dial 1989, Cooper 1994, Cooper 1998). In aquatic systems, chemosensory abilities likely play a dominant role in the detection of predators (Miner and Stein 1996, Kats and Dill 1998). For instance, amphibians tend to spend less time in areas with fish chemicals which indicate the presence of predatory fish (Petranka et al. 1987, Stauffer and Semlitsch 1993). Chemosensory abilities to detect predators are particularly important in systems where the other primary senses are inhibited (i.e. visually obstructive areas, murky waters, etc. – Hartman and Abrahams 2000). When detecting predators across large areas, olfaction is less likely to be an important cue for birds, though there is evidence that birds can assess predation risk extent using olfaction *(e.g.* Roth et al. 2008, Amo et al. 2008*)*. Presumably, birds mainly integrate both auditory and visual detections of predators to assess risk at a large spatial scale, but there is little direct study of such effects (but, see Lima 2009). Detecting the general presence of predators via auditory cues is probably also important in mammals (Abramsky et al. 1997, Lyly et al. 2018).

Predator detection on a smaller spatial scale will often involve the detection of dangerously close-by predators, an imminent attack, or even an attack already underway. Two important issues here are the identity of the possible threat and an assessment of the imminent risks involved. Olfaction could function at this scale in some cases, but visual and auditory cues are likely to dominate in most predator-prey systems. Here, nearby, large animals are likely to be deemed threatening until proven otherwise. Sudden movement by large objects is very likely a universal cue of a possible attack. In aquatic systems, sudden pressure waves and vibrations may be the main cues of dangerous situations. Vibrations could also be the main cue in many invertebrate systems (e.g. Sitvarin et al. 2016). These topics are generally not well studied, but predator detection at smaller spatial scale probably involves a number of sensory modalities.

Vision is arguably the most heightened sense in birds, and undoubtedly plays a critical role in the detection of a dangerous encounter or an approaching predator. For instance, birds, and very likely most vertebrates, have specialized neural systems that can visually detect looming (incoming) objects and yield an accurate indication of when that object will reach the bird (Wang and Frost 1992). The strongest responses are to symmetrically looming objects, which implies direct approach towards the viewer (Blackwell et al. 2009, Lima et al. 2015). Objects with predator-like profiles are also most likely to yield a strong response (Curio 1993, Canty and Gould 1995). Although not well studied, it is likely that birds can very quickly recognize the identity of a predator in flight by sight alone (Edelaar and Wright 2006). In encounter situations with a less imminent risk of attack, birds may assess the direction of a predator's gaze and respond appropriately (Carter et al. 2008). Birds can also detect and identify predators whose features are partly occluded by vegetation or other objects (Tvardíková and Fuchs 2010). The finer details of potential predators, such as the feather texture, are also important aspects of threat assessment by birds (Beránková et al. 2015, Nemec at al. 2015).

Despite birds being highly visual animals, auditory cues are also important in predator detection and recognition. Virtually all work on auditory cues has focused on alarm calls, which are given by almost all social birds (Caro 2005). Several species of passerines can assess predation risk and modify their alarm calls based on that assessment (Templeton et al. 2005, Freedberg 2008, Suzki 2014). Many species also use referential alarm calls that provide information on the nature of the predator (Rainey et al. 2004, MacLean and Bonter 2013) and even the current behavior of the predator (Griesser 2008). Receivers of these alarm calls respond appropriately to modified calls (Freedberg and Lucas 2002). Eavesdropping on heterospecific alarm calls is also a large component of the auditory detection of threats by birds (Magrath et al. 2015, Fallow et al. 2011); heterospecifics may include mammals as well as other birds (Rainey et al. 2004). Additionally, chickadees can discriminate between predator vocalizations and provide alarm calls that are specific to the type of predator that is heard (Billings et al. 2015). This ability to distinguish the calls of predators is probably widespread in birds. Very similar phenomena have also been identified in several mammalian alarm-calling systems (Klump and Shalter 1984, Petracca and Caine 2013). Predator detection based on auditory cues is not limited to alarm calls. Stress calls can also provoke antipredatory behaviors in prey (Searcy and Caine 2003).

Non-vocal cues of immediate danger, the focus of this study, have received much less attention in birds than alarm calls. Work here, once again, has focused on noises made by conspecifics or social heterospecifics. One of the most commonly encountered and potentially informative non-vocal sounds is the wing flapping of birds as they fly away from a group. Such departures may reflect an approaching threat, and in some systems may be the main alarm signal (Lima 1995, Butler et al. 2017). Such departures, however, involve both a visual (the bird in flight) and auditory component (wing flapping sounds). Nevertheless, flight sounds alone can cause flush responses in nearby birds (Lima and Zollner 1996, Hingee and Magrath 2009). Flight departures of conspecifics can contain important information about the risk of predation at a given time (Boujja-Miljour et al. 2017). The flight feathers of some species, especially doves and pigeons, emit unique sounds that convey information about the nature of departure (Boujja-Miljour et al. 2017, Clark and Prum 2015). Rock pigeons may also use intention movements to alert flock members to an upcoming (non-threat-driven) flight departure (Davis 1975).

Sounds made by the predators themselves are perhaps the most threatening stimuli beyond actually viewing an attack directly: many predators are as stealthy as possible during an attack, thus the detection of such auditory stimuli very likely indicates a precariously dangerous situation, with a predator close-by or in mid-attack. Since predators often cannot achieve complete silence during an attack, it is likely that prey auditory abilities are finely tuned to detect and respond to such sounds. Additionally, different types of predators will undoubtedly make different noises (e.g. terrestrial vs. aerial), signaling the need for different responses. Very little work, however, has addressed the responsiveness of animals to these sorts of non-vocal predatory sounds. One exception concerns the ability of some types of nocturnal rodents to hear the flight of owls (Webster and Webster 1971, Webster and Strother 1972), whose flight feathers produce little sound compared to other raptors (Wagner et al. 2017, Lepiane and Clark 2017). There appears to be little similar work on birds, both regarding any special auditory adaptations or general ability to discern possible predatory (non-vocal) noises and differentiate among types of predators by sound alone. In related work, however, Quinn et al. (2006) found that finches will increase visual scanning in a noisy environment that might mask predatory sounds, suggesting that birds may routinely monitor the environment for such sounds.

Thus, the basic goal of my work is to provide an initial assessment of the extent to which birds can detect and assess a threat based on non-vocal sounds of danger. The study species are wintering dark-eyed juncos (*Junco hyemalis)* and other emberizid sparrows. These sparrow species generally deal with ambush predators like *Accipiter* hawks that depend on the element of surprise for a successful attack. These sparrows should possess an ability to detect the salient sounds that might be made by such hawks when on the attack and respond accordingly.

I focus in part on wingbeats, the noise made in flapping flight. My predatory wingbeat stimuli were from a sharp-shinned hawk (*Accipiter striatus*) and red-tailed hawk (*Buteo jamaicensis*). I expected the birds to be maximally responsive to these hawk wingbeats, and particularly to the more dangerous sharp-shinned hawk (see below). Other wingbeat stimuli were wingbeats of conspecific juncos and another non-threatening small bird, Carolina chickadees (*Poecile carolinesis*). These latter stimuli should be less threatening, but nevertheless could indicate an incoming threat (Lima 1995, see also below). Additionally, I examined the salient features of the most threatening or evocative auditory stimulus, by manipulating the cadence of stimuli, and the range of frequencies in the stimuli as per the apparent auditory abilities of small sparrows. Another focus was the ability of these birds to detect and respond appropriately to the sounds of an approaching terrestrial predator, since small, ground-feeding birds also face threats from mammalian mesopredators. I utilized two terrestrial stimuli that varied in their tempo, a dog walking and running.

First, I begin with a description of the methods general to all experiments. I then discuss each of my 3 experiments (in temporal sequence) in self-contained sections. Each section presents the methods specific to that experiment followed by the corresponding results. Finally, these sections are followed by a general discussion of the overall results and their implications.

GENERAL METHODS

Study Species

The birds visiting my study sites were emberizid sparrows, dominated numerically by dark-eyed juncos (*Junco hyemalis*, 70% of birds observed). Other relatively common species were American tree sparrows (*Spizelloides arborea,* 24%), and white-throated sparrows (*Zonotrichia albicollis,* 5%). These closely-related sparrows often feed in mixed flocks and react similarly in the context of anti-predatory behavior (e.g. Carr and Lima, 2012). Low-level emberizid visitors at each site were song sparrows (*Melospiza melodia)*, swamp sparrows (*Melospiza georgiana)* and fox sparrows *(Passerella iliaca*). Northern flickers (*Colaptes auratus*), red-bellied woodpeckers (*Melanerpes carolinus*) and mourning doves (*Zenaida macroura*) were also occasional visitors to the sites. Observations were not made when these large birds were present, as their presence appeared to have a large effect on the sparrows.

Study Sites

This study was carried-out from January through March 2018 at two study sites in Vigo County, IN, separated by 26 km. Both feeding sites were centered on ground-level concrete pads (6 x 5 m) in generally open areas with nearby large, open-canopy trees (within 10 m) that provided little immediate safety from predators. The concrete pads allowed food to remain dry and readily available to the birds. The food used was finely ground, yellow cornmeal, placed uniformly within 1.5 m of a pad’s edge closest to cover. Finely ground cornmeal can be picked up only by the emberizid sparrows, thus limiting feeding birds to the target species. Enough food was provided each day to avoid depletion before the end of the day. At least 80 birds visited each study site, as judged by the number of birds feeding at dawn on cold days.

Present at each site was an observation blind and protective cover. Each blind (1.5 x 1.2 x 1.2 m) was placed about 1.5 m from the edge of the concrete pad and opposite cover. Protective cover in the form of leafless, woody brush, was placed adjacent to (0.5 m away from) each concrete pad. Cover at both sites was arranged in a pile roughly 1.2 x 1.2 x 5 m in extent, with the long axis parallel to the pad's edge. The tendency for birds to flush to cover was a key behavioral metric in my study (see below).

