

Heterospecific eavesdropping in a nonsocial species

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Many species respond to heterospecific alarm calls, and the majority are social taxa and possess complex alarm calls themselves. Thus, the ability to respond to heterospecific alarm calls may be facilitated by possessing both these traits. Gunther's dik-dik (*Madoqua guentheri*) is a monogamous, territorial, and nonsocial miniature antelope with a simple vocal repertoire. Dik-diks are highly vulnerable to predation and could benefit from eavesdropping on heterospecific alarm calls. We broadcast recordings of white-bellied go-away bird (*Corythaixoides leucogaster*) alarm calls to dik-diks to test whether they could respond to heterospecific alarm calls. On hearing a go-away bird alarm call, dik-diks increased their likelihood to run to cover, decreased their foraging activity, increased their rate of head turning, and increased their period of vigilance compared with a nonthreatening bird song. Thus, predation risk alone, in the absence of complex sociality or complex communicative abilities, may be sufficient to drive the evolution of heterospecific eavesdropping. *Key words:* associative learning evolution, eavesdropping, dik-dik, heterospecific alarm call. [*Behav Ecol* 19:1041–1046 (2008)]

Alarm calls function as a targeted alert system used in several contexts to: alert conspecifics of potential danger (Weary and Kramer 1995), warn a predator that it has been spotted (Hasson 1991), and recruit nearby individuals for mobbing defense (Curio et al. 1978) or to call in the predator of the predator (Grim 2008). Recent studies suggest that alarm calls elicit responses not only from predators and conspecifics but also from eavesdropping or cooperating heterospecifics (Oda and Masataka 1996; Shriner 1998; Fichtel 2004). Eavesdropping, also known as information parasitism, occurs when an individual other than the intended receiver cues in on public sensory information (McGregor 2005). Though eavesdropping is a well-studied phenomenon (Mennill et al. 2002), we do not know the extent of eavesdropping nor do we have a predictive theory that explains which species should eavesdrop.

Sociality and mixed species associations can reduce group members' risk of predation through dilution effects, predator deterrence, and improved detection (Bshary and Nôe 1997; Treves 2000). However, a positive association between group size and predator detection efficiency relies on the ability of members to communicate. The evolution of social complexity is associated with the evolution of a large vocal alarm repertoire (Blumstein and Armitage 1997b; Blumstein 2003). Thus, it is likely that social species with large alarm call repertoires are predisposed to respond to heterospecific alarm calls. We define sociality as group living in which members interact and form relationships. Some nonsocial species that are capable of heterospecific alarm call discrimination live in dense aggregations and are highly vulnerable to predation (Laurie 1981; Wauters and Dhondt 1992). Therefore, predation alone may be a sufficient factor to drive the evolution of the ability to respond to heterospecific alarm calls.

We studied the Gunther's dik-dik (*Madoqua guentheri*), a nonsocial, territorial, monogamous (Estes 1991), yet highly

vulnerable prey species with a simple alarm call repertoire, to see if vulnerability without sociality was sufficient for the evolution of heterospecific alarm call recognition. We acknowledge that what we refer to as an "ability" is likely to be a learned trait (Shriner 1998). Nonetheless, some species may be predisposed to learn about specific biologically important things (Seyfarth et al. 1980; Marler 2004).

Dik-diks are miniature antelope, approximately 3.7–5.5 kg, inhabiting dry regions of low shrubby bush with adequate vegetative cover (Haltenorth and Diller 1980). Pairs maintain territories of approximately 5–30 ha (Kingdon 1997). The large territory size suggests that couples are acoustically isolated from neighbors, and therefore, their single, breathy, "zik-zik" alarm whistle is used for communication between closely associated pairs (Estes 1991). They are locally abundant in acacia woodlands (approximately 5 dik-diks km⁻²) and fall prey to >20 species of aerial and terrestrial predators such as leopards, lions, wild dogs, hyenas, vultures, and eagles. (Estes 1991). To conceal themselves from predators, dik-diks spend much of their lives in dense cover (Kingswood and Kumamoto 1996). Thus, they may benefit from eavesdropping on a species that has a better view of potential predators.

