

Research



Cite this article: Collier K, Radford AN, Stoll S, Watson SK, Manser MB, Bickel B, Townsend SW. 2020 Dwarf mongoose alarm calls: investigating a complex non-human animal call. *Proc. R. Soc. B* **287**: 20192514. <http://dx.doi.org/10.1098/rspb.2019.2514>

Received: 28 October 2019

Accepted: 27 August 2020

Subject Category:

Behaviour

Subject Areas:

behaviour

Keywords:

alarm call, combinatoriality, dwarf mongoose, syntax, vocal communication, vocal complexity

Author for correspondence:

Katie Collier

e-mail: katie.collier@hotmail.fr

†Joint last authors.

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.5124519>.

Dwarf mongoose alarm calls: investigating a complex non-human animal call

Katie Collier¹, Andrew N. Radford², Sabine Stoll^{3,4,5}, Stuart K. Watson^{4,5}, Marta B. Manser^{1,5}, Balthasar Bickel^{4,5,†} and Simon W. Townsend^{1,4,5,6,†}

¹Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

²School of Biological Sciences, University of Bristol, 24 Tyndall Ave, Bristol BS8 1TQ, UK

³Psycholinguistics Laboratory, and ⁴Department of Comparative Language Science, University of Zurich, Plattenstrasse 54, 8032 Zurich, Switzerland

⁵Center for the Interdisciplinary Study of Language Evolution (ISLE), University of Zurich, Switzerland

⁶Department of Psychology, University of Warwick, Coventry CV4 7AL, UK

KC, 0000-0002-3286-8088; ANR, 0000-0001-5470-3463; SWT, 0000-0003-1504-1801

Communication plays a vital role in the social lives of many species and varies greatly in complexity. One possible way to increase communicative complexity is by combining signals into longer sequences, which has been proposed as a mechanism allowing species with a limited repertoire to increase their communicative output. In mammals, most studies on combinatoriality have focused on vocal communication in non-human primates. Here, we investigated a potential combination of alarm calls in the dwarf mongoose (*Helogale parvula*), a non-primate mammal. Acoustic analyses and playback experiments with a wild population suggest: (i) that dwarf mongooses produce a complex call type (T_3) which, at least at the surface level, seems to comprise units that are not functionally different to two meaningful alarm calls (aerial and terrestrial); and (ii) that this T_3 call functions as a general alarm, produced in response to a wide range of threats. Using a novel approach, we further explored multiple interpretations of the T_3 call based on the information content of the apparent comprising calls and how they are combined. We also considered an alternative, non-combinatorial interpretation that frames T_3 as the origin, rather than the product, of the individual alarm calls. This study complements previous knowledge of vocal combinatoriality in non-primate mammals and introduces an approach that could facilitate comparisons between different animal and human communication systems.

1. Background

Communication plays an essential role in the social lives of many species [1–4], with considerable interspecific variation both in the modality used (e.g. auditory, visual, olfactory) and in complexity [5]. Communicative complexity has long been defined in several ways: for example, by the number of structurally and functionally distinct elements or the amount of bits of information, with the presence of more elements or bits representing more complex systems [6,7]. Recently, one measure of communicative complexity in the vocal domain—the capacity to combine calls together into larger structures—has received increasing attention. Comparative and theoretical work suggests that combining calls not only serves to increase the communicative output of a species but, compared with the creation of new calls, does so in a more efficient way [8,9] and with a reduced error risk for the receiver [10,11].

To date, the majority of research on signal combinations in non-human vocal communication has focused on primate species, not least because of their close phylogenetic relationship to humans and thus the potential to

