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Urgency-related alarm calling in Arabian babblers, *Turdoides squamiceps*: predator distance matters in the use of alarm call types

Christina Sommer [a,*], **Dietmar Todt** [a], **Roni Ostreiher** [b] **and Roger Mundry** [a,c]

[a] Freie Universität Berlin, Institut für Biologie/Verhaltensbiologie,
Takustr. 6, 14195 Berlin, Germany
[b] Hazeva Field Study Centre, M.P. Arava 86815, Israel
[c] Max Planck Institute for Evolutionary Anthropology,
Deutscher Platz 6, 04103 Leipzig, Germany
[*]Corresponding author's e-mail address: christina.sommer@fu-berlin.de

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Abstract

Alarm call systems can be broadly categorised into functionally referential and urgency based. In the former, different categories of predators evoke structurally distinct call types which elicit different responses also in the absence of the predator stimulus. In the latter, call parameters and/or call use vary gradually with the degree of perceived risk. However, call types that are typically uttered in the presence of a certain predator category may occasionally occur also in response to other predators. Such 'cross taxon calling' indicates the possibility that also the differential use of acoustically distinct call types could be urgency based. The call system of Arabian babblers (*Turdoides squamiceps*) comprises three structurally distinct alarm call types. Two of them seem to be predominantly used towards two different predator types, but all call types also occur simultaneously in the same predator context. We hypothesised that in Arabian babblers the differential use of alarm call types reflects an urgency based alarm call system. To test this, we confronted groups of Arabian babblers with an owl dummy in two different distances ('near' and 'far'), representing two degrees of risk or response urgency. We found that not general call type occurrence but call use differed between the two treatments: birds started trilling earlier in the near treatment and uttered more barks in the far treatment. We conclude that the differential use of call types is mediated by the degree of threat a caller perceives. Finally, we synthesize our results together with the findings of other field studies on alarm calling in Arabian babblers and suggest different functions for the three different call types based on their distance related occurrence and acoustic characteristics.

Keywords

alarm calls, antipredator behaviour, Arabian babbler, call system, distance to predator, response urgency.

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1. Introduction

Many animals produce alarm calls when they are threatened by a potential predator (reviewed in Zuberbühler, 2009). Alarm call systems of different species have been categorised into functionally referential and urgency based. In a functionally referential call system animals utter structurally distinct call types in response to different categories of predators (Marler et al., 1992). Thus, the occurrence of a certain call type labels a certain predator category (such as ground or aerial predator) and is connected with a respective flight strategy which is evoked by these calls even in the absence of the original stimulus (context independence, Evans, 1997; Blumstein, 2002; Kiriazis & Slobodchikoff, 2006). Characteristics of functionally referential call systems were, for instance, reported in primates (e.g., Struhsaker, 1967; Seyfarth et al., 1980a,b; Macedonia, 1990; Zuberbühler et al., 1997; Zuberbühler, 2000, 2001; Kirchhof & Hammerschmidt, 2006) and birds (e.g., Evans et al., 1993a; Seddon et al., 2002). However, such calling does not per se indicate that a caller communicates exclusively information about a certain type of predator. That is, additional information can be encoded in alarm calls, such as predator colour, size or shape (Ackers & Slobodchikoff, 1999; Slobodchikoff et al., 2009).

In urgency based systems the degree of danger an animal perceives influences its calling behaviour. Here, call parameters and/or call use gradually vary with the degree of perceived risk. The outcome is diverse and can concern call rate, repetition of single elements and/or acoustic structure of single calls in relation to distance, size or speed of the predator, or the callers' age, and social or environmental variables such as group size or refuge distance. For instance, size and speed of an aerial predator influenced the number of calls uttered in domestic chickens (*Gallus gallus*, Evans et al., 1993b), the size of a predator was reflected in the number of 'dees' in chickadee calls (*Poecile atricapilla*, Templeton et al., 2005; *P. carolinensis*, Soard & Ritchison, 2009). Call rate varied with the distance to a predator in yellow-bellied marmots (*Marmota flaviventris*, Blumstein & Armitage, 1997) and juvenile Richardson's ground squirrels (*Spermophilus richardsonii*, Warkentin et al., 2001). The number of elements in the call as well as the minimum frequency varied with the distance to a predator in white-browed scrubwren (*Sericornis frontalis*, Leavesley & Magrath, 2005), and alarm calling rates increased with decreasing group size in chacma baboons (*Papio cynocephalus ursinus*, Cowlishaw, 1997).

