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Editor's choice

Original Article

Kalahari skinks eavesdrop on sociable weavers to manage predation by pygmy falcons and expand their realized niche

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Eavesdropping on community members has immediate and clear benefits. However, little is known regarding its importance for the organization of cross-taxa community structure. Furthermore, the possibility that eavesdropping could allow species to coexist with a predator and access risky foraging habitat, thereby expanding their realized niche, has been little considered. Kalahari tree skinks (*Trachylepis spilogaster*) associate with sociable weaver (*Philetairus socius*) colonies as do African pygmy falcons (*Polihierax semitorquatus*), a predator of skinks and weavers. We undertook observational and experimental tests to determine if skinks eavesdrop on sociable weavers to mitigate any increase in predation threat that associating with weaver colonies may bring. Observations reveal that skinks use information from weavers to determine when predators are nearby; skinks were more active, more likely to forage in riskier habitats, and initiated flight from predators earlier in the presence of weavers compared with when weavers were absent. Playback of weaver alarm calls caused skinks to increase vigilance and flee, confirming that skinks eavesdrop on weavers. Furthermore, skinks at sociable weaver colonies were more likely to flee than skinks at noncolony trees, suggesting that learning is mechanistically important for eavesdropping behavior. Overall, it appears that eavesdropping allows skinks at colony trees to gain an early warning signal of potential predators, expand their realized niche, and join communities, whose predators may otherwise exclude them.

Key words: **alarm call, antipredator behavior, communities, ecological engineers, heterospecific eavesdropping, mixed-species groups.**

INTRODUCTION

Eavesdropping is common in animal and plant communities (Bradbury and Vehrencamp 1998; Karban and Maron 2002; Vitousek et al. 2007; Magrath et al. 2015) with information regarding predation threats being particularly valuable. Individuals that are able to eavesdrop on predator-related information gain immediate and clear benefits (Magrath et al. 2015), including enhanced predator detection and increased foraging efficiency resulting from reduced vigilance (Sullivan 1984; Doligez et al. 2002; Mcgraw and Bshary 2002; Vitousek et al. 2007; Oommen and Shanker 2010; Schmidt et al. 2010; Sharpe et al. 2010; Baigrie et al. 2014). However, little is known regarding the importance of eavesdropping for the organization of community structure, including cross-taxa communities (Goodale et al. 2010). Joining a community may expose new members to increased risk (Götmark and Andersson 1984; Groom 1992), including from other community members. Eavesdropping could in principle offset such costs and facilitate community membership (Oommen and Shanker 2010). Furthermore, risk-related information from heterospecifics within communities could increase access to higher-risk habitat and, therefore, expand species' realized niches (Goodale et al. 2010; Ridley et al. 2014; Martinez et al. 2018). Here, we seek to identify whether eavesdropping allows individuals to join communities, whose predators may otherwise exclude them. We also seek to determine if community members use eavesdropping to expand their realized niche within communities by enabling them to exploit new habitat.

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To date, research on eavesdropping has demonstrated that heterospecific alarm calls can elicit increased vigilance (Vitousek et al. 2007; Müller and Manser 2008; Kitchen et al. 2010) and increase the distance at which individuals flee from approaching predators (flight initiation distance [FID]; Ydenberg and Dill 1986). By contrast, nonalarm calls can indicate the lack of a predator, allowing individuals to increase foraging success by reducing vigilance when other species are present (Baigrie et al. 2014; Lilly et al. 2019). Eavesdropping could also affect spatial variation in perceived predation risk (Martinez et al. 2017), known as the landscape of fear (Brown et al. 1999; Laundré et al. 2001). Animals behaviorally avoid habitat where predation risk is high; therefore, by reducing the costs of accessing habitat with higher predation risk, eavesdropping could enable individuals to expand their realized niche and exploit additional habitat. This would be particularly valuable for organisms that make decisions to forage and/or move to habitat patches that provide additional food (Gil et al. 2017). To date, this possibility has been largely overlooked, although research has demonstrated that some birds and reptiles expand their niche when associated with heterospecifics (Whiting and Greeff 1999; Ridley et al. 2014; Martinez et al. 2018). Therefore, it is not only of interest to determine if species eavesdrop on other species, enabling them to expand their realized niche, but also whether organisms also gain additional benefits when in the presence of heterospecifics on whom they eavesdrop. By reducing predation risk, eavesdropping could enable organisms to join communities, including those where predatory members would otherwise exclude them (Oommen and Shanker 2010).

For individuals to benefit from predator information within communities, eavesdropping must provide relevant and reliable information. Heterospecific alarm calls are only relevant if the calling species and eavesdropper are vulnerable to the same predators (reviewed by Magrath et al. 2015; Meise et al. 2018). For example, New Holland honeyeaters *Phylidonyris novaehollandiae* share more predators with white-browed scrubwrens *Sericornis frontalis* than superb fairy-wrens *Malurus cyaneus*. Consequently, honeyeaters flee more often to scrubwrens, than fairy-wrens, alarm call (Magrath et al. 2009a). Therefore, the type of taxa that heterospecifics eavesdrop on is less relevant as long as they are able to mechanistically recognize the information.