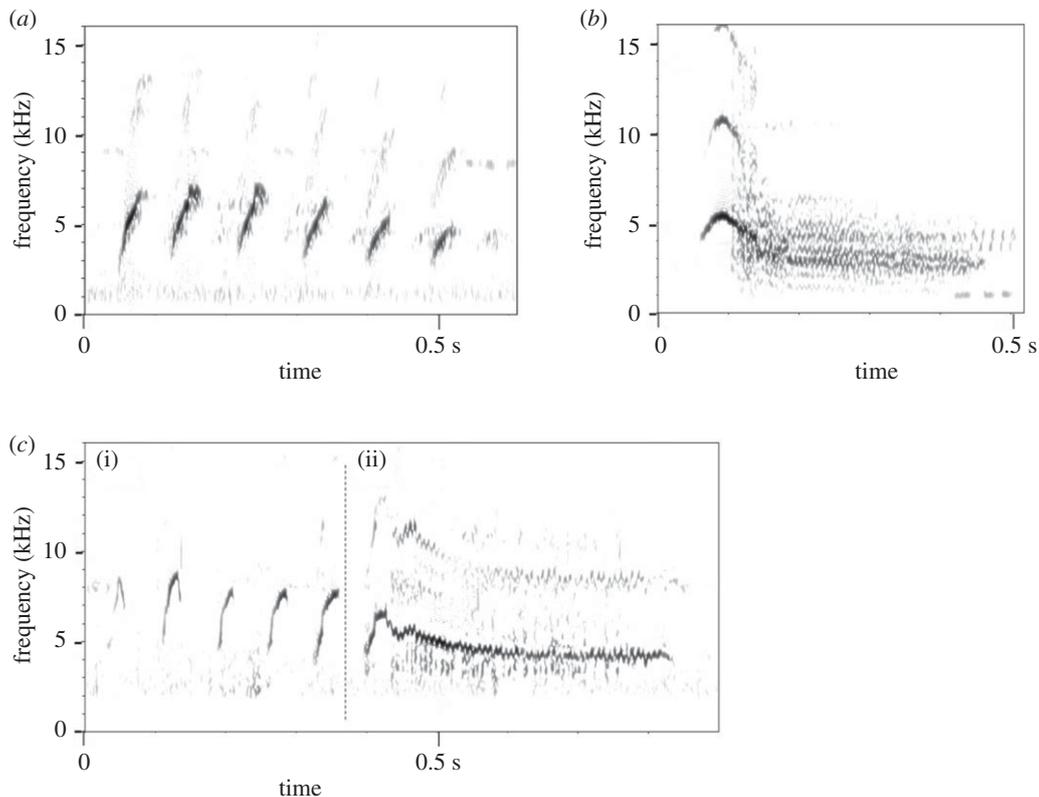


Figure 1. Spectrograms of dwarf mongoose alarm calls. (a) Aerial alarm call. (b) Terrestrial alarm call. (c) Type 3 or T_3 alarm call composed of two parts: (i) pulsed first segment ($T_{3,1}$) and (ii) noisy second segment ($T_{3,2}$). Window length = 0.05 s, dynamic range = 70 dB.

shed light on the evolution of our own highly combinatorial communication system. Combinatorial capacities have, for example, been demonstrated in both primate alarm and long calls (black-fronted titi monkeys, *Callicebus nigrifrons* [12,13]; Bornean orang-utans, *Pongo pygmaeus wurmbii* [14]; putty-nosed monkeys, *Cercopithecus nictitans* [15,16]; white-handed gibbons, *Hyllobates lar* [17]) and their social calls (chimpanzees, *Pan troglodytes* [18]; bonobos, *Pan paniscus* [19,20]; red-capped mangabeys, *Cercocebus torquatus* [21]; Diana monkeys, *Cercopithecus diana diana* [22]). One combinatorial signal in Campbell's monkeys (*Cercopithecus campbelli campbelli*) has received particular attention, primarily due to its structural similarity with compositionality in the human language where meaning-bearing units (e.g. words) are combined together into larger meaningful structures [23,24]. Specifically, Campbell's monkeys have been shown to affix an acoustically distinct 'oo' unit to their predator-specific alarm calls [25,26]. The addition of this affix changes the meaning of different alarm calls in a predictable way, from specific to general, and has therefore been interpreted as a rudimentary combinatorial or even compositional system [27–29].

Despite an emphasis on primates, recent research suggests similar combinatorial capacities are also present in taxa more distantly related to humans. For example, two bird species have been demonstrated to produce remarkably similar combinations of calls. Both pied babblers (*Turdoides bicolor*) and Japanese great tits (*Parus minor*) combine alert vocalizations (used to indicate threats) with a recruitment call (used to recruit conspecifics in a variety of events) into a larger structure when encountering threats, such as snakes, that require recruitment [30,31]. Playback experiments have confirmed that these call combinations are meaningful to receivers, conveying information on both the context and the required action [30,31]. There also exists

intriguing, detailed observational data documenting call combinations in non-primate mammals (banded mongooses, *Mungos mungo* [32]; meerkats, *Suricata suricatta* [33]). In comparison to birds and primates, however, experimental verification of the structure and function of these combinations is still needed (though see [34] for an example in dingos, *Canis familiaris dingo*). If we are to capture the complexity of animal vocal communication systems, data on the production and perception of call combinations are required across a wide range of species and taxa. Such data are particularly important for understanding the role that combinatoriality might play in facilitating the emergence of complex communication systems [35]. Here, we aim to further existing knowledge by experimentally investigating combinatorial-like structures in the alarm-call system of a non-primate mammal, the dwarf mongoose (*Helogale parvula*).