Each concrete pad also had wooden planks (10 cm in height when placed on edge, 2.5 m in length) for visual obstructions. These obstructions were oriented perpendicular to cover, and spaced 1 m apart. Visual obstructions were used to prevent birds from easily assessing their surroundings before flushing, thus forcing more flushes than might otherwise be observed. This allowed for clearer assessments of risk perception by the birds. Obstructions also provided birds with the option of jumping on the wooden planks to survey their surroundings, rather than immediately flushing to cover.

Auditory Stimuli and Recording Methods

Details of the various sound stimuli used in my study are provided in the sections on specific experiments (see below). To summarize, Experiment 1 covered a range of auditory stimuli, some potentially threatening and others less so. Threatening stimuli included wingbeat sequences from two species of hawks, as well as the sounds of dogs walking and running. Other stimuli consisted of wingbeat sequences from flying juncos and chickadees.

Experiments 2 and 3 used experimentally modified stimuli to isolate some of the key auditory features of the more evocative stimuli, as indicated by the results of Experiment 1.

Appropriate sound stimuli were recorded with a Sennheiser (Model ME66) microphone. The microphone was connected to a Studio Six Digital (iAudioInterface), which in turn was connected to an Apple iPod touch. Recorded files were saved directly to the iPod. I used Adobe Audition CS6 editing software for the preparation of sound stimuli. A sound level meter (Larson Davis model LX1T) was used to measure the general volume of various auditory stimuli. All sounds were measured in decibels (dBA). A Karman/Hardon speaker (beige in color, 18 cm tall and 11 x 9.5 cm wide) was used in the playbacks of sound stimuli. The speaker was placed 20 cm off of ground and about 1 m from the edge of the feeding pad opposite cover, directly in front of the observation blind. To human ears, this speaker accurately replicated sounds as recorded, much better than other available options.

Playback Methods

Playback sessions were performed each day, weather permitting, alternating between the two study sites. Days with precipitation in the form of rain or snow were avoided. Sessions began 30 min after sunrise and generally lasted 60 - 90 min.

Stimuli were played to a target flock size of 5 to 15 birds present on the feeding pad, dominated numerically by juncos (≥ 50% of birds present). Only flocks stable in size with normally feeding birds were presented with playbacks. There was at least a 7-min period between one playback and the next. This time between playbacks allowed ample time for the study species to return to a calm state before being exposed to another stimulus (the birds usually resumed feeding within 20 sec). The typical time elapsed between stimuli playbacks was 7-10 min, sometimes longer when proper target situations were slow to develop. During this time, there was typically much turnover of birds that visit the feeding pad. Despite the large number of playbacks at each site over the course of this study, there was little indication of habituation to any of the stimuli presented.

Video Recording and Analysis

Behavioral responses to stimulus presentations were recorded for subsequent analysis with a Panasonic HC-W570 digital video recorder from within the observational blind. Birds typically responded to most stimuli with a sudden and synchronous partial flush (involving only a portion of the flock) or complete flush (100% of flock) to cover. Thus, my main metric for characterizing responses was the proportion of the flock that flushed to cover. This proportion focused on this first wave of synchronous flushes (with exception of the dog stimuli; see below). The birds that did not flush to cover invariably adopted a distinct alert or vigilant/freezing posture for a few seconds. This vigilant posture is easily distinguishable from the brief scans that such birds make while feeding, which are usually under 0.5 s in length (Bednekoff and Lima 1998). These "frozen" birds often subsequently flushed to cover as well, but I conservatively refer to them as non-flushing birds. I also characterized the destination of each immediately flushing bird. Individual flushes to cover were categorized as exposed or interior. Exposed flushes refers to birds who flew to perches on the exterior or exposed top portions of the cover pile. Interior flushes involved flight into the interior, safest portion of cover. Following these immediate or delayed flushes to cover, I determined the time elapsed for the first, second, and third individual to return to feeding.

Certain sound stimuli consistently failed to produce flushes. To characterize the behavioral response to such stimuli, I determined the proportion of birds that became vigilant (frozen posture) during the stimulus presentation. This metric is only useful when no flushes occurred, since two or more flushing birds invariably elicited freezing in the birds that did not immediately flush (Lima 1995). I analyzed responses to the terrestrial threat (dog stimuli) by characterizing the initial and secondary responses to the looming stimuli (see below for details).

Statistical Analyses

My study used unmarked birds, since leg bands (the only practical marking technique) would be obscured by belly feathers on many days due to heat-saving postures adopted by birds (Carr and Lima 2012). Without knowledge of individual birds, I adopted the approach of characterizing the response to each stimulus presentation (as mentioned above) by the proportion of the flock that flushed, or the proportion of the flock that adopted an alert, vigilant posture, depending on the stimulus presented. These measures were assumed to be an independent estimate of the behavior of the groups of birds visiting my study sites. This is a reasonable approach, given that the birds routinely entered and departed the feeding pad on a minute-to-minute basis, thus producing an ever-changing array groups present during and across sessions. The same group of birds was probably rarely if ever sampled repeatedly, since these birds do not form distinct, stable subflocks across a winter (Roth and Vetter 2008). As such, the statistical results technically apply only to the birds at my study sites, but the populations of birds were not unusual in any way.

My analysis made extensive use of non-parametric (rank-based, distribution-free) statistics because the data were usually markedly and irretrievably non-normal. I used Kruskal-

Wallis tests (Pohlert 2018) for analyses of the tendency for birds to flush to cover or become vigilant across several experimental treatments. Wilcoxon Rank Sum tests (R Core Team 2018) were used for two-sample comparisons. Parametric statistics (ANOVA, t-tests) were used in a few cases when appropriate. All analyses were conducted in Program R (R Core Team 2018). The results were nearly identical across study sites; thus data were pooled over sites in all statistical tests.

EXPERIMENT 1: COMPARISON OF BASIC STIMULI

Rationale

The basic question for this experiment is whether the study species can detect and recognize an incoming attack via only auditory cues of attack. The key stimuli used in this experiment were wingbeat sequences from a sharp-shinned hawk (SSHA), a red-tailed hawk (RHTA), dark-eyed juncos (DEJU), and Carolina chickadees (CACH). I also used the recorded footsteps of a domesticated dog as a simulated, terrestrial threat. Other stimuli used were background noise and simulated woodpecker drumming.

If the study birds can distinguish auditory cues by flight noises (wingbeats), then their collective responses should reflect the relative danger implied by each. Predatory wingbeats should elicit stronger behavioral responses than non-predatory stimuli. Expected stronger responses include larger proportions of flock flushing to cover, longer return times, and greater increases in vigilance (in the event of no birds flushing to cover). Furthermore, I expected the sparrows to respond more strongly to a sharp-shinned hawk wingbeats than those of the red-tailed hawk. Sharp-shinned hawks and red-tailed hawks represent differing levels of threat to the target species. Red-tailed hawks have a diet that consists primarily of mammals and larger bird species (Preston and Beane 2009), whereas sharp-shinned hawks prey entirely on small birds like sparrows during the winter (Roth et al. 2006).

The sounds of a dog walking and running in leaf litter should imply the approach of a terrestrial threat. I recorded these sounds such that they are looming, auditory stimuli in which the sound intensity grows as the playback proceeds to completion. I expected the sparrows to respond more strongly and quickly to the dog-running stimulus than to the dog-walking stimulus, since the former represents a more immediate threat. Responses such as increased vigilance rather than quick flight to cover might also be expected, since a moving mammal does not pose the same danger as a flying raptor.

This experiment used DEJU and CACH flight recordings as non-predatory wingbeat stimuli. Carolina chickadees sometimes feed in the same environment as the target species, and should thus be familiar to the target sparrows. Juncos are the primary study species of this experiment, and they undoubtedly hear DEJU wingbeat sounds very often. The sparrows at my site should presumably be much less responsive to these stimuli, as compared to the predators. However, the DEJU and CACH wingbeat sequences could nevertheless indicate an incoming threat to the target species (Hingee and Magrath 2009, Boujja-Miljour et al. 2017). Nevertheless, the departure of a single conspecific (as per my stimuli) should be less threatening than multiple, simultaneous departures (Lima 1995, Lima and Zollner 1996).

Two control sounds were used in this experiment, which should evoke few antipredator responses. One was a woodpecker drumming sound that the sparrows were likely to hear within their environment. The other control sound was the unavoidable noise embedded in the “background” of the hawk recordings, a mechanical hum (from an airhandling system) sound that is likely not routinely heard by the sparrows.

All stimuli, except the dog-derived stimuli, were played at two sound levels, soft and loud. Here, I expect heightened behavioral responses to loud stimuli than to soft stimuli. Soft stimuli (50 dBA) were not much louder than the external environment at each site (roughly 45 dBA) and, thus, should be more difficult for the sparrows to discern from the environmental noise at each site. I suspect, however, that approaching predators would strive to keep their sound production in the soft range, hence these stimuli are directly relevant to my overall goals.

Sampling

During December 2017, Carolina chickadee and dark-eyed junco wingbeat recordings were obtained by placing the microphone set-up immediately adjacent to a 1 x 1 m feeding platform. These recorded departures were normal, unprovoked departures that occurred when a bird simply left the feeder. The microphone was generally 0.5 m away from the departing birds. Two clear recordings from different individuals were used from each species. Only a single, unprovoked departure was involved in these stimuli. The wingbeat frequency was 21 beats s^{-1} in CACH sequences and 16 beats s^{-1} in DEJU sequences.

I recorded wingbeat sequences from an adult female RTHA and a juvenile SSHA. Both birds were held for purposes of falconry by local falconers. Hawks were recorded as they flew from one perch to another, covering a distance of 10 m. The hawks flew in the direction of the microphone, the auditory scenario that the study species would likely experience during an attack. The playback recordings covered only the end of a flight. I used two clear recordings from each individual hawk. These recordings were about 1.5 s in length, the RTHA frequency was about 7.5 beats s^{-1} and SSHA was 9 beats s^{-1}.

