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Title: Behavioural responses of Eastern grey squirrels, Sciurus carolinensis, to cues of risk while foraging.

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Abstract: Previous studies have shown that Eastern grey squirrels modify their behaviour while foraging to offset risks of social and predatory costs, but none have simultaneously compared whether such modifications are performed at a cost to foraging. The present study directly compares how grey squirrels respond to cues of these risks while foraging. We simulated social risk and predatory risk using acoustic playbacks of stimuli that grey squirrels might be exposed to at a foraging patch: calls of conspecifics, heterospecifics (competitor and non-competitor) and predators. We found that grey squirrels responded to predator, heterospecific competitor and conspecific playbacks by altering their foraging and vigilance behaviours. Foraging was most disrupted by increased vigilance when we played calls of predators. Squirrels' response to calls of heterospecific competitors did not differ from their response to conspecific calls, and they resumed foraging more quickly after both compared to predator calls: whereas they showed little response to calls of non-competitor heterospecifics and a white noise control. We conclude that squirrels respond differentially to calls made by conspecifics, heterospecific competitors and predators, with the most pronounced response being to calls of predators. We suggest that squirrels may view conspecific and corvid vocalisations as cues of potential conflict while foraging, necessitating increased vigilance.

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01 May 2015

Faculteit Biologie
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For the Attention of: Professor Johan Bolhuis, Editor in Chief,

Dear Professor Bolhuis,

Re: Submission of Research Paper to Behavioural Processes

I hereby submit the revised manuscript entitled "Behavioural responses of Eastern grey squirrels, *Sciurus carolinensis*, to cues of risk while foraging" by K Jayne, S. E.G. Lea and L. A. Leaver for publication as a research paper in Behavioural Processes.

I confirm that all final recommendations for revision have been adhered to as set out by the reviewer in your email dated 14th April 2015.

I look forward to receiving your correspondence in due course.

Yours sincerely

Kimberley Jayne
(Corresponding author).

Revisions based on reviewers comments

Manuscript: Behavioural responses of Eastern grey squirrels, Sciurus carolinensis, to cues of risk while foraging.

Reviewers comment	Revision note
On line 328, a $p<0.05$ is considered non-significant. I assume this is because the authors used an adjusted alpha level due to the Bonferroni correction they applied. It would be good to know what this new alpha level was OR alternatively, if they did the Bonferroni correction the other way around (by multiplying the p-value by the number of tests, so the alpha remains 0.05).	I have now inserted the level of the Bonferroni correction applied.
Line 357: no time by condition interaction with $p=0.051$. Given that there are only 5 white noise playbacks in that analysis, the power of the analysis may be a bit low to detect a significant pattern. Given that such an interaction would make interpretation clearer, I wonder if it would make sense to analyse this again with just the corvids and other passerines...	The data was re-analysed in the manner the reviewer suggested (with just the corvid and the passerine data). However, little difference was made to the outcome of the tests upon the interpretation of the results. Thus we have opted to keep the white noise control condition in our analysis for consistency when compared to the data from season 1.
Line 286: "analysis" instead of "analyses".	Corrected.

Highlights

- We compare behavioural responses by squirrels to cues of risk while foraging.
- Squirrels responded to playbacks by reducing their foraging behaviour.
- Foraging was most disrupted by the perceived presence of predators.
- Response to conspecific calls suggests they viewed them as sources of conflict.
- They were sensitive to auditory presence of corvids that compete for resources but ignored non-competitor species.

Title: Behavioural responses of Eastern grey squirrels, *Sciurus carolinensis*, to cues of risk while foraging.

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Behavioural responses of Eastern grey squirrels, *Sciurus carolinensis*, to cues of risk while foraging.

Previous studies have shown that Eastern grey squirrels modify their behaviour while foraging to offset risks of social and predatory costs, but none have simultaneously compared whether such modifications are performed at a cost to foraging. The present study directly compares how grey squirrels respond to cues of these risks while foraging. We simulated social risk and predatory risk using acoustic playbacks of stimuli that grey squirrels might be exposed to at a foraging patch: calls of conspecifics, heterospecifics (competitor and non-competitor) and predators. We found that grey squirrels responded to predator, heterospecific competitor and conspecific playbacks by altering their foraging and vigilance behaviours. Foraging was most disrupted by increased vigilance when we played calls of predators. Squirrels' response to calls of heterospecific competitors did not differ from their response to conspecific calls, and they resumed foraging more quickly after both compared to predator calls: whereas they showed little response to calls of non-competitor heterospecifics and a white noise control. We conclude that squirrels respond differentially to calls made by conspecifics, heterospecific competitors and predators, with the most pronounced response being to calls of predators. We suggest that squirrels may view conspecific and corvid vocalisations as cues of potential conflict while foraging, necessitating increased vigilance.

Keywords:

Competition; foraging; playback; predation; *Sciurus carolinensis*.

1. Introduction

Grey squirrels frequently forage within a context of conspecifics, heterospecifics (including competitors) and potential predators. Social foraging can benefit the individual in a number of ways, including providing information about optimal foraging conditions and reducing costs associated with predation risk. However there are fitness costs associated with increased competition from social foraging, and there is some evidence to suggest that there might be a trade-off between reducing the risks posed by predation and competition. In the current study we examined whether grey squirrels are differentially sensitive to different cues of risk while foraging, and we looked at how their behaviour is modified in response to social and predatory risks.

1.1. Foraging among conspecifics: the costs and benefits

The social environment can influence an individual's decisions on where and when to forage. Foraging alongside others can benefit individuals by allowing them to more easily locate resources through a process of local enhancement (Adams & Jacobs 2007; Heyes et al. 2000), and informing them about the optimal place to search for food (Galef & Giraldeau 2001). Conspecifics can provide information about when it is safe to forage (Galef & Giraldeau 2001), reduce the need for vigilance during feeding (Lima 1995), and reduce predation risk by dilution (Bednekoff & Lima 1998; Elgar 1989; Galef & Giraldeau 2001; Rausch et al. 2012).

However, social foraging also presents a fitness cost to the forager. Individuals must compete with one another for the same food resources while foraging and during cache recovery, and increased competition can increase the possibility of antagonistic encounters (Gerber et al. 2004). Dominant grey squirrels have been found to use their rank to monopolise a food patch to sequester food to eat and store (Allen & Aspey 1986; Flyger 1955; 1960; Horwich 1972; Koprowski 1996; Pack et al. 1967; Taylor 1966; Thompson 1978). Some grey squirrels will act in ways that help to avoid antagonistic interaction with conspecifics while foraging, such as transporting food away from a food patch (Hopewell et al. 2008), increasing their vigilance levels (Tarigan 1994), or demonstrating alarm behaviour including tail flagging, barking and vigilance which may serve to ward off potential competitors (Partan et al. 2010; Partan et al. 2009). All these behaviours can only be performed at a cost to time spent foraging.

1.2. Foraging among competing heterospecifics: the costs and benefits

Foraging in the presence of heterospecifics that share similar food sources, habitats or predators may have some of the same advantages as foraging with conspecifics. Avarguès-Weber et al. (2013) suggest that heterospecifics could provide as much valuable information as conspecifics. For instance, some sciurids eavesdrop on the alarm calls of sympatric bird species in order to obtain information on predation risk (red squirrel, *Sciurus vulgaris*: Randler 2006a; Eastern chipmunk, *Tamias striatus*: Schmidt et al. 2008). However, fewer studies have investigated whether heterospecifics could enhance information about optimal foraging locations, with the majority of these on invertebrates and birds (Avarguès-Weber et al. 2013), though squirrels are known to forage at the same food patches as other species and compete with them for access (Bekoff et al. 1999; Fisler 1977; Wauters et al. 2001; Wauters et al. 2000).

