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Original Article

Sentinel dominance status influences forager use of social information

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Animals in social groups can acquire information about the need for antipredator behavior by personally sampling the environment or from information provided by others. Use of such social information is expected to be adjusted according to its reliability, but experimental tests are rare and tend to focus just on alarm calls. We use detailed behavioral observations, acoustic analyses, and playback experiments to investigate how differences in sentinel dominance status affect the behavioral decisions of foraging dwarf mongooses (*Helogale parvula*). Dominant individuals acted as sentinels considerably more often than subordinate group members and used higher sentinel posts for guarding, making them potentially higher-quality sentinels in terms of experience and optimal positioning for predator detection. Surveillance calls produced during sentinel bouts contained vocal information about dominance status. Playback experiments showed that foragers used surveillance calls to detect sentinel presence and identity, and adjusted their vigilance behavior accordingly. When a dominant sentinel was on duty, compared with a subordinate groupmate, foragers increased reliance on social information, gathered less information through personal vigilance, and focused more on foraging. Our study contributes novel evidence that a major benefit of individual- and class-specific vocalizations is the potential to assess differences in caller information quality.

Key words: **antipredator vigilance, reliability, sentinel behavior, social information, vocal communication.**

INTRODUCTION

To make informed decisions, animals use "personal" information from their own experiences and "social" information gathered from other individuals (Giraldeau et al. 2002; Danchin et al. 2004). Although social information can be obtained quickly and relatively cheaply (Giraldeau et al. 2002), there is discernible variation in quality (Blumstein, Verneyre, et al. 2004). Where using poor-quality information is costly to the receiver, individuals should adjust their reliance on social information according to its potential quality (Barrera et al. 2011). By compiling information gathered during prior interactions, receivers can maximize use of high-quality sources while ignoring other individuals (van Bergen et al. 2004; Dall et al. 2005).

Variation in quality has been best studied in a predatory context with respect to alarm calls, vocalizations given to warn of approaching danger (Hollén and Radford 2009). Individuals in mixed-species groups discriminate between the alarm calls of heterospecifics, responding more strongly to species with whom they share most threats, or which are more accurate in their classification of predators (reviewed in Magrath et al. 2015). Receivers might also be expected to discriminate between conspecific alarm callers, given that the threat of predation differs depending on intrinsic biological factors such as age, sex, and body condition (e.g., Werner et al. 1983; Lima 1988; Lea and Blumstein 2011), "personality" (Dall et al. 2004), and experience with predators (Dill 1974; Stankowich and Blumstein 2005). Although individuals in some species disregard acoustic differences in alarm calls and respond similarly to all callers (Schibler and Manser 2007), several studies have found that receivers discriminate between reliable and unreliable callers (Cheney and Seyfarth 1988; Hare and Atkins 2001; Blumstein, Verneyre, et al. 2004), often on the basis of age class (e.g., adult/juvenile; Gouzoules et al. 1996; Hanson and Coss 2001; Blumstein and Daniel 2004).

Sentinel behavior, in which an individual adopts a raised position, scanning for predators and warning others of danger, has been documented in a range of social bird and mammal species (reviewed in Bednekoff 2015). Benefits accrued to groupmates from sentinel behavior (early warning of predators, decreased forager vigilance, and increased biomass intake; Manser 1999; Hollén et al. 2008; Ridley et al. 2010) are likely to vary depending on the quality of the sentinel. Individuals may differ in their ability to detect and correctly identify a threatening stimulus for a variety of reasons, including variation in ecological conditions, motivation, visual acuity, sentinel position, and experience. Groupmates would be expected to adjust their own vigilance behavior depending on sentinel quality, reducing vigilance effort when foraging in the presence

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of better sentinels. To our knowledge, however, only one study has examined this possibility: Radford et al. (2009) found that pied babbler (*Turdoides bicolor*) foragers reduced vigilance more when sentinels were positioned higher.

In several species, individuals produce low-amplitude surveillance calls when acting as a sentinel (Manser 1999; Hollén et al. 2008; Kern and Radford 2013). Surveillance calls are known to provide key information about sentinel presence, satiation level and height (Manser 1999; Hollén et al. 2008; Radford et al. 2009; Bell et al. 2010; Radford et al. 2011), and an estimate of current risk levels (Bell et al. 2009; Kern and Radford 2013), thus allowing receivers to optimize their foraging (Manser 1999; Hollén et al. 2008; Bell et al. 2010). Surveillance calls can also provide information about sentinel identity (Manser 1999), including age, sex, and dominance status. Foragers could potentially use this vocal information in combination with prior knowledge about individual reliability, to adjust their vigilance and foraging behavior accordingly, but this possibility remains unexplored.

