

White-Crowned Sparrow respond to the alarm calls of local species but do not discriminate among them

KATHERINE ZISKA^{1,2}, DANIEL BLUMSTIEN^{1,3}

¹ Rocky Mountain Biological Laboratory, Gothic 81224, Colorado, USA

² Department of Fundamentals: Texts and Issues, University of Chicago, Chicago 60637, Illinois, USA

³ Department of Ecology & Evolutionary Biology, University of California Los Angeles, Los Angeles 90095, California, USA

Abstract

Eavesdropping is recognizing and gleaning information from a communication intended for someone else. Eavesdropping on alarm calls can benefit eavesdroppers by decreasing the time they spend allocated to vigilance, giving them more time for other behaviors such as foraging. Although there have been many studies done on eavesdropping on heterospecifics among birds, there have been few studies on migratory birds and their ability to learn heterospecifics alarm calls of local species in their breeding ranges. We conducted a playback on white-crowned sparrows (*Zonotrichia leucophrys oriantha*) using alarm calls from Lincoln's sparrows (*Melospiza lincolnii*), yellow-bellied marmots (*Marmota flaviventris*), gray jays (*Catharus minimus*), American robins (*Turdus migratorius*), and white-crowned sparrows to try and understand if they listened to these acoustically variant alarm calls and gained any different information from each of them. We found that while sparrows responded to all playbacks, they did not discriminate amongst treatments. Thus, sparrows obtain general information about threats in their territories but do not respond in ways consistent with the alarm calls providing differential information about these threats. We speculate that fledglings probably learn the alarm calls of local species before migration, and remember them when they return to breed themselves.

KEY WORDS: Alarm call, heterospecifics eavesdropping, mountain White-crowned sparrow, migration

INTRODUCTION

Interspecies interactions are seen when individuals from two species interact with each other such that there are positive (+), negative (-), or neutral (0) consequences for one or both participants. Mutualism (+/+) or commensalism (+/0) is commonly seen among many species of birds and mammals when they respond to heterospecific alarm calls (Shriner 1998; Magrath et al. 2007). For example, superb fairy-wrens (*Malurus cyaneus*) and white-browed scrubwrens (*Sericornis frontalis*) have a mutualistic relationship because they respond in a graded, risk-based way to one another's alarm calls (Fallow & Magrath 2010). Birds can also respond to heterospecific alarm calls by unrelated species. For example red-breasted nuthatches (*Sitta canadensis*) respond to chick-a-dee alarm calls, which is an example of commensalism as there is no evidence that black-capped chickadees (*Poecile atricapillus*) respond to nuthatch's alarm calls (Templeton & Greene 2007).

Responding to other species' alarm calls may be beneficial because individuals can allocate less time to monitoring predators because they can rely on others to alarm if they see a predator approaching (Bell et al. 2009; Radford et al. 2011; Ridley et al. 2013). A recent review by Magrath et al. (2015) states that 70 vertebrate species have been experimentally shown to respond to heterospecifics alarm calls, making eavesdropping a widely practiced survival strategy. There are two mechanisms by which animals could respond to other species' calls: they could respond to acoustically similar alarm calls or they could learn the calls of another species (De Kort & Ten Cate 2001; Ghirlanda & Enquist 2003).

How much of the ability to respond to heterospecifics is a result of learning and how much is innately recognized by birds is difficult to isolate. There is evidence that birds and mammals can learn alarm calls that are dissimilar to their own (Griffin et al. 2005; Vitousek et al. 2007; Magrath et al. 2008, 2009; Ito & Mori 2009). There are also studies that have shown that birds may be innately predisposed to recognize and respond to sounds that are acoustically similar to their own (Marler 1957; Davies et al. 2005; Fallow et al. 2011, 2013; Randler 2012). But it is not as clear-cut as similar sounds are innately responded to and dissimilar sounds must be learned. Superb fairy-wrens respond to white-browed scrubwrens only when they live sympatrically, but do not respond to white-browed scrubwrens when they do not live together despite the similarity of their alarm calls (Magrath et al. 2008).