As with conspecifics, there are disadvantages as well as advantages in foraging with heterospecifics. Corvids live alongside grey squirrels and compete for some of the same resources while foraging and storing food. Some species of corvid could pose a particular threat because they have been demonstrated to possess good observational spatial memory, which can increase their accuracy for locating caches they have seen being made by others (Mexican jays, *Aphelocoma ultramarine*, and pinyon jays, *Gymnorhinus cyanocephalus*: Bednekoff & Balda 1996a; 1996b; Western scrub jays, *Aphelocoma californica*: Watanabe & Clayton 2007). There is also evidence of corvids following grey squirrels and raiding their caches after observing them being made (Vernelli 2013). Two studies have directly investigated the role that corvids might play as competitors for caches. Schmidt and Ostfeld (2008) used playbacks of jay vocalisations at varying distances to simulate pilferage risk to caching grey squirrels. They found that squirrels reduced their effort when recovering cached food if recordings of blue jays, *Cyanocitta cristata*, were played closer to the foraging patch while they were caching. However, when actually storing food, squirrels do not appear to be sensitive to a corvid audience in the same way as they are to a conspecific audience. Leaver et al. (2007) reported that grey squirrels spaced their caches father apart in the presence of conspecifics, and oriented with their backs to conspecifics when caching, but they did not do this when caching in the presence of corvids. They suggest that facing away from corvids while caching may not provide the cache protection advantages that it has to a conspecific audience, given that corvids can fly to observe the caching squirrel from an aerial location. Given that corvids pose similar risks as conspecifics to foraging and caching grey squirrels there are good reasons to expect squirrels to react to them as heterospecific pilferers.

1.3. Predation risk while foraging

A further factor that impacts upon foraging is the threat of predation. Urban grey squirrels are prey to a variety of species including red foxes, *Vulpes vulpes* (Booth et al. 2012; Müller-Schwarze 2009; Rausch et al. 2012), raptors such as red-tailed hawks, *Buteo jamaicensis* (Temple 1987), and domestic animals such as dogs, *Canis familiaris* (Makowska & Kramer 2007). Frequently there is a trade-off between foraging efficiency and reducing predation risk. Grey squirrels engage in anti-predator behaviour, including bipedal vigilance (Makowska & Kramer 2007), and alarm vocalisations (Bakken 1959; Horwich 1972; Lishak 1977; Partan et al. 2010; Partan et al. 2009), all of which can incur a cost to time spent foraging (Makowska & Kramer 2007; Shonfield 2011). Predation risk also affects decisions about where to forage and for how long. In locations where predation risk is high, grey squirrels reduce their foraging time compared to areas under tree canopy or shade (Booth, et al. 2012; Bowers et al. 1993; Brown et al. 1992; Kilpatrick 2003; Newman et al. 1988), and will transport food to eat in an area of cover (Lima & Valone 1986; Lima et al. 1985).

However, often locations that are less exposed to predation also have increased foraging competition. Thus, sometimes individuals forage and cache in locations more exposed to predators in order to avoid interactions with more dominant competitors (willow tit, *Parus montanus*: Ekman 1987;

Koivula et al. 1994; Lahti et al. 1998; crested tit, *Parus cristatus*: Lens et al. 1994). Grey squirrels have also been found to trade-off the risk of cache theft against the risk of predation, preferring to cache more profitable food items in open areas exposed to predators compared to storing non-profitable items closer to tree-cover where there is also a higher risk of cache theft (Steele et al. 2014). These studies demonstrate that foraging individuals do not always act in ways to simply minimise predation risk, but that the role of the social environment heavily influences foraging and hoarding decisions about predation risk. However, less is known about what contribution social and predatory risks make to overall foraging decisions.

1.4. Risks while foraging: conspecific-and heterospecific-competition and predation risk

It is clear that squirrels face a multi-way trade-off in choosing where and when to forage, in terms of the costs and benefits of social foraging and the costs of predation. They engage in different behavioural strategies to offset these risks while foraging and storing food, such as engaging in vigilance behaviour (Partan et al. 2010; Partan et al. 2009; Tarigan 1994), or changing how they forage, cache and recover food (Hopewell & Leaver 2008; Hopewell et al. 2008; Leaver et al. 2007; Steele et al. 2008; Schmidt & Ostfeld 2008). While elements of this trade-off have been considered before so that we know how grey squirrels respond to individual cues, the full system has not, so less is known about how responses to different risk factors compare against one another. The current study isolates responses to different cues of risk while foraging to determine what relative contribution they make to foraging decisions.

In the current study we used auditory playbacks to simulate some of the risks that wild grey squirrels might face while foraging: risks posed by other squirrels, risks posed by other species that compete for the same resources as squirrels (corvids), and risks posed by predators. We compared these with calls of non-competitor passerine species to determine their response to non-competitors that frequently forage within the same patch, as well as incorporating a white noise control condition in order to determine whether responses noted were specific to sound type *versus* general responses to any noise. We monitored behavioural changes in alert behaviour (vigilance, escape and vocalisations) and foraging duration and distance from safety, across three time periods (before, during or after playback). Auditory playbacks provide a powerful tool in many behavioural studies of wild animals and can be particularly useful for monitoring behavioural responses to risk cues (e.g., Murphy et al. 2013). This technique allowed us to isolate responses to the three different risk factors in order to determine their relative significance in modifying squirrels' foraging and alert behaviours.

We predicted that if squirrels respond to the calls of conspecifics and corvids (as opposed to other passerine species) as potential competitors for resources, then they should act in ways which maximise foraging, including engaging less time in alert behaviour (being vigilant, escaping to areas of safety, vocalising) and more time spent foraging. On the other hand, if they respond to conspecifics and heterospecifics as sources of antagonistic interaction, then we predicted that they would act in ways to minimise potential contact by increasing their alert behaviour, and foraging farther away from trees where there might be fewer competitors. Finally we predicted that the predator playback would increase the time squirrels engaged in alert behaviour, which would be performed at a cost to foraging, and that they would respond by seeking areas closer to safety, or escape into trees.

2. Method

2.1 Study sites and sample

Two seasons of observations were carried out in urban parkland in South and East Devon between 0900-1600 hours from October 2012 through January 2013 and again from October through December 2014 to coincide with the peak foraging season of grey squirrels in this region. Sites were selected where squirrels were foraging or had previously been seen foraging. We visited a total of 97 different locations, observing one squirrel at each site. For the first season of observations (2012-2013) forty of these locations provided satisfactory independent experimental observations of adult squirrels that remained in view for the necessary length of time to conduct observations (criteria are discussed later in detail). The sites where a playback failed in the first season were revisited in 2014, where we successfully obtained data from an additional 21 sites. All sites were more than 300 metres apart from one another (monitored using Free GPS iPhone application by Code Burners and verified by www.itouchmap.com) to avoid overlapping home ranges between individuals (the maximum known linear measure of home range size recorded for a grey squirrel is 136.7 metres: Doebel & Mc Ginnes 1974, a measure which has been used for the same purpose in other recent grey squirrel studies, e.g., Getschow et al. 2013); therefore we can say with a good degree of certainty that our observations at different sites are independent. Neighbouring sites were not tested on the same day in order to minimise effects of playbacks being overheard by nearby squirrels.

2.2. Experimental design and playback stimuli

This study used a between subjects design so that each squirrel was exposed to one playback condition. During the first testing season we exposed one squirrel at each of the independent sites one of the following playbacks: squirrel call (N=10), heterospecific competitor corvid call (N=10), predator call (N=10), or white noise (N=10). During the second testing season we exposed one squirrel at each of our testing site one of the following playbacks: calls of heterospecific non-competitor neighbour species, namely non-corvid passerines (N=9), corvid calls (N=7), or white noise (N=5). Each playback was unique and only used once during the study, to minimise the possibility for pseudoreplication and control for the potential referential content of the calls (Kroodsma 1989), excluding the white noise playback which was used as a control stimulus and played at 15 different sites (specific details on the playbacks used is available as supplementary material). In an effort to have a roughly equal number for each of the conditions during each testing season, the order that each playback stimuli was presented was predetermined.