Here, we investigate information available in dwarf mongoose (*Helogale parvula*) surveillance calls, and its use by foraging group members. Dwarf mongooses are cooperatively breeding carnivores living in groups of up to 30 individuals (Rasa 1977). The dominant pair monopolizes reproduction, with related and unrelated subordinates of both sexes helping to rear offspring (Rood 1980). Dwarf mongooses search for the majority of their prey by digging, and so are unable to forage and be fully vigilant simultaneously (Rasa 1989). They are at risk from a wide range of avian and terrestrial predators (Rasa 1986), and sentinels are often posted (Sharpe et al. 2010; Kern and Radford 2013). Dwarf mongoose sentinels produce low-amplitude surveillance calls in approximately half of sentinel bouts, predominantly calling when guarding in denser habitats and when group members are more spread out (Rasa 1986; Kern and Radford 2013). Subordinate sentinels are more likely to vocalize than dominants, though the likelihood of a dominant sentinel vocalizing increases in larger groups (Kern and Radford 2013).

Using a combination of natural observations, acoustic analysis of sound recordings, and field playback experiments, we answer 4 main questions. First, do foraging dwarf mongooses use vocal cues to detect the presence of a sentinel and adjust their behavior accordingly, as has been shown in other species (Manser 1999; Hollén et al. 2008)? Second, do dominant and subordinate individuals differ in their contributions to sentinel behavior and choice of sentinel post height? Third, do vocal cues provide information about sentinel dominance status? Fourth, do foragers adjust their vigilance behavior according to vocal information about sentinel dominance status?

MATERIALS AND METHODS

Study site and population

This study took place on Sorabi Rock Lodge Reserve, a 4 km^2 private game reserve in Limpopo Province, South Africa (24°11′S, 30°46′E), part of southern Africa's Savanna Biome (see Kern and Radford 2013 for full details). Data were collected from 8 groups of wild dwarf mongooses (mean group size = 8.3; range = 3–17), habituated to close observation (<5 m) on foot (Kern and Radford 2013). All animals are individually identifiable either from markings of blonde hair dye (Wella UK Ltd, Surrey, UK) applied with an elongated paintbrush or from natural features such as scars or facial irregularities. The population has been monitored since 2011; thus, the age of most individuals is known; individuals can be sexed through observations of ano-genital grooming.

Observational data collection

To investigate contributions to sentinel duty by individuals of different dominance status, observations were conducted between January 2014 and March 2015. Once groups had left the overnight refuge to begin foraging, scan samples were carried out every 30 min to record whether a sentinel was present and, if so, the sentinel's identity (and thus sex and dominance status), sentinel post height (to the nearest 10 cm), and group size. Individuals younger than 1 year seldom contribute to sentinel behavior (Kern JM, unpublished data); therefore, group size included only individuals of 12 months and older. Adult group members were classified as either "dominant" (male and female pair) or "subordinate" (the remaining individuals). The dominant pair could be identified through observations of aggression, feeding displacement, scent marking, and greeting behavior (Rasa 1977). Sentinels were defined as individuals whose feet were at least 10 cm above ground and who were actively scanning the surroundings, whereas groupmates were engaged in other activities, primarily but not exclusively foraging (Sharpe et al. 2010; Kern and Radford 2013, 2014).

Acoustic recordings and analysis

To investigate acoustic variation in the surveillance calls of dominant and subordinate sentinels, vocal recordings were collected in tandem with observations of sentinel behavior from December 2012 to September 2013. Vocalizations from known individuals were recorded from a distance of 0.5–10 m at a sampling rate of 44.1 kHz with a 16-bit resolution onto a SanDisk SD card (SanDisk, Milipitas, CA), using a Marantz PMD660 professional solid-state recorder (Marantz America, Mahwah, NJ) and a handheld highly directional Sennheiser ME66 shotgun microphone (Sennheiser UK, High Wycombe, Buckinghamshire, UK) with a Rycote Softie windshield (Rycote Microphone Windshields, Stroud, Gloucestershire, UK). Whole bouts were recorded (mean ± standard error [SE], bout duration = 157.3 ± 34.8 s, range = 0.3–18.9 min, N = 101).