Mammals and birds can learn to recognize heterospecific alarm calls throughout their lives. (Vieth et al. 1980; Shriner 2001; Griffin 2004; Nocera et al. 2008). In birds, fledglings can learn rapidly and it takes young white-browed scrubwrens only a few weeks, to respond to heterospecifics alarm calls with as much accuracy as adults (Haff & Magrath 2013). It has also been shown that birds can adapt their responses to familiar alarm calls if they learn that the alarm call is unreliable (Nocera & Ratcliffe 2009). For instance, captive European blackbirds (*Turdus merula*) can learn to recognize an enemy through cultural transmission if they perceive mobbing call choruses from conspecifics or heterospecifics (Curio et al. 1978; Vieth et al. 1980).

Migratory birds face a unique problem: they winter with one set of species and breed surrounded by another. Thus, if they are to benefit from a heterospecific alarm call

network, they may have to learn to respond to other species or they must respond to acoustically similar alarm calls or those with specific acoustic attributes. Since there is evidence that birds actively learn and distinguish heterospecific alarm calls throughout their lives, it would seem likely that migratory birds would be able to adapt to new environments and integrate into local alarm call networks. Although there have been studies on alarm call networks in established mixed-species bird flocks (Dolby & Grubb 1998; Goodale & Kotagama 2005, 2008), there are few studies on alarm call networks on migratory birds that do not flock during the breeding season. The studies that do investigate migratory birds tend to focus on stop over locations with familiar heterospecific alarm calls (Reudink et al. 2007; Nocera & Ratcliffe 2009).

Only a few studies have investigated migratory birds ability to learn and integrate into local mobbing networks with unfamiliar alarm calls. For instance, Nearctic-Neotropical migrant species (Swainsons' thrush (*Catharus ustulatus*) ovenbird (*Seiurus aurocapilla*), Kentucky warbler (*Geothlypis Formosa*), wood thrush (*Hylocichla mustelina*), and gray-cheeked thrush (*Catharus minimus*) typically inspect antipredator mobbing of heterospecifics to discover local predators (Nocera et al. 2008). However, it has not been shown that migrants learn from such interactions. Migrants rarely join mobs if they are passing through, because they risk their own safety without receiving a reward because they have nothing to protect in that area (Nocera et al. 2008). Being able to identify local predators at one's breeding site is likely to have both personal and direct fitness consequences, and we are not aware of studies that specifically addressed migrant birds listening to non-mobbing alarm calls as fledglings and then being able to reintegrate into the alarm call system once they return to breed themselves.

We studied the response of a migratory population of white-crowned sparrows (*Zonotrichia leucophrys oriantha*) to a set of heterospecific alarm calling species during their breeding season. At our Colorado study site, sparrows migrate in as the snow melts in May and establish territories and breed. They live in close proximity with a number of species that emit alarm calls but do not overtly compete with them, including American robins (*Turdus migratorius*), gray jays (*Perisoreus Canadensis*), and yellow-bellied marmots (*Marmota flaviventris*). They have overlapping territories and compete for resources with Lincoln's sparrows (*Melospiza lincolni*). Of these species, marmots and jays produce the loudest alarm calls and could potentially serve as a long-distance alarm. White-crowned sparrows likely share aerial predators with the birds (raptors), and, because they nest on the ground, terrestrial predators (foxes, coyotes) with the marmots. By selecting species of different sizes and with acoustically different alarm calls, and broadcasting calls to the sparrows, we asked the following questions. First, do sparrows respond to other species' alarm calls? We asked this on two time frames, immediately upon hearing a call, and over one minute following playback. Second, do sparrows differentially respond to alarm calls? If so, can we interpret these differential responses as being associated with the relative information value to sparrows?

MEATHODS

We studied the responses of white-crowned sparrows to broadcast alarm calls and a control white-crowned sparrow song in the East River Valley in and around the Rocky Mountain Biological Laboratory (RMBL) from 13 June to 12 July 2018. This is when

males are courting females and defending territory, which makes them easier to find and ensures there is little pseudo replication, as territories remain fairly stable. We conducted our playback experiments between 05:30 and 10:30 because the morning chorus makes it easy to find singing males and there is typically little to no wind or other atmospheric disturbance.