In the East African savannah, the go-away birds (*Corythaixoides spp.*) are named and known for their alarm calls, warning surrounding conspecifics, and eavesdropping heterospecifics of approaching danger (Simmons 2000). The go-away bird is often spotted perched on or near the top of trees, enabling it to spot approaching raptors and ground predators from a distance. Although it is speculated that neighboring animals respond to the go-away's alarm call (Simmons 2000), we are unaware of a published study recording which heterospecifics respond to this public information.

We conducted playback experiments to dik-diks using multiple recorded exemplars of the go-away bird alarm call and song from a nonthreatening bird as a control. If vulnerability, rather than complex sociality or complex communicative abilities, was sufficient to select for the ability to respond to heterospecific alarm calls, dik-diks would discriminate between the 2 sounds and modulate their antipredator behavior appropriately.

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Received 7 January 2008; revised 13 May 2008; accepted 13 May 2008.

METHODS

Literature analysis

We compiled all playback studies that documented heterospecific eavesdropping on alarm calls and categorized them according to whether each species were social or lived in mixed species groups, whether they emitted alarm calls, and if so, whether the calls were predator specific or varied in rate. For species not reported to produce alarm calls, we noted whether they were nonvocal, had seasonal variation in vocalizations, or emitted multiple vocalizations.

Obtaining alarm calls and control vocalizations

We conducted playback experiments in October 2007 at the Mpala Research Centre (00° 17' 52N, 6° 53' 11.6W) in Laikipia, Kenya. We broadcast recordings of white-bellied go-away bird alarm calls and slate-colored boubou (*Laniarius funebris*) songs to dik-diks, over a 48-km² area. We recorded (16 bit, 44 kHz) approximately 25 exemplars of raptor-elicited go-away bird aerial alarm calls and 25 boubou songs with a line and gradient condenser microphone (AT835b, Audio-Technica US, Stow, OH) onto a direct to disk digital recorder (Marantz PMD670, Marantz America, Mahwah, NJ). Based on pilot observations, we noticed that dik-diks did not alter their behavior when nearby slate-colored boubous sang; we assumed boubou songs were nonthreatening to dik-diks and could serve as an appropriate control.

We selected 4 exemplars (from unique individuals) of each stimulus (go-away alarm calls and boubou song controls; Figure 1) with the greatest signal to noise ratio and the least background noise. We then normalized each exemplar to 95% of its maximum amplitude and created playback tracks (.aif files) with each stimulus preceded by 30 s of silence and followed by 60 s of silence. All exemplars were modified using SoundEdit 16 (Adobe Systems, 1997).

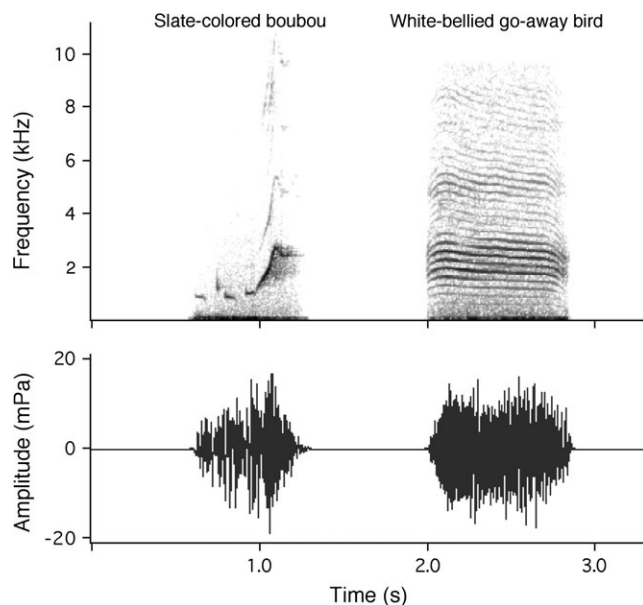


Figure 1
Spectrograms (FFT size = 1024, overlap = 99.22%, filter bandwidth = 1066.32 Hz, frequency grid resolution = 43.07 Hz) and waveforms of naturally elicited slate-colored boubou song and white-bellied go-away bird alarm calls.