From recordings, spectrograms were created in Raven Pro 1.5 using a 1024 point fast Fourier transformation (Hamming window, 69.9% overlap, 1.45-ms time resolution, 43-Hz frequency resolution). From spectrograms of 3 randomly selected surveillance calls per individual (N = 44; 16 dominants, 28 subordinates), the following parameters were measured: 1) peak frequency of the fundamental (kilohertz), defined as the frequency at which maximum power occurs within the lowest formant; 2) bandwidth (kilohertz), defined as the difference between the upper- and lower-frequency limits of the call; 3) duration of the first element (seconds); 4) total call duration; and 5) the number of elements per call (Figure 1). Raven's manual selection tool was used to select the time and frequency range of the element to be analyzed (by J.M.K.); means were calculated for each parameter for each individual. Selected calls came from recordings with good signal-to-noise ratio (at least 20 dB above ambient noise). Where possible (N = 18; 8 dominants, 10 subordinates), each call came from a separate sentinel bout. Where fewer than 3 bouts were available for an individual, calls came from 2 bouts (N = 10; 3 dominants, 7 subordinates) or 1 bout (N = 16; 5 dominants, 11 subordinates).

Playback experiments

To assess the influence of both a vocalizing sentinel and vocal cues to sentinel dominance status on forager vigilance, 2 playback experiments were conducted in August–September 2013 and April–May 2014. In the first experiment, 7 groups were presented

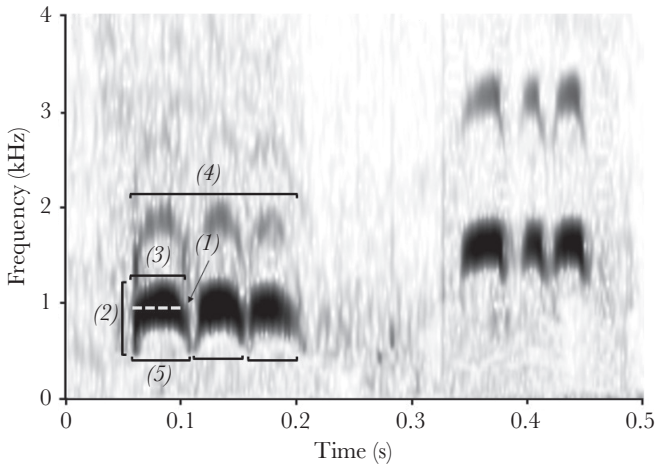

Figure 1
Spectrogram of a surveillance call showing variables analyzed: 1) peak frequency of the fundamental, 2) bandwidth, 3) duration of the first element, 4) total call duration, and 5) number of elements per call.

with 2 treatments: surveillance calls of the group's dominant male and ambient noise (as per Hollén et al. 2008). The eighth group contained no subordinate female focal at the time which precluded their inclusion in the first experiment. In the second experiment, 8 groups received 2 treatments: surveillance calls with the best signal-to-noise ratio of the group's dominant male and of a subordinate adult male from the same group from whom surveillance calls had been recorded. All playback tracks were 3 min in duration and included recording of ambient noise from the center of the territory of the focal group made at similar times of day. Playback tracks of sentinel presence also included surveillance calls, recorded opportunistically from the relevant male in the focal group, and inserted at 12-s intervals to create a uniform call rate of 5 calls per minute; previous research has found this to be the mean call rate during sentinel bouts taking place more than 10 min since an alarm call (Kern and Radford 2013). Tracks did not include any other vocalizations, from conspecifics or heterospecifics.

During both experiments, each group was presented with one pair of playback trials in a counterbalanced order. Calls were broadcast from an mp3 player connected to single SME-AFS portable field speaker (Saul Mineroff Electronics Inc., New York) positioned at a height of 1 m. Playback amplitude was standardized to the natural amplitude of ambient noise (peak amplitude: 40 dB sound pressure level A [SPLA] at 1 m) and of dwarf mongoose surveillance calls (peak amplitude: 55 dB SPLA at 1 m) using a HandyMAN TEK1345 sound meter weighting A (Metrel UK Ltd., Normanton, West Yorkshire, UK). The 2 trials to the same focal individual in a given experiment were separated by a minimum of 1 h and played when the entire group was foraging in the same habitat type. Playbacks took place when there was no natural sentinel on duty, when there had been no sentinel present for at least 5 min, and no natural alarm call for at least 10 min. Following any major disturbances, such as an intergroup encounter or snake mobbing, a minimum of 15 min was left before the next playback took place.

Observers conducted behavioral observations in tandem with playback experiments. The same female forager was selected in both trials to the same group in a given experiment. Using a stopwatch and tally counter, observers measured the number of vigilance scans performed and the cumulative time spent vigilant. Trials were abandoned ($N = 3$) if a natural alarm call occurred during the 3 min, if a natural sentinel went on duty, or if the forager ceased foraging to interact socially with another group member (e.g., grooming, feeding displacement) and were later repeated after at least 1 h.