Each audio stimulus was taken from digital recordings of vocalisations coming from a single individual. Using Audacity 2.0.3, recordings were edited to be monophonic, background noise was removed, and they were cut to provide 15 seconds of playback. During the 15 second playback the audio was intermittent rather than continuous, but it was edited so that there was no more than 3 seconds of silence between each sound made. During the 15 seconds of playback each of the sounds emitted was unique, in that they were not digitally edited to be repeated, but naturally followed on from one another in the original digital recording.

The calls were levelled using iTunes. The amplitude for each call was adjusted using a sound level meter (Cirrus Research Limited Sound Level Meter, verified using Free GPS Version 3.6.2 iPhone application) at 1 metre from the source in the type of natural environment in which the experiments took place, to the average natural peak amplitude of the stimulus species. All of the types of vocalisations chosen ranged between 50-100dB and were relatively similar in structure to one another across categories (sample spectrograms available as supplementary material). The average squirrel playback amplitude was at a natural peak of 70dB (Lishak 1982, 1984); average corvid peak playback amplitude was 75dB (Blumstein et al. 2000; Goodson & Adkins-Regan 1997; Heinrich 1988; Searcy & Caine 2003); average predator calls peaked at 80dB (raptor: Chu, 2001; Jurisevic & Sanderson 1998; Krüger 2002; Searcy & Caine 2003; fox: Frommolt et al. 2003; domestic dog: Randler 2006b); average non-competitor passerine peak playback amplitude was 80dB (Ritschard et al. 2012 and references therein); and white noise was at a constant 90dB (which has been used as the maximum sound intensity in previous playback studies with grey squirrels, e.g., Schmidt & Ostfeld 2008). Calls were played using an iPhone4S (volume adjusted to pre-determined dB level for each call) connected by a 25 metre audio cable to an X-mini™ II speaker at full volume, so that the observer could operate the calls at a distance to the speaker away from the main observation area.

2.3 Procedure and measures

Three principal observers were involved in collecting data for this study. We achieved high levels of inter- observer reliability (between 76-100% agreement for all measures, calculated using the index of concordance technique reported in Martin & Bateson 1993), but worked in pairs for the majority of observations (N = 27 out of 40) to ensure consistency in recording. Observers sat at the edge of the observation site (starting observations at a minimum of approximately 20m from the nearest squirrel), close to shrubs or a tree. The speaker was placed on the ground in the centre of the observation area, a minimum of 5m away from the base of a tree/shrub, covered with leaves or grass, and operated from a distance using an iPhone4S. Observation of a focal individual would commence 5 minutes after arriving at the study site to allow the animal time to habituate to our presence.

A focal squirrel was selected using opportunity sampling of any squirrel that was on the ground, and a description of its behaviour was recorded using a digital audio voice recorder (iPhone4S or Olympus DM-450). Continuous sampling was used to monitor the start and end times of all behaviours and changes in location of the focal squirrel. Observers recorded the following behaviours, focussing on activities that might affect fitness (McGregor 2000). (1) Vigilance: while on ground, individual stops current behaviour, becomes bipedal with body in a stretched upright position with head high, ears forward, and not eating or manipulating food, but can be holding food, may also be tail flagging, or foot tapping (adapted from Blumstein & Arnold 1995, & Partan et al 2010). (2) Escape: fleeing to an area of refuge. (3) Foraging: searching for food, manipulating items, eating food, carrying food, caching food; can be bipedal or quadrupedal, but must be on the ground. (4) Vocalisation. (5) Mean distance to an area of refuge, to the nearest .5m: refuge included any natural or man-made structure that would provide safety from a terrestrial or aerial predator.

Before commencing playback, observers collected 3 minutes of continuous behavioural data from one focal squirrel. After this time the 15 second auditory stimulus was played if the conditions adhered to the following criteria: the squirrel had remained on the ground for a minimum of 75 seconds immediately prior to the onset of the playback, had not engaged in alert behaviours (vigilance, vocalisation, escape) during the prior 30 seconds, was within 10-30 metre range of the speaker, and had not been exposed to the natural auditory presence of conspecifics, passerine species, or predators. Observers continued watching the focal squirrel for a further 3 minutes after the playback had ended if it remained in sight. If it escaped up a tree and was still visible we continued to monitor behaviour for a further 3 minutes, and waited to record its latency to return from the tree if this continued beyond 3 minutes (maximum latency was 196 seconds). In the first season of observations a total of 56 out of 97 observations were discarded before playback commenced because the observations did not meet these criteria (essentially squirrels were not in sight long enough), and one observation was discarded during playback because the focal squirrel went out of sight at the time of the playback; in the second season of observations, all 56 locations were visited where an observation had failed in the previous season, a total of 35 observations were discarded before playback commenced because the observations did not meet these criteria.

2.4. Statistics

Analyses were conducted separately for each season of observations. For the first season we carried out a 3 x 4 mixed design repeated measures analysis of variance (ANOVA) to examine the main effects of time-period (pre-, during- and post-playback) and condition (conspecific, corvid, predator, control), and the time-period by condition interactions on the following dependent measures: vigilance duration, foraging duration and foraging/vigilance mean distance to refuge. For the second season we carried out a 3x3 mixed design repeated measures ANOVA to examine the main effects of time period (pre-, during- and post-playback) and condition (non-competitor passerine, corvid, white noise) and time by condition interactions on the following measures: vigilance duration, foraging duration and foraging/vigilance distance to refuge. Data for the measure 'distance' were transformed using a square root transformation which corrected violated assumptions of sphericity, homogeneity of variance and equality of covariances. We used the more robust Pillai's Trace significance test. $P \leq 0.05$ was the criterion to further examine the outcome of the model. All follow-up pairwise comparison contrast tests were conducted with a Bonferroni adjustment to account for multiple comparisons.

We performed a separate chi-square analysis to assess differences between conditions and time-periods on frequency of escape behaviour across the two seasons.

If the focal squirrel had responded to the playback by demonstrating any alert behaviour (the individual stopped foraging, and commenced vigilance, vocalisation, or escape behaviour during the stimulus playback) we measured the time it took for the squirrel to resume foraging from the time the call was played. Data were transformed using a square root transformation which corrected violated assumptions of homogeneity of variances. Once again, two separate one-way between subjects ANOVAs were conducted to examine differences in latencies between the four conditions for the first season, and the three conditions for the second season. Subsequent planned follow-up pairwise comparison contrast tests were conducted using a Bonferroni adjusted alpha level.

We used Microsoft Excel 2010 and SPSS Version 16.0 to carry out the analyses.

3. Results

Descriptive statistics for vigilance and foraging durations across the playback conditions in each season during the three time periods are displayed in Table 1.

Insert Table 1

Table 1. *Descriptive statistics showing mean (and standard deviation) of behaviour during the three playback periods for each of the conditions in (a) season one and (b) season two.*

3.1. Foraging and vigilance durations and distance to cover

3.1.1. Season one

A mixed ANOVA (with condition as the between-subjects factor and time-period as the within subjects factor) showed no main effect of time-period or condition on distance to refuge (P > .05. There were significant main effects of time-period on vigilance duration ($F_{2,72}$ = 14.11, P < .001, sphericity assumed) and foraging duration ($F_{2,72}$ = 6.40, P = 0.003, sphericity assumed), both with a moderate effect size (Partial Eta squared .28 and .15 respectively), and these are illustrated in Figure 1. There was no time-period by condition interaction on distance to refuge (lower bound test, P > .05), but there was a significant time-period by condition interaction on vigilance duration ($F_{6,72} = 3.67$, $P = 0.003$, sphericity assumed) and foraging duration ($F_{6,72} = 3.40$, $P = .005$, sphericity assumed), both with a moderate effect size (Partial Eta squared .23 and .22 respectively).