These urgency based call systems differ fundamentally from functionally referential call systems with stimulus-specific call type production. However, also a combination of both systems is possible: for example, Manser (2001) found that suricates (*Suricata suricatta*) give acoustically different alarm calls to different aerial and terrestrial predators, and, furthermore, they vary the acoustic properties within these call types in relation to levels of urgency (distance to the predator). Correspondingly, the flight reactions qualitatively differed in response to playbacks of different call types, but also varied with the presumed urgency level in which the calls were uttered (Manser et al., 2001). Thus, the suricates' graded call system combines referential information with information about perception of urgency (Manser et al., 2002). Also for some primate species a mixed call system has been shown (redfronted lemurs, *Eulemur fulvus rufus*, and white sifakas, *Propithecus verreauxi verreauxi*, Fichtel & Kappeler, 2002). Here, the call system is functionally referential for one predator class but urgency based for others.

In addition, the occurrence of acoustically distinct calls in response to different predator categories can also be mediated by the degree of danger a predator presents, rather than by its specific category (reviewed in Evans, 1997). 'Cross taxon calling' is a phenomenon indicating the possibility that the differential use of structurally distinct call types can be mediated by the degree of threat a caller perceives (Macedonia & Evans, 1993). It refers to the finding that calls typically uttered in the presence of a certain predator class (e.g., bird of prey) occasionally occur also in response to other predators (e.g., mammal; Owings & Virginia, 1978; Robinson, 1980; Sherman, 1985; Greene & Meagher, 1998). Such cross taxon calling might indicate an urgency based call system in which a certain predator category is usually, but not always, associated with a certain degree of response urgency and, thus, in most cases elicits a specific call type (Macedonia & Evans, 1993). Other examples indicating an urgency based use of different call types come from birds. For instance, blue tits (*Parus caeruleus*) and turkeys (*Meleagris gallopavo*) utter different calls in response to models simulating low and high flying birds of prey (Schleidt, 1961; Klump & Curio, 1983). Furthermore, in an experimental field study of mobbing behaviour, Naguib et al. (1999) found that Arabian babblers (*Turdoides squamiceps*) used the same two call types simultaneously in two different predator contexts, but one call type was more common in the presence of an owl dummy while the other was predominant during experiments with a cat. Accordingly, they hypothesised that differential call use in the presence of different predators could be mediated by different degrees of risk they presented. A descriptive field study on Arabian babbler alarm calling behaviour points to that at least two of their three different alarm call types were correlated to the distance to the predator (Sommer, 2011), but this finding lacks experimental evidence.

In this study we experimentally investigated whether the differential use of alarm call types could be mediated by the degree of danger of the predator situation in Arabian babblers. Their call type production seems to lack stimulus specificity, but instead they may use acoustically distinct call types and/or their combinations to signal the perceived risk, or response urgency. To address this we experimentally confronted groups of Arabian babblers with an owl dummy in two different distance categories, representing two different degrees of risk or degrees of response urgency. We expect the birds to use the three different alarm call types differently with regard to the distance in which they detected the dummy. That is, we expected that general call type occurrence, numbers or latencies to call a certain call type differ between the two distance categories.