Statistical analysis

All analyses were performed using R version 2.15.1 (R Development Core Team 2012). All tests were 2 tailed and were considered significant at $P < 0.05$. Parametric tests were conducted where data fitted the relevant assumptions of normality and homogeneity of variance. Logarithmic transformations were conducted to achieve normality of errors in some cases (Crawley 2005); nonparametric tests were otherwise used. The specific nature of independent and dependent variables as well as the statistical technique used to address each of our 4 questions are outlined below.

Do foragers use vocal cues to detect the presence of a sentinel and adjust their behavior accordingly?

Data on the number and duration of vigilance scans collected during the first playback experiment (surveillance calls vs. ambient noise) were analyzed using Wilcoxon signed-rank tests.

Do dominant and subordinate individuals differ in their contributions to sentinel behavior and choice of sentinel post height?

Observers conducted 2970 scans on 420 sample days in 8 groups (mean ± SE scans per group = 371 ± 23), with a natural sentinel present in 1678 (56.5%) scans. To investigate variation in contributions to sentinel duty and the height adopted by dominant and subordinate individuals, linear mixed models (LMMs) and generalized linear mixed models (GLMMs) were used to analyze behavioral data from scan samples. Mixed models allow the incorporation of both fixed and random terms, the latter allowing repeated measures from the same group or individual to be taken into consideration. Model simplification was conducted using stepwise backward elimination (Crawley 2005) with terms sequentially removed until the minimal model contained only terms whose elimination significantly reduced the explanatory power of the model. Removed terms were returned to the minimal model individually to confirm that they were not significant. χ^2 and P values were obtained by comparing the minimal model with models in which the term of interest had been removed (for significant terms) or added (for nonsignificant terms). For fixed terms, presented effect sizes ± SE were obtained from the minimal model, as were estimated variance components for random terms.

For assessment of sentinel contributions, 2 GLMMs with binomial error structure were conducted using the glmer function in package "lme4" (Bates et al. 2012). In both models, the proportion of sentinel bouts performed by each individual was included as the response variable. The first model bound the number of scan samples in which a given individual was acting as a sentinel with the number of scans conducted that day when that individual was not a sentinel, testing the likelihood of an individual being a sentinel over a given period. The second model bound the number of scan samples in which a given individual was acting as a sentinel with the number of scans during which a different individual was acting as a sentinel, testing the likelihood of a sentinel being a dominant individual. In both models, group size, dominance status, and sex were fitted as fixed effects, with both individual identity nested in group identity and observation day included as random terms. All 2-way interactions of biological interest were included in the maximal model. To investigate the influence of age as well as status,

2 additional GLMMs were conducted using a subset of the data containing just the dominant pair and the oldest subordinate male and female from each group. Eight individuals in 5 groups changed dominance status (from subordinate to dominant) over the course of the study period, providing a natural experiment, and so 2 further GLMMs considered scans involving these reduced datasets.

For the assessment of sentinel post height, 2 LMMs were used following logarithmic transformation of the data. Sentinel dominance status and sex were fitted as fixed effects, with individual identity nested in group identity included as a random term for both the complete data set (N = 1430 bouts, 75 individuals, 8 groups), and a reduced data set containing only the 7 individuals who changed status and for which height data were available before and after the switch.

Do vocal cues provide information about sentinel dominance status?

Differences between dominance classes in peak frequency of the fundamental, bandwidth, and duration of the first element were analyzed using independent-samples t-tests, and number of elements using Wilcoxon signed-rank tests. All tests were performed on the mean values for each individual. Total call duration was not analyzed as this was strongly correlated with the number of elements (Spearman rank correlation: Rs = 0.93, N = 130, P < 0.0001). As multiple comparisons were made, the sequential Bonferroni method was used to correct those parameters reaching significance (Rice 1989).

Do foragers adjust their vigilance behavior according to vocal information about sentinel dominance status?

To investigate whether foragers alter vigilance behavior depending on the dominance status of a sentinel, data from the second playback experiment (dominant surveillance calls vs. subordinate surveillance calls) were analyzed using a paired t-test (number of vigilance scans) and a Wilcoxon signed-rank test (duration of vigilance scans).

RESULTS

Do foragers use vocal cues to detect the presence of a sentinel and adjust their behavior accordingly?

Foraging dwarf mongooses conducted significantly fewer vigilance scans (Wilcoxon signed-rank test: Z = 27, N = 7, P = 0.034; Figure 2a) and spent significantly less time vigilant (Z = 26, N = 7, P = 0.047; Figure 2b) when subjected to playback of surveillance calls compared with playback of ambient noise.

Do dominant and subordinate individuals differ in their contributions to sentinel behavior and choice of sentinel post height?

