

# Cooperative Sentinel Calling? Foragers Gain Increased Biomass Intake

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## Summary

Many foraging animals face a fundamental tradeoff between predation and starvation [1, 2]. In a range of social species, this tradeoff has probably driven the evolution of sentinel behavior, where individuals adopt prominent positions to watch for predators while groupmates forage [3]. Although there has been much debate about whether acting as a sentinel is a selfish or cooperative behavior [3–6], far less attention has focused on why sentinels often produce quiet vocalizations (hereafter known as “sentinel calls”) to announce their presence [7, 8]. We use observational and experimental data to provide the first evidence that group members gain an increase in foraging success by responding to these vocal cues given by sentinels. Foraging pied babblers (*Turdoides bicolor*) spread out more, use more exposed patches, look up less often, and spend less time vigilant in response to sentinel calling. Crucially, we demonstrate that these behavioral alterations lead to an increase in biomass intake by foragers, which is likely to enhance survival. We argue that this benefit may be the reason for sentinel calling, making it a truly cooperative behavior [9].

## Results and Discussion

### Behavioral Responses to Sentinels

Pied babblers are cooperatively breeding birds that live in groups of 3–15 individuals [10]. Group members spend more than 95% of their foraging time on the ground as a loose flock, probing beneath the sand and pecking the surface for invertebrate prey [10], and they are preyed on by a variety of raptors, terrestrial mammals, and snakes [11]. Foraging groups have a sentinel (an individual perched at least 1 m above the ground and actively scanning for predators [11]) in place about 30% of the time [11], and these individuals tend to be the first to detect a predator and give an alarm call [11]. All adult group members act as sentinels on some occasions, with bouts lasting between 0.2 and 6.3 min (mean  $\pm$  standard deviation [SD] =  $1.6 \pm 1.3$  min,  $n = 152$  bouts by 27 individuals).

Because group members generally forage within 20 m of one another, continuous monitoring of their positions is possible

[12, 13]. Paired observational data from scans of the whole group showed that 2 min after the start of a sentinel bout, foraging group members had spread out more (Figure 1A) and were more likely to be foraging in the open (Figure 1B), whereas 2 min after the end of a sentinel bout, foraging individuals had moved closer together (Figure 1A) and were less likely to be foraging in the open (Figure 1B). Because pied babblers dig for invertebrate prey in the sand, they must raise their head to look for predators; hence, it is easy to score antipredator vigilance [12]. Paired observational data from focal watches of individual foragers showed that they looked up less often (Figure 1C) and spent a smaller proportion of time vigilant (Figure 1D) in the 2 min period after the start of a sentinel bout compared to the 2 min period beforehand, and they looked up more often (Figure 1C) and spent a greater proportion of time vigilant (Figure 1D) in the 2 min period after the end of a sentinel bout compared to the 2 min period beforehand.

### Behavioral Responses to Sentinel Calling

Because pied babbler sentinels produce frequent sentinel calls throughout each bout (mean  $\pm$  SD call rate =  $19.4 \pm 8.8$  calls/min, range = 5.3–56.9 calls/min,  $n = 152$  bouts by 27 individuals), foraging individuals may be adjusting their behavior in response to visual and/or vocal cues. A playback experiment demonstrated that foragers can use the vocal cues alone to detect the presence of a sentinel and then adjust their behavior accordingly (see also [7]): Foraging group members spread out more (Figure 2A), were more likely to forage in the open (Figure 2B), looked up less often (Figure 2C), and spent a smaller proportion of time vigilant (Figure 2D) in response to the playback of sentinel calls compared to the playback of background noise. Previous work on pied babblers showed that foraging individuals also pay attention to vocal cues from other foragers to gain information about group size and relative spatial position and that they then adjust their antipredator vigilance accordingly [12].