A 17 kg dog served as a representative terrestrial predator. These stimuli were recorded by placing the microphone set-up at the end of a lane (12 m long) of dry leaf litter and having a dog walk or run down the lane towards the microphone set-up. This simulates an approaching terrestrial animal, one moving slowly and the other rapidly. The dog was on a leash and the owner was setting the pace by walking/running beside the dog in a cleared lane to prevent human footsteps from being recorded. Two clear recordings were used for each of the slow and fast stimuli. These recordings ranged from 5 s for running to 10 s for walking. These stimuli varied in volume from 46 dBA at the start to 63 dBA at the end.

The woodpecker stimulus was a 1 s playback of simulated woodpecker drumming. This playback was manufactured by tapping sharply on a small, hard cardboard box. A single tap was multiplied using Adobe Audition to a sequence of taps set to the 19 taps s^{-1} of redbellied woodpeckers (Shackelford et al. 2000). This woodpecker is a common bird near my study sites. To human ears, this recording is a realistic and rather startling noise, especially when played relatively loudly. Background noises found in recordings of hawk wingbeats were isolated and converted to their own playback stimulus. Two clear recordings were used for the playbacks of this control stimuli, each 1 s long. This control sound was played only at the loud setting (see below).

Stimuli were played at two sound intensities that were designated as “soft” and “loud”, corresponding to 50 and 60 dBA sounds. Decibels are measured on a logarithmic scale, thus a 10 dBA difference is a distinctly noticeable difference (at least to humans). In the field, 50 dBA was clear and could be heard, but was somewhat faint. In contrast, 60 dBA stimuli could be heard easily over the general environmental noise. Such differences appear to be perceived similarly by the sparrows.

All of the above stimuli were presented during each observation session, in a randomly arranged order. During a session, a given stimulus was played only at one of the two specified sound intensities. I also played only one of the two dog approaching stimuli (fast or slow tempo) during a given session. The sequence of stimuli played within a given session was randomized using a random number generator. Once the sound/tempo levels were determined for a session at a given site, the opposite sound/tempo levels were used during the next session at that site. After this second session, a new randomized sequence was determined and the process repeated. This experiment covered 34 sessions, yielding 17 observations for each stimulus at a given sound intensity; 17 observations were also produced for each speed (slow and fast) of the dog-based stimuli.

As mentioned above, the main behavioral response metric was mainly the proportion of the flock that flushed to cover, or the proportion that became vigilant in a situation with no birds flushing to cover. For the looming, dog-based stimuli, we characterized the first (immediate) and secondary behavioral response for each individual on the pad. The first response was either vigilance or an immediate flush to cover. The second response (for those not flushing immediately) was dictated by the second movement that each individual made after the first response was recorded. These secondary responses were recorded as “vigilant” if they simply remained vigilant for the entire playback, “fly” if they flew to cover, “run” if they ran/hopped to cover and “enhanced vigilance” for birds that jumped on top of visual obstructions but otherwise remained vigilant. As before, the statistical approach focused on the proportion of birds adopting these various behavioral options.

Results and Discussion

The results suggest that hawk wingbeats elicited the strongest behavioral responses, and that relatively loud stimuli elicited uniformly stronger responses than the soft stimuli. The proportion of the flock that flushed to cover in response to each wingbeat stimulus is shown in Figure 1 (loud presentations) and Figure 2 (soft presentations). For loud stimuli, complete flushes typically followed loud hawk presentations. Complete flushes were seen in 65% of SSHA wingbeat presentation and 53% of RTHA wingbeat presentation. Partial flushes to loud hawk playbacks generally involved more than 75% of the flock to flush to cover. There was, however, no obvious or statistical differences in the responses to the two hawk stimuli (Wilcoxon Rank Sum test, W = 130, p = 0.588), indicating that both were equally “scary”.

Loud DEJU and CACH wingbeats also elicited several complete flushes to cover (in 41% and 29% of presentations, respectively). Compared to hawks, there was a greater tendency for incomplete flushes, especially apparent in response to CACH playbacks. There was no statistical difference between flush responses to the CACH and DEJU stimuli (Wilcoxon Rank Sum test, W = 175, p = 0.287). Responses to pooled hawk stimuli were generally greater when compared to pooled responses of the DEJU and CACH stimuli (Wilcoxon Rank Sum test, W = 729, p = 0.0497). The study birds were nevertheless responsive to non-hawk stimuli, at least when played at a relatively loud sound level. As mentioned above, even non-hawk wingbeat sequences could indicate an incoming attack (Lima 1995, Hingee and Magrath, 2009), and perhaps a loud playback indicates a more powerful flight response indicative of a true escape flight.

In response to soft stimuli (Fig. 2), the sparrows were also more likely to flush to cover in response to hawk wingbeats than CACH or DEJU wingbeats, but complete flushes were generally not observed. The birds were more responsive to SSHA than RTHA, but the difference was not statistically significant (Wilcoxon Rank Sum test, W = 127, p = 0.493). Responses to DEJU and CACH stimuli were broadly similar, with most cases involving no birds flushing (Fig 2). Comparing hawks pooled to DEJU-CACH pooled, there was a significantly stronger tendency for more flushing in response to hawk wingbeat sequences (Wilcoxon Rank Sum test, W = 698.5, p = 0.0489).

Considering only cases in which birds showed vigilance in response to soft stimuli but none flushed (Fig. 3) reveals clearer differences among responses to different wingbeat stimuli (Kruskal-Wallis test, chi-squared = 12.794, df = 3, p = 0.0051). A greater proportion of non-flushing birds adopted an alert, vigilant posture in response to soft SSHA stimuli (Fig. 3). The same held in response to RTHA wingbeats, but to a lesser extent (with 2 cases of no overt response). The difference between the two hawk stimuli was not statistically significant (Wilcoxon Rank Sum test, W = 69, p = 0.529). Several cases with no overt response were seen to DEJU and especially CACH soft stimuli, although responses to DEJU and CACH were not significantly different (Wilcoxon Rank Sum test, W = 129, p = 0.0579).

Control stimuli rarely elicited more than a vigilance response. Loud control stimuli – background hawk-recording noise or woodpecker drumming – evoked some flushing in only 1 of 17 presentations of each (data not shown). The response to the woodpecker control was a bit surprising, since the sudden hammering sound is fairly startling to a human observer. Considering the many cases without flushes, birds showed a tendency to become vigilant in response to the loud woodpecker drumming, sometimes with 100% of flock members doing so (Fig. 4). Still, many birds seemed to ignore the drumming. Loud background noise continued to evoke little behavioral response, even at the level of vigilance.

Return times (time to resume feeding after complete flushes to loud stimuli) tended to be longer in response to the hawk stimuli (Fig. 5), but the differences between means were not statistically significant (ANOVA, F = 1.313, df = 3, 28, p = 0.29). However, a direct comparison of responses between the SSHA and CACH treatments indicated significantly shorter return times following the latter stimulus (two sample t-test, t = 2.6, df = 14.9, p = 0.019). The birds generally resumed feeding within 20 s following a complete flush and, often within 10 s. Once in cover, they were alert and surveyed their surroundings. Apparently, they quickly assess the situation as safe, regardless of the nature of the sound stimulus.

The response to the walking and running dog stimuli were qualitatively different to those of wingbeats, hence I analyze their effects separately. Recall that these two stimuli have a looming nature, with the crackling noise of leaves starting soft but steadily increasing in volume over several seconds. Thus, the birds' responses varied over time during a stimulus presentation, and I examine the first and second responses of the sparrows.

The vast majority of first responses involved the adoption of a vigilant (frozen) posture by all birds in a flock. Such first-response vigilance followed 88% of the dog-walking presentations and 77% of the dog-running presentations. In 2 of 17 and 4 of 17 cases for the walking and running dog stimuli, respectively, at least one bird's first response was to flush to cover. In all such instances, only a minority of flock members flushed as their first response.

However, the time elapsed between the start of the playbacks and first responses differed substantially between walking and running stimuli (Wilcoxon Rank Sum test, W = 251.5 p = 0.0002, Fig. 6). The rapidly increasing volume of the running stimulus yielded a response within 1 s, whereas the birds' first overt vigilance response to the walking stimulus generally occurred within about 1 – 2.5 s. A faster auditory, looming sound clearly elicited a faster vigilance response. Overall, the crackling sounds of leaves got the attention of all feeding birds, and at rates far beyond the control stimuli.

The second response to the terrestrial threat (considering only cases/flocks with no flushing as first response) involved four distinct behaviors, and thus a much greater variety of responses than seen for other stimuli. As before, birds often flew to cover. Vigilance as the second response was defined as a bird remaining vigilant during the entire stimulus playback. Two other unique responses were observed. Running to cover occurred when a bird ran (hopped) to cover instead of flying to cover. Enhanced vigilance occurred when an already vigilant bird jumped up onto the nearby visual obstructions (10 cm in height), presumably to obtain a better look at its surroundings.

The distribution of these four, secondary responses differed between the two dogrunning stimuli (Fig. 7). Flying to cover was a prominent secondary response in response to both dog-walking stimuli, but was significantly greater in response to the running dog (Wilcoxon Rank Sum test, $W = 81$, $p = 0.0291$). A primary source of this difference was a much greater tendency to simply remain vigilant for the entire duration of the playback of the walking-dog stimulus. Enhanced vigilance was also a frequent observation in response to the walking dog, being recorded in 8 out of 15 relevant presentations; this behavior was observed in only two presentations of the running dog. The tendency to run to cover was about the same across the two stimuli. Overall, the dog-running stimulus was clearly perceived as more threatening, and the great majority of birds went directly to cover (flying or running) on their second response.

These results suggest that the dog-based stimuli were perceived as an approaching threat, but not one that required an immediate, maximal response. This interpretation is most obvious in the dog-walking stimulus, to which many birds simply stayed alert on the pad during the entire playback rather than move to cover. The enhanced vigilance responses also suggest that the birds recognized the dog footsteps as a terrestrial animal, one that they attempted to see better by jumping up onto the visual obstructions. Such responses were never observed in wingbeat playbacks, and would be a particularly maladaptive response to an attacking hawk. Flushes to cover were also different between the dog-based and wingbeat playbacks. In response to dog-based stimuli, birds tended to flush to the highest exposed branches or similar branches on side of cover, likely for a better view. In contrast, wingbeatdriven flushes caused birds to go deeper into the center of cover (data not shown).