Playback Stimuli

We broadcast alarm calls from five different species to the sparrows: white-crowned sparrows, American robins, gray jays, Lincoln's sparrows and yellow-bellied marmots (Figure 1). We also used white-crowned sparrow song as a positive control. We elected to not include a negative control because a previous study using the same methods found no response to a tropical kingbird (*Tyrannus melancholicus*) song (Connover et al. unpublished data). Robin, jay, Lincoln sparrow and white-crowned sparrow alarm vocalizations were sourced from Xeno-Canto (<http://www.xeno-canto.org>), while we used previous recordings we had made of white-crowned sparrow song and yellow-bellied marmot alarm calls. We selected five high quality (high signal:noise ratio) exemplars for each species except for the American robin for which we selected four high quality exemplars. Each exemplar was normalized using Audacity 2.1.0 (www.audacityteam.org/) and edited into a playback stimulus and saved as an AIF file. All stimuli began with 30 s of silence, the broadcast stimulus, followed by 60 s of silence. Stimuli were stored and broadcast on an Apple iPhone 7 (Apple Inc., Cupertino, CA) and broadcast through an Anker Soundcore Sport XL Outdoor Portable Bluetooth Speaker (Anker Innovations., San Francisco, CA). We calibrated playback amplitude so that each exemplar was broadcast at 85 dB measured at 1 m using a digital sound level meter (Radioshack 33-2055, weighting level A, peak response).

Playback protocol

A single observer conducted all experiments. The observer walked slowly through suitable habitat (in and around willows, *Salix* spp., and corn lilies, *Veratrum californicum*). By walking through different parts of the valley on different days, the opportunity for pseudoreplication was avoided. When a sparrow was identified the observer approached to within 15 m and began the playback, dictating quietly behavioral transitions into a digital recorder. The first 30 s quantified baseline behavior; the 60 s following the playback quantified the response. Our ethogram included 9 behaviors and was modified from (Slaughter et al. 2013) (Table 1). If a bird flew away during the baseline period, we aborted the playback. For each successful playback we recorded the date and time, GPS location, cloud cover, wind speed on the Beaufort scale, whether there were any heterospecifics or conspecifics within 10 m of the focal subject, the height of the bird off the ground, as well as the initial response to the broadcast sound. Following a playback the observer moved at least 40 m away so as to avoid both acoustic carry-over effects and to ensure that the next subject was a different individual (Ralph & Pearson, 1971; Patterson & Petrinovich, 1978). Playbacks were broadcast in a Latin Square design to reduce any impact of carry-over effects. To avoid acoustic interference we avoided habitat next to quickly flowing water and only conducted playbacks when the wind was 0-3 on the Beaufort scale. We scored the recorded behavioral transitions using JWatcher 1.0 (Blumstein & Daniel, 2007) and used JWatcher to calculate time budgets.

We used ArcGIS 10.5 (ESRI 2017, Redlands, CA) to calculate the distance between playbacks and removed a playback from our data set if it was within 40 m of another one so as to avoid pseudoreplication. Because distance to road and distance to nearest building accounted for significant variation in sparrow breeding behavior and behavioral responses in previous studies (Connover et al. unpublished ; Crino et al. 2011; Dietz et al. 2013), we used ArcGIS to calculate the distance to road, distance to forest edge, distance to the nearest marmot colony, distance to trail, and distance to the nearest building.

Did the sparrows respond differently immediately following playback?

To ask if sparrows varied their initial response, we performed a contingency table [analysis](#). We first defined three levels of the first response as high, medium, and none. High included fly and chink (chinks are alarm calls). Medium was defined by looking, and none was defined as no reaction. We calculated Chi-square test and standardized residuals (i.e., cell Chi-square values) using SPSS v. 24 ((IBM, New York, NY).

Did the sparrows respond differently on a longer time scale?