2. Material and methods

2.1. Study species and study site

Arabian babblers are cooperative breeders, live in stable groups and maintain territories all year round. Most groups consist of a breeding pair and helpers which are the breeders' direct offspring, other close relatives, or unrelated conspecifics (Zahavi, 1990; Cramp & Perrins, 1993). Helpers usually do not reproduce (Lundy et al., 1998), however, they participate in defending the territory, incubation and feeding the offspring etc. (Zahavi, 1990; Cramp & Perrins, 1993; Wright, 1998). Groups of Arabian babblers exhibit a cooperative system of vigilance (Wright et al., 2001a,b; Edelaar & Wright, 2006): In turns, a sentinel is standing guard in a conspicuous position, scanning the area, while other group members forage in relative safety, presumably making the whole group more efficient in both, foraging and predator avoidance (for review see Bednekoff & Lima, 1998; Clutton-Brock et al., 1999). The vocal repertoire of the species comprises a number of distinct call types (Cramp & Perrins, 1993). Three of these call types (barks, trills and tzwicks, Figure 1) occur during encounters with potential predators, sometimes but not always simultaneously (Cramp & Perrins, 1993; Naguib et al., 1999;

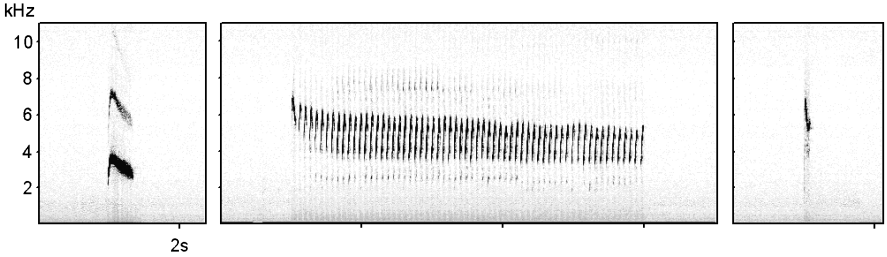

Figure 1. Spectrograms of alarm calls of Arabian babblers. Shown are a bark, a trill and a tzwick (from left to right).

Regosin, 2002; Ostreiher, 2003; Sommer, 2011). Tzwicks are also produced in other situations potentially presenting a threat, e.g., in reaction to sudden, fast or close movements, such as non-predatory birds or conspecifics flying nearby (Cramp & Perrins, 1993; Sommer, 2011) or when nest sites are approached by conspecifics from neighbouring territories (Regosin, 2002). The study site was located in the Arava valley, Israel. The investigated birds were part of an ongoing study and the population is subject of extensive observation and research since 1971 (for details, see Zahavi, 1989, 1990). Most individuals are colour-banded and to a great extend habituated to the presence of human observers. The size of tested groups ranged from 3 to 13 subjects (median (1st; 3rd quartile): 7 (6; 7); $N = 9$ groups). To control for group size and social effects due to group composition we used a paired experimental design (see below).

2.2. Experimental set-up and data recording

For an experiment we presented a dummy owl resembling a long-eared owl (*Asio otus*), a resident predator in the area (Sommer, 2011). The dummy (size ca. 28 cm) was built of styrofoam covered with feathers from Peacocks (*Pavo cristatus*) and domestic chickens. To increase the probability that the Arabian babblers detect the dummy, its wings could be moved by pulling an attached nylon string by an experimenter hidden behind vegetation. The wings were only moved before the first Arabian babbler called and not during the actual experiment or call recordings. Therefore, we are confident that the results were not affected by the wing movements of the owl dummy. We used two different distances in each group, a 'near' distance ranging from 14 to 28 m (mean ± SD 21.4 ± 5.2) and a 'far' distance ranging from 48 to 89 m (mean ± SD 69.0 ± 14.9). The exact distances were influenced by possibilities to place the dummy in a natural and sufficient position as well as by the movements of the bird group. For an experiment we fixed the covered dummy on a perch of a tree and orientated its eyes towards the centre of the bird group. In each experiment, we uncovered it, when all group members were foraging in close vicinity to each other (all subjects within a radius of approximately 20 m or less). If no suitable tree was available, we fixed the dummy on a branch that was then placed in an upright position. The height of the owl above the ground ranged from ca. 1 to ca. 3.5 m.