The likelihood of an individual conducting a sentinel bout at the time of a scan sample was significantly affected by the interaction between dominance status and group size (GLMM: χ^2 = 7.99, degrees of freedom [df] = 1, P = 0.0047, random terms: group < 0.0001, individual in group = 0.236, occurrence = 0.092, intercept = −2.574 ± −0.268). Dominants were more likely to act as a sentinel than subordinates, but that difference was most apparent in large groups (Figure 3a). Individual sex did not significantly influence sentinel contribution (χ^2 = 0.55, df = 1, P = 0.460).

The likelihood of a given individual conducting a particular sentinel bout was significantly affected by dominance status: Dominant individuals were more likely to act as a sentinel than subordinate individuals (GLMM: χ^2 = 21.20, df = 1, P < 0.005, random terms: group < 0.0001, individual in group = 0.242, observation day < 0.0001, intercept = −0.312 ± 0.212; Figure 3b). Individuals were also significantly more likely to act as sentinel in smaller groups (χ^2 = 25.22, df = 1, P < 0.005), but individual sex did not significantly influence sentinel contribution (χ^2 = 0.47, df = 1, P = 0.494).

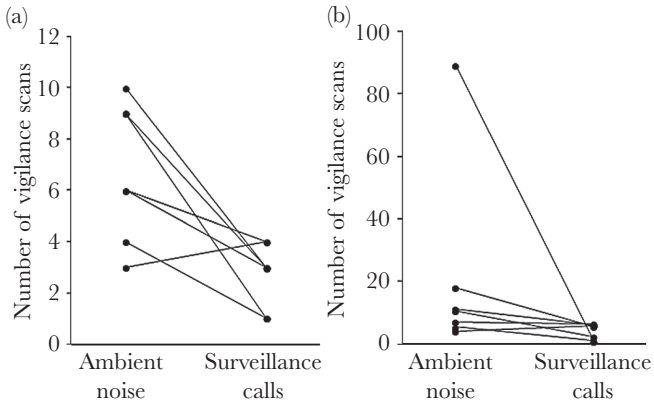

Figure 2
Response—(a) total number of vigilance scans and (b) total duration of vigilance scans—of foraging dwarf mongooses to the playback of sentinel surveillance calls and ambient noise. Lines join values for the same individuals in the 2 treatments (N = 7).

When analyzing the subset of the data containing only the dominant pair and the oldest subordinate male and female from each group, dominant individuals were still more likely to act as a sentinel than subordinate groupmates. Dominant individuals were significantly more likely to conduct a sentinel bout at the time of a scan sample than the oldest subordinates (GLMM: χ^2 = 6.65, df = 1, P = 0.011, random terms: group = 0.07, individual in group = 0.39, observation day = 0.15, intercept = −2.11 ± 0.105). None of group size (χ^2 = 0.015, df = 1, P = 0.903), sex (χ^2 = 0.16, df = 1, P = 0.689), or the interaction between group size and status (χ^2 = 2.17, df = 1, P = 0.338) significantly influenced sentinel contribution. Dominant individuals were also significantly more likely to conduct a particular sentinel bout than the oldest subordinate group members (χ^2 = 6.80, df = 1, P = 0.009, random terms: group < 0.0001, individual in group = 0.16, occurrence = 0.000, intercept = −0.437 ± 0.24). All individuals were significantly more likely to conduct a sentinel bout in smaller groups (χ^2 = 16.42, df = 1, P < 0.0001), but there was no significant interaction between group size and status (χ^2 = 0.93, df = 1, P = 0.337), and individual sex did not significantly influence sentinel contribution (χ^2 = 0.09, df = 1, P = 0.767).

When analyzing the subset of the data containing only the 8 individuals whose status changed, qualitatively the same results were obtained as with the overall dataset: Dominant individuals were more likely to be acting as a sentinel than subordinate groupmates, but that effect was more pronounced in larger groups. There was a significant interaction between group size and dominance status when considering the likelihood of an individual conducting a sentinel bout at the time of a scan sample (GLMM: χ^2 = 12.82, df = 1, P = 0.0003, random terms: group < 0.0001, individual in group = 0.049, intercept = −2.536 ± 0.350), but no significant effect of sex (χ^2 = 1.54, df = 1, P = 0.214). There was also a significant interaction between group size and dominance status when considering the likelihood of an individual being on duty in a given sentinel bout (χ^2 = 9.10, df = 1, P = 0.003,