We used JWatcher (Blumstein & Daniel, 2007) to calculate the proportion time in sight allocated to looking, flying, vocalizing, relaxed behavior (vocalization + walking + preening + foraging) for the 30 s baseline time bin and in 15 s intervals following playback and in 30 s intervals following playback. To standardize each individual's responses, we subtracted the post-playback response from the baseline response and plotted these changes in time allocation as a function of the playback treatment. After exploring responses graphically, we elected to conduct formal analyses using 30 s time bins because this is where we saw the most variation [and the time bins used in previous analyses of white-crowned sparrows](#) (Blumstein et al. 2004)).

Our formal analyses involved first plotting means and 95% confidence intervals of the difference from baseline for each of our behavioral categories. Any deviation from 0 would indicate that sparrows responded to the playback. For those time intervals where sparrows responded to the playback, we fitted general linear models [\(in SPSS\)](#) to see if they differentially responded to the different stimuli. If the models were significant, we calculated Fisher LSD post-hoc tests to explore which treatments were significantly different. We did not control for multiple comparisons.

Testing for confounding factors

We tested for potentially confounding factors by fitting [general linear models](#) on the following variables: day of year, height of bird, distance to speaker, wind speed, cloud cover, number of conspecifics within 10 m, number of heterospecifics within 10 m, distance to road, distance to forest edge, distance to marmot colony, distance to trail, distance to building, and distance to nearest playback. If these did not vary systematically by treatment, they could not be confounding.

RESULTS

We conducted a total of 122 playbacks in total: 20 for each category except for white-crowned sparrow song, which had 22. Thirteen of these playbacks were conducted

less than 40 m away from the nearest playback. To avoid pseudoreplication we eliminated these, which reduced our sample size to 109 playbacks: 19 white-crowned sparrow songs, 18 white-crowned sparrow alarm calls, 19 American Robin alarm calls, 19 gray jay alarm calls, 18 Lincoln's sparrow alarm calls, and 16 yellow-bellied marmot alarm calls. We found that the baseline time allocation did not differ significantly as a function of stimulus type (all p-values > 0.32), except for looking (p = 0.032). To control for this difference and, more importantly, to permit us to identify response to the playback, all analyses are conducted on the change in time allocation from baseline time allocation.

Did the sparrows respond differently immediately following playback?

While the overall contingency table suggests that sparrows responded differently to the playback (p = 0.011), none of the standardized residuals for the cells in the contingency table significantly deviated from that expected by chance (all cell Chi-square values < 1.96). Thus, we conclude that sparrows' immediate response to broadcast sounds was similar across treatments.

Did the sparrows respond differently on a longer time scale?

By examining the average $\pm$ 95% C.I. response to playback, we found that sparrows responded to broadcast heterospecific alarm calls (Figure 2). In the first 30 s following playback, sparrows engaged in significantly more time allocated to flying in response after hearing white-crowned sparrow song and grey jay alarm calls. Sparrows engaged in significantly less time allocated to vocalizing in response to hearing grey jay alarm calls. Sparrows engaged in significantly less time allocated to relaxed behavior following grey jay alarm call playback. In the second 30 s following playback, sparrows allocated significantly less time to looking after hearing white-crowned sparrow song as well as in response to alarm calls from American robins, gray jays, and yellow-bellied marmots. They also engaged in significantly more relaxed behavior in the second time bin after hearing American robin alarm calls.

While these results show that sparrows *responded* to some of the playbacks, the results of our analysis of responses using general linear models shows that they did not *differentially* respond to playbacks (vocalizing 0-30 s: p = 0.233; relaxed 0-30 s: p = 0.0153; relaxed 30-60 s: p = 0.593; looking 30-60 s: p = 0.201). There were significant differences in the time allocated to flying in the first 30 s following playback (p = 0.032), and post-hoc tests identified significant difference from white-crowned sparrow song to alarm calls from American robins (p = 0.027) and yellow-bellied marmots (p = 0.021), from American robins to white-crowned sparrow song (p = 0.027) and gray jay alarms (p = 0.013), from gray jay to American robin (p = 0.013) and yellow-bellied marmot alarm calls (p = 0.010), and from yellow bellied marmot and gray jay alarm calls (p = 0.010) to white-crowned sparrow song (p = 0.021) (Figure 2).