Subsequent planned contrast tests were carried out using a Bonferroni adjusted alpha level for the main effects of time period on vigilance and foraging durations. For vigilance duration there were significant differences between the pre- and during-playback conditions ($P < .001$) and between the during- and post-playback conditions ($P < .001$). Figure 1(a) shows that squirrels spent significantly more time being vigilant when the call was being played compared to the pre- and post-playback time periods, indicating that they attended to the playbacks. For foraging duration there was a significant difference between the pre- and during-playback conditions ($P = .002$), and the differences between the pre- and post-playback conditions approached significance ($P = .028$ NS, using a Bonferroni adjusted alpha level of $P \leq .017$). Figure 1(b) shows that squirrels spent significantly more time foraging prior to the playback compared to when the call was being played, and there was a trend for them to spend more time foraging after the call had been played compared to when the call was being played.

Insert Figure 1

For the time-period by condition interaction we conducted planned follow-up analyses to examine differences between the four conditions at the ‘during-playback’ and post-playback periods. We conducted a MANOVA with condition as a fixed factor and vigilance duration during playback and foraging duration during playback as dependent measures. During playback we found significant effects of condition for vigilance duration ($F_{3,36} = 3.98$, $P = .015$) and foraging duration ($F_{3,36} = 4.64$, $P = .008$), both with a moderate effect size (Partial Eta squared .25 and .28 respectively), and these are illustrated in Figure 2. However, there were no significant differences between conditions post-playback ($P > 0.05$). Subsequent planned contrast tests using a Bonferroni adjusted alpha level revealed significant differences between both vigilance duration and foraging duration for the predator and control conditions during playback (P = .002, P = .001 respectively). During the experimental playback period, squirrels exposed to predator calls spent significantly more time being vigilant compared to the control condition, and spend significantly less time foraging than during the control condition.

Insert Figure 2

3.1.2. Season two

A mixed ANOVA (with condition as the between-subjects factor and time-period as the within subjects factor) showed no main effect of time period or condition on distance to refuge (P > .05). There was a significant main effect of time period on vigilance duration ($F_{2,34}$ = 3.99, P = .028, sphericity assumed, moderate effect size .19), a significant main effect of condition on vigilance duration ($F_{2,17}$ = 20.90, $P \leq$ .001, high effect size .71), but no time by condition interaction on vigilance duration ($F_{4,34}$ = 5.72, P = .051). There was also a significant main effect of condition on foraging duration ($F_{2,18}$ = 4.76, P = .022, moderate effect size .35), but no significant main effect of time period on foraging duration (P > .05), and no significant time by condition interaction on foraging duration (P > .05).

Subsequent planned contrast tests were carried out using a Bonferroni adjusted alpha level for the main effects of time period and condition on vigilance duration, the results of which are included in Figure 3. For time period there were significant differences between the pre- and during periods ($P < 0.05$), with squirrels spending significantly more time being vigilant during the playback than before the playback, as seen in Figure 3(a). For condition, squirrels spent significantly more time being vigilant in the corvid condition compared to the non-competitor passerine condition ($P \leq$ .001), and significantly more time being vigilant in the corvid condition compared to the white noise condition ($P \leq$ .001) as seen in Figure 3(b).

Insert Figure 3.

For the effect of playback condition on foraging duration, follow-up planned contrast tests revealed a significant difference between the corvid and non-competitor passerine conditions (*P* = .022). Figure 4 shows that squirrels spent significantly more time foraging in the non-competitor passerine condition compared to the corvid condition.

Insert Figure 4.

3.2. Frequency of escape behaviour

A chi square test was carried out to assess differences between conditions and between the time periods for frequency of escape behaviour for each season. We did not find any significant differences in the amount of escape behaviour demonstrated between the conditions or for the different time periods (*P* > .05).

3.3. Latency to resume foraging post-playback-initiated-alert-behaviour

3.3.1. Season one

Except in the control condition, focal squirrels nearly always stopped foraging to some form of alert behaviour during playback; only one squirrel in each of the conspecific and corvid conditions (and none in the predator condition) appeared to ignore the playback. In contrast, seven of the ten squirrels in the control condition did not change their behaviour in response to the white noise. Figure 5 shows latency to resume foraging after displaying alert behaviour during playback, and reveals that squirrels responded similarly to the conspecific and corvid playbacks, and in both cases latencies to return to foraging were longer than in the control condition. Squirrels took even more time to resume foraging behaviour when exposed to the predator playback compared to the three other conditions. These data were analysed using a one-way between subjects ANOVA which revealed a statistically significant difference between the conditions ($F_{3,36} = 26.90$, $P < .001$) with a large effect size (Partial Eta squared .69). Subsequent planned contrast tests using a Bonferroni adjusted alpha level, revealed significant differences between all conditions ($P < .001$), excluding the conspecific and corvid conditions whose condition means were not significantly different from one another ($P > 0.008$), see Figure 5.

Insert Figure 5

3.3.2. Season two

We recorded alert behaviour in the same manner as per season one. On 3 out of 9 occasions, the focal squirrel responded to the call of the non-competitor passerine species by demonstrating alert behaviour for 4 seconds or less; on the other 6 occasions that this call was played the focal squirrel showed no behavioural response to the call. In the control condition, one focal individual demonstrated alert behaviour. In contrast, all focal squirrels responded to the corvid playbacks by switching from foraging to alert behaviour. Figure 6 shows average latency to resume foraging after displaying alert behaviour during playback, and reveals that squirrels responded similarly in response to the non-competitor passerine and control playbacks, and in both cases latencies to return to foraging were ≤1 second. Squirrels took more time to resume foraging behaviour when exposed to the corvid playback compared to the other two conditions. These data were analysed using a one-way between subjects ANOVA which revealed a statistically significant difference between the conditions ($F_{2,18} = 9.53$, $P = .002$) with a moderate effect size (Partial Eta squared .51). Subsequent planned contrast tests using a Bonferroni adjusted alpha level revealed significant differences between the corvid and non-competitor passerine conditions ($P = .003$), and the corvid and control conditions ($P = .007$), see Figure 6.

Insert Figure 6

4. Discussion

Across both seasons we found a strong effect of time-period on vigilance duration, and a strong effect of time-period on foraging duration in season one. During the period when the stimulus was being played, there was an overall decrease in foraging and an increase in vigilance. In particular, squirrels displayed more vigilance and less foraging when exposed to predator playbacks compared to the control white noise playbacks. Across both seasons we also found significant differences between latencies to resume foraging depending upon which call was played. Squirrels exposed to the predator playback took longer to resume foraging after the playback compared to the corvid and conspecific conditions to which squirrels responded similarly, taking longer to resume foraging than those squirrels in the non-competitor passerine and control condition who scarcely responded to the playback.

Overall our results show that grey squirrels responded to the playbacks of corvids and conspecifics similarly by displaying alert behaviour when the calls were played and delayed recommencing their foraging behaviour after the calls had ceased, while they were unresponsive to calls of non-competitor species. This finding implies that there are potential costs associated with the auditory presence of conspecifics and corvids, in comparison to the auditory presence of other passerines who do not necessitate the need for increased vigilance. This supports our hypothesis that squirrels respond to corvids and conspecifics as sources of potential antagonistic encounters, acting in ways that increase their ability to monitor their surroundings by pausing their foraging behaviour, as opposed to increasing their foraging to offset the increased competition. Likewise, squirrels responded to predator calls by increasing the time they were engaged in alert behaviour during the playback, which was performed at a cost to foraging as we predicted. However, our study shows that although the different cues of risk had similar disruptive effects on foraging, there were differences in degree of response, with predatory cues bringing about longer disruption to foraging than other social cues; clearly the cost of not spotting a predator would be higher than for not attending to social cues.