EXPERIMENT 2: NUMBER AND CADENCE OF HAWK WINGBEATS

Rationale

Based upon the results of Experiment 1, I explored further the most evocative of stimuli, the SSHA wingbeat sequence. A basic question here is just how many wingbeats it takes for the birds to recognize the possible threat of an incoming hawk attack. The quick recognition of a predator would be necessary for a bird to gain any sort of advantage in such a high-speed predator-prey interaction. Perhaps one wingbeat is not enough to elicit much of a response, but 2 or 3 wingbeats should suffice (e.g., Lima 1994).

In this experiment, wingbeat playbacks consisted of one isolated wingbeat, or two or three wingbeats in a natural sequence. I expected that the birds' responses would be stronger as the number of wingbeats increased. I also varied the cadence of wingbeats by slowing them to 33% and 50% of the natural SSHA frequency of 9 beats s^{-1}. I classified these modified cadences as medium and slow, respectively. I expected that the regular, naturally-paced stimuli would be the most evocative, whereas the longest pacing would have the lowest response rate.

Sampling

Using Adobe Audition C66, I first extracted a clean sequence of three natural wingbeats from the two SSHA recordings used in the first experiment. From these, I further extracted two consecutive wingbeats and one isolated wingbeat. Spacing was then added between wingbeats to produce the two slower cadences. The natural, unaltered wingbeat cadence is 9 beats s^{-1}. This cadence was slowed to a medium pace of 6 beats s^{-1} and then further to a slow pace of 4.5 beats s^{-1}. The wingbeats themselves were unaltered, but there was extra time inserted between beats. For the slower cadences, noise that was between natural wingbeats of the original recordings was used for between-wingbeat spacing to simulate a natural wingbeat noise to the extent possible. The alternative (not implemented) was empty space between beats, which produced a sound more mechanical than natural.

I played the resulting stimuli in random sequences in each of 20 sessions conducted from February 17 through March 13, 2018. I played 5 stimuli at each playback session in a randomized order. I ordered the stimuli in a way such that after every third playback session, each stimulus would have been played twice. The result over 20 sessions was 14 presentations of each stimulus.

Results and Discussion

A natural cadence of 2 or 3 wingbeats elicited an obviously stronger behavioral responses than the slower cadences or a single beat? (Fig. 8, Kruskal-Wallis test, chi-squared

= 19.366, df = 5, p = 0.0016). These multiple-beat stimuli often led to complete or nearly complete flushes. Three natural wingbeats were more evocative than 2 wingbeats (Fig. 8), but the difference was not significant (Wilcoxon Rank Sum test, W = 105.5, p = 0.74), suggesting that 2 or 3 wingbeats with a natural cadence are enough to be perceived consistently as a threat. One wingbeat alone was clearly not enough to consistently evoke strong responses, although there were several complete or nearly complete flushes to a single wingbeat.

Another clear result in Figure 8 is the nearly equivalent flushing response across all stimuli excluding the normal-cadence multiple-wingbeat stimuli (Kruskal-Wallis test, chisquared = 0.839, df = 4, p = 0.9332). Multiple-wingbeat stimuli slowed to 50% or 33% of the natural cadence produced results essentially identical to a single wingbeat. This result suggests that the birds may have perceived the slowed cadences of wingbeats as single wingbeats or perhaps not a sequence of wingbeats. Nonetheless, these altered stimuli still occasionally elicited complete flushes to cover (Fig. 8).

I could not prepare faster-than-normal cadences without altering the wingbeats themselves, thus I do not know whether the birds are simply more responsive to increasingly faster cadences of hawk wingbeats. However, I note that the faster wingbeat cadence of chickadees (21 beats s^{-1}) and juncos (16 beats s^{-1}) were not inherently more evocative than the natural SSHA frequency of 9 beats s^{-1} (Figs. 1-3). I suspect that the faster cadence of the CACH and DEJU stimuli signifies (in part) their less threatening nature.

EXPERIMENT 3: SPECTRAL ATTRIBUTES OF HAWK WINGBEATS

Rationale

In this experiment I addressed further the salient features of the sharp-shinned hawk wingbeat in evoking behavioral responses in the emberizid sparrows. I focus specifically on the range of sound frequencies that are necessary to evoke a significant response by the sparrows.

How much of the SSHA wingbeat can an emberizid sparrow hear? The SSHA wingbeat covers a range of frequencies from under 200 Hz to about 18 kHz, with greater power in the lower frequencies below about 3–4 kHz (Fig 9). However, emberizid sparrows closely related to those in my study have hearing that is increasingly poor below 2 kHz (Schwartzkopff 1955, Beason 2004). This fact suggests that the birds respond mainly to the spectral portion of a SSHA wingbeat that is above 2 kHz. It is nevertheless conceivable that the lower frequency sounds are important to wingbeat stimulus recognition.

I thus modified natural SSHA 3-wingbeat sequences to remove key ranges of frequencies to determine whether part or all of the spectral frequencies are needed for a maximal response. Specifically, I used 2 kHz and 4 kHz frequency cutoffs, keeping only sound above or below each selected frequency. The 2 kHz cutoff (as per Schwartzkopff 1955) addressed the question of whether the low range frequencies are important in predator detection. I used a cutoff at 4 kHz to determine whether a greater sweep of low-frequency sound influences responsiveness to wingbeats. I expected that the sparrows would respond to the 2 kHz and above wingbeats similarly to the full, natural wingbeat, based on the auditory sensitivity of emberizid sparrows (see Beason 2004). I additionally expected less responsive to the 4 kHz cutoff stimuli, as both of these stimuli would presumably be perceived as irregular or odd wingbeats.

I also explored the spectral frequency of dog footsteps (see Experiment 1), and whether a hawk-equivalent stimulus could be created from dog footsteps. A single dog footstep in leaves has much power above 3 kHz (well within the hearing range of sparrows), and otherwise resembles a hawk wingbeat in sound, timing and spectral frequency. Conceivably, part of the responsiveness to dog footsteps might reflect some similarity to hawk wingbeats.

Sampling

Using Adobe Audition, I created the following 5 stimuli (see Fig. 10).

1) A natural, unaltered three wingbeat sequence that encompasses the full frequency of sound in the SSHA recording;
2) A wingbeat sequence consisting of frequencies 2 kHz and above. This range of frequencies is presumably that most easily heard by the birds;
3) A sequence with only frequencies under 2 kHz, which are those presumably less audible to the birds;
4) 4 kHz and above, prepared as per the 2 kHz stimulus, but with a higher cutoff;
5) Below 4 kHz, which are lower frequencies but apparently at least in part within audible range of the birds.

I also created a “3-wingbeat” version of dog footsteps in dry leaves (the “dog-to-hawk” stimulus), to determine whether the birds can distinguish between dog steps and SSHA wingbeats when each is presented similarly. A dog-to-hawk stimulus was made in Adobe Audition by isolating three, single footsteps and merging them to match the timing of the 3

SSHA wingbeat sequence (Fig. 11). To the human ear, this dog-to-hawk stimulus sounds like (or “similar to”) a natural hawk wingbeat. This could also be the case for the sparrows, if their hearing is poor below 2 kHz. Each stimulus created for this experiment had two different playbacks for presentation one from different hawk wingbeat sequences.

All 6 resulting stimuli were played during each playback session, in random order, alternating between study sites. Sessions ran from 15–28 March 2018 with a total of 12 sessions. Measurements were made once again to ensure that all stimuli were presented at 60 dBA, or “loud”. As per Experiment 2, my principle behavioral metric was the proportion of the flock that flushed to cover when exposed to the various auditory stimuli.

Results and Discussion

The natural wingbeat stimulus, with its full frequency range, elicited the strongest behavioral response. The response to the complete wingbeat stimulus is obviously greater than that to all other stimuli (Fig. 12). The birds did not react very strongly to the above-2kHz stimulus, despite the likelihood that this stimulus is in the main hearing range of the birds (Beason 2004). However, they were uniquely unresponsive to the below-2-kHz stimulus. Note, however, that the birds often showed a complete or nearly complete vigilance response to the below-2-kHz stimulus, indicating that they could hear the playbacks (data not shown). These results suggests that the full-spectrum wingbeat stimulus is needed to consistently evoke flush responses. Accordingly, the above and below 4 kHz stimuli produced relatively low-level reactions, which did not differ significantly (Wilcoxon Rank Sum test, W = 53.5, p = 0.284). The responses to the above-2-kHz, above-4-kHz and below-4-kHz stimuli were statistically indistinguishable (Kruskal-Wallis test, chi-squared = 1.41, df = 2, p = 0.495, Fig. 12).

While primarily composed of high frequency noise, the dog-to-hawk stimulus never elicited a strong flush response (always under 50% flush). Overall, responses to the dogtohawk stimulus did not differ statistically from the other high frequency stimuli of 2 kHz above

(Wilcoxon Rank Sum test, W = 70.5, p = 0.953) and 4 kHz above (Wilcoxon Rank Sum test, W = 67.5, p = 0.812). Thus, even though the dog footsteps were modified to fit the same pacing and encompassed much of the natural wingbeat frequency, the birds were able to quickly discriminate this particular stimulus from the natural wingbeats.