We conducted experiments in December 1998 and April 1999. In both periods, none of the groups made breeding attempts. In total we conducted 29 experiments using 16 different groups. From these we excluded all experiments during which a predator or a neighbouring group suddenly appeared ($N = 6$), or that did not evoke a vocal response ($N = 2$) because the group changed its travelling direction and did not detect the predator dummy. Finally, we excluded three groups from the analysis that we failed to test a second time. The resulting data set consisted of nine groups tested with either design. All data presented refer to these nine groups. Two experiments carried out in the same group were separated by at least one day and at most three days without any experiment. Experiments took place in the morning (between 0640 and 1045 h) and in the afternoon (between 1500 and 1925 h). We are aware that long-eared owls hunt mainly at dusk and dawn, but for two reasons it seems justified to conduct the experiments also during daytime: first, even if owls hunt crepuscularly, they would be encountered perched in trees during the rest of the day and on these occasions they elicit alarm calls and mobbing behaviour in Arabian babblers (personal observations, Sommer, 2011), and second, for our hypothesis it is only important to compare two treatments of differing risk (near and far distance to predator), even if this risk may be generally rather low. We conducted the experiments in a randomised order (‘near’ treatment first: 5 groups; ‘far’ treatment first: 4 groups). During the experiments we made stereo recordings of vocalisations of Arabian babblers on one channel and commented on the closest distance of the callers or other group members on the other channel. We used Sennheiser ME 66 microphones and a Sony TC-D5 M tape recorder. Comments on the callers’ distances were based on vegetation structures, measured and noted in a sketch of the experiment site after the treatment.

2.3. Data acquisition and statistical analysis

Since we were interested in factors independent from both, group size and social organisation, we used, first, a paired experimental design, and second, treated the vocal response as group response. We digitised the vocal reaction of groups of Arabian babblers using AVISOFT-SASLab Pro (R. Specht, 1998) with a sample rate of 44.1 kHz. Arabian babblers often approached the owl dummy during the experiment, making the far to a near treatment. Therefore, we restricted the analysis in all experiments to the 30 s after the initial vocal reaction (the shortest response before birds approached the dummy in a 'far' treatment and, therefore, the longest usable time span applicable to all treatments). The initial vocal reaction was defined as the first alarm call (bark, trill or tzwick) uttered after uncovering the predator dummy. For the 30-s interval following this call we determined the following parameters: number of tzwicks and barks, time trilling, type of the first, second and third call type uttered, and latency to the first trill (the latency of the first alarm call was, by definition, set to 0 s). We did not use the number of trills (as for the other two alarm call types), but the time trilling, because trills consist of a series of elements and vary a lot in duration whereas barks and tzwicks are single element calls showing relatively minor variation in their duration (Figure 1). We defined time trilling as the time between the onset of the first and the end of the last element of a trill, summed up for all trills. Periods of overlapping trills by several group members were considered only once. All temporal measures were taken to the nearest 0.1 s using cursors on the onscreen waveform display.

To analyse the vocal response with regard to the general occurrence (yes/no) of call types in the two treatments we used a McNemar test. A Wilcoxon signed-ranks test was applied to compare the number of different call types in the two treatments. To test whether the first call type uttered differed between the two treatments we used a permutation test (Adams & Anthony, 1996; Manly, 1997). For this we used chi-square (derived for treatment vs. first call type uttered) as a test statistic and permuted first call types within groups. We applied an exact permutation test, i.e., derived the sampling distribution by enumerating all possible arrangements of the data. To further analyse the vocal response with regard to the frequency of occurrence of call types within experiments we first conducted a Principal Components Analysis (PCA, rotation method: varimax). Since this method does not allow for missing values in the data set we included only those parameters for which we had obtained measures from each experiment (latency to the first trill, time trilling, numbers of barks and tzwicks). Using a PCA was justified from the data structure (Kaiser–Meyer–Olkin measure of sampling adequacy: 0.539; Bartlett's test of sphericity: $\chi^2 = 21.6$, df $= 6$, $p < 0.01$; McGregor, 1992). The PCA revealed two principal components with an Eigenvalue in excess of one. The first component explained 52% and the second 33% of the total variance. Two of the four variables loaded most on the first component (number of barks: 0.91, latency to the first trill: 0.94), the other two loaded most on the second component (time trilling: 0.74, number of tzwicks: 0.92). We, thus, used the factor scores extracted from the principal components as composite measures of vocal response. We then used Wilcoxon signed-ranks tests to compare, first, the factor scores between the two treatments, and thereafter, the original parameters (latency to the first trill, time trilling, numbers of barks, number of tzwicks) as post-hoc comparisons following a significant main result. Statistical tests were chosen according to the rationales and assumptions described in Siegel & Castellan (1988) and Bortz et al. (1990). We used exact non-parametric tests since small sample sizes required their use (Siegel & Castellan, 1988; Mundry & Fischer, 1998). All standard tests were calculated using SPSS 10.07; the permutation test was programmed in R (R Development Core Team, 2009) using the package gtools (Warnes, 2009). We indicate two-tailed p-values throughout.