In general, the vocal announcement of sentinel presence (commonly called the “watchman’s song”; [14]) might be particularly beneficial in species that forage in habitats where lines of sight are regularly obscured [8, 15, 16]; vocal cues may be less important for species foraging in open habitats [17]. Although pied babblers live in open habitats, however, foragers spend much of their time with their heads in holes, searching for subterranean prey. Consequently, they may be unable to check visually for the presence of a sentinel by using peripheral vision [18], and need to suspend foraging and lift their head to do so. Vocal cues prevent the need for visual checking in this way and thus maximize foraging time. For communication to be efficient in this regard and allow foragers the greatest flexibility in their behavior, sentinel calls need to be given throughout a bout, as is the case in pied babblers (this study), meerkats [7], and dwarf mongooses [8]. Calls that are only given at the start and end of a bout, as in white-browed sparrow weavers [15], or simply at the end of a bout, as in jungle babblers [16], might aid coordination of sentinel bouts by different individuals but are unlikely to play such a key role in the adjustment of behavior by foragers.

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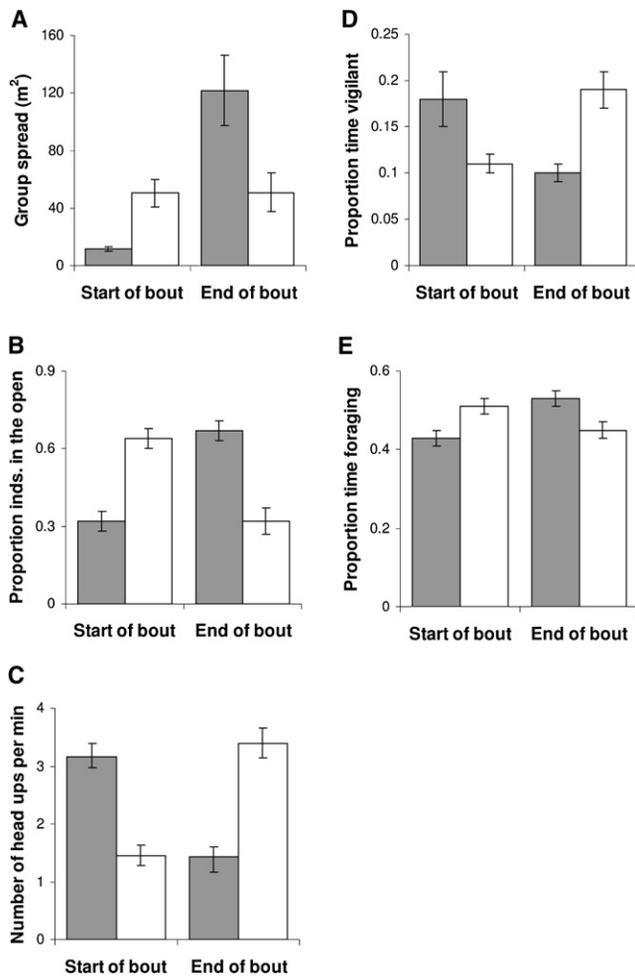


Figure 1. Change in Behavior of Foraging Pied Babblers after the Start or End of a Sentinel Bout

Shown are mean  $\pm$  SE: (A) group spread (LMM, start:  $\chi^2 = 76.32$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 60$ ; end:  $\chi^2 = 44.04$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 34$ ); (B) proportion of individuals foraging in the open (GLMM, start:  $\chi^2 = 72.10$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 48$ ; end:  $\chi^2 = 35.50$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 34$ ); (C) head-up rate (LMM, start:  $\chi^2 = 58.38$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 103$ ; end:  $\chi^2 = 61.16$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 105$ ); (D) proportion of time spent vigilant (LMM, start:  $\chi^2 = 20.91$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 103$ ; end:  $\chi^2 = 39.63$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 105$ ); and (E) proportion of time spent foraging (LMM, start:  $\chi^2 = 19.62$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 103$ ; end:  $\chi^2 = 13.08$ ,  $df = 1$ ,  $p < 0.001$ ,  $n = 105$ ). Sample sizes refer to the number of paired scans or focal periods. In (A) and (B), behaviors were recorded 0 min (gray bars) and 2 min (white bars) after the change in sentinel status. In (C)–(E), behaviors were recorded in the 2 min period before (gray bars) and after (white bars) the change in sentinel status.