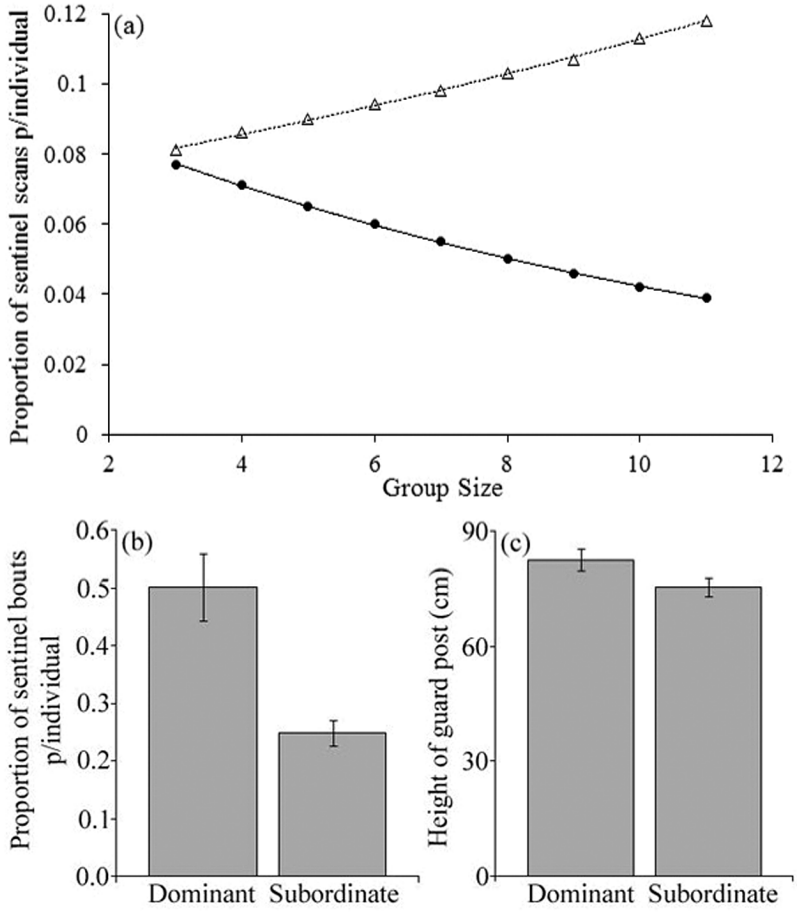

Figure 3
The effect of dominance status on (a) likelihood of acting as a sentinel during a given scan sample (dominant: open triangles and dotted line, subordinate: black circles and solid line), (b) likelihood of an individual being the sentinel during a given sentinel bout, and (c) height of guard post. For (a), lines were plotted using back-transformed means predicted from GLMM. For (b) and (c), mean and SEs calculated from raw data are shown.

random terms: group = 0.123, individual in group = 0.028, intercept = −0.866 ± 0.497), but no significant effect of sex (χ^2 = 1.91, df = 1, P = 0.167).

The height at which sentinels positioned themselves ranged from 10 to 600 cm (mean ± SE = 72.8 ± 1.8 cm, N = 1430 bouts, 75 individuals, 8 groups). Dominant sentinels used significantly higher posts than subordinate sentinels (LMM: χ^2 = 6.73, P = 0.009, random terms: group = 0.076, individual in group = 0.092, intercept = 1.773 ± 0.03; Figure 3c). Sentinel sex did not significantly influence height choice (χ^2 = 1.83, P = 0.17). When analyzing only those bouts performed by individuals who changed status (N = 179 bouts, 7 individuals, 7 groups), the same result was found: Individuals guarded from significantly higher posts when dominant than when they were subordinate (χ^2 = 12.02, P < 0.001, random terms: group < 0.001, individual in group = 0.16, intercept = 1.75 ± 0.07). Sentinel sex did not significantly influence height choice (χ^2 = 0.47, P = 0.489).

Do vocal cues provide information about sentinel dominance status?

Surveillance calls of dominants had a significantly lower peak frequency of the fundamental (independent-samples t-test: t_{40} = 6.97, P < 0.0001), reduced bandwidth (t_{41} = 2.83, P = 0.0035), and longer first element (t_{37} = 4.91, P < 0.0001) (Figure 4; audio files of dominant and surveillance calls can be found in the Supplementary Material). No significant difference was found in the number of elements per call (dominant: 2.29 ± 0.23, subordinate: 2.00 ± 0.18; Wilcoxon signed-rank test: T = 241.5, N = 43, P = 0.53).

Do foragers adjust their vigilance behavior according to vocal information about sentinel dominance status?

Sentinel status did not significantly influence the number of scans performed by a forager (paired t-test: t_7 = 1.23, P = 0.259; Figure 5a), but foragers spent significantly less time vigilant in response to the playback of surveillance calls from a dominant individual than a subordinate group member (t_7 = 2.55, P = 0.038; Figure 5b).