Playbacks were broadcast from an iPod (Apple, Cupertino, CA) through a PAL speaker (Tivoli Audio, LLC, Cambridge, MA). Controls were broadcast at 77–79 dB SPL and experimental stimuli at 93–95 dB SPL (measured 1 m away from a Radio Shack Digital Sound Level Meter Model #33-2055, Fort Worth, TX.). Amplitudes were selected to mimic the natural intensities of go-away bird alarm calls and boubou song. Although not precisely measured, we are confident that the boubou's natural song was emitted at a lower amplitude than go-away bird alarm calls at an identical distance.

Playback paradigm

Dik-diks have 3 peaks of activity at midnight, dawn, and dusk (Estes 1991). We conducted our experiments during 0600–1030 h and 1500–1730 h, times when boubous and go-away birds were also active. We drove a Land Rover across 70.6 km of dirt road around the study site at a slow speed (5–10 k h⁻¹). When a dik-dik was spotted, we stopped, turned off the vehicle, and began an experiment: the speaker was placed at the window (1.4 m above the ground); we noted the dik-dik's baseline behavior during the 30 s of silence as well as the animal's response during the post-playback 60-s period. We also noted the sex of each dik-dik, identifying males by their horns (Estes 1991). We did not conduct experiments during periods of rain, wind >Beaufort scale 4–5, human interference, or when we could see natural predators.

We dictated behavioral transitions onto a microcassette recorder using a precompiled ethogram of common dik-dik behaviors. Two of the authors trained until they were consistently scoring behavior and then recorded all behavioral observations. Our ethogram included stand look (legs stationary, head erect), sit look (weight resting on belly, legs tucked under body with torso on ground), walk (slow quadrupedal movement), run (rapid quadrupedal movement), stand forage (4 legs on the ground with head in/near vegetation), groom (head turned to lick torso), scratch (short lifting of hind leg to upper body or head), body, ear, head, leg and nose twitch/shake (short quiver or spasm of the torso, ear, head, leg or nose), foot stamp (foot lifted and brought down on ground heavily), tongue flick (short exposure of tongue), vocalization, and out of sight. We later scored these focal observations in JWatcher 1.0 (Blumstein and Daniel 2007) for use in subsequent analysis. After each completed focal sample, we recorded the playback location using an Etrex GPS (Garmin Corp., Salem, OR) and measured the speaker to dik-dik distance in meters.

To minimize the possibility of resampling individuals, a minimum distance of 50 m separated all playback sites. We alternated experimental and control stimuli to avoid influencing baseline behavior of nearby dik-diks. If dik-diks were found in pairs, we sampled both individuals simultaneously with the same playback. Later, we randomly selected one of the paired individuals for use in analysis.

Statistical analyses

Using a Chi-square test, we examined the effect of treatment on the proportion of dik-diks that ran within 5 s of hearing the playback. Dik-diks that ran out of sight immediately reacted strongly to the playback; however, their absence for the next 55 s made any further exploration of their behavior impossible. Therefore, in the following analyses conducted in StatView (SAS Institute, 1993), we excluded any focal individuals that were out of sight for 90% or more of the post-playback period.

We calculated the proportion of time spent engaged in each behavior for the 30 s baseline period and subtracted this from time allocation measurements for the 15 s after the onset of the

playback. This allowed us to quantify the change in measured behaviors (e.g., Adams et al. 2006; Coleman et al. 2008). We focused on the 15 s after playback because dik-dik responses were sometimes brief and dik-diks often moved out of sight over longer periods of time. We explored the effects of treatment on all recorded activities but focused formal analyses on the following behaviors (thought to be associated with an increase in dik-dik alertness; Brotherton and Rhodes 1996): time spent foraging, rate of looking, and time spent stand looking. These variables are associated with antipredator and vigilance behaviors (Caro 2005) and were therefore an appropriate way to test our hypotheses about risk perception.