The mechanisms allowing individuals to respond accordingly to the alarm calls of other species are only beginning to be determined (Magrath et al. 2015). Those that respond to heterospecific alarm calls innately are able to do so without previous experience, thereby reducing exposure to predators (Hollen and Radford 2009), whereas learned responses require exposure to other species in predator alarm contexts (Ramakrishnan and Coss 2000; Magrath et al. 2009b). Consequently, when learning plays a primary role, only individuals with an opportunity to learn would show full capacity for eavesdropping. Research on bird–bird and mammal–mammal alarm eavesdropping has considered whether responses result from learning or potentially simple overlap in signal characteristics through shared phylogeny and similar alarm vocalizations (Magrath et al. 2009b; Randler 2012; Dutour et al. 2017; Meise et al. 2018). However, where eavesdropping occurs between phylogenetically distant taxa that exploit different communication modalities (e.g., sight, sound), they are unlikely to respond to other taxa's alarm signals due to overlap with species' own alarm systems (Magrath et al. 2015).

Here, we consider the interactions between Kalahari tree skinks (*Trachylepis spilogaster*), sociable weavers (*Philetairus socius*), and African pygmy falcons (*Polihierax semitorquatus*), henceforth "skinks," "weavers," and "falcons," respectively. These skinks occur in the arid savannah of southern Africa (Broadley 2000) and live in small groups of 3.9 ± 0.54 individuals on average (Brain 1969; Rymer et al. 2014). They largely forage on trees and on the ground close to trees but retreat to trees when disturbed, indicating that the ground represents a higher-risk foraging habitat (Brain 1969). They are strongly associated with weaver colonies, being found in greater numbers on trees with colonies (Rymer et al. 2014). Skinks appear to gain substantially from weaver colonies, including through refuge, basking, and foraging benefits (Rymer et al. 2014). Weaver colonies vary in size, often increasing with age, and can contain between 2 and 250 nesting chambers housing hundreds of weavers (Maclean 1973). Weaver colonies host a wide range of other species, across multiple taxa, including many invertebrates. Weaver colonies also host falcons, whose diet largely consists of small lizards (Maclean 1970), including skinks, whose remains are often found under falcon nests when falcons are breeding (Lowney AM, Thomson RL, personal observation). However, trees with colonies inhabited by falcons do not have fewer skinks than colony trees without falcons (Rymer et al. 2014). Falcons do not build their own nests and, in southern Africa, rely solely on weaver colonies for breeding and roosting (Maclean 1970). Falcon territories may contain multiple colonies, with falcons often moving between these colonies throughout the year.

Weavers have the potential to provide information to skinks about predators through both their behavior and vocalizations. Falcons likely present only a low threat to adult weavers given the low proportion of the falcon diet they make up (Maclean 1970) and the association between the species. Nevertheless, weavers alarm when a falcon is visible (Maclean 1970) and disperse when they approach (Lowney AM, Thomson RL, personal observation). Weavers usually occur in large groups around their colonies; their alarm calling when a falcon approaches the colony tree is conspicuous and unmistakable (Lowney AM, Thomson RL, Flower TP, personal observation). Skinks, therefore, have the opportunity to eavesdrop on predator presence information provided by weavers. Eavesdropping could facilitate their membership in this community in the face of predation risk by falcons. They might even exploit such information to expand their niche use at the weaver colony by spending more time foraging on the ground and further from the tree refuge.

Here, we explore the association between skinks and weavers to identify distinct association benefits. To do this, we focus on whether skinks eavesdrop on weavers to gain information. Certain reptiles have been shown to eavesdrop on other species (Whiting and Greeff 1999; Vitousek et al. 2007). Broadley's flat lizards (*Platysaurus broadleyi*) use signals from red-eye bulbuls (*Pycnonotus nigricans*) and pale-winged starlings (*Onychognathus nabouroup*) to locate food (Whiting and Greeff 1999), whereas the Galapagos marine iguana (*Amblyrhynchus cristatus*) use alarm calls of Galapagos mocking bird (*Mimus parvulus*) as a warning that Galapagos hawks (*Buteo galapagoensis*) are nearby (Vitousek et al. 2007). The information gained from eavesdropping in the aforementioned studies have distinctively different benefits, and these are not typically considered together. First, we investigate whether skinks use eavesdropping to expand their realized niche at colony trees by joining a cross-taxa community, despite the increased likelihood of a predator. Second, we test to determine if skinks gain early warning of predators from weavers and flee to cover earlier in response to approaching predators in the presence of weavers. Third, we experimentally test whether skinks eavesdrop on weaver alarm calls to reduce predation risk. Finally, to determine whether eavesdropping is mechanistically dependent on learning through familiarity with weaver vocalizations, we additionally compare alarm responses of skinks from colony versus noncolony trees.