3. Results

In general, subjects responded clear and strong to the dummy once it was detected. Responses consisted of uttering (at least one of the) alarm call types, bark, trill or tzwick. Furthermore, subjects often displayed typical mobbing postures, such as spreading their tail and wings. In most experiments several Arabian babblers called at a time and often some subjects or the whole group approached the dummy to distances sometimes less than 10 m while continuously calling. Vocal responses could last up to more than 10 min and often did not cease until we finished the experiment by covering the dummy.

Either of the three call types (barks, trills and tzwicks) occurred in both experimental treatments, near and far. In 14 out of 18 experiments Arabian babblers uttered two or three different call types within one treatment with a tendency to produce more call types in the far than in the near treatment

Table 1.
Occurrence of different alarm call types in the two experimental treatments ‘near’ and ‘far’.

Call type	Treatment	
	Near	Far
Bark	3	8
Trill	9	9
Tzwick	6	6

Indicated are numbers of experiments during which the respective call types occurred at least once within the first 30 s of vocal response to the artificial owl ($N = 9$ experiments with either treatment).

(Wilcoxon signed-ranks test, $T^+ = 15$, $N = 5$ groups (4 ties), $p = 0.063$). All groups uttered trills in both treatments. Tzwicks were uttered either in both treatments (six groups) or in none of the two (three groups). Eight groups uttered barks in the far treatment whereas only three groups uttered barks in the near treatment (McNemar test: $p = 0.0625$, Table 1). With regard to the very first call type uttered we found no significant difference between the two treatments (permutation test: $p = 0.156$; Table 2). Nevertheless, it was remarkable that a bark was uttered as the very first call in none of the near treatments but in four out of nine far treatments.

However, a closer look at the vocal responses revealed clear effects: The factor scores extracted from the first principal component differed signifi-

Table 2.
Initial vocal response of Arabian babbler groups to an artificial owl.

Call type	Treatment	
	Near	Far
Bark	0	4
Trill	6	3
Tzwick	3	2

Indicated are the numbers of experiments in which a bark, a trill or a tzwick, respectively, was the first call type uttered in the two different treatments, ‘near’ and ‘far’ ($N = 9$ experiments with either treatment).