DISCUSSION

Our work has demonstrated that dominant dwarf mongooses of both sexes act as sentinels considerably more often than subordinate group members, and that the surveillance calls produced during sentinel bouts contain vocal information about dominance status. Our playback experiments showed that foragers not only use surveillance calls to detect the presence of sentinels (as in other species; Manser 1999; Hollén et al. 2008) but also to determine the dominance status of the sentinel and alter their vigilance accordingly. Foragers reduced their vigilance in the presence of dominant

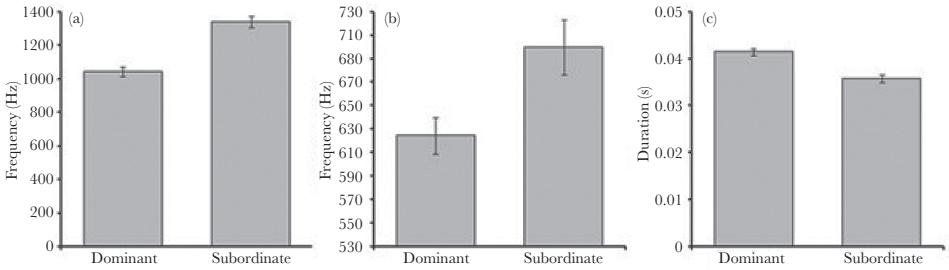

Figure 4
Acoustic variables differing significantly between dominance classes: (a) peak frequency of the fundamental, (b) bandwidth, and (c) duration of the first element. Means ± SE shown ($N = 43$; 16 dominants, 27 subordinates).

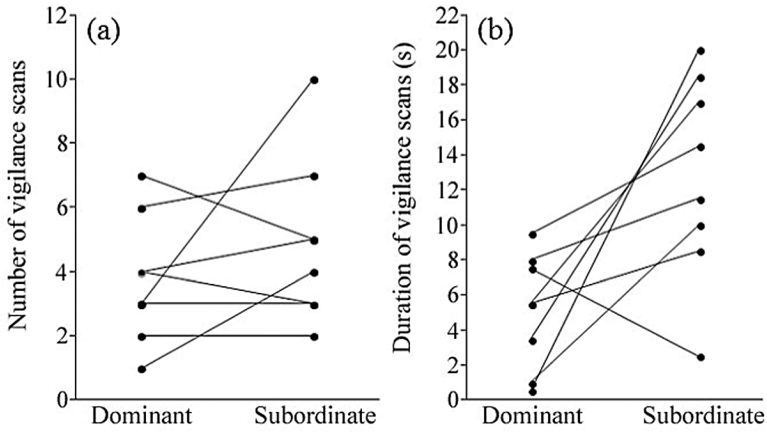

Figure 5
Response—(a) number of vigilance scans and (b) duration of vigilance scans—of foraging dwarf mongooses to the playback of sentinel calls by different classes. Lines join values for the same individuals in the 2 treatments ($N = 8$).

sentinels compared with when subordinate groupmates were acting in that role. We therefore provide novel empirical evidence from a field study that whether and to what extent animals exploit social information depends on the identity of the information provider.

There are a number of possible reasons why foragers might show a stronger response to the surveillance calls of dominant compared with subordinate sentinels. First, surveillance calls of dominant individuals may be easier to detect as they have lower peak frequency of the fundamental and longer duration, traits generally associated with greater ease of detection (Wiley and Richards 1982). Because dominance is closely related to age in dwarf mongoose groups (Rood 1980), differences in response may stem from age-related differences between dominant and subordinate sentinels. Many species consider alarm calls given by younger individuals to be less reliable (Gouzoules et al. 1996; Hanson and Coss 2001; Blumstein and Daniel 2004), and the same may be true of surveillance calls. However, unlike alarm-call studies that have traditionally compared juveniles and adults, 2 classes that are known to differ in their vulnerability to predation (Lea and Blumstein 2011), our study compared only adult sentinels.

Alternatively, differences in response to dominant and subordinate sentinels may relate to differences in height adopted by these classes of individual. By guarding from higher posts than subordinates in general, the probability of dominant sentinels detecting predators is likely to be greater, increasing the reliability of information provided (see also Radford et al. 2009). Speaker height was the same throughout experimental trials, so foragers could not have been responding to differences in height at the time of playback, but they may associate dominant sentinels with higher posts. Another possible reason for the differences in response to sentinels of different dominance status relates to an individual's experience as a sentinel. Dwarf mongoose group composition remains relatively stable, with some group members cohabiting for years at a time (Rood 1983), thereby facilitating the accumulation of class- or individual-specific information about sentinel behavior. Dominant individuals contribute more to sentinel duty when compared both with all subordinates and with only the oldest same-sex subordinate. The results from the natural experiment, comparing the same individuals before and after they switched from being subordinate to dominant, also demonstrated these differences in sentinel behavior; after reaching a position of dominance, individuals were more likely to contribute to sentinel duty (and to guard from higher posts) than when they were subordinate group members. By contributing more to sentinel duty, individuals gain considerably more experience once they become dominant, and may therefore be expected to provide higher-quality information, such as a more accurate assessment of background risk level, or what constitutes a threatening stimulus. To explore this fully would require the manipulation of individual reliability, such as has been done with alarm calls (Hare and Atkins 2001; Blumstein, Verneyre, et al. 2004).