GENERAL DISCUSSION

Overall, the results suggest that predator/threat recognition by birds can be based entirely on non-vocal auditory cues of incoming threats. Of the stimuli presented to the birds, hawk wingbeat sequences generally elicited the strongest responses. This result was clear in the response to the loud stimuli presentations. However, when these stimuli were played softly, the results are perhaps the clearest with flushes (the strongest behavioral response) was primarily seen in the hawk wingbeat sequences. Vigilance responses to the soft stimuli were strongest to the hawk stimuli, especially sharp-shinned hawk stimulus. This result clearly shows that soft hawk stimuli received the bird’s attention. These results probably explain, in part, why *Accipiter* hawks like SSHA complete ambush attacks in a slow glide whenever possible (Lima, S.L., pers. obs.). Even though a hawk is generally not in view of the targeted prey in the late stages of an attack, a few wingbeats could alert the prey to the attack. The importance of detecting such stimuli, however, could explain why vigilance in prey birds is elevated in noisier environments that might mask soft auditory cues (Quinn et al., 2006). I expected that the study birds would be more responsive to sharp-shinned hawk than red-tailed hawk wingbeats, but there was not much solid evidence that the birds distinguished between the two hawk stimuli. The sharp-shinned hawk-based stimuli, however, always evoked the greater response.

Sparrows were generally responsive to wingbeats, which could signal attacks in different ways. Wingbeat stimuli from Carolina chickadees and dark-eyed juncos, to some extent, caused immediate flushes to cover. This was especially true for loud presentations of wingbeats. These stimuli could indicate an attack detected by a nearby conspecific or heterospecific, as documented in other avian systems (Hingee and Magrath 2009). It seems likely that loud noises would generally be interpreted as a nearby threat that would demand some attention. Nevertheless, even soft sharp-shinned hawk wingbeats nearly always generated a response, even if only an alert scan of the environment. Soft chickadee and junco wingbeats stimuli evoked relatively few responses, perhaps indicating that a distant conspecific/heterospecific departure may not be of immediate importance to the birds. It is also likely that birds can discriminate small from large birds by wingbeats s^{-1} and the relative brevity of the wingbeats themselves; chickadee and junco wingbeat rates were about double that of the sharp-shinned hawk.

The details of hawk wingbeats were also clearly important in threat recognition. A brief sequence of 2 or 3 natural-cadence wingbeats usually caused complete flushes to cover. A single hawk wingbeat was less effective, but also evoked several large-scale flushes. These findings suggest that more than one wingbeat sound is essential for full identification of a threat. Slowing down the wingbeats lowered their effectiveness in evoking flushes to about that of a single wingbeat. The full frequency spectrum of wingbeats also appeared to be important in threat recognition; all partial-spectrum wingbeats were much less evocative. This result was somewhat surprising, since the above-2-kHz stimulus incorporates the frequency range most audible to sparrows. There was no tendency to flush in response to the below2kHz wingbeat stimulus, which presumably was enriched in inaudible wingbeat sounds. There may be more power in the low frequency range of a natural wingbeat, but this low frequency range in itself is clearly not enough to elicit responses.

Not all potential threats are aerial predators. The results suggest that juncos and other sparrows can distinguish the approach of a terrestrial threat, as simulated by an approaching dog. Such threats are not as dangerous as hawks, and the birds' responses were unlike those to hawk wingbeat stimuli. The birds' first response was almost invariably to become alert and assess the environment. During slow approaches, alertness was the only response for many birds during the entire playback. Other birds jumped onto the visual obstructions for a better view. Many flushes to cover ended with birds up on top of cover rather than in cover, where they too have a better view. This enhanced vigilance response strongly suggests that birds were not expecting an aerial predator. My attempt to create a hawk-wingbeat stimulus from dog footsteps failed to produce a large effect, although weak partial flushes often occurred (with no enhanced vigilance responses). Overall, it seems that footsteps are distinctly different from wingbeats, with the distinction being made very quickly by the birds, likely due to the lack of spectral power in the low-frequency range. Other terrestrial noises, such as twigs snapping, nearby scratchy noises, rustling leaves, etc., are likely to be perceived as similarly non-threatening.

In the bigger picture of predator detection, vision almost certainly plays a dominant role in small birds. This fact is reflected in their large investment in visual vigilance while feeding (Bednekoff and Lima 1998), as demonstrated across a large phylogenetic range of birds (Beauchamp 2015). It is clear that birds also have the ability to quickly discriminate (visually) predators from non-predators (Fuchs 2012). Nevertheless, such threatening visual stimuli are also associated with auditory stimuli, which I have demonstrated are sufficient to generate full-blown escape responses. Acoustical vigilance, or time and effort devoted specifically to detection of auditory signals of danger, also seems likely to occur, but this phenomenon has received almost no attention (but see Quinn et al. 2006). This type of vigilance is likely to be seen in noisy eaters, like sparrows, whose seed crunching, undoubtedly affects their hearing. Acoustical monitoring of the environment has likely shaped behavior of both avian prey and their predators over evolutionary time.

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FIGURES

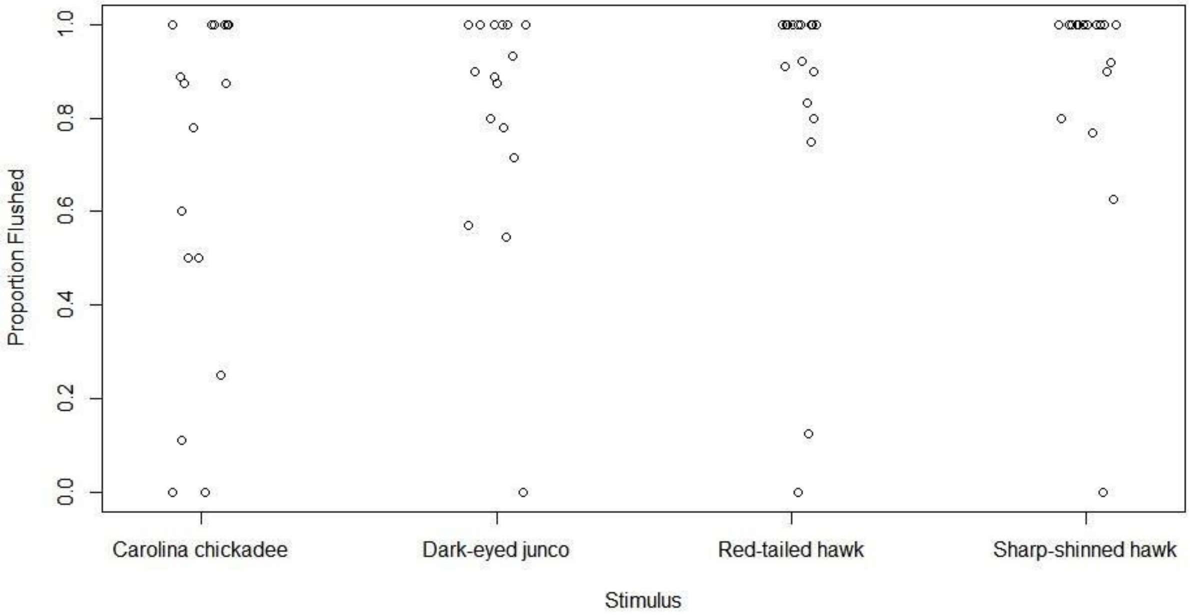

Figure 1. Proportion of the flock to flush when presented with loud wingbeat stimuli.

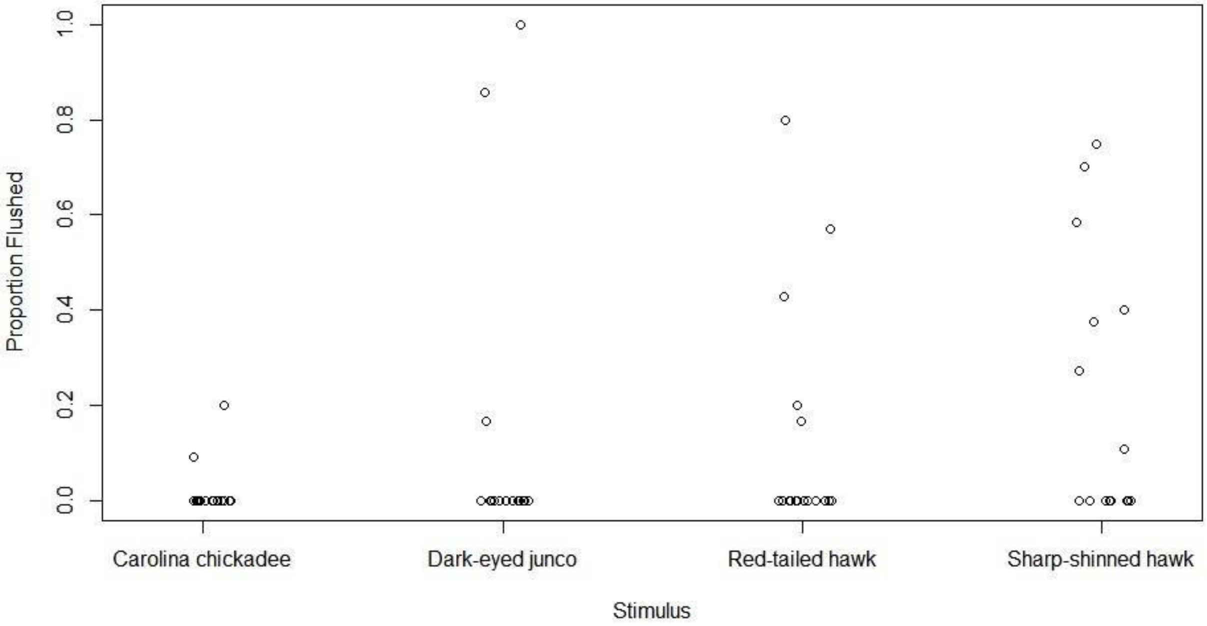

Figure 2. Proportion of the flock to flush when presented with soft wingbeat stimuli.