METHODS

Field site

This study was carried out at Tswalu Kalahari, a reserve in the Northern Cape, South Africa (27°13′30″S and 22°28′40″E), that is approximately 114 000 ha. Our main study area consists of 130 km^2 containing over 250 sociable weaver colonies, mostly in the two dominant tree species camelthorn (*Vachellia erioloba*) and shephard's tree (*Boscia albitrunca*; Rymer et al. 2014). Falcon occupation of weaver colonies averaged 14% (±0.77 standard error [SE]) annually of ~250 colonies monitored (Bolopo et al. 2019). Ground vegetation is patchily distributed and dominated by Kalahari sourgrass (*Schmidtia kalihariensis*) and small shrubs. We focused our study on an area of 6 ha and on skinks at camelthorn trees only. All colonies used were within known falcon territories but did not host falcons at the time of study. Additionally, falcons were not breeding at the time of study. All observations are by A.M.L. Additionally, the time of day has been demonstrated to affect skinks behavior (Huey and Prianka 1977). Therefore, we carried out balanced treatments that equally represented different times of the day. Our research was approved by the University of Cape Town Research Ethics Committee (2015/V14/RT).

Skink abundance and movement

To investigate whether weaver presence expanded habitat use by skinks at colony trees, we counted skinks visible and whether they were on the ground or the tree at times when weavers were present at their colony or absent. Skink counts were undertaken between December 2016 and January 2017 at 20 colony trees from four locations around a colony tree, each lasting 4 min. Each observer location was at least 50 m from the tree and, after each count, the observer moved to the next location ~90° around the tree. Once the full rotation of the tree had been carried out, a further 5 min was used for the observer to slowly walk toward and around the tree; this helped identify individuals on the floor as these individuals were difficult to see from a distance of 50 m. In addition, this clarified any uncertainties about whether some individuals may have been counted twice (Rymer et al. 2014). Counts were undertaken using a spotting scope (Kowa TSN-881 and Kowa ×20–60 eyepiece), and we noted the number of skinks (active and, therefore, exposed) and their position as either low risk (on the tree) or high risk (on the ground) when first observed. An entire tree count would last ~25 min. Counts were done twice at a given tree (paired), once with weavers present and once when absent. Paired counts were always done on the same day and the order of counts was alternated between each paired count.

Skink FID in response to predators

To investigate whether weavers facilitate earlier escape responses by skinks and, therefore, reduce predation risk, we used an approaching human as a model predator to generate FIDs for both weavers and skinks. We undertook trials with skinks at trees with colonies and weavers present and we paired these with noncolony trees where weavers were absent. Weavers were on the ground during trials with weavers present. To control for habitat differences, paired trees were always within 200 m of each other and both trials were conducted within 60 min (21.2 min ± 2.55). One trial was carried out at each colony and each paired noncolony tree and the order of trials was alternated between samples. We searched for skinks from >50 m away using the spotting scope. Once a skink was located, the observer walked directly toward the skink at ~3 m/s, keeping the skink in sight. Weaver FIDs were also recorded at the colony trees where weavers were present to determine whether this affected skink FIDs. Different color markers were dropped to mark when skinks or weavers initiated escape and FID was measured (meters) after the trial.

We chose noncolony trees as controls as this prevented habituation to the approaching "predator" and reduced the amount of time that passed between paired trials. We could not account for when and how long weavers would be at a given colony, and weavers would often return immediately after the "predator" had retreated. Therefore, using noncolony trees as controls helped reduce the amount of time that passed between each trial. Additionally, when FIDs were carried out at control trees first, we could use the scope to observe when weavers were present at the paired colony tree and then start the FID at the noncolony tree. This increased the likelihood of weavers still being at the colony tree when the FID trial at the control was complete.

Skink eavesdropping on weaver alarm calls

Recording of weaver calls

We used a playback experiment to confirm that skinks eavesdrop on weaver alarm calls and flee to cover in response and investigate whether this eavesdropping behavior is learned or innate. To determine if skinks eavesdrop on weaver alarm calls, skinks at colony trees were presented with playback stimuli of weaver alarm (alarm) and nonalarm contact vocalizations (control), when weavers were not present. In addition, to determine whether eavesdropping is learned through familiarity with weavers, or is innate, these playbacks were repeated to skinks at noncolony trees, again making sure that no weavers were present at the time of experiment. Stimuli were created using recordings collected with a Sennheiser ME66 directional microphone attached to a tripod, placed 20 m from a colony tree that currently hosted falcons and coupled with a Marantz PMD660 recorder. Once the recording was started, the observer moved to a distance of >50 m from the colony tree and noted when weavers were present, how many there were, and the context of any calls (when foraging, weaving, resting, or when a predator approached). When alarm calls were produced, the species that triggered the alarm response was also noted. This allowed for the use of alarm calls produced specifically in response to approaching falcons. Nonalarm vocalizations were those produced when weavers were at the colony provisioning or weaving and no predator was observed, nor weaver antipredator behaviors.

Playback stimuli

Recordings from 20 unique colonies were used to produce one alarm stimulus and one nonalarm playback stimulus paired for each colony (40 playback stimuli in total) in Raven 1.4 (www.birds.cornell.edu/raven). Each stimulus consisted of 30 s of silence followed by 30 s of vocalization. The 30 s of vocalization stimulus were created using sound segments from a single recording. Chosen segments were those that had better signal to sound ratio. Where possible, full 30-s segments were used (29/40); however, where this was not possible, smaller segments were pieced together. These were filtered with a high-pass filter set at 500 Hz, with amplitudes standardized across recordings.