It is important to point out that all of these calls were, essentially, false alarms from the squirrels' point of view. As a result, we cannot conclude with confidence that their behaviour would have been similar had they actually located the source of the sounds. The squirrels in this study heard but failed to visually locate another animal. Had they actually spotted an animal with the corresponding playback whilst foraging, they may have made other behavioural changes in response to the particular individual, such as increasing foraging, or moving away from the competitor, which were not present in this study. Observational studies of actual responses to natural predators and competitors in conjunction with controlled experiments allowing more direct comparisons will help to give a broader understanding of the nuanced trade-offs made by foraging squirrels.

4.1. Foraging among competitors

Previous studies demonstrate that while there are benefits to social foraging (reviewed in Galef & Giraldeau 2001), for an asocial species like the grey squirrel (Koprowski 1996) there are a number of costs associated with foraging nearby either conspecifics or heterospecifics who use the same resources. The increased competition for resources fosters a need to spend more time foraging (Pravosudov & Lucas 2000), and the potential for agonistic encounters encourages more vigilance behaviour (Tarigan 1994), but is performed at a cost to foraging (Makowska & Kramer 2007; Shonfield 2011). Our study clarifies how grey squirrels respond to potential sources of competition while foraging in comparison to non-competitor species. In response to the risks of conspecific and corvids, squirrels predominately acted in ways to indicate that they viewed these calls as a signal of potential antagonistic interaction, as opposed to a signal of increased foraging competition, though as we pointed out earlier, we cannot conclude that they would respond similarly to the actual presence of a competitor.

The effect of the playback on foraging was not prolonged: *after* the playback had *ended* squirrels re-started foraging in an average of 12 seconds in the conspecific condition and 15 seconds for the heterospecific condition. It seems that squirrels benefit by being wary of nearby competitors, but resume foraging soon after the threat of competition ceases. It is reasonable that squirrels should not remain disturbed for an extended period after the auditory risk has ceased, as it is more profitable for them to maintain a consistently high level of foraging and engage in occasional bouts of vigilance after exposure to a risk cue. In particular, there may be high costs associated with reduced foraging at a time of year when squirrels are increasingly busy caching food for the approaching winter months. It is possible that alert behaviours might extend for a longer period of time at other times of year when the associated foraging costs are not as high.

In comparison to other passerines, corvids share similar resources with squirrels and are also known to pilfer their caches (Vernelli 2013). However, based upon the past literature it was unclear how squirrels would react to the corvid playbacks. Leaver et al. (2007) report that squirrels do not change their behaviour *during* caching in the presence of corvids, and Schmidt and Ostfeld (2008) report that they do alter their behaviour when *recovering* caches made in the presence of corvids. Our current study provides evidence that squirrels are sensitive to the auditory presence of corvids in comparison to other passerines of whom they tend to ignore. Furthermore, they respond to corvid vocalisations in a similar manner to the alarm calls of conspecifics while foraging. A recent study has found that grey squirrels are responsive to alarm calls made by passerine species if they are acoustically similar to squirrel calls (Getschow et al. 2013). However, in our study the corvid calls were not alarm calls but instead contact calls directed at other birds. Corvids vocalising to one another could pose an aggressive hazard to a lone foraging squirrel; they are often larger than grey squirrels, and frequently forage with other corvids for the same resources as squirrels. Thus it seems adaptive that the squirrels respond by engaging in alert behaviour temporarily until the potential threat has passed. The specific risk which corvids pose to squirrels, whether as competitors for food, cache thieves, sources of aggression, or all three, is still open to more investigation, but our current study highlights that further research in this area would be valuable in order to more fully understand interspecific foraging competition.

4.2. Foraging among competitors and predators

Our study also contributes to the existing literature of how predation risk affects the foraging behaviour of grey squirrels. When under increased perceived risk of predation grey squirrels engage in more vigilance behaviour (Partan et al 2010; Partan et al. 2009), which incurs a cost to the amount of time spent foraging (Brown et al. 1992; Makowska & Kramer 2007; Shonfield 2011). In addition, because we have isolated responses to social and predatory risk cues, our study directly compares the contribution that each of these make to overall behavioural responses during foraging. Previous research has shown that while some individuals preferentially forage and eat in areas closer to safety (Booth, et al. 2012; Bowers et al. 1993; Brown et al. 1992; Kilpatrick 2003; Lima & Valone 1986; Lima et al. 1985; Newman et al. 1988), some will forage or cache in locations more exposed to predators when the risk of competition is high (Ekman 1987; Koivula et al. 1994; Lahti et al. 1998; Steele et al. 2014). In the current study we have shown that squirrels responded similarly to both predatory and social risks by interrupting their foraging behaviour and engaging in alert behaviours, social risks had less enduring disruptive effects to foraging than the predator cues. Further research of this nature could help to determine whether the presence of foraging competitors reduces the cost of defence against predators. Indeed separate studies have reported that squirrels will monitor alarm calls of both competing conspecifics (Partan et al. 2010; Partan et al. 2009) and heterospecifics (Randler 2006a; Schmidt et al. 2008) and change their vigilance behaviour accordingly. Thus being alert to calls of competitors reduces the need for sustained vigilance to calls of predators. Nevertheless, in an environment where all three cues of risk would be present it is likely that squirrels would be tolerant to nearby heterospecifics and conspecifics despite their potential disruptive effects to foraging. It is also likely that the squirrels’ differential responses to predator *versus* competitor cues was due to the differential cost of failing to locate a potential predator (death) compared to that of failing to locate a potential competitor (loss of food items).

It is possible that our conspecific playback stimuli also signalled predation risk. Squirrels communicate through a variety of means (auditory, Horwich, 1972; Lishak, 1982; Lishak, 1984; olfactory, Taylor, 1977; visual, Thompson, 1978) yet most of their communication tends to relate to aggression or threatening conditions (Clark, 2005; Horwich 1972; Gurnell 1987; Steele & Koprowski, 2001) and is primarily used for resource guarding (Thompson, 1978), during mating (Thompson, 1977) and as predator alerts directed at both other squirrels and the predator itself (Lishak, 1984), particularly tail signals and vocalisations (Partan et al. 2009; Partan et al. 2010). The vocalisations used in our study were combination “kuk” and “quaa” alarm calls (Horwich 1972; Lishak 1984) which are more likely to be displayed when conspecifics are present (Partan et al. 2010) and therefore our playbacks could be signalling the risk of conflict with another squirrel, but it is possible that they may also signal predator presence. It is not currently known whether there are subtle differences in the nature of calls when directed at a conspecific or otherwise. If subjects were responding to conspecific calls as predator alerts then we might expect a similar response to the conspecific playback as to the predator playback. Our results demonstrate that this is not the case; the conspecific vocalisations appear to present a lesser risk than those of the predator calls. Squirrels reacted to conspecific calls by interrupting foraging to a lesser degree than when they heard a predator call, and this suggests that the response may be associated with avoidance of intraspecific conflict rather than cue of predation, as well as highlighting the likelihood of there being different costs from ignoring calls made by different species.

4.3. Conclusion

This study has shown that squirrels responded differently to cues of predation than to cues of conspecific and heterospecific presence, illustrating how they pose different risks to foraging. Squirrels responded to these different cues of risk by demonstrating alert behaviour and limiting their foraging. The perceived presence of competitor species appeared to have short-term disruptive effects on foraging, rather than facilitating it, suggesting that these calls may signal sources of inter- and intra-specific conflict. Squirrels did not respond to cues of non-competitor species. Foraging was disturbed for a greater length of time after predator calls because of more time engaged in alert behaviour when potential predators could be around. Overall, these behavioural changes were somewhat short-lived, possibly indicating that there were high costs associated with reduced foraging.

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Figure captions

Figure 1. The effects of time-period on (a) vigilance and (b) foraging behaviours in season one, including outcome of planned follow-up analyses. ** indicates *P* < 0.01, *** indicates *P* < 0.001, and error bars represent 95% confidence intervals.

Figure 2. The effects of condition on (a) on vigilance duration and (b) on foraging duration during playback in season one. The outcome of the planned follow-up analyses conducted on the time-period by condition interaction are displayed. ** indicates *P* < 0.01, *** indicates *P* < 0.001, and error bars represent 95% confidence intervals.