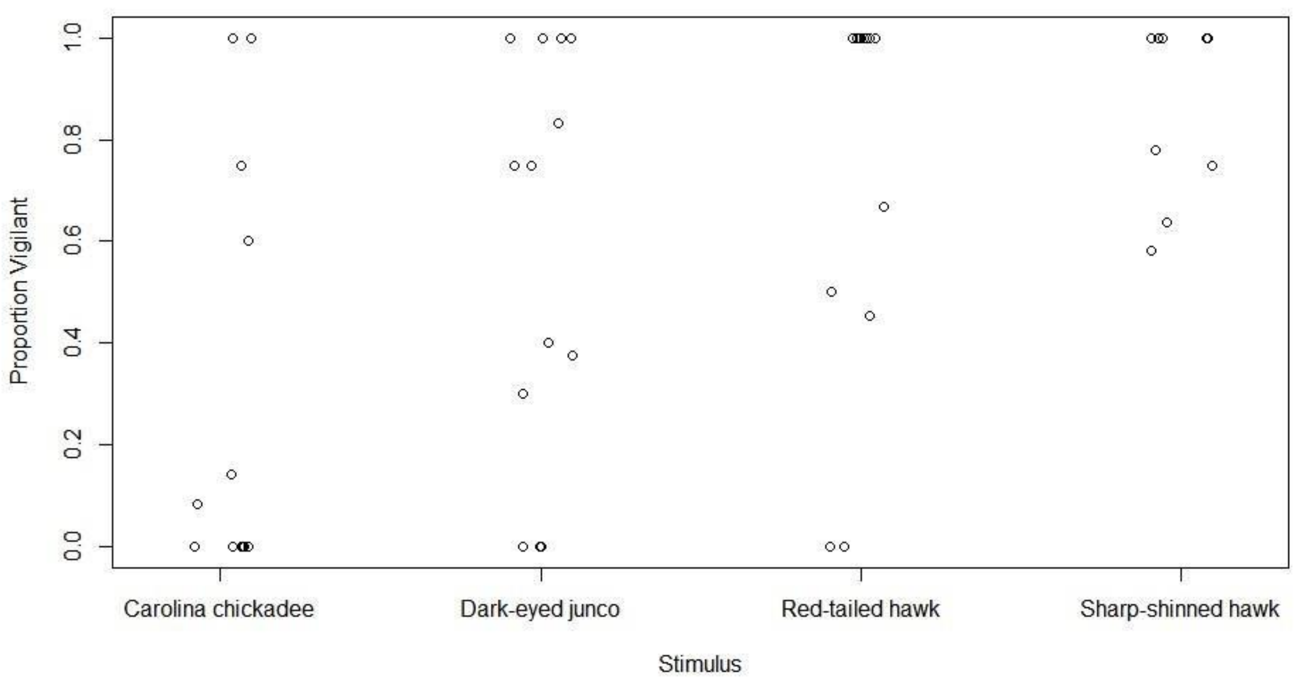

Figure 3. Proportion of flock to become vigilant when presented with soft stimuli. Included are only those cases in which a stimulus did not evoke a flush response (partial or complete).

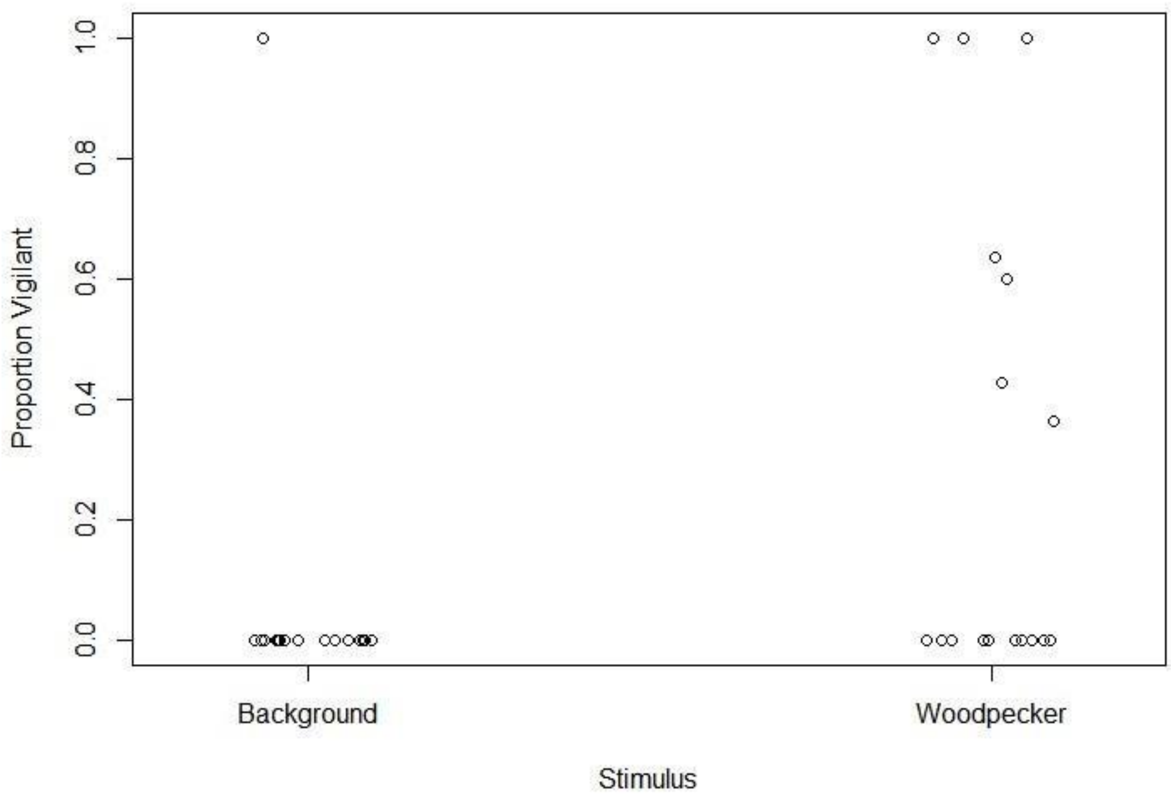

Figure 4. Proportion of flock vigilant when presented with a loud, control stimulus. These data are from cases in which the stimuli do not produce a flush response in the flock (partial or complete).

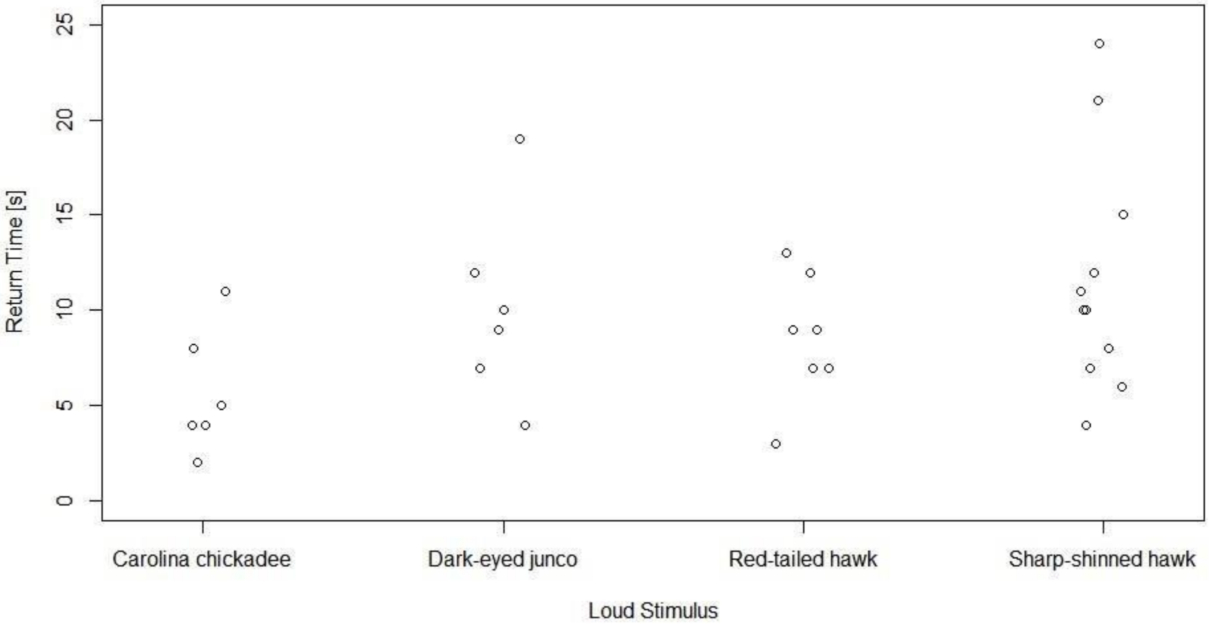

Figure 5. Time for the first bird to return to the feeding pad after a complete flock flush, driven by a loud stimulus.

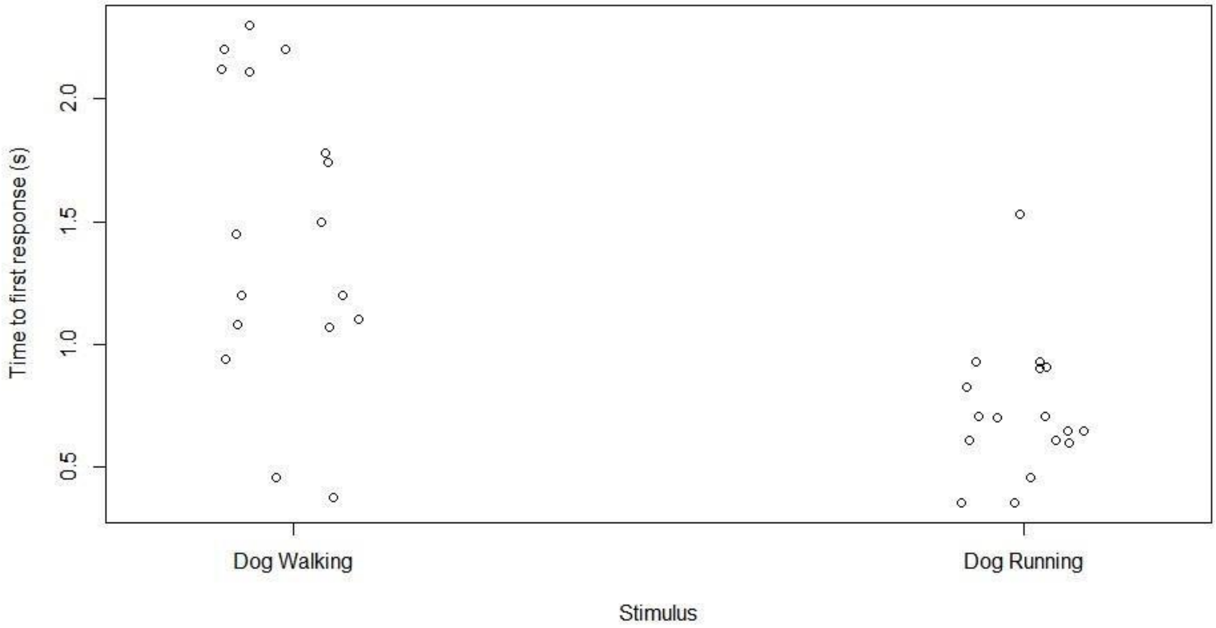

Figure 6. Time after the start of a playback for the first response to be elicited by dog-based stimuli.