Experimental design and procedure

Playbacks trials were conducted at 40 different trees: 20 with a weaver colony and 20 without (paired). All paired trees were located within 250 m of one another. Each tree received two playback trials; one alarm and one nonalarm resulting in a total of 80 trials (20 paired trials at colony trees and 20 at noncolony trees). We ensured that the recording playback pair was from a different colony to that where playbacks occurred.

Playback trials were undertaken using a wireless speaker (FOXPRO Fury GX7 Digital Game Call) positioned on the tree where the experiment was carried out. The observer retreated to >25 m and used the scope to locate skinks. Once a skink was located on the tree, the observer would operate the speaker via a remote (TX-500) transmitter. To account for carryover effects, the order of stimulus presented was changed between each experiment. Skink behavior during each trial was observed through the scope. Response parameters were whether a skink ran from view (yes/no), and the total number of vertical and lateral head movements. An increase in vigilance may result in an increase in the number of head movements as skinks scan for potential predators. This has been shown to be true with other reptiles (Ito and Mori 2010). An individual skink would be presented with two trials: one alarm and one nonalarm vocalization. If skinks are shown to respond appropriately (increased vigilance to alarm calls but not change in behavior when presented with the control) at colony trees but not at noncolony trees, then this would imply a role of call learning and not simply innate knowledge of weaver alarm vocalizations. If a skink fled during the first trial, we would wait until a skink returned to the same area before repeating the process with the second trial. Occasionally, a skink would be quite distinct (missing part of a tail) and these would return to the same basking sites, suggesting that individuals have preferred locations and trials were conducted on the same individuals. However, many skinks were indistinguishable; therefore, we could not guarantee that the second trial was conducted using the same individual as the first. Nevertheless, random playback order ensures that any effect is balanced between treatments. Once a skink returned to the area, we waited for 60 s before presenting the second stimulus. This was to allow the individual to resume foraging or basking behavior. All trials were conducted when there were no weavers present. If weavers did appear during the trial, the experiment was abandoned and a different colony/noncolony tree pair was selected for the experiment.

Statistical analyses

All data were analyzed using the R statistical package 3.4.0. (R Core Team 2017). Generalized linear mixed models (GLMMs) were undertaken using the glmmTMB package (Brooks et al. 2019). This package was used due to its ability to handle zero-inflated models. Where count data were overdispersed, models were fitted with either a quasi-Poisson or negative binomial distributions (Hara and Kotze 2010). Trees, where paired treatments were undertaken, were given unique IDs that were then used as random terms in the relevant models. For analyses where interactions were fitted, we explored interactions where P values were less than 0.1 using post hoc tests. Those that had a value greater than 0.1 or where post hoc tests revealed no significant differences were subsequently removed from the models. Tukey post hoc tests were carried out using emmeans function (Lenth 2018). For each response variable, the full model terms and structure and the error distribution used are detailed in Appendix 1.

To explore whether weaver presence influenced skinks foraging site and behavior, a GLMM with a negative binomial distribution was first fitted to test whether weaver presence (present/absent) influenced the number of skinks visible at colony trees. A Poisson distribution was then used to compare the number of observed skinks foraging away from the tree when weavers were and were not present, fitted as an explanatory term, and tree ID was included as a random term. Time has been demonstrated to affect skinks behavior, with peak activity occurring earlier and later in the day (Huey and Prianka 1977); therefore, we included time of observation/experiment as an additional explanatory term in this and all subsequent models.

A negative binomial GLMM was used to determine whether weaver presence influenced skink FID. Colony presence (present/absent) and time of day were used as explanatory terms. Paired trees were given a unique pair ID and this was used as a random term. A Pearson's correlation was used to determine to what extent weaver FID influenced skink FID.

To test our assumption that skinks are able to eavesdrop on weaver alarm calls and whether this depended on their familiarity with weavers, we carried out GLMMs considering vigilance during playback trials fitted with a quasi-Poisson distribution. Our model used the number of head movements as the response variable and stimulus type (alarm/control), playback period (pre/during), tree type (colony/noncolony), and time of day as explanatory terms. Paired and individual trees were given unique IDs and these were used as random terms, with tree ID being nested within pair ID. We fitted a three-way interaction between the playback period, stimuli type, and tree type to determine whether skinks respond differently to the playback treatments.

We also tested the likelihood that skinks flee for cover to further identify whether skinks familiar with weavers more often show appropriate escape responses to alarm versus control calls. Again, this would imply a role for call learning and not simply innate knowledge of weaver alarm vocalizations. Here, we used stimulus type (alarm/control), tree type (colony/noncolony), and time of day as explanatory terms. Tree ID nested within playback pair ID was used as a random term. We included an interaction between tree type and stimulus type to explore whether skinks familiar with weavers better distinguish control versus alarm weaver calls.

RESULTS

During 59.5 h of acquiring playback recordings, we observed falcons approaching colonies on 108 occasions. Weavers alarmed to 90% of all falcon approaches and, in 87% of these approaches, the birds flew away from the spot where they had been perched.