Figure 3. The effects of (a) time period and (b) condition on vigilance duration in season two, including outcome of planned follow-up analyses. * indicates *P* < 0.05 *** indicates *P* < 0.001, and error bars represent 95% confidence intervals.

Figure 4. The effects of condition on foraging duration in season two, including outcome of planned follow-up analyses. * indicates *P* < 0.05, and error bars represent 95% confidence intervals.

Figure 5. Differences in season one for mean latencies to resume foraging across the playback conditions if alert behaviour was demonstrated. *** indicates *P* > 0.001, and error bars represent 95% confidence intervals (*N*=40).

Figure 6. Differences in season two for mean latencies to resume foraging across the playback conditions if alert behaviour was demonstrated. ** indicates *P* > 0.01, and error bars represent 95% confidence intervals (*N*=21).

Captions for supplementary material

1. Descriptions of playbacks used as stimuli. All calls were obtained from the National Sounds Archive, London, UK, FreeSound.org and personal recordings. Each stimulus was played only once, excluding white noise.

2. Spectrogram of typical playback for each of the experimental conditions (generated using Audacity 2.0.3).

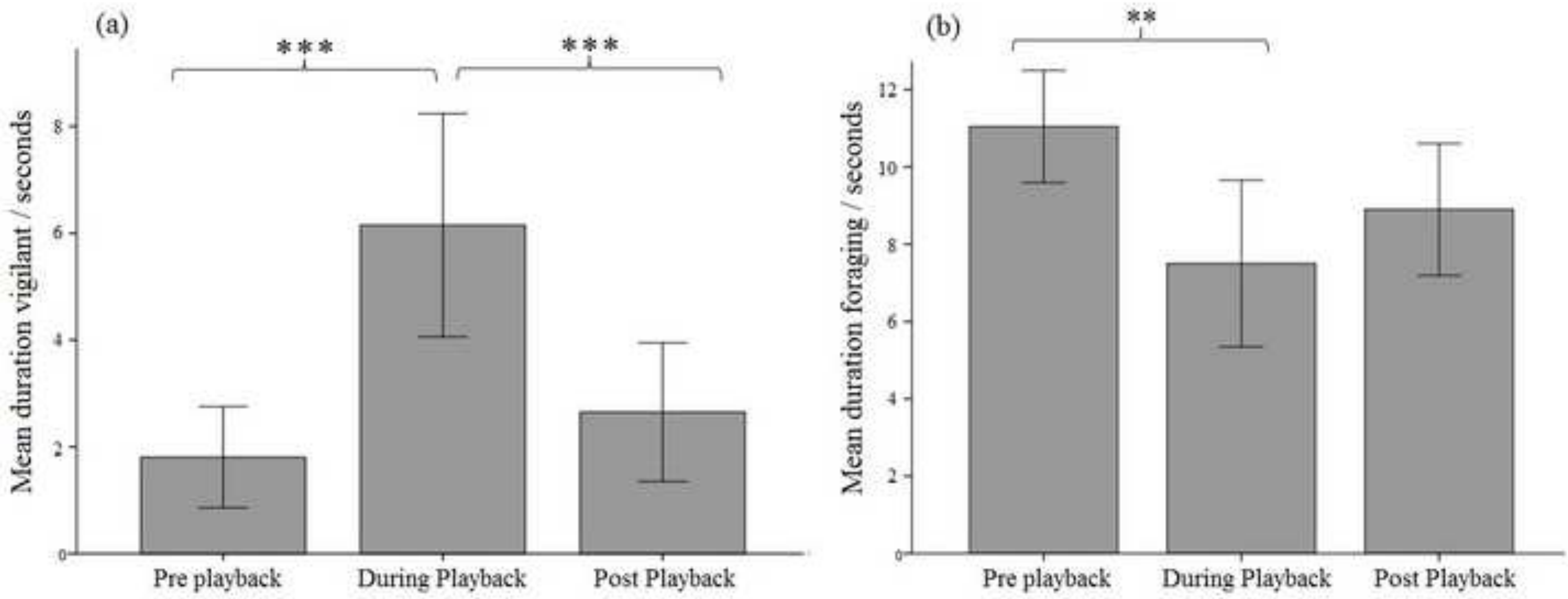
Table 1

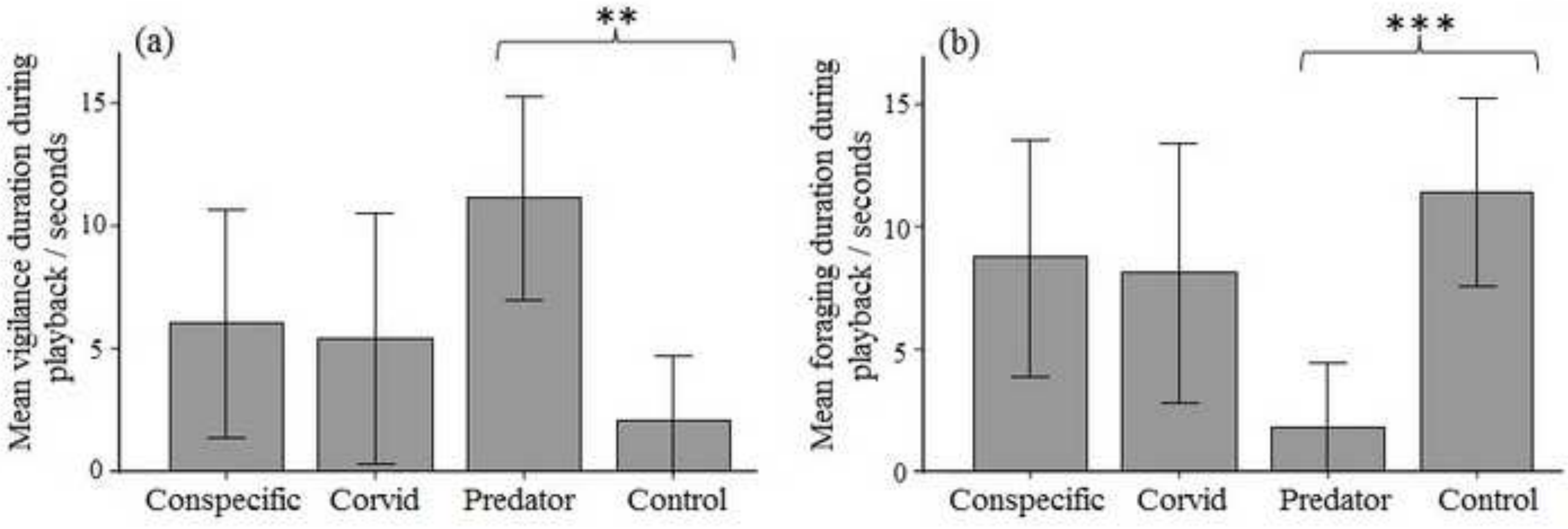
(a)

	Conspecific *n*=10			**Corvid *n*=10**			**Predator *n*=10**			**White noise *n*=10**		
	Pre	During	Post	Pre	During	Post	Pre	During	Post	Pre	During	Post
Vigilance duration /seconds	1.54	6.00	4.14	2.96	5.40	2.10	.60	11.10	3.66	2.12	2.10	.70
	(.73)	(2.04)	(1.55)	(1.50)	(2.25)	(1.28)	(.35)	(1.84)	(1.46)	(.76)	(1.14)	(.41)
Foraging duration /seconds	9.60	8.70	7.36	11.26	8.10	10.70	12.40	1.80	7.80	10.92	11.40	9.74
	(1.73)	(2.13)	(1.75)	(1.41)	(2.35)	(1.77)	(1.25)	(1.16)	(1.84)	(1.39)	(1.69)	(1.39)

(b)