### Foraging Success

The pervasive assumption in previous studies is that a reduction in antipredator vigilance in the presence of a sentinel (as shown above) will result in additional foraging time and improved foraging success (e.g., [3, 6, 7]). Although the link between time spent vigilant and time spent foraging has sometimes been examined [7], the resultant impact on foraging success has never been investigated empirically. Paired observational data from focal watches showed that pied babblers increased the proportion of time spent foraging after the start of a sentinel bout and decreased the proportion of time spent foraging after the end of a bout (Figure 1E). Crucially, our data also showed that an increase in the proportion

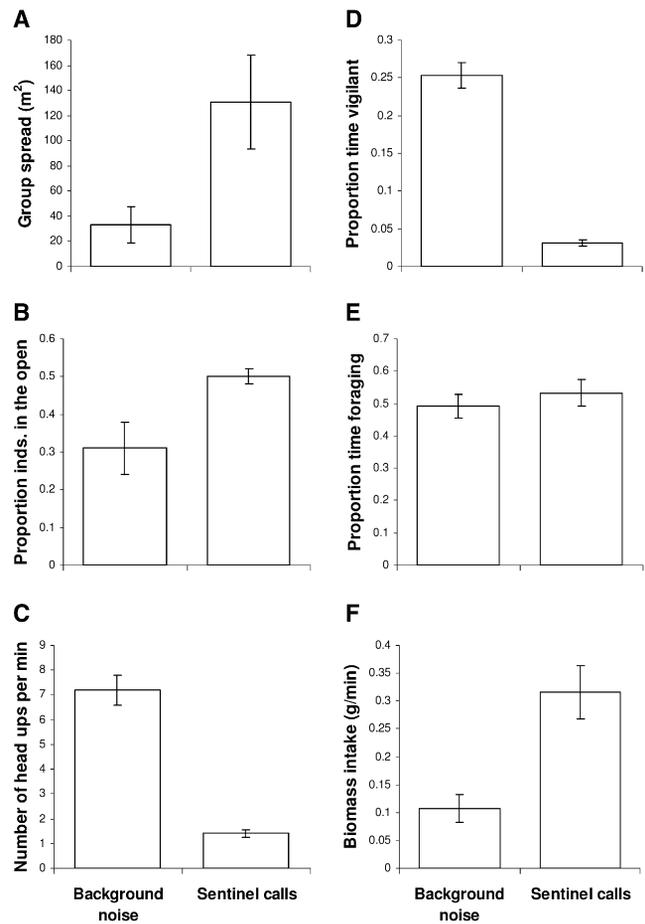


Figure 2. Response of Foraging Pied Babblers to the Playback of Sentinel Calls and Background Noise

Shown are mean  $\pm$  SE: (A) group spread (paired t test:  $t = 5.10$ ,  $n = 8$ ,  $p = 0.001$ ); (B) proportion of individuals foraging in the open ( $t = 2.47$ ,  $n = 8$ ,  $p = 0.043$ ); (C) head-up rate ( $t = 11.86$ ,  $n = 8$ ,  $p < 0.001$ ); (D) proportion of time spent vigilant ( $t = 15.40$ ,  $n = 8$ ,  $p < 0.001$ ); (E) proportion of time spent foraging ( $t = 0.551$ ,  $n = 8$ ,  $p = 0.599$ ); and (F) rate of biomass intake ( $t = 3.38$ ,  $n = 8$ ,  $p = 0.012$ ) during the 5 min trials.  $n = 8$  groups for (A) and (B), and  $n = 8$  individuals for (C)–(F).

of time spent foraging led to an increase in biomass intake per unit time (Table 1).