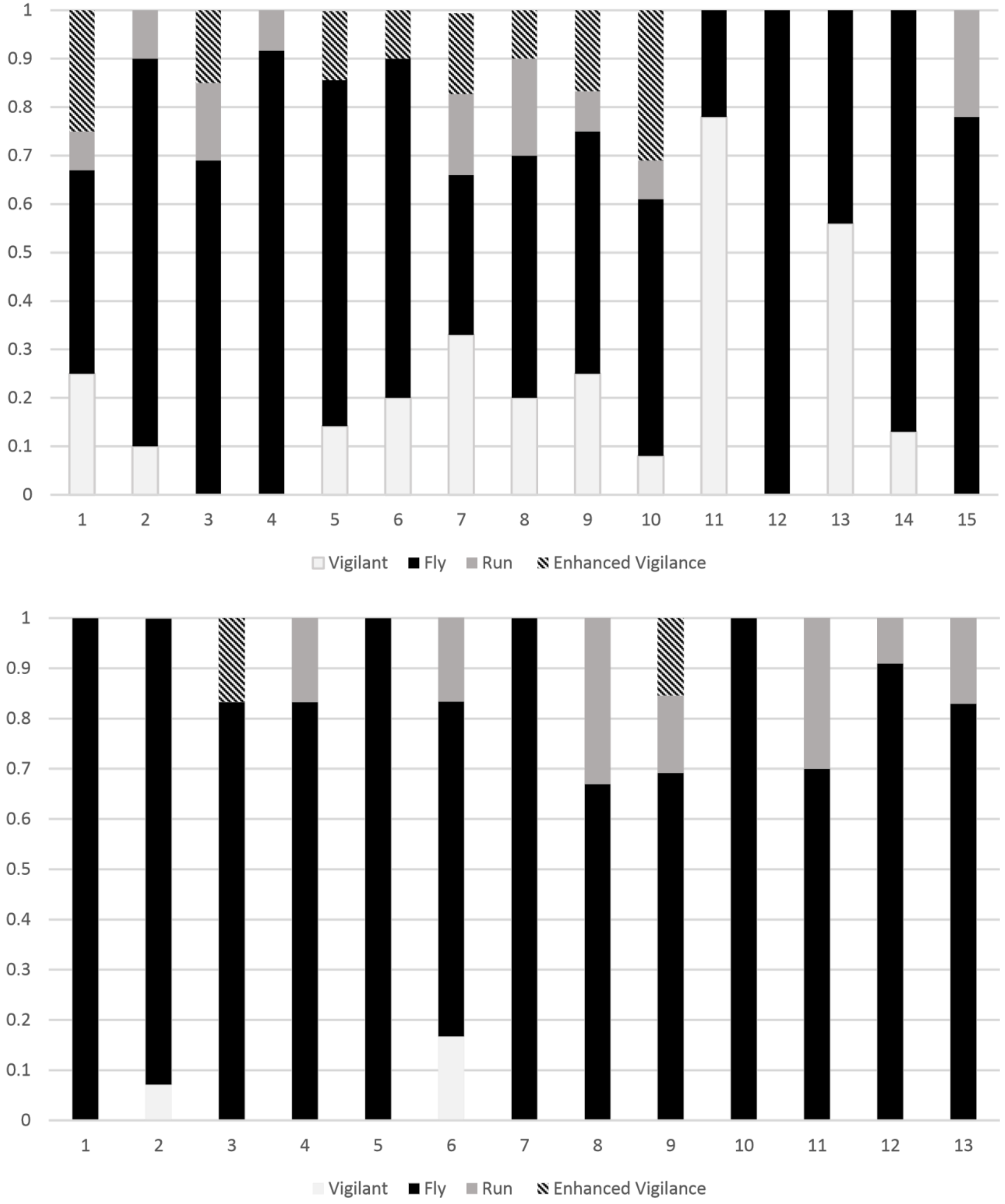

Figure 7. Second responses within the flock when presented with the (top) dog-walking stimulus and (bottom) dog-running stimulus. These data include only cases in which the first response of all flock members was a vigilance posture (no flushes). Each set of bars indicate the proportion of a targeted flock that adopted a given behavior. Numbers on x-axis refer to individual flock/playbacks.

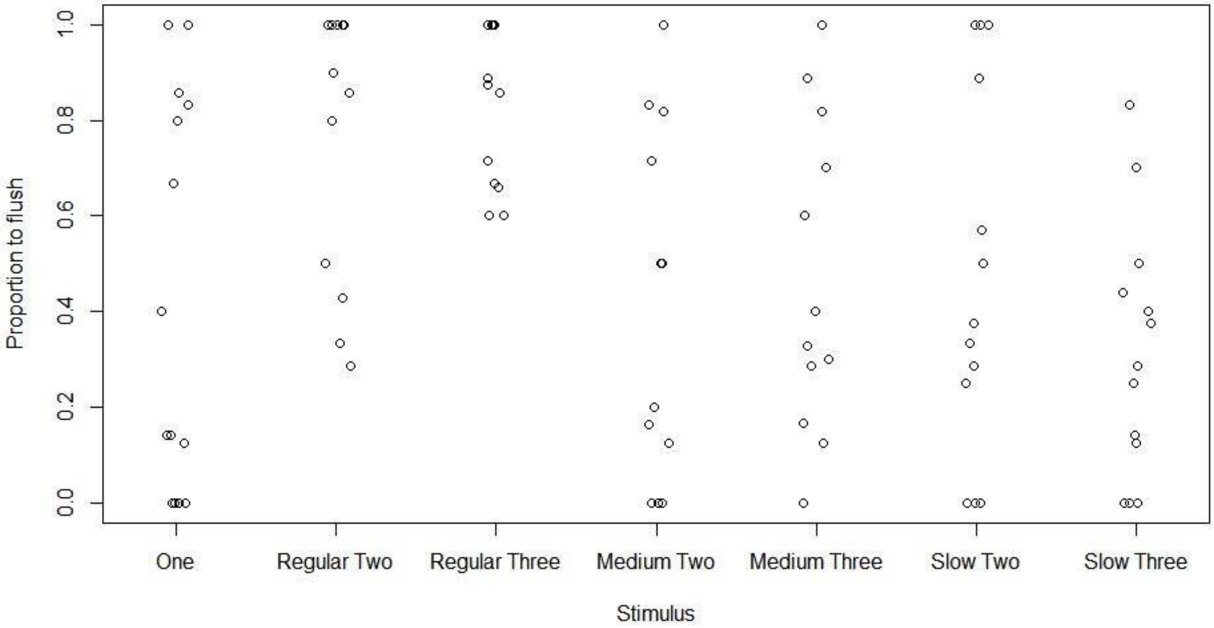

Figure 8. Proportion of the flock that flushed to cover when exposed to wingbeat sequence that differ in number and cadence. “One” represents a solitary wingbeat. “Regular two” and “regular three” are two and three wingbeat sequences with a natural cadence of 9 beats s^{-1}.

“Medium two” and “medium three” are wingbeat stimuli slowed by 33%; “slow two” and “slow three” were slowed by 50%.