Skink abundance and movement

In total, 75 skinks were observed, of which 19 were recorded on the floor foraging away from the tree. Consideration of whether weaver presence promotes skink activity on colony trees revealed that twice as many skinks were observed when weavers were present (Figure 1a; Table 1a). Furthermore, five times as many skinks were observed foraging on the ground when weavers were present compared with when weavers were absent (Figure 1b; Table 1b).

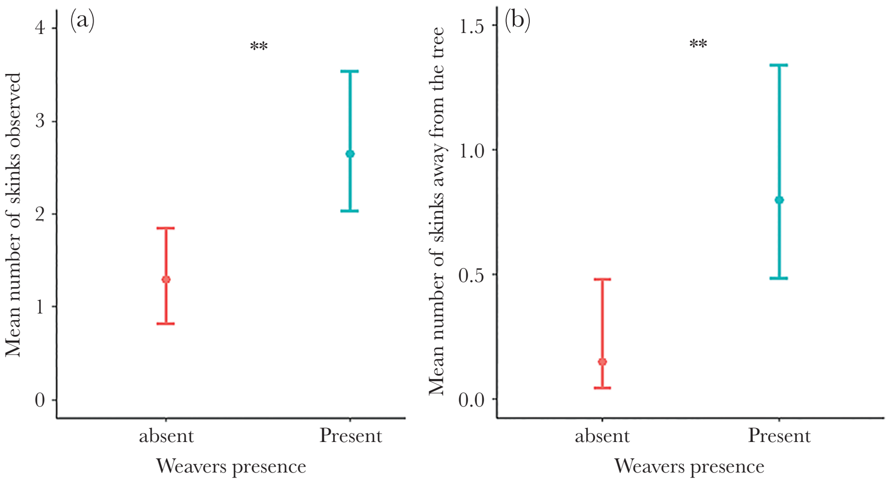

Figure 1
Mean (+95% confidence interval) number of skinks when weavers were present and absent at colony trees: (a) total skinks observed (n = 75); (b) proportion foraging away from the tree (n = 19; $^{**}P < 0.01$).

Table 1
GLMM (negative binomial and Poisson, respectively) of whether the number of skinks observed is influenced by the presence of sociable weavers (a) at colony trees only and (b) around colony trees. Time was recorded in the 24-h format and was converted to decimal (e.g., 12:30 became 12.5). Bold values demonstrate that skink presence increase the number of individuals observed at colony trees ($P = 0.0013$) and the number of individuals foraging in riskier habitats away from the tree ($P = 0.007$)

Response variables	Explanatory variables	Estimate	±SE	χ^2	P
(a) Total number of skinks n = 20	Weavers present (yes/no)	0.778	0.24	10.38	**<0.01**
	Time	0.066	0.03	3.63	0.06
(b) Skinks away from the tree; n = 20	Weavers present (yes/no)	1.70	0.63	7.17	**<0.01**
	Time	0.02	0.07	0.08	0.78

Skink FID in response to predators

In total, 68 FID experiments were undertaken: 34 at colony trees with weavers present and 34 at paired noncolony trees with weavers absent. The human “predator” could approach significantly closer to skinks at noncolony trees, before skinks fled for cover, compared with colony trees with weavers present (Figure 2; Table 2). There was a strong positive correlation between the weavers and skinks FID (Pearson’s correlation coefficient $|r| = 0.85$). Both species initiated their escape at the same distance in 23 of the 34 trials. During the other 11 trials, the weavers always dispersed first.

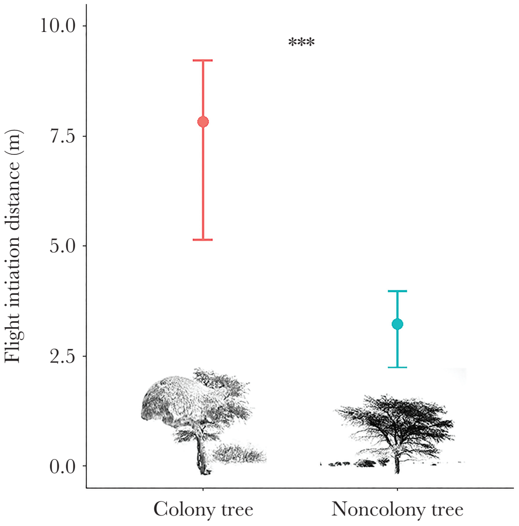

Figure 2
Mean (of the raw values + 95% confidence interval) flight initiation distance of Kalahari tree skinks at noncolony trees compared with when weavers were present at colony trees ($^{***}P < 0.001$).