Testing for confounding factors

Our results were not confounded by other factors that could explain variation in response. None of the covariates we recorded differed significantly between stimulus categories (day of the year--p = 0.935; height of bird--p = 0.168, distance to speaker--p = 0.783, wind velocity--p = 0.695, cloud cover--p = 0.997, number of conspecifics within

10 m— $p = 0.793$, number of heterospecifics, within 10 m— $p = 0.671$, distance to road— $p = 0.235$, distance to forest edge— $p = 0.815$, distance to marmot colony— $p = 0.968$, distance to trail— $p = 0.701$, distance to building— $p = 0.869$, or distance from nearest playback— $p = 0.493$).

DISCUSSION

Taken together, our evidence is consistent with the hypothesis that white-crowned sparrows have a generalized heightened response to heterospecific alarm calls for a set of birds and a mammal with which they live. Because the calls that we used were acoustically quite diverse (Figure 1), and because white-crowned sparrows return to the place they were born to breed, we speculate that these birds may have learned heterospecific alarm calls as fledglings. This is a more likely hypothesis than learning it upon arriving at the breeding grounds as fledglings are at a much higher risk of predation and must learn alarm calls quickly in order to survive (Haff & Magrath 2013).

A notable finding was that white-crowned sparrows reacted to alarm calls by allocating less time to looking 30-60 s after the alarm call. This result matches that in Blesdoe and Blumstein (2014), in which they found that the main responses of white-crowned sparrows to white noise and downward frequency jump was that 30-60 s after playback the sparrows spent less time allocated to relaxed behaviors. This might reflect observer's creating a ceiling effect—there was no immediate response because observers had already triggered heightened vigilance by approaching to conduct the experiment. Over time, as the observer silently recorded a subject's behavior, sparrows became habituated to their presence. All else being equal, we would assume that the rate of habituation should be a constant as the observer was an equal distance away. Thus, it was the experience of hearing an alarm call that modified the longer-term response and permits us to interpret the response 30-60 s following playback.

Furthermore, white-crowned sparrows reacted similarly to the song of a conspecific as they did to alarm calls, implying the response to an intruder is the same whether it is a predator or competitor. This may be explained by the need to defend their territories. Breeding sparrows engage in considerable territory defense and upon detection, males respond by chasing the intruder out of the territory.

The results are not explained merely by alarm call duration where we might expect longer-duration stimuli might elicit heightened responses. White-crowned sparrow song was our longest stimulus and although sparrows spent more time flying in response to song and the gray jay alarm calls, we found no evidence that they discriminated them from the other stimuli. So although these sparrows listen to a diverse range of alarm calls, they are not obviously responding in a way that suggests that some species' calls are more reliable or informative than others.

Some species are known to differentiate between reliable and unreliable alarm callers on a species, as well as individual level (Hare & Atkins 2001; Blumstein et al. 2004; Magrath et al. 2009). Some callers are less reliable than others and this can result in either an increase in alertness, as in yellow-bellied marmots, or a decrease found in Richardson's ground squirrels (*Urocitellus richardsonii*) (Hare & Atkins 2001; Blumstein et al. 2004). The only behavioral differences in response that we found was that sparrows flew more in response to white-crowned sparrow songs and gray jay alarm

calls than to American robin alarm calls and yellow-bellied marmot alarm calls. However, if sparrow and jay calls were more reliable, we would have expected to see heightened responses to more of the behaviors we examined and patterns of discrimination to be more consistent. However, our findings suggest the contrary.

On the other hand, the sparrow's generalized response may be due to universal caller unreliability. The species we chose have partially overlapping predators with white-crowned sparrows. This makes them all partially unreliable alarm callers, making it necessary for the sparrows to assess the risk themselves by flying to investigate and maintaining heightened vigilance for a longer period of time. Yellow-bellied marmots also spend more time verifying risk themselves upon hearing an unreliable alarm (Blumstein et al. 2004).