	Non corvid passerine *n*=9			**Corvid *n*=7**			**White noise *n*=5**		
	Pre	During	Post	Pre	During	Post	Pre	During	Post
Vigilance duration /seconds	.53	1.00	1.38	1.00	10.43	5.46	1.52	.25	1.25
	(.84)	(1.58)	(1.80)	(1.73)	(4.61)	(5.94)	(1.27)	(.50)	(2.50)
Foraging duration /seconds	13.00	13.11	12.956	10.83	6.29	8.97	11.88	12.00	12.40
	(1.65)	(2.76)	(4.09)	(5.24)	(6.55)	(5.49)	(2.53)	(6.71)	(3.76)


(a)
***
***
Mean duration vigilant / seconds
0
2
4
6
8
Pre playback
During Playback
Post Playback
(b)
**
Mean duration foraging / seconds
0
2
4
6
8
10
12
Pre playback
During Playback
Post Playback


(a)
Mean vigilance duration during playback / seconds
0
5
10
15
**
Conspecific
Corvid
Predator
Control
(b)
Mean foraging duration during playback / seconds
0
5
10
15
***
Conspecific
Corvid
Predator
Control

Figure

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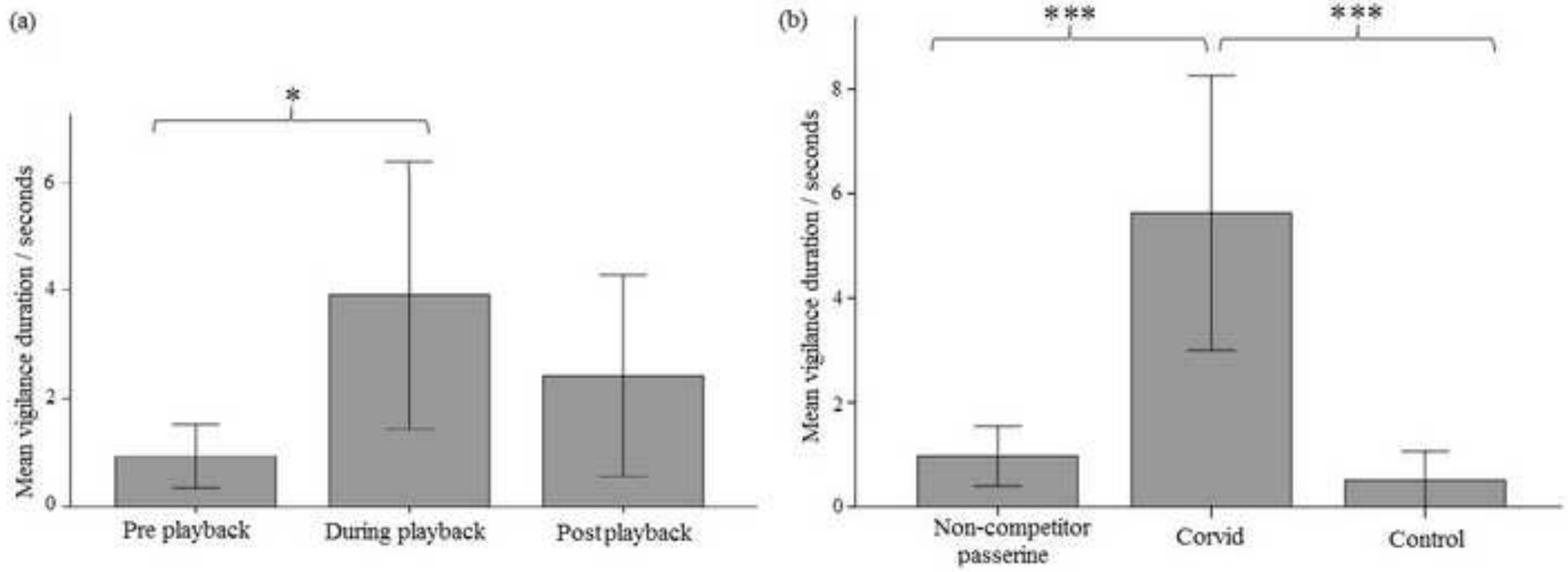

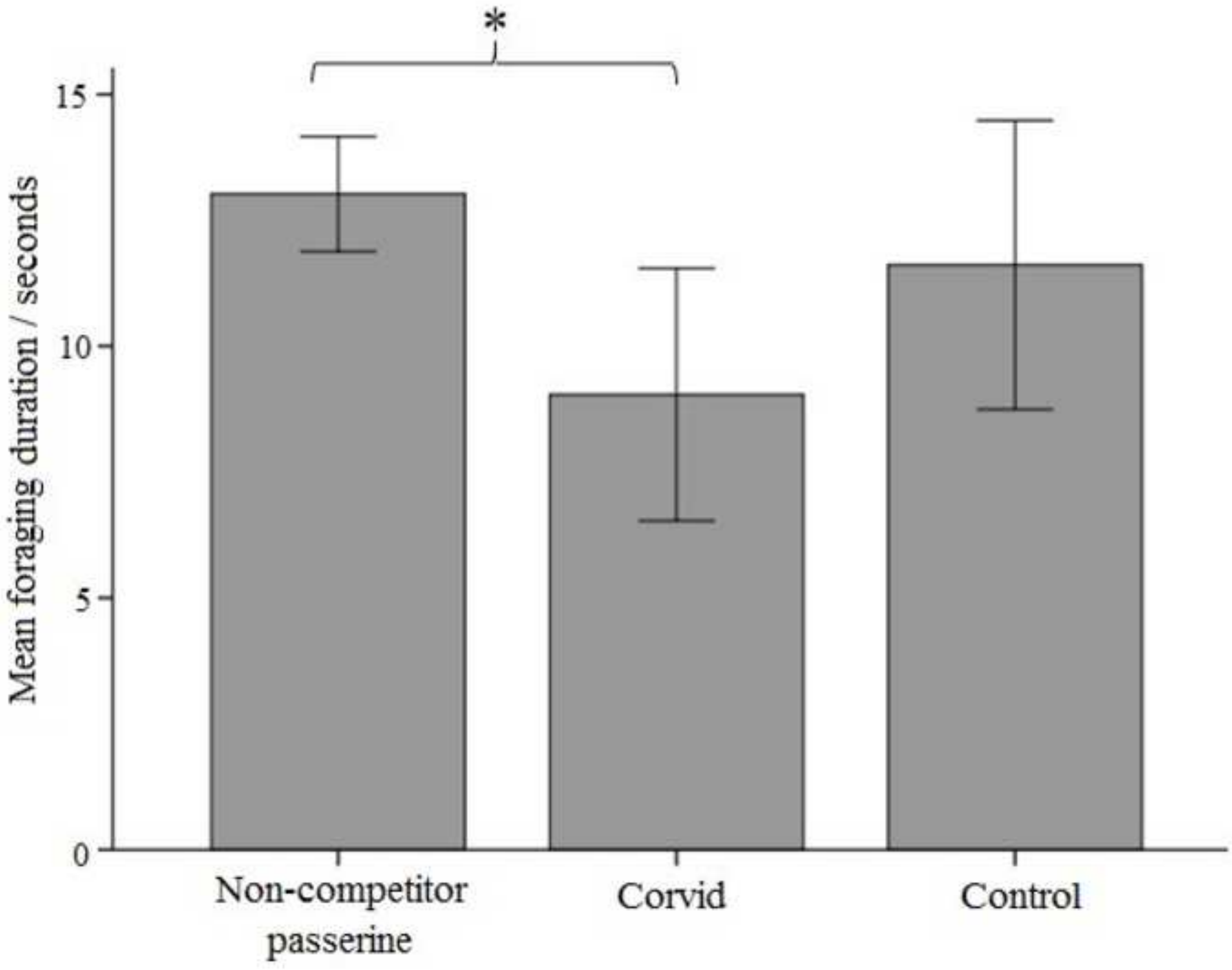
*
Mean foraging duration / seconds
15
10
5
0
Non-competitor passerine
Corvid
Control