Skink eavesdropping on weaver alarm calls

Vigilance response to playback stimulus

In response to weaver call playbacks, the interaction between playback period, stimulus type, and colony presence explained much of the variation (Table 3). Post hoc comparison of the preplayback and playback period revealed that skinks significantly increased their vigilance when presented with an alarm stimulus compared with the preplayback period at both colony (type, $z = -5.514$, $P < 0.001$; Figure 3a) and noncolony trees (type, $z = -5.761$, $P < 0.001$; Figure 4c). However, skinks at colony trees did not increase their vigilance when presented with a control stimulus (type, $z = -1.644$, $P = 0.723$; Figure 3b), whereas skinks at noncolony trees did (type, $z = -3.848$, $P < 0.01$; Figure 3d). Comparison between responses to alarm versus control stimuli in the playback period showed that skinks were significantly more vigilant when presented with an alarm than a control stimulus at both colony (type, $z = -4.412$, $P < 0.001$; Figure 4a,b) and noncolony trees (type, $z = 3.124$, $P < 0.05$; Figure 3c,d). Comparison between skinks at colony and noncolony trees, when presented with an

Table 2

GLMM (negative binomial) of whether sociable weaver presence influenced skink FID in response to predators. Time was recorded in the 24-h format and was converted to decimal (e.g., 12:30 became 12.5) before being used in the models. Bold values represent the increase in distance that skinks initiated FID ($P < 0.001$) when weavers were present

Response variables	Explanatory variables	Estimate	±SE	χ^2	P
Skink FID; $n = 64$ (32 paired)	Weavers present (yes/no)	0.838	±0.17	24.23	**<0.001**
	Time	0.004	±0.031	0.02	0.89

Table 3

Skink response to playback stimuli (quasi-Poisson and binomial respectively), skink vigilance (a) and the likelihood that skinks flee (b) when presented with alarm and control stimuli in response to playback stimuli. Time was recorded in the 24-h format and was converted to decimal (e.g., 12:30 became 12.5). Bold values represents that interactions between Playback period × Treatment × Colony tree ($P = 0.07$) and Treatment x Colony ($P = 0.02$) that explained much of the variation for differences in skink vigilance, and the likelihood that skinks flee for cover, respectively

Response variables	Explanatory variables	Estimate	±SE	χ^2	P
(a) Vigilance; $n = 160$	Playback period (pre/stimuli)			71.1	<0.001
	Treatment (alarm/control)			19.97	<0.001
	Colony tree (yes/no)			8.02	<0.01
	Time of trial	0.03	0.04	0.67	0.41
	Treatment order (first/second)			0.77	0.38
	Playback period × Treatment	−0.41	0.47	6.22	<0.05
	Playback period × Colony tree	0.73	0.55	0.01	0.93
	Treatment × Colony tree	0.76	0.67	1.33	0.25
	Playback period × Treatment × Colony tree	−1.40	0.77	3.30	**0.07**
(b) Flee (yes/no); $n = 80$	Treatment (alarm/control)			1.04	0.31
	Colony tree (yes/no)			5.45	<0.05
	Time	−0.73	0.73	1.02	0.31
	Treatment order (first/second)	4.50	2.98	2.29	0.13
	Treatment × Colony tree	−20.62	8.88	5.49	**0.02**

alarm stimulus, revealed no differences in vigilance. Skink vigilance was higher in response to control stimuli at noncolony trees than colony trees (type, $z = -2.863$, $P = 0.09$; Figure 4b); however, this was not statistically significant.

Likelihood skinks flee when presented with different playback stimuli

Our model testing the likelihood skinks flee for cover when presented with weaver call stimuli, revealed that skinks at colony trees were more likely to flee when presented with an alarm stimulus than skinks at noncolony trees ($z = -3.232$, $P < 0.001$; Figure 5a,b; Table 3). No difference was observed when comparing responses to the control stimuli. Post hoc tests also revealed that skinks at colony trees are more likely to flee when presented with an alarm than a control stimulus; however, this was not deemed to be statistically significant ($z = 2.512$, $P = 0.07$; Figure 5a; Table 3) but, at noncolony trees, no significant difference was more clearly observed.

DISCUSSION

Our results suggest that associating with weaver communities and eavesdropping on alarm vocalizations enable skinks at colony trees to reduce predation risk and exploit riskier habitat, despite exposure to a predatory community member, the pygmy falcon. Associating with weavers facilitates skink foraging and basking by allowing them to increase activity, venture further from refuges, and sit in more exposed locations. We show experimentally that skinks respond decisively to weaver alarm responses and specifically eavesdrop on weaver alarm calls. Furthermore, eavesdropping appears at least partially learned because skinks at colony trees respond more strongly to weaver alarm calls than controls and show appropriate escape responses, whereas skinks at noncolony trees do not clearly distinguish controls and alarms. It is possible but highly unlikely that there is a subpopulation of “weaver specialist” skinks within the species with a genetically driven weaver alarm response and preference for weaver colonies. However, this explanation appears less parsimonious given the lack of evidence for reproductive isolation between trees. Together, our results demonstrate that skinks eavesdrop on weaver alarm vocalizations toward falcons, which enables them to reduce predation risk and expand their realized foraging niche, potentially mitigating the costs of living with a predatory community member.

Many studies have focused on responses of eavesdroppers to alarm signals but, here, we also emphasize that eavesdropping may allow organisms to expand their realized niche (Vitousek et al. 2007; Magrath et al. 2015). By foraging in the presence of weavers, skinks can reduce their risk in the “landscape of fear.” This could enable skinks to reduce vigilance as demonstrated for other species (Sullivan 1984; Doligez et al. 2002; Mcgraw and Bshary 2002; Schmidt et al. 2010; Sharpe et al. 2010) and/or expand the area of habitat or resources exploited for a given risk threshold as results indicate here. The skink’s strategy will be a trade-off between gaining more protection and exploiting the weavers to get more food. This decision likely depends on skink energetic state with less satiated individuals more likely to exploit foraging benefits for an equal predation risk (Heithaus et al. 2007). We suggest that further research assess when animals exploit eavesdropping to expand their habitat use and/or foraging in comparison to reducing exposure to predators.