Dwarf mongooses are a highly social, small carnivore species from eastern and southern Africa. They live in groups of up to 30 individuals [36], composed of a dominant pair and subordinate individuals of both sexes who can be related or unrelated to the dominant male and female [37]. They forage for insects and small vertebrates as part of a group. During foraging sessions, individuals often perform sentinel behaviour, standing in an elevated position and alerting the rest of the group to threats by producing alarm calls [38]. Among other calls, dwarf mongooses produce two predator-specific alarm calls upon detecting aerial and terrestrial predators [39]. A third alarm call, type 3 (T_3), appears to be a combination of aerial and terrestrial alarm calls [39] (figure 1), with the structure resembling an aerial alarm call (hereafter $T_{3,1}$) always preceding the structure resembling a terrestrial alarm call (hereafter $T_{3,2}$). Previous observations indicate that T_3 functions as a general alarm call (i.e. a call given to a wide range of disturbances which contains no specific

Table 1. Simplified contexts in which the different dwarf mongoose alarm calls were produced, both during natural encounters and predator presentations (derived from [39]), as well responses of subjects to the different alarm call types during playback experiments. **X**: call primarily given to this stimulus or main response to the playback of an alarm call. **x**: alarm call rarely given to a stimulus type or secondary reaction to the playback of an alarm call type. **0**: call never given to a stimulus or response never recorded in reaction to the playback of an alarm call.

	production in response to				main response when hearing alarm call			
	aerial stimuli	helium balloon	dog	secondary cues	observer	run for cover	vigilance	look at the sky
aerial alarm call	X	X	x	0	X	X	x	X
terrestrial alarm call	x	0	X	X	X	x	X	0
T ₃ alarm call	X	X	X	x	X	X	X	X

information about the eliciting context [40]) and can occur in ambiguous predation contexts [39], potentially suggesting that the meaning of T₃ is related to the meaning of its parts. However, an experimental demonstration that the T₃ alarm call functions to communicate general threats is lacking.

Building on prior work, here we used field-based playback experiments and acoustic analyses to investigate further the function and acoustic structure of T₃ alarm calls and to determine the extent to which the overall meaning of the combination is derived from its parts. First, if T₃ serves as a general alarm call, we expected to observe general anti-predator behaviours in response to its playback. Second, if T₃ has this function by virtue of being, at least at the surface level, a combination of an aerial and a terrestrial call: (i) the acoustic structure of T₃'s component parts should be similar to the acoustic structures of the corresponding alarm call types; and (ii) playbacks of the different parts of T₃ in isolation should reveal similar responses to the aerial and terrestrial alarm calls.

2. Methods

(a) Study site and population

Our research was carried out between November 2014 and June 2015, and in January–February 2016, as part of the long-term Dwarf Mongoose Research Project. Subjects were adult (greater than 1 year) dwarf mongooses living in their natural habitat located on Sorabi Rock Lodge, South Africa [41] and belonged to seven wild but habituated groups composed of 6 to 15 individuals (mean group size = 11). Individuals were habituated to close observations, allowing sound recordings from 1 to 3 m and detailed data collection from field-based playback experiments [39,41]. All mongooses were individually identifiable by small blonde dye-marks or distinguishable features such as scars [41].

(b) Alarm call collection and acoustic analysis

Alarm calls for acoustic analysis were collected by employing the same methods as in previous work [39]. Dwarf mongooses were followed during two daily sessions, one in the morning and another in the evening, during which we recorded, *ad libitum*, all alarm calls produced. When possible, the eliciting stimulus, the mongooses' response and the caller's identity were noted. To collect additional alarm calls, in particular, those produced in the presence of terrestrial predators (none of which we obtained naturally), we carried out predator presentations. We

used a domestic dog (husky crossbreed, approx. 60 cm at the shoulders) on a leash as a substitute terrestrial predator and a helium balloon to simulate an aerial predator [39].