We defined the rate as number of looks over total time spent looking; this number denotes the rate at which dik-diks moved their head to scan their surroundings, presumably in an attempt to acquire more information about the true predation risk. We then used *t*-tests to compare the change in rates of foraging and looking over 15 s post-playback intervals. A chi-square test was used to examine the effect of treatment on the probability of dik-diks to increase time allocated to stand looking. To determine effect size, we examined the contingency coefficients (for all chi-square tests) and *d* scores (for all *t*-tests). Cohen's *d* scores near 0.2 indicate a small effect, 0.5 a medium effect, and 0.8 a large effect (Cohen 1988).

Our final data set consisted of 51 females (average distance to speaker = 23.2 mean \pm 8.6 SD), 45 males (average distance to speaker = 27.1 mean \pm 12.4 SD), and 4 unknowns (average distance to speaker = 24.1 mean \pm 15.4 SD). This data set divided into 54 (31 female, 21 male, 2 unknown, average distance to speaker = 24.7 mean \pm 10.0 SD) go-away bird playbacks and 46 (20 females, 24 males, 2 unknown, average distance to speaker = 25.4 mean \pm 11.8 SD) control playbacks, for a total of 100 playbacks to unique individuals. For each focal observation, we quantified and recorded possible confounding factors, and later tested these variables by fitting a logistic regression (for whether an individual ran in the first 5 s after playback) or general linear models (for the remaining continuous dependent variables).

RESULTS

Literature analysis

We found that birds respond to other birds and mammals to other mammals, but documented cases across taxonomic groups were not as common (Table 1). We also found that the majority of species studied live in social or mixed species groups (24/27 studies, 18/21 species). Of the 18 studied social species that respond to heterospecific alarm calls, 13 species have complex alarm calling behavior, 12 species produce predator specific calls, and 1 species varies calling rate to convey urgency. The remaining 5 social species are reported to emit only a single type of alarm call but have more than 1 vocalization.

Playback study

We used StatView (SAS Institute, 1993) to fit the logistic regressions and SuperANOVA (Abacus Concepts, 1991) to fit the general linear models. None of the examined covariates or factors—distance to speaker (all *P* values >0.24), number of conspecifics in view (all *P* values >0.12), distance to cover (all *P* values >0.14), exemplar (all *P* values >0.30), sex of focal individual (all *P* values >0.58), or amplitude (all *P* values >0.30)—significantly explained variation in the response to playback. Observer effects did not significantly explain variation (all *P* values >0.11) in response to 3 variables (running within 5 s of post-playback, rate of looking, and

proportion of time spent stand looking) and did not significantly interact (*P* = 0.948) with the fourth (proportion of time spent foraging).

Dik-diks were more likely to run within the first 5 s of hearing a white-bellied go-away bird alarm call (20/54 ran) compared with a slate-colored boubou song (2/46 ran - $\chi^2 = 15.5$, *P* < 0.0001, contingency coefficient = 0.366). Those dik-diks that remained decreased their proportion of time spent foraging on hearing the heterospecific alarm call ($t_{84} = -2.10$, *P* = 0.039, Cohen's *d* = 0.458; Figure 2a) and increased their rate of looking/head turning compared with those that heard the control bird song ($t_{96} = 2.86$, *P* = 0.005, Cohen's *d* = 0.583; Figure 2c). The proportion of time standing and looking was not influenced by playback stimulus ($t_{96} = 0.425$, *P* = 0.672, Cohen's *d* = 0.07; Figure 2b). In the first 15 s after playback, 17/54 individuals increased the amount of time allocated to standing and looking after hearing a go-away bird compared with 6/46 individuals after hearing the boubou ($\chi^2 = 4.77$, *P* = 0.029, contingency coefficient = 0.213).

DISCUSSION

The combined results of immediate running, decreased time spent foraging, increased looking rate, and increased time spent stand looking suggest an increase in dik-dik alertness in response to go-away bird alarm calls. Most reported cases of heterospecific alarm call discrimination are in species more social than dik-diks (24/27 studies, 18/21 species), and it is thus noteworthy that territorial, nonsocial dik-diks also possess the ability to respond to heterospecific alarm calls.