Individuals can obtain risk estimates by visually monitoring the behavior of surrounding groupmates (Pays et al. 2010), but it has become increasingly apparent that foragers also make use of vocal information (Radford and Ridley 2007; Hare et al. 2014).

A growing body of evidence over recent years has highlighted the importance of vocal cues in sentinel systems (Manser 1999; Hollén et al. 2008; Bell et al. 2009; Radford et al. 2009; Bell et al. 2010; Radford et al. 2011; Kern and Radford 2013), especially for species foraging in denser habitats, where line of sight is interrupted, or whose feeding strategies prevent simultaneous foraging and scanning. Through use of surveillance calls, dwarf mongoose foragers gain valuable information without the need to interrupt digging behavior and scan the environment for themselves, thereby increasing foraging efficiency and reducing risk of starvation (Manser 1999; Hollén et al. 2008). Class and individual differences in call structure further allow receivers to fine-tune behavioral responses depending on the identity of a social partner, thereby minimizing fitness costs associated with inappropriate responses (Pollard 2010). Such acoustic differences have been found in a multitude of call types (Stoddard et al. 1991; McCowan and Hooper 2002; Rendall 2003; Sharp and Hatchwell 2005; Charrier et al. 2009), yet whether receivers attend to potential differences in caller identity has received little attention outside of alarm calling situations. There are several other signaling contexts, however, where caller identity might considerably impact receiver fitness, such as mobbing calls, food calls and vocalization coordinating group travel (Conradt and List 2009; Boeckle et al. 2012; Micheletta et al. 2012).

The finding that dominants do more sentinel duty raises the question as to why. Whether an individual acts as sentinel is closely related to its nutritional state (Clutton-Brock et al. 1999; Wright et al. 2001; Bell et al. 2010). Dominants, with access to higher-quality resources, and being older and more experienced at finding food (Heinsohn 1991), are usually in a better state than subordinates, and therefore may be expected to do more. Dominants may gain additional benefits from sentinel behavior, using elevated posts not only to scan for predators but also to observe the behavior of group members, although subordinates could also gain additional benefits from sentinel behavior, using it to search for potential roving opportunities. Alternatively, there may be trade-offs between contributions to different cooperative activities, including babysitting, pup provisioning, and territorial defense. Dominants may perform more sentinel behavior but reduce effort to other helping activities. Were contributions moderated by effort to other activities, one might expect dominant females to do less because they suffer considerable energetic costs associated with reproduction (Clutton-Brock et al. 1999). Somewhat surprisingly, however, we found no effect of sex on sentinel behavior.

A further question raised by our results is why dominants generally guard from higher posts. Variation in post height is likely to influence the probability of a sentinel detecting a predator: Higher sentinels may be better placed to detect predators sooner (especially terrestrial predators), able to see further and with a wider field of view (Blumstein, Fernández-Juricic, et al. 2004; Fernández-Juricic et al. 2004; Radford et al. 2009). On the other hand, post height is also likely to influence a sentinel's risk of predation, with higher sentinels more vulnerable to detection by aerial predators. Dominant individuals, being more experienced sentinels, may be better able to afford the risk entailed by guarding from higher posts. Alternatively, if dominants also use sentinel duty to monitor the behavior of subordinates, they may adopt higher posts in an effort to watch more of the group, as well as to enhance predator detection.

Use of vocal information, such as surveillance calls, facilitates optimization of the foraging–vigilance trade-off by foragers. Where information quality varies, reliable information should be weighted more heavily (McLinn and Stephens 2006). Our results demonstrate that the dominance status of a sentinel is a key factor taken into consideration by receivers when determining the value of social information. When a dominant sentinel is on duty, foragers rely more heavily on social information, gather less information through personal vigilance and concentrate on foraging. Dominant individuals gain more experience of sentinel duty and guard from higher posts, thus may potentially be able to provide higher-quality information about risk. Our study contributes novel evidence that a major benefit of individual- and class-specific vocalizations is the potential to assess differences in information between callers, and we suggest that future work should investigate the presence of reliability assessment in different call types.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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