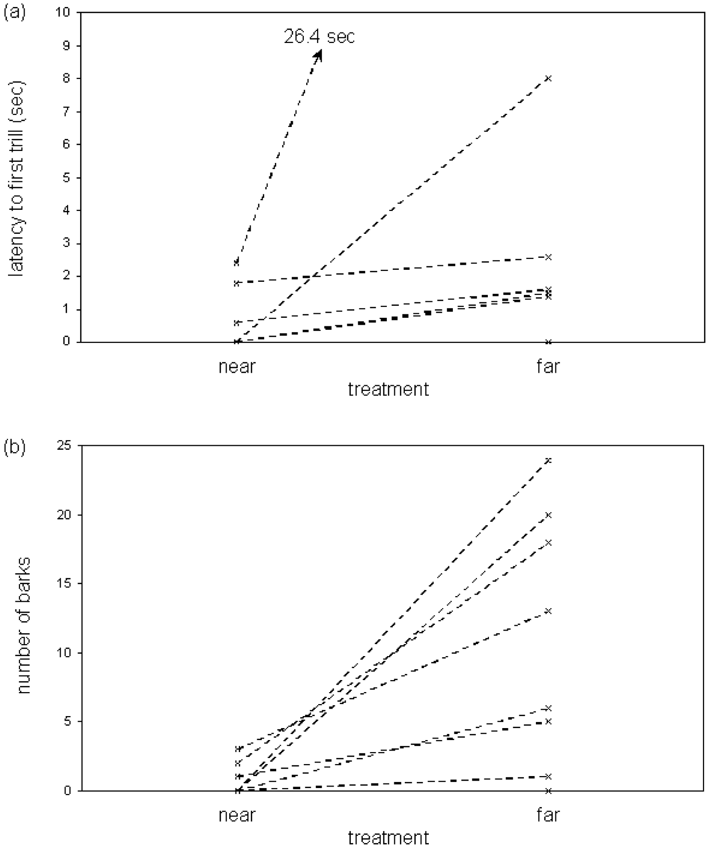

Figure 2. Two parameters of vocal response of Arabian babblers' groups to the two experimental treatments ('near' and 'far'). Each pair of connected crosses indicates values for one respective group. Indicated are (a) the latency to the first trill and (b) the number of uttered barks within the first 30 s of vocal response to the artificial owl.

cantly between the two treatments ($T^+ = 41$, $N = 9$, $p < 0.03$), and correspondingly, also the two variables loading most on this component: Arabian babblers started trilling earlier in the near treatment ($T^+ = 21$, $N = 6$ groups (3 ties), $p < 0.05$, Figure 2a) and uttered more barks in the far treatment ($T^+ = 36$, $N = 8$ groups (1 tie), $p < 0.01$, Figure 2b). The scores from the second principal component (with high loadings of time trilling and number of tzwicks) did not vary between the treatments ($T^+ = 23$, $N = 9$, $p = 1$). To summarise, the general pattern of call type occurrence did not differ between the treatments, while the details of call use did.

4. Discussion

All three call types generally occurred in both treatments, independently from the distance to the predator dummy. There was also no relation between the initially uttered call type and the distance, although barks occurred as the initial call only in the far treatment. In the majority of experiments Arabian babbler groups uttered two or three different call types simultaneously, with a tendency to utter more call types in the far treatment. Furthermore, Arabian babblers uttered more barks in the far treatment and started trilling earlier in the near treatment, whereas the time trilling and the number of tzwicks did not differ. Thus, the general occurrence of alarm call types in Arabian babblers did not differ between the two treatments, but the use of these call types did: the vocal reaction varied with regard to the distance in which Arabian babblers detected the predator dummy.

We do not think that these results are an artefact due to the quality of our dummy, because, first, the birds' calling behaviour was comparable to natural encounters with living predators. Arabian babblers commonly utter barks and trills as well as combinations of these calls with tzwicks in the presence of flying or perched birds of prey and owls (Regosin, 2002; Sommer, 2011). An Eagle owl (*Bubo bubo*) perched in daylight 5 m from a group of Arabian babblers and later flying and withdrawing to 60 m, elicited all three alarm call types as well as approach and typical mobbing behaviour in Arabian babblers (own observation). And second, the calling behaviour of subjects during experiments with the near artificial owl was similar to that reported by Naguib et al. (1999) who used another owl model (a stuffed short-eared owl, *Asio flammeus*) that was presented in distances similar to those we used in the near treatment (15–30 m). We, therefore, assume that the vocal behaviour we observed is comparable to Arabian babblers' natural calling behaviour in the presence of near and far owls, respectively. Furthermore, we have to consider that alarm calling in highly sociable Arabian babblers is influenced by, e.g., dominance hierarchy or sex of individual birds. For instance, during snake-directed mobbing subordinate group members mobbed longer than dominants and females mobbed longer than males (Maklakov, 2002). However, in our study we controlled for social effects by applying a paired experimental design and treating the vocal response of the entire group. Hence, regardless of whether calling was, in addition, influenced by the behaviour or calling of group mates or not, the finding that calling differed between the two treatments remains unambiguous and interesting. Hence, we are confident that the used artificial owl was sufficient for studying the call system in relation to the distance to a potential predator. One additional analysis would complement our investigation: the birds' approach in the far treatment (making it a near treatment after some time) may suggest a comparison between call use in the far and near distance within one experiment. However, in the six cases of approach, only some group members approached and others stayed behind. That is, the subsequent 'group response' contained only a part of the group or even only one bird. This situation was, to our opinion, not comparable to the initially 30 s and we, therefore, refrained from this additional analysis.