Learning processes, like other traits, are shaped by natural selection (Shettleworth 1993). In social species, the ability of group members to respond to conspecific alarm calls is often explained through associative learning (Griffin 2004). In this model, the predator cue (conditioned stimulus) is presented immediately before the conspecific alarm call (unconditioned stimulus), eventually leading group members to associate the 2 stimuli and respond to either stimulus with antipredator behavior (Shettleworth 1998). Furthermore, Griffin and Galef (2005) recently showed that the order in which the stimuli are presented does not matter. In other words, group members have evolved a means of learning that does not require a specific presentation order between predator cue (conditioned stimulus) and alarm call (unconditioned stimulus). This selected mode of social learning allows individuals to associate alarm calls with antipredator behavior independent of a predator cue and furthermore suggests an increased level of behavioral plasticity (Griffin and Galef 2005). This learning ability increases the likelihood of a social animal associating a novel predator with a familiar conspecific alarm call (Griffin 2004) or, conversely, a familiar predator with a novel heterospecific alarm call.

Dik-diks neither produce complex alarm calls nor do they live socially, yet their extreme vulnerability to predators (50% fawn survival rate; MacDonald 1985) creates a strong selective force that may drive the evolution of associative learning abilities in this nonsocial species. We can apply this logic to other heterospecific eavesdroppers such as the Galapagos marine iguana (*Amblyrhynchus cristatus*), the golden-mantled ground squirrel (*Spermophilus lateralis*), and the red squirrel (*Sciurus vulgaris*). Like dik-diks, iguanas do not have complex alarm communication (Vitousek et al. 2007). Like dik-diks, golden-mantled ground squirrels and red squirrels do not live socially (Tonkin 1983) and are vulnerable to predators.

Our results suggest that high predation risk is itself a key factor in the evolution of an individual's ability to respond to heterospecific alarm calls. Future research should tease apart how predation risk and sociality interact; however, our results

Table 1

Past heterospecific eavesdropping playback studies: caller, responding heterospecific, sociality of responding heterospecific, specificity of the alarm call or vocalizations of the responding species, and references