Figure

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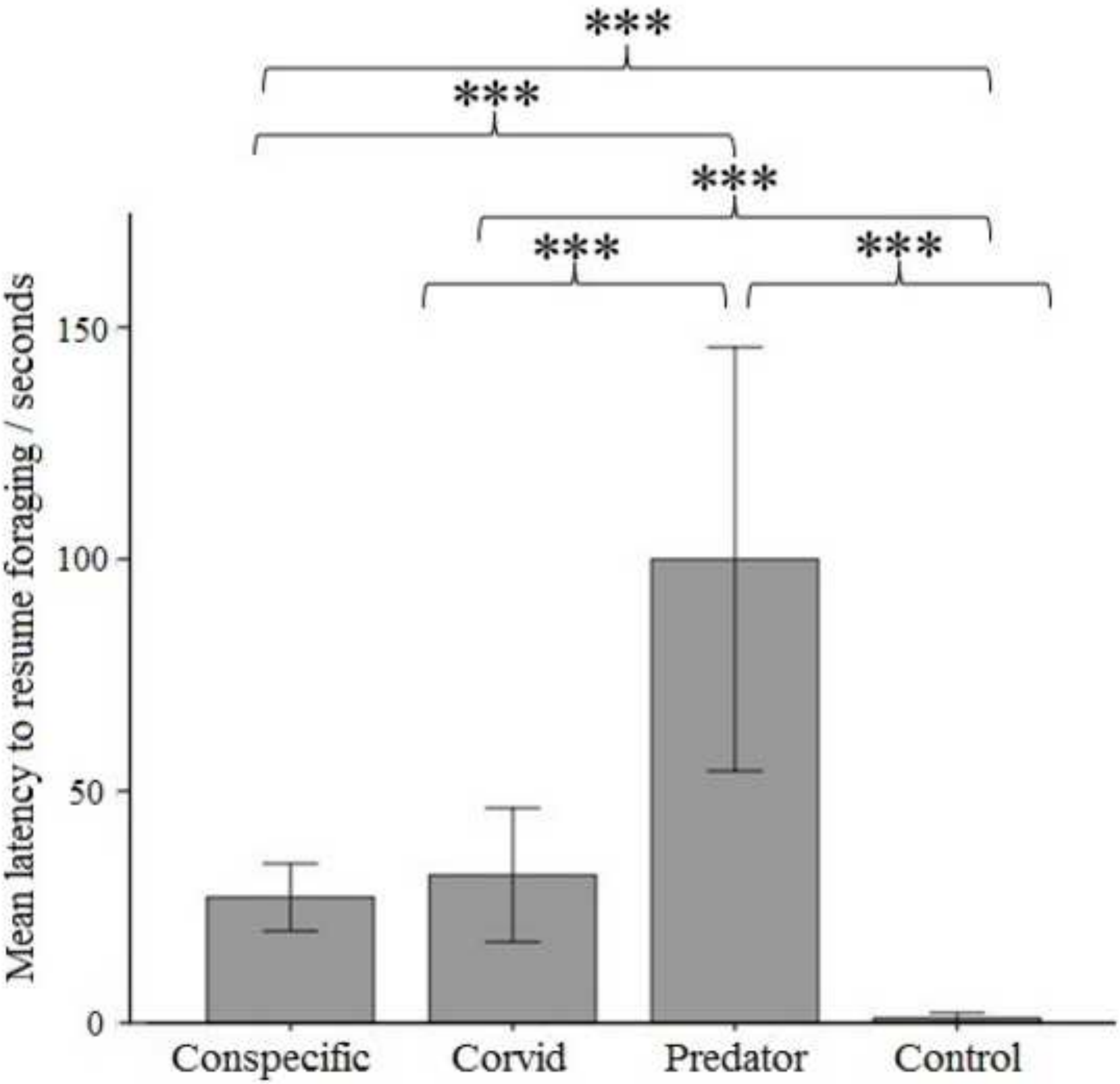

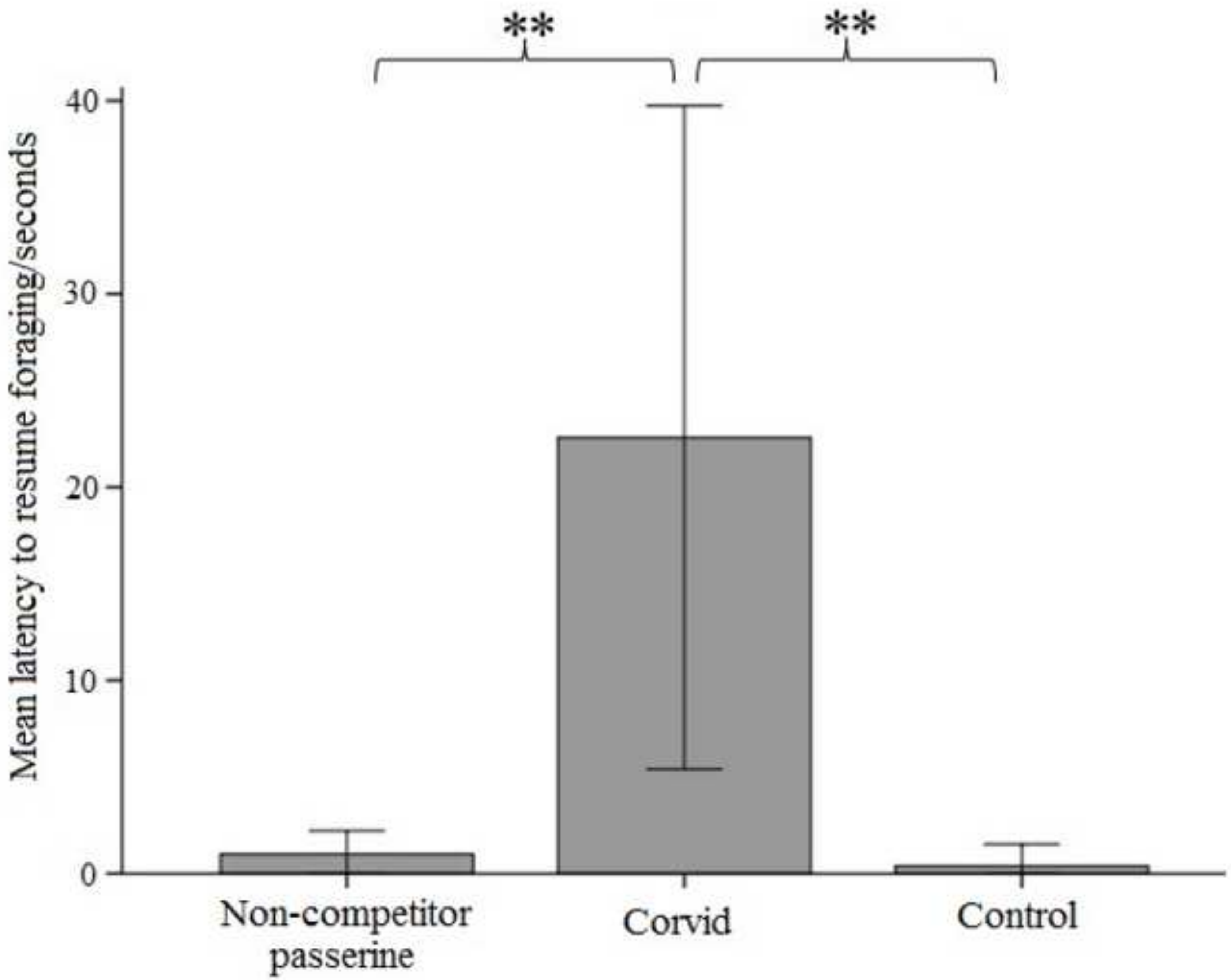
**
**
40
30
20
10
0
Mean latency to resume foraging/seconds
Non-competitor passerine
Corvid
Control