Rainey et al. (2004) found that yellow-casqued hornbills (*Ceratogymna elata*) discriminated between Diana monkeys (*Ceropithecus diana*) leopard (*Panthera pardus*) and crowned eagles (*Stephanoaetus coronatus*) alarm calls by vocalizing and moving towards the playback significantly more in response to the monkey's eagle alarm call and the eagle shriek. The species we used in our study have not been shown to have unique calls for different predators, it follows that we would not observe discrimination from the white-crowned sparrows. Rainey's et al. study found flying as a response to an alarm call, which is also observed in the following studies: De Kort & Ten Cate 2001; Goodale & Kotagama 2008; Fallow et al. 2011, 2013; Haff & Magrath 2013. Therefore, white-crowned sparrows may be able to discriminate information encoded into alarm calls that discriminate predators, however further research is needed.

Furthermore, discriminating among alarm calls might not be important for migratory birds. Another possible interpretation of our results is that white-crowned sparrows generalized response to general alarm calls may be beneficial for migrants, as being able to respond to acoustically dissimilar alarm calls may help them survive in unfamiliar environments throughout their migration. Nocera et al. (2008) found that migrants inspect, but do not often participate in mobbing alarm calls when passing through. They concluded that migrant species may be able to appropriately respond a wider range of species than residence, which respond more to familiar calls. This correlates with our experiment that shows that sparrows respond to a broad range of species.

In summary, white-crowned sparrows have a generalized response to local species that share some predators. Their lack of discrimination could be because of the partial predator overlap and lack of discrimination in the alarm calls themselves. A generalized response to acoustically dissimilar alarm calls could be beneficial to migratory birds in avoiding predation in unfamiliar environments. This is supported by evidence that migrants may have a boarder range of acoustic understanding (Nocera et al. 2008). The local species alarm calls were probably learned as fledglings as there is more selective pressure on fledglings to learn quickly as they are more vulnerable to predation, however more research is needed in order to determine migratory birds capacity to learn acoustically dissimilar alarm calls.

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Table 1. Ethogram of behaviors recorded during play-backs (following Slaughter et al. 2013).

Behavior	Description
Stand and look	On ground or perching, scored each time head moved and fixated
Forage	Moving head towards the ground to find food or having food in beak
Preen	Moving beak through feathers
Walk	Taking steps, moving legs individually
Hop	Jumping from one location to another, scored by each discrete jump
Chink	Chirping, each chirp scored individual
Vocalization	Singing or non-song vocalization, excluding chinks
Flight	Gliding or flapping wings in the air while in sight
Out of sight	No longer visible to observer

Figure 1. Waveform (top) and spectrogram (bottom) of representative exemplars. Spectrogram parameters: Hamming window, 1000 samples; time grid—0 percent overlap, 1000 sample hop size; frequency grid: 1024 DFT, 43.1 Hz grid spacing.