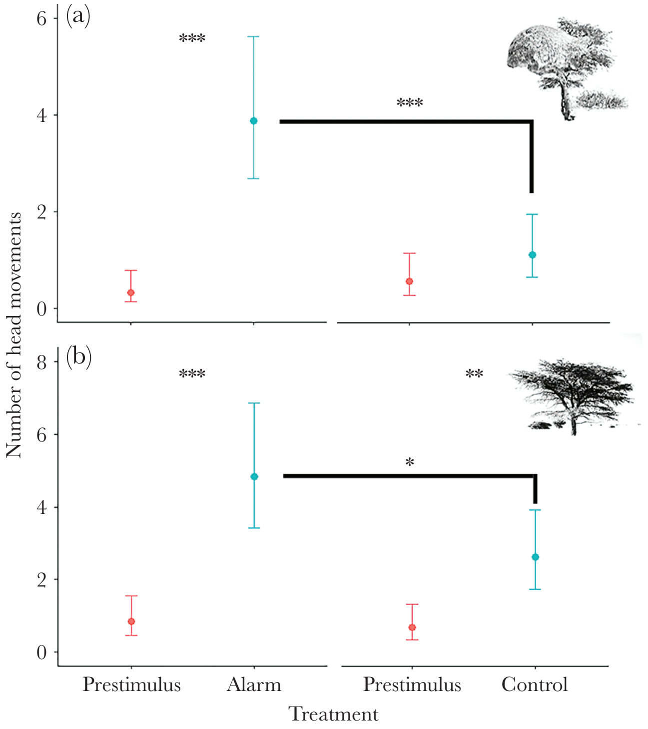

Figure 3
Skink vigilance measured as head movements (mean + 95% confidence interval). (a) Skink vigilance significantly increased when presented with the alarm call playback stimulus at colony trees but not control playbacks. Vigilance was also significantly greater to alarm than control playbacks. However, vigilance did not significantly change when presented with a control stimulus. In contrast, at noncolony trees (b), vigilance significantly increased when presented with either stimulus. Vigilance was also significantly greater to alarm than control playbacks (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

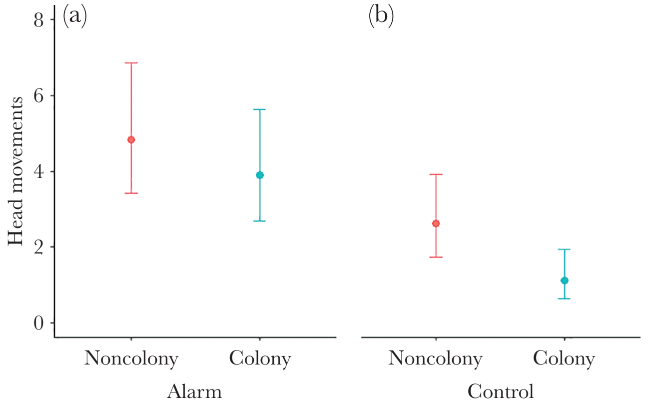

Figure 4
Skink vigilance (mean + 95% confidence interval) in response to alarm (a) and control (b) stimuli. (a) Skinks at colony and noncolony trees were more vigilant in response to alarm than control stimuli, but skinks at noncolony trees showed greater vigilance to control stimuli (b).

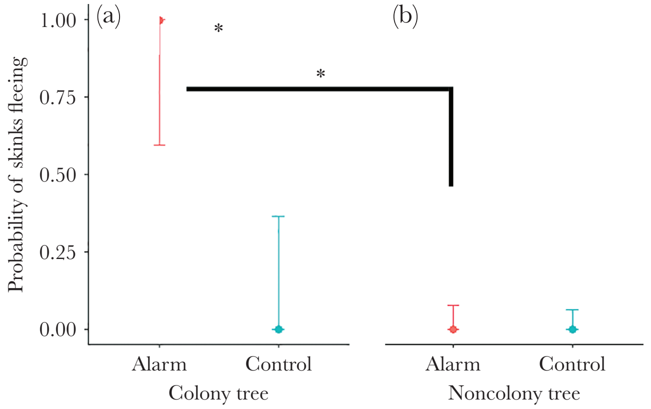

Figure 5
The likelihood (+95% confidence interval) of skinks fleeing during playback periods at colony and noncolony trees. Skinks at colony trees were more likely to flee in response to alarm stimuli than control stimuli, but skinks at noncolony trees did not show this relationship. Furthermore, in response to alarm stimuli, skinks at colony trees were more likely to flee to cover than skinks at noncolony trees (**$P < 0.01$).

Skink's eavesdropping on weavers illustrates how exploitation of beneficial relationships within communities can mitigate the costs of negative interactions with other community members. Skinks may gain numerous benefits from joining weaver communities, including through increased foraging returns and by mitigating risk. However, association with weavers likely exposes them to enhanced predation by pygmy falcons. Nevertheless, skinks can mitigate the risk through additional eavesdropping interactions with weaver community members. Therefore, we may expect to see that, when animals join mixed-species associations, natural selection will favor the evolution of beneficial species interactions that specifically mitigate the costs of negative interactions with other community members. For example some bird species nest near a potential predator, who by forming a protective umbrella around its own nest can exclude mutual predators (Bogliani et al. 1999).