We performed an acoustic analysis to compare the different types of alarm calls emitted and to determine whether T₃ is structurally a combination of an aerial and a terrestrial alarm. We first visualized the calls using Praat v. 5.3.85 (www.praat.org) and selected good-quality alarm calls with a high signal-to-noise ratio for the analysis. Using the acoustic program Luscinia [42], we then extracted several temporal and spectral parameters from these calls (electronic supplementary material, table S1). We did this for each of the natural alarm call types (aerial, terrestrial and T₃) but also for the first and second halves of T₃ (T_{3,1} and T_{3,2}), respectively, resembling an aerial and a terrestrial alarm call.

(c) Playbacks

Following on from previous work investigating the contexts in which the different dwarf mongoose alarm-call types are produced [39] (results summarized in table 1), we aimed to clarify T₃'s status as a general alarm call by considering the responses to playbacks of three natural alarm calls: aerial, terrestrial and T₃. For natural alarm calls, we performed a total of 18 playbacks each for aerial and terrestrial calls (to 17 individuals belonging to seven groups) and 15 playbacks for T₃ alarms (to 14 individuals belonging to seven groups; in all cases, the individual that received two playbacks of the same call type was tested in two different field seasons).

To test whether subjects perceived the T₃ alarm call as a combination of aerial and terrestrial alarms, we carried out paired playbacks of three sets of stimuli: (i) T₃ and artificial T₃ alarms (T_{3art}), created by sequentially concatenating the recordings of individually produced aerial and terrestrial calls; (ii) aerial and T_{3,1}; and (iii) terrestrial and T_{3,2} alarms. The aim was to conduct the paired playbacks to 10 focal mongooses, belonging to seven different groups, but set (i) could only be played back to eight individuals. For all playbacks, we selected calls with a good signal-to-noise ratio as stimuli, providing 15 exemplars of aerial, 12 of terrestrial and 9 of T₃ alarm calls. Each stimulus consisted of a single call recorded from a foreign group to avoid the focal individual hearing its own alarm call during the experiment. We played back the alarm calls from a height of about 1 m to simulate a call from an individual acting as a sentinel (raised guard) [41]. We implemented playbacks when the focal mongoose was foraging in the open and its response was filmed from 3 to 5 m using a handheld camcorder (Canon Legria HF R506; Cannon Inc., Tokyo, Japan). All behavioural measurements were taken from the resulting videos. We noted

the focal individual's immediate response to the playback and, in line with previous work [39], scored its strength according to the activity or energy required by the different responses, which also corresponds to the scale of disruption that the response causes to mongoose foraging activity. Specifically, we scored 1 = no reaction (no visible change in behaviour); 2 = vigilance (mongoose paused foraging and scanned the area horizontally); 3 = moved (mongoose started moving but stopped short of cover); or 4 = ran for cover (mongoose moved quickly to the nearest bush or rocks). We also determined the focal individual's latency to relax; that is, latency to resume foraging or engage in auto- or allo-grooming. Furthermore, we noted whether, within the minute following playback, the mongoose engaged in additional anti-predator behaviours: looking-up behaviour (i.e. looking at the sky), which may facilitate the detection of aerial predators; or initiating a sentinel bout, which could allow subjects to detect any type of predator. To ensure accurate coding of the videos, 15 randomly selected videos (26% of trials) were blind-coded by a second naïve observer. Interobserver analyses suggest a reliable agreement between observers: (% agreement varied between 73% and 86% for the different categories of behaviours; strongest reaction ($r = 0.89$, $p < 0.001$), looking-up (adjusted kappa: 0.73 [CIs: 0.19, 0.97]) and becoming a sentinel (adjusted kappa: 0.6 [CIs: 0.04, 0.91]) [43,44]. Experimental trials only took place if no conspecific or heterospecific alarm calls had been heard within the last 10 min and the mongooses were showing no signs of alarm or arousal from a previous event (predator encounter or intergroup interaction). At least 1 h separated two successive playbacks, with a maximum of three playbacks per session (morning or afternoon). All stimuli were presented in a random order.

(d) Statistical analysis

(i) Acoustic analysis

We compared the three natural call types, obtained from five different groups, to each other ($n = 7$ calls per group per type), as well as aerial and terrestrial alarm calls to $T_{3,1}$ and $T_{3,2}$ respectively (aerial and $T_{3,1}$: $n = 7$ calls per group per type; terrestrial and $T_{3,2}$: $n = 10$ calls per group per type), using the measured acoustic parameters (see electronic supplementary material, table S1). We started by removing any collinear parameters, as determined by their variance inflation factors (VIF). We calculated VIFs for all parameters and discarded the parameter with the highest VIF and then repeated these steps until all remaining parameters had VIFs with values lower than 10 and therefore should not be collinear [45]. We then used the remaining parameters to run a discriminant function analysis (DFA). Given that multiple calls obtained from the same group contributed to the dataset, we implemented permuted DFAs (pDFA) using a function provided by R. Mundry. Unlike conventional DFAs, pDFAs allow for repeated measures due to multiple recordings of an individual or group and do not return inflated p -values [46]. Ideally, we would also have controlled for potential repeated measures at the individual level, but this was not possible due to difficulties reliably identifying callers on a regular basis. All analyses were performed using R v. 3.2.1 [47] with the packages usdm [48] and MASS [49].