The finding that call use varied with the distance in which Arabian babblers detected the owl dummy clearly supports our hypothesis that alarm calling in the Arabian babbler represents an urgency based system. Also differences in Arabian babblers' calling behaviour during encounters with different types of predators, as reported by Naguib et al. (1999), do not necessarily occur due to the type of predator per se but could also be mediated by the degree of danger the predator presents. Regosin (2002) reported that Arabian babblers produced only tzwicks in response to a live dog (*Canis familiaris*, in distances comparable with our near treatment) and mainly trills in response to a stuffed perched peregrine falcon (*Falco peregrinus*). Taken together, the results of these two studies and our experiment suggest that the occurrence of acoustically distinct call types in Arabian babblers is not stimulus-specific and that their call system is clearly not functionally referential. The picture of call type occurrence is even astonishingly homogeneous, if one sorts the reported experiments by the presumed degree of danger they represent (overview in Table 3): Assumed high risk (near live cat, Naguib et al., 1999; near live dog, Regosin, 2002) is related to the occurrence of mainly or exclusively tzwicks, intermediate risk (near perched stuffed owl, Naguib et al., 1999; near owl dummy, this study; near stuffed falcon, Regosin, 2002) evokes more and/or earlier trilling, and low risk (far owl dummy, this study), elicits more barks. A similar picture arises for the initial call type in these experiments. However, the findings of the study at hand provide direct evidence that also the use of acoustically distinct call types evoked by different predator categories can be mediated by the degree of danger a predator presents and may reflect an urgency based alarm call system. Our findings also suggest further experimental studies on alarm calling in the Arabian babbler. If our interpretation is correct, then we predict that an owl presented in very

Table 3.
Occurrence of Arabian babblers' alarm call types in relation to the presumed degree of danger of the experimental situations.

	Experiment and study	Distance (m)	Call type occurrence			Initial call type			Call timing and other remarks
			Tzwick	Trill	Bark	Tzwick	Trill	Bark	
→ Presumed degree of danger → → →	Moving live dog$^{1)}$	20–30	◯	–	–	◯	–	–	
	Caged live cat$^{2)}$	15–30	◯	∘	∘	◯	–	–	Longer tzwick periods, more tzwicks before trill
	Stuffed falcon$^{1)}$	10–30	○	○	∘				
	Stuffed owl$^{2)}$	15–30	∘	◯	∘	○	○	–	Longer trill periods
	Dummy owl near$^{3)}$	14–28	○	◯	○	○	○	–	Earlier trilling
	Dummy owl far$^{3)}$	48–89	○	◯	◯	∘	○	○	Later trilling, more barks

Shown are the results of this study and results reported by Regosin (2002) and Naguib et al. (1999). The size of the circles denote the proportion of call types (please note that only records of the same study are directly comparable), – denotes no occurrence of call type and an empty cell denotes no record.

$^{1)}$ Regosin (2002): $N = 14$, dog: 1 min analyzed, stuffed falcon: 3–5 min analyzed.

$^{2)}$ Naguib et al. (1999): $N = 6$, paired design, first 2 min analyzed.

$^{3)}$ this study, $N = 9$, paired design, first 30 s analyzed.

close distances would mainly evoke tzwicks, or that a cat presented in very far distances would provoke mainly trills or even barks.