However, individuals did not increase the proportion of their time spent foraging in response to the playback of sentinel calling compared to background noise (Figure 2E), despite reducing their time spent vigilant. Instead, foragers spent more time moving between patches (mean  $\pm$  standard error [SE] proportion of time, sentinel calling:  $0.43 \pm 0.04$ ; background noise:  $0.26 \pm 0.02$ ; paired t test:  $t = 9.63$ ,  $n = 8$ ,  $p < 0.001$ ). But, even though they did not increase their foraging time, foragers still had a higher biomass intake per unit time during playbacks of sentinel calling compared to that during playbacks of background noise (Figure 2F). This increase in biomass intake was the result of increased numbers of prey items found ( $t = 4.32$ ,  $n = 8$ ,  $p = 0.003$ ) rather than an increase in the average size of prey items eaten ( $t = 1.87$ ,  $n = 8$ ,  $p = 0.104$ ). There are a number of possible explanations for the increase in biomass intake despite no increase in foraging time. First, by spreading out more widely, individuals may be less likely to encounter foraging patches already depleted by other group members. Second, because individuals venture

Table 1. Terms Affecting the Rate of Biomass Intake by Foraging Pied Babbler Individuals

Full Model	df	$\chi^2$	p
Proportion of time spent foraging	1	115.78	<0.001
Rainfall (mm)	1	17.37	<0.001
Foraging group size	1	3.78	0.054
Individual status <sup>a</sup>	2	5.63	0.070
Habitat <sup>b</sup>	3	3.68	0.303
Wind condition	1	0.49	0.486
Individual sex	1	0.10	0.757
Group breeding status <sup>c</sup>	1	0.22	0.639
Minimal Model	Effect	SE	
Constant	-1.625	0.043	
Proportion of time spent foraging	3.262	0.303	
Rainfall (mm)	0.010	0.003	

Results from a linear mixed model were based on 493 focal samples from 54 individuals in ten groups. Group identity, individual identity, and focal watch were included as random terms. The rate of biomass intake was log transformed prior to analysis.

<sup>a</sup> Independent fledgling, subordinate adult, dominant adult.

<sup>b</sup> Dune, open, grass, thicket.

<sup>c</sup> Presence or absence of dependent fledglings.

into the open more, they may have a wider choice of foraging patches and thus have access to those of better quality. Third, because individuals look up less often, foraging bouts are longer and less interrupted, which is likely to be beneficial when they are chasing mobile prey that can burrow into the sand. These possibilities are not mutually exclusive and remain to be tested in detail.

## Conclusions

Our results provide the first empirical evidence that foragers benefit from an increase in foraging success in the presence of a sentinel. By altering their behavior in response to the vocal cues provided by sentinels, pied babbler foragers increased their rate of biomass intake, which probably has profound consequences for survival and reproduction in such an arid environment (see [19]). Moreover, this increase in foraging success is not necessarily due simply to an increase in time spent foraging, a possibility that has important implications for a wide range of studies, including those investigating the vigilance behavior of foraging individuals, mate guarding, and the food-allocation decisions of parents.

Previous studies have shown that sentinel calling aids coordination of sentinel bouts by different individuals [7, 8]. This coordination may lead to short-term selfish benefits to sentinels because, on finishing a bout, they can forage in the presence of another sentinel [7]. However, if the foraging success and survival of groupmates increases as a consequence of the behavioral changes made in response to sentinel calling, as suggested by this study (see also [7]), then sentinels might also benefit through kin selection [20], because group members in cooperative societies are often close kin [21], and/or group augmentation [22], because group size is a key determinant of predation risk [23] and successful territory defense [24]. Hence, although our results say nothing about the selection pressures driving the initial evolution of sentinel calling, they strongly suggest that benefits to groupmates play a role in its maintenance. As such, sentinel calling would classify as

truly cooperative because it provides a benefit to other individuals (the recipients) and is selected for because of this beneficial effect on the recipients [9].

## Experimental Procedures

### Study Site and Species

Fieldwork was carried out on the Kuruman River Reserve in the southern Kalahari, South Africa (26°58'S, 21°49'E) [25]. We studied 11 color-ringed, habituated groups (containing 3–12 individuals; mean  $\pm$  SD = 5.2  $\pm$  2.0), which could be observed from approximately 2–3 m away, thus enabling the accurate scoring of individual foraging success [10]. Fledglings were independent once they obtained 95% of their food from self-feeding; prior to this they were dependent. Adults were individuals older than 12 months and were divided into dominants (the putative breeding pair) and subordinates (the remainder of the adults). Breeding females always incubate the eggs overnight; breeding males were identified from midair courtship chases and copulations with breeding females. Pied babblers are sexually monomorphic in plumage, so subordinates and fledglings were sexed with a DNA test (for details of capture, bleeding, and DNA extraction and analysis, see [10, 13]).