Skinks may not only eavesdrop on signals but also attend to weaver cues, including foraging and flight behavior. In nonalarm contexts, skinks may use weaver chatter signals or foraging/weaver behavior as cues that predation risk is low. Studies have suggested that heterospecifics taking flight in response to an approaching predator should also be a reliable cue in alarm contexts (Morse 1977), yet few studies have indicated that relaxed behavior can be used as a reliable cue (Sullivan 1984; Sullivan 1985; Ridley et al. 2014; Lilly et al. 2019). Although we did not test for this, we did observe fewer false responses to control calls at colony trees and, therefore, suggest that this be explored in future studies. Moreover, to the best of our knowledge, only one study has explicitly determined through experimentation that heterospecific relaxation is a cue to the absence of a predator (Lilly et al. 2019). Such behavior is likely widespread in mixed-species assemblages, and research to explore this possibility would represent an exciting new avenue to determine how community members exploit both heterospecific signals and cues to moderate risk in the landscape of fear.

Skinks use cross-taxa eavesdropping to avoid predation, further demonstrating that eavesdropping is likely driven by shared information value rather than phylogeny. Eavesdropping is commonly used in species associations, especially between species within the same taxonomic and functional group (Lea et al. 2008). Eavesdropping will be favored by any organism when information from the environment reliably correlates with a context in the environment that affects individual fitness (Danchin et al. 2004; Shettleworth 2010). Intuitively, between-taxa eavesdropping should, therefore, be no less likely than within-taxa eavesdropping, assuming that signal detection is possible and predators overlap.

However, studies have mainly focused on within-taxa eavesdropping (Kitchen et al. 2010; Baigrie et al. 2014; Ridley et al. 2014; Meise et al. 2018). In particular, research has considered how the alarm calls of different bird species often share acoustic similarities, which may facilitate heterospecific recognition (Marler 1957; Hurd 1996). Overlap in information value and sensory systems to detect signals may be less likely between taxa; nevertheless, for organisms of the same trophic level, requiring similar habitat and which share predators, overlap might be high (Goodale et al. 2010).

The mechanism behind skink eavesdropping appears to be in part learnt through familiarity, but other factors may contribute. Our finding that skinks at colony trees better discriminated alarm and control stimuli and were more likely to show flee responses to alarm calls, indicates that learning plays a role in the acquisition of eavesdropping responses appropriate for signal context. By contrast, skinks at noncolony trees showed limited discrimination, nor an appropriate flee response to alarms. The overall high response to alarm and control signals by skinks at noncolony trees may result from a low threshold for unfamiliar sounds. The lack of evidence for reproductive isolation between trees suggests that individual skinks may change location, develop in different places and also experience weaver flocks in their territory providing opportunities for learning. Overall, our results support the benefits available from a learning mechanism that enables individuals to exploit available information within a heterogeneous environment (Griffin 2004). Such learning mechanisms likely play an important role for species that exploit mixed-species associations where community membership may be variable, especially across a species' range.

In summary, we demonstrate how across-taxa eavesdropping allows skinks to expand their realized niche and join communities including predatory members, which may otherwise exclude them. Such habitat use expansion may be an important aspect of mixed-species assemblages that are facilitated by eavesdropping. Eavesdropping is likely possible through learning in skinks and, more generally, a learning mechanism may allow individuals to be flexible in response to changes in local community composition (Griffin 2004). Our study highlights the broad benefits of eavesdropping for risk management, specifically through niche expansion, thereby highlighting its potential importance in facilitating community associations and habitat use.

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Appendix 1

Complete list of models used, including response, explanatory and random effects. Distribution, zero inflation, and overdispersion parameters are also shown. All models were carried out in the glmmTMB package using the glmmTMB function (Brooks et al. 2019)

Response variables	Model	Distribution	Explanatory variables	Random effects	Zero inflation	Overdispersion parameter
Skink abundance and movement						
(a) Total number of skinks	GLMM	Poisson	Weavers present (yes/no) Time	Colony ID	No	
(b) Skinks away from the tree	GLLM	Poisson	Weavers present (yes/no) Time	Colony ID	No	
Skink FID in response to predators						
Skink FID		Negative binomial	Weavers present (yes/no) Time	Paired ID	No	2.25
Skink eavesdropping on weaver alarm calls						
(a) Skink vigilance	GLLM	Quasi-Poisson	Playback period (pre/stimuli) Treatment (alarm/control) Colony tree (yes/no) Time of trial Treatment order (first/second) Playback period × Treatment Playback period × Colony tree Treatment × Colony tree Playback period × Treatment × Colony tree	Pair ID Tree ID	No	0.577
(b) Skinks fleeing (yes/no)	GLLM	Binomial	Treatment (alarm/control) Colony tree (yes/no) Time Treatment order (first/second) Treatment × Colony tree	Pair ID Tree ID		