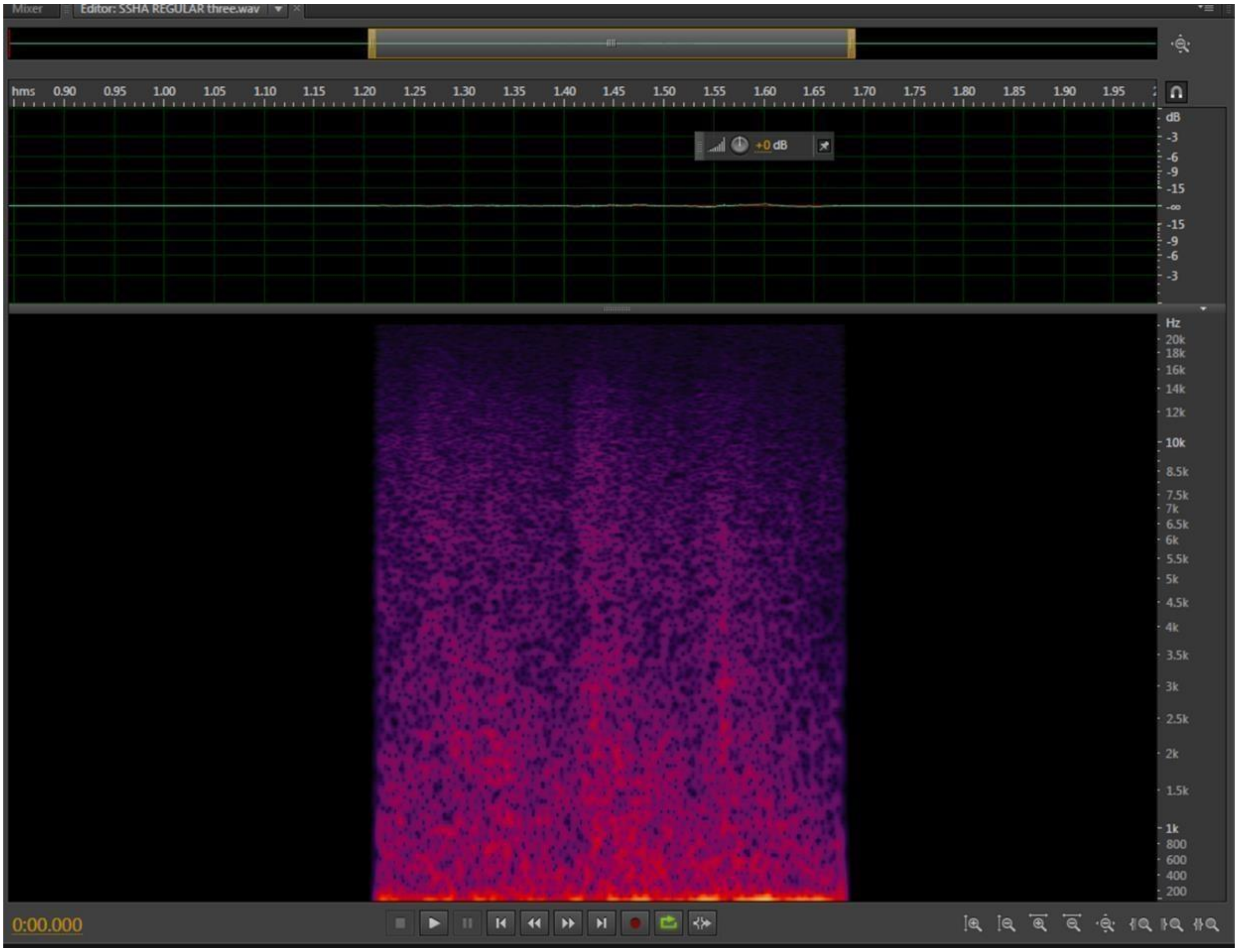

Figure 9. Spectral display of the three-wingbeat sharp-shinned hawk stimulus at a naturalcadence. Frequencies of the wingbeats range from 200Hz-18kHz, with most of the power (brighter coloration) between 200Hz and 2kHz. Figure generated from Adobe Audition C66.

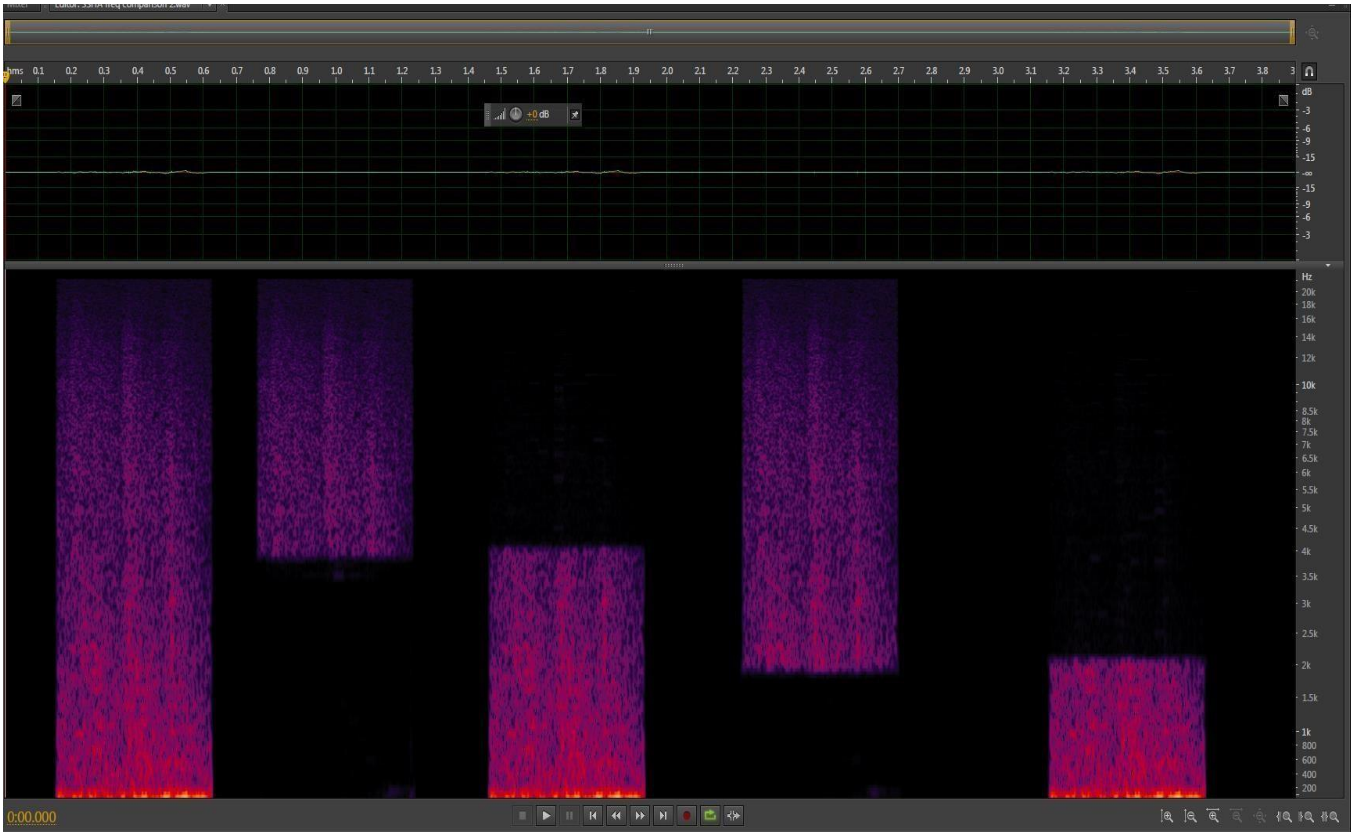

Figure 10. Spectral display of the five stimuli created for Experiment 3. From left to right: three natural wingbeats, 4 kHz and above, 4 kHz and below, 2 kHz and above, 2 kHz and below. All are based on three wingbeats in a natural cadence. Figure generated from Adobe Audition C66.

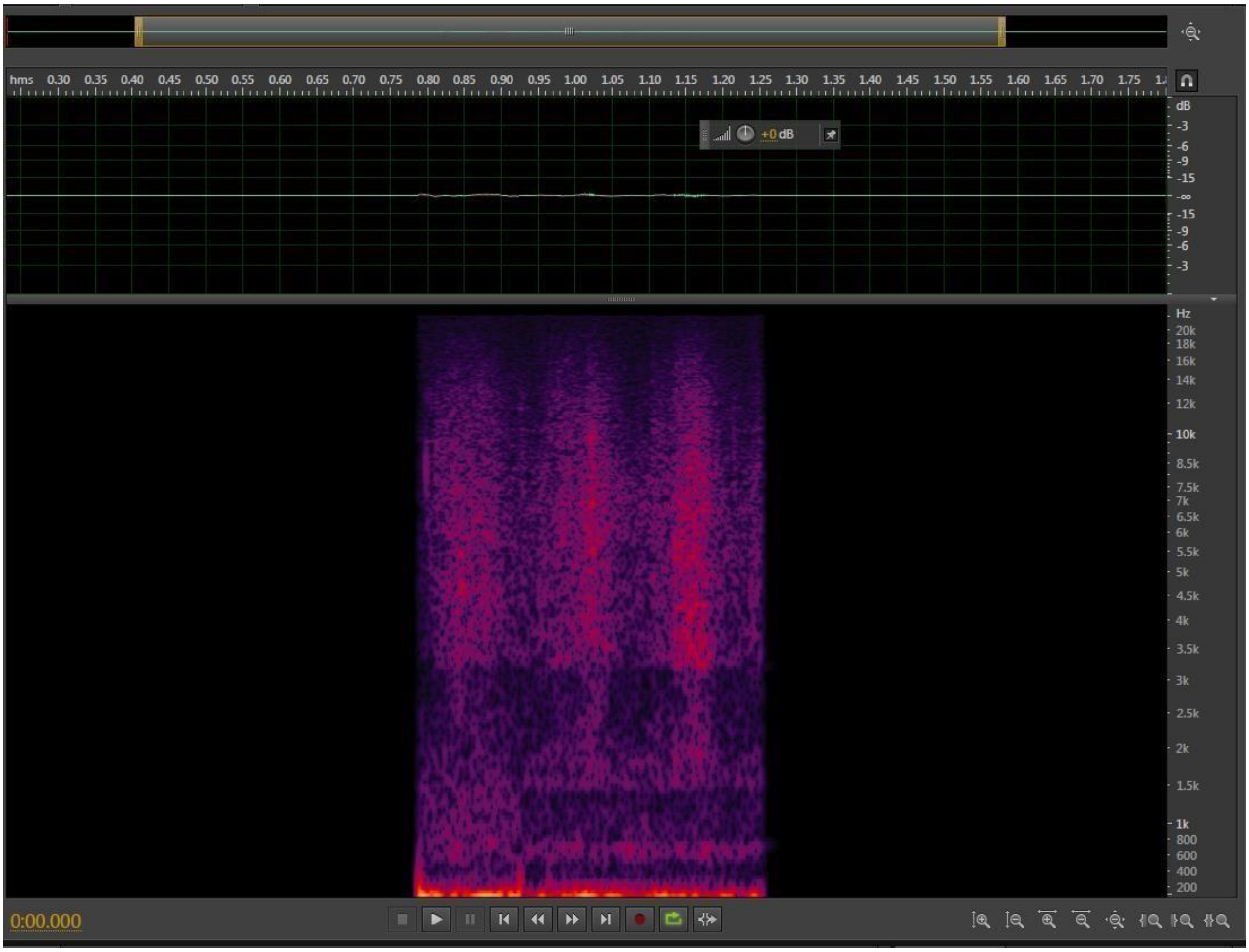

Figure 11. Spectral display of the dog-to-hawk stimulus created in Adobe Audition C66. Note color intensity above 3 kHz, indicating relatively little power in the lower frequencies.