### Observational Data Collection

Data were collected for 4–5 hr after dawn and for 4 hr before dusk between November 2006 and June 2007. We collected paired-scan data to ascertain how the presence of a sentinel influences the spread of the foraging group (group spread; the estimated distance between the two foragers furthest apart multiplied by the distance between the two foragers furthest apart on a perpendicular axis) and the proportion of individuals foraging in the open (clearly visible) as opposed to under cover (for example, foraging at the base of a bush). When an individual started a sentinel bout, and as long as there had been no sentinel in the previous 5 min, we immediately recorded group spread and the exposure (open, cover) of each foraging individual. To assess the impact of the sentinel's presence, we collected the same data 2 min later, as long as the sentinel had remained on duty during that time. We repeated this paired-scanning protocol at the end of a sentinel bout, as long as no new sentinel started a bout within 2 min. We discarded any paired scans in which the habitat type (dune, open, grass, thicket) or foraging group size changed within the 2 min period; analyzed scan pairs were matched for potential confounding variables. Scans were not conducted if there had been an alarm call in the previous 5 min; group members generally return to foraging within 2 min of an alarm call (A.N.R., unpublished data).

We also conducted continuous focal watches on foraging adults and independent fledglings (mean  $\pm$  SE length of focal watch = 4.64  $\pm$  0.19 min, range 0.13–25.83 min, n = 57 individuals; mean  $\pm$  SE focal watches per individual = 13.6  $\pm$  1.1, range = 1–35, n = 759 watches). Focal watches continued until an alarm call occurred, the group moved to a new habitat, or the focal individual flew off or became a sentinel. At least 1 hr was left between watches on the same individual so that pseudoreplication could be minimized. During focal watches, we recorded the behavior of the individual as (1) foraging (whenever it was pecking or probing), (2) vigilant (whenever it had its head raised), or (3) moving. We also recorded each successful foraging attempt and the size of prey captured (see [10]), which was used for the calculation of the biomass intake of individuals per minute of observation time, and each change of sentinel status. All data were recorded onto a Palm TX PDA (Palm, Sunnyvale, California), which automatically noted the time of each event.

### Playback Experiment

To test whether foraging group members respond to the vocal cues given by sentinels, we presented eight groups with two trials; one involved 5 min playback of the sentinel calls of the group's dominant male, and the other involved 5 min playback of background noise from the group's territory (as a control). Trials to the same group were in randomized order and on separate days. Playbacks were of the same sound intensity as natural sentinel calls, were broadcast from a Sony SRS-A35 speaker positioned 2.5 m above the ground, and were conducted when no natural sentinel had been present for at least 5 min and there had been no alarm calls for at least 10 min. One observer conducted scan samples at the end of each minute of the trial to record group spread and the proportion of individuals foraging in the open; a second observer continuously recorded the vigilance and foraging behavior of the group's dominant female.

#### Data Analysis

We analyzed observational data with mixed models because these allow the inclusion of random as well as fixed terms and can thus take account of repeated measures of the same group, individual, scan pair, and focal watch. All models had a normal error structure (linear mixed model [LMM]), except those examining the proportion of individuals foraging in the open, which had a binomial error structure and a logit link function (generalized linear mixed model [GLMM]). To assess the influence of sentinel presence on group spread and the proportion of individuals foraging in the open, we conducted separate models on paired scans conducted 0 min and 2 min after the start of a sentinel bout and paired scans conducted 0 min and 2 min after the end of a sentinel bout. We included group identity and scan pair as random terms. To assess the influence of sentinel presence on head-up rate, the proportion of time spent vigilant, and the proportion of time spent foraging by individual foragers, we conducted separate models with paired focal-watch data from the 2 min period before and after either the start or end of a sentinel bout. We included group identity, individual identity, and focal-watch pair as random terms. We also used data from the focal watches to investigate the importance of proportion of time spent foraging by individuals on their rate of biomass intake per unit time (see Table 1).

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