During a single experiment with our predator model Arabian babblers usually uttered two or even three of their alarm call types. Also for confrontations with a cat or an owl dummy Naguib et al. (1999) described the regular occurrence of two different call types (trills and tzwicks), and also during natural encounters with potential predators all three call types are likely to occur in combination within the same encounter (Sommer, 2011). Regosin (2002) even reported mixed calling, that is, two or three call types were acoustically melted into a single call. Using call type combinations during a single confrontation with a predator again indicates that in the Arabian babbler a certain type of alarm call is not a functional referent. However, a simultaneous occurrence of structurally distinct call types is not a necessary prerequisite for an urgency-based call system (graded changes within one call type would meet the same requirements), but such simultaneous use of different call types, is known also for some marmot species (Blumstein, 1999). Moreover, for putty-nosed monkeys (*Cercopithecus nictitans*) Arnold & Zuberbühler (2006a,b, 2008) conclude that meaning is encoded in the call sequences containing different alarm call types, but not by individual calls, and that combinatorial signalling increases the variety of messages that can be generated with a limited call repertoire. Furthermore, American red squirrels (*Tamiasciurus hudsonicus*) produce mixed bouts of two alarm call types to predators of different types which led Digweed & Rendall (2009a,b) to suggest that calls might be directed primarily at conspecifics, or at the predators themselves and function to announce their detection and possibly aid in deterring or repelling them.

Based on the results for the calling behaviour in Arabian babblers from the different field studies (Naguib et al., 1999; Regosin, 2002; Sommer, 2011; this study) we suggest distance-related functions of the different call types. Certain alarm calls might signal to the detected predator and serve to deter it (Zuberbühler et al., 1999; review on rodent species: Shelley & Blumstein, 2005). The use and acoustic structure of barks are especially suitable for this purpose because of two reasons: First, such a signal is more appropriate in low risk situations, that is, when the predator is spotted in a distance and not when already attacking, forcing the potential prey to dive into cover. Second, barks are of low pitch, compared to trills and tzwicks and, thus, have a higher potential to travel over larger distances (Wiley & Richards, 1978) and to be detectable for an avian predator. However, to give evidence for the function of barks as a signal to the predator, direct experiments with predators are needed. The potential function of the other two call types, however, remains widely unclear from our experiments. Naguib et al. (1999) hypothesised that tzwicks could indicate a ‘higher urgency, risk, or uncertainty’. Observations that tzwicks are evoked predominantly by potential predators that were detected in short distance and by birds that were precedingly not engaged in vigilance behaviour (Sommer, 2011) support this idea. Also the fact that tzwick-like calls regularly occur during fights between Arabian babblers (Cramp & Perrins, 1993) indicate that they are related to high degrees of risk or urgency. From our results, however, we can neither support nor reject this hypothesis, because we found no differences in the number of tzwicks uttered during the two treatments. However, it might be that even an owl presented in a short distance generally presents only a minor risk (Naguib et al., 1999), and, accordingly, that the number of tzwicks uttered was not affected by further increasing the distance. Particularly interesting is the potential function of trills. This call type is most common in situations that assumedly present an intermediate threat. Accordingly, Naguib et al. (1999) hypothesised that such long calls, like trills, 'are not well suited for symbolising immediate threat but are more effective in transferring information that requires no immediate reaction'. However, trills are long series of similar elements that are repeated at regular intervals, and such calls seem to have a large potential to indicate changes in a situation through irregularities in the series (Morton & Shalter, 1977; Owings & Virginia, 1978; Bayly & Evans, 2003). Such changes of a situation, however, could be most important in situations of predator surveillance that present an intermediate threat.

To summarise, in this study we provide experimental evidence that the occurrence of acoustically distinct alarm call types can be mediated by 'urgency'. The call system of Arabian babblers is urgency based with three acoustically distinct call types and the use of these call types is related to the distance to the predator. Taking together our and results of other field studies on alarm calling of Arabian babblers we suggest that tzwicks indicate high response urgency (a predator being close), whereas trills have the potential to serve predator surveillance in situations of intermediate threat (and distance). Barks may, in addition, signal the predator its detection from far.

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