Caller	Responding heterospecific	Social?	Specificity of		References
			Alarm call?	Non-alarm vocalizations?	
Across taxa					
White-bellied go-away bird (<i>Corythaixoides leucogaster</i>)	Guenther's dik-dik (<i>Madoqua guentherii</i>)	No ^a	No	Yes ^b	This study
Superb starling (<i>Spreo superbus</i>)	Vervet monkey (<i>Cercopithecus aethiops</i>)	Yes	Yes ^c		1–3
Crested guinea fowl (<i>Guttera pucherani</i>)	Diana monkey (<i>Cercopithecus diana</i>)	Yes ^d	Yes ^c		4, 18
Eurasian Jay (<i>Garrulus glandarius</i>)	Red squirrel (<i>Sciurus vulgaris</i>)	No ^a	Yes ^c		6–8
Galapagos mockingbird (<i>Nesomimus par vulus</i>)	Galapagos marine iguana (<i>Amblyrhynchus cristatus</i>)	No ^c	Nonvocal	Nonvocal	27
Diana monkey (<i>Cercopithecus diana</i>)	Yellow-casqued hornbill (<i>Ceratogymna elata</i>)	Yes ^d	No	Yes ^f	4, 5, 31
Mammal–mammal					
Moustached tamarin (<i>Saguinus mystax</i>)	Saddleback tamarin (<i>Saguinus fuscicollis</i>)	Yes ^d	Yes ^c		28
Saddleback tamarin (<i>Saguinus fuscicollis</i>)	Moustached tamarin (<i>Saguinus mystax</i>)	Yes ^d	Yes ^c		28
Diana monkey (<i>Cercopithecus diana</i>)	Campbell's monkey (<i>Cercopithecus campbelli</i>)	Yes ^d	Yes ^c		19
Campbell's monkey (<i>Cercopithecus campbelli</i>)	Diana monkey (<i>Cercopithecus diana</i>)	Yes ^d	Yes ^c		18
Chimpanzee (<i>Pan troglodytes</i>)	Diana monkey (<i>Cercopithecus diana</i>)	Yes ^d	Yes ^c		18
Campbell's monkey (<i>Cercopithecus campbelli</i>)	Diana monkey (<i>Cercopithecus diana</i>)	Yes ^d	Yes ^c		19
Putty-nosed monkey (<i>Cercopithecus nictitans stamplii</i>)	Diana monkey (<i>Cercopithecus diana</i>)	Yes ^d	Yes ^c		29
Nilgiri langur (<i>Trachypithecus johnii</i>)	Bonnet macaque (<i>Macaca radiata</i>)	Yes ^d	Yes ^c		9, 10
Sambar deer (<i>Cervus unicorn</i>)	Bonnet macaque (<i>Macaca radiata</i>)	Yes ^d	Yes ^c		10
Hanuman langur (<i>Semnopithecus entellus</i>)	Bonnet macaque (<i>Macaca radiata</i>)	Yes ^d	Yes ^c		10
Redfronted lemur (<i>Eulemur fulvus rufus</i>)	Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Yes	Yes ^c		12–14
Ringtailed lemur (<i>Lemur catta</i>)	Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Yes	Yes ^c		33
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Redfronted lemur (<i>Eulemur fulvus rufus</i>)	Yes	Yes ^c		13, 15
Verreaux's sifaka (<i>Propithecus verreauxi</i>)	Ringtailed lemur (<i>Lemur catta</i>)	Yes	Yes ^c		30
Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Yes	Yes ^g		20, 22
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	Golden-mantled ground squirrel (<i>Spermophilus lateralis</i>)	No ^a	No	Yes ^b	20, 21
Bird–bird					
White-browed scrubwren (<i>Sericornis frontalis</i>)	Superb fairy-wren (<i>Malurus cyaneus</i>)	Yes ^d	Yes ^c		11
Superb fairy-wren (<i>Malurus cyaneus</i>)	White-browed scrubwren (<i>Sericornis frontalis</i>)	Yes ^d	Yes ^c		11
Forester's tern (<i>Sterna forsteri</i>)	Western grebe (<i>Aechmophorus occidentalis</i>)	Yes ^{d,h}	No	Yes ^b	16, 17, 25, 32
American avocet (<i>Recumirostra americana</i>)	Dunlin (<i>Calidris alpina</i>)	Yes ^{d,h}	No	Yes ^b	23, 25
American avocet (<i>Recumirostra americana</i>)	Western Sandpiper (<i>Calidris mauri</i>)	Yes ^{d,h}	No	Yes ^b	23–25
Black-capped chickadee (<i>Poecile atricapillus</i>)	Red-breasted nuthatch (<i>Sitta canadensis</i>)	Yes ^{d,h}	No	Yes ^b	25, 26

Sociality is defined as group living in which group members interact and form relationships.

1—Isbell (2005), 2—Cheney and Seyfarth (1985), 3—Seyfarth et al. (1980), 4—Rainey et al. (2004), 5—Rasa (1983), 6—Randler (2006), 7—Greene and Meagher (1998), 8—Wauters and Dhondt (1992), 9—Coss et al. (2007), 10—Ramakrishnan and Coss (2000), 11—Magrath et al. (2007), 12—Lawler et al. (2005), 13—Fichtel (2004), 14—Brockman et al. (2001), 15—Vick and Pereira (1989), 16—Nuechterlein (1988), 17—Nuechterlein (1981), 18—Zuberbühler (2000a), 19—Zuberbühler 2000b, 20—Shriner (1998), 21—Bartels and Thompson (1993), 22—Blumstein and Armitage (1997a), 23—Leger and Nelson (1982), 24—Johnson (2005), 25—Poole (2005a, 2005b, 2005c, 2005d), 26—Templeton and Greene (2007), 27—Laurie (1981), 28—Kirchhof and Hammerschmidt (2006), 29—Eckardt and Zuberbühler (2004), 30—Oda and Masataka (1996), 31—Rainey and Zuberbühler (2007), 32—Nuechterlein and Buitron (2006), 33—Oda (1998).

^a Territorial all year.

^b Multiple vocalizations but only 1 alarm call.

^c Predator specific alarm call.

^d Live in mixed species groups or flocks (for all or majority of year).

^e Colonial.

^f Seasonal call with variation.

^g Alarm call conveys information about urgency.

^h Territorial during breeding season.