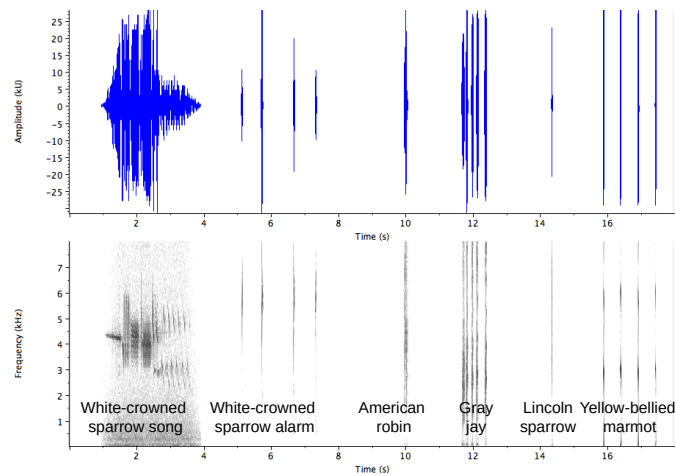
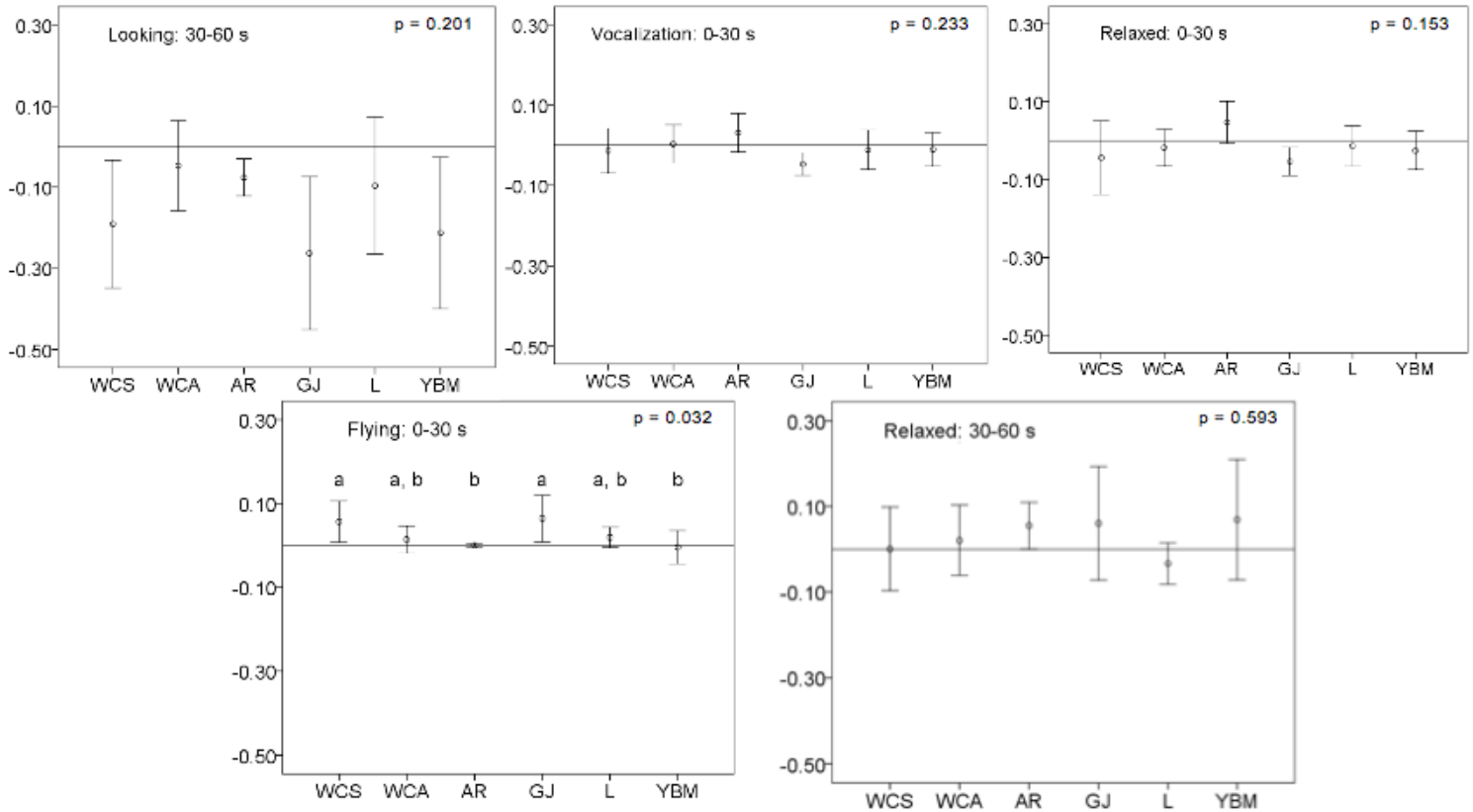


Figure 2. Mean $\pm$ 95% confidence intervals for behaviors that significantly differed from baseline time allocation. WCS=White-crowned sparrow song; WCA=White-crowned sparrow alarm call; AR= American robin alarm call; GJ=gray jay alarm call; L=Lincoln's sparrow alarm call; YBM= yellow-bellied marmot alarm call. When there was evidence of statistically different responses as a function of playback stimulus, we conducted pairwise tests; identical letters illustrate non-significant differences.



Map

Map. Purple numbered dots are playback locations. The red is outlining marmot colonies. White lines are trails.