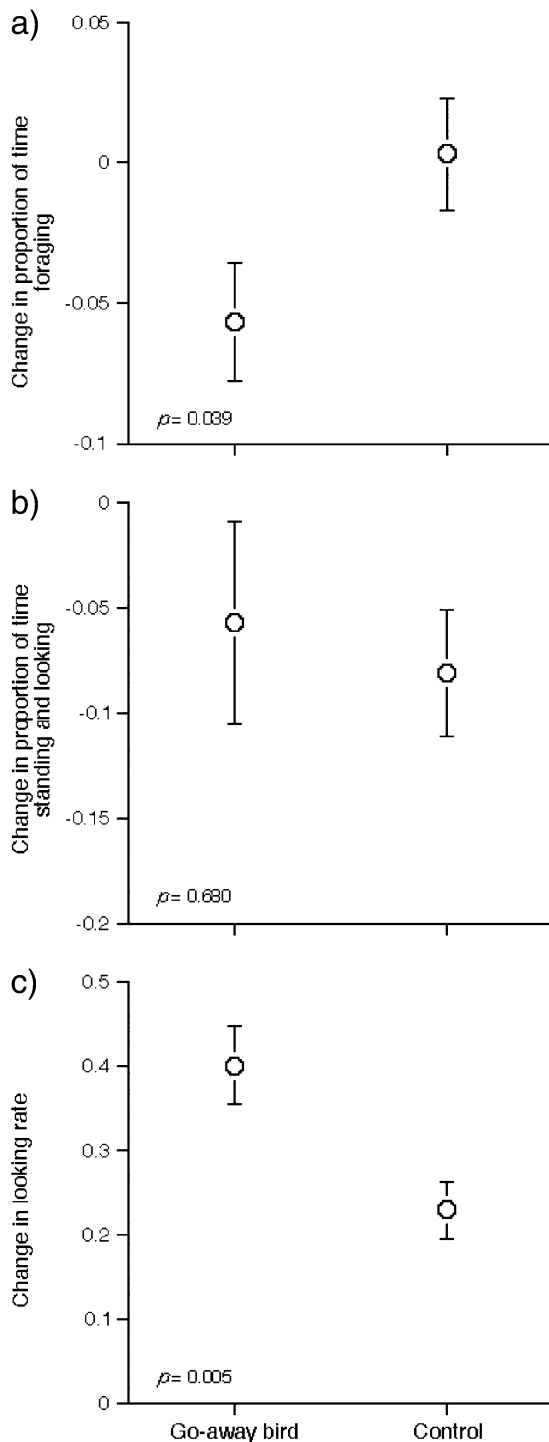


Figure 2
Change (mean difference between the first 15 s after playback and the 30 s baseline period \pm standard error) of (a) proportion of time spent foraging; (b) proportion of time spent standing and looking; and (c) looking rate (N head turns/s) as a function of playback stimulus (go-away bird alarm call, boubou song).

suggest that sociality is not a necessary prerequisite for the evolution of flexible associative learning abilities. Shettleworth (1998) suggests that animals more easily acquire learning behaviors that increase their chances of survival. The fitness benefit of flexible associative learning may therefore be increasingly important in highly vulnerable species, explaining

heterospecific alarm call response in Galapagos marine iguanas, golden-mantled ground squirrels, red squirrels, and dik-diks. Further studies are needed in highly social species with little to no predation, as well as nonsocial species with extreme predation, to further address this question.

We thank the UCLA Department of Ecology and Evolutionary Biology, the UCLA Office of Instructional Development, and the Lida Scott Brown Endowment for support. We thank the Kenyan Ministry of Science and Technology for permission to work at Mpala. We are extremely thankful to Director Margaret Kinnaird, Christopher Odhiambo, and the staff of Mpala who welcomed and facilitated our work. George Aike provided GIS assistance. Finally, we thank our guides Mathew Namoni, Jacob Waitthaka, and Jacob Egirigiri, as well as Tom Smith, Robert McMoran, Allison Alvarado, and Brenda Larison for help conducting playbacks, and Mark Hauber and 2 anonymous reviewers for astute and very constructive comments.

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