(ii) Playbacks

To investigate the strength of reaction when hearing the three different natural alarm calls, we used a cumulative link mixed model (CLMM), fitting stimulus type as a fixed effect and individual nested within the group as a random effect. When a significant result was returned, we carried out post hoc pairwise CLMMs between the treatments (aerial versus terrestrial, aerial versus T_3 , terrestrial versus T_3) and p -values were adjusted for multiple testing using Bonferroni's correction. Models of the same format were

used to compare the strength of reaction between paired stimuli (aerial and $T_{3,1}$, terrestrial and $T_{3,2}$, T_3 and T_{3art}).

To compare latencies to relax in response to the three different natural alarm calls, we carried out a linear mixed model (LMM) with stimulus type as a fixed effect and individual nested within the group as a random effect. Inspecting plots of the model residuals showed that our data did not violate the assumptions of linearity, homoscedasticity and normality of the residuals. However, this was not the case for the data from the paired playbacks, so we used non-parametric Wilcoxon signed-rank tests to compare latencies to relax in this case.

To test whether the expression of the additional anti-predator behaviours (looking-up and acting as a sentinel) differed in response to different playback stimuli, we performed generalized linear mixed models (GLMMs) with a binomial family and a logit link function with stimulus type as a fixed effect and individual nested within the group as a random effect. This was done for all playbacks except in the case of looking-up behaviour in paired playback set (iii), as this behaviour was not expressed in reaction to the stimuli used. For all the models, p -values were obtained using likelihood ratio tests comparing full models, including all the explanatory variables, to reduced models including the same explanatory variables but without the variable of interest. Analyses were performed using R [47] with the packages ordinal [50] and lme4 [51].

3. Results

(a) Acoustic analysis

The three natural alarm call types were distinguishable by the measured acoustic parameters (pDFA: $n_{\text{calls}} = 105$, $p = 0.002$, percentage correctly cross-classified = 82%). Aerial alarms and the first element of T_3 ($T_{3,1}$) could not reliably be distinguished from each other by acoustic parameters alone ($n_{\text{calls}} = 70$, $p = 0.091$, percentage correctly cross-classified = 68%), whereas terrestrial alarms and the second element of T_3 ($T_{3,2}$) could be discriminated ($n_{\text{calls}} = 100$, $p = 0.026$, percentage correctly cross-classified = 94%).

(b) Function of T_3 alarm calls

The strength of reaction by dwarf mongooses to playbacks of natural alarm calls depended on the alarm call type (CLMM $\chi^2_2 = 6.88$, $p = 0.03$; figure 2). While we have previously shown that subjects reacted differently to aerial and terrestrial alarms [39], Bonferroni-corrected post hoc pairwise comparisons of the current data indicated that reaction strength was not significantly different in response to aerial and T_3 alarm calls ($\chi^2_1 = 1.27$, $p_{\text{adj}} = 0.78$) and to terrestrial and T_3 alarm calls ($\chi^2_1 = 2.01$, $p_{\text{adj}} = 0.48$). The absence of differences in reaction strength to T_3 and aerial or terrestrial calls, in addition to its previously defined use in multiple and ambiguous predator contexts [39], is highly suggestive of T_3 's status as a general alarm call. In addition, there was no significant difference in latency to relax (LMM: $\chi^2_2 = 1.90$, $p = 0.39$) or sentinel behaviour ($\chi^2_2 = 0.28$, $p = 0.87$), in response to playback of the different natural alarm calls. Furthermore, there was no significant difference in subsequent looking-up behaviour (GLMM: $\chi^2_2 = 4.98$, $p = 0.083$).

(c) Playback of paired natural and experimentally modified alarm calls

We found that the strength of response did not differ significantly to T_3 and T_{3art} (CLMM: $\chi^2_1 = 0.22$, $p = 0.26$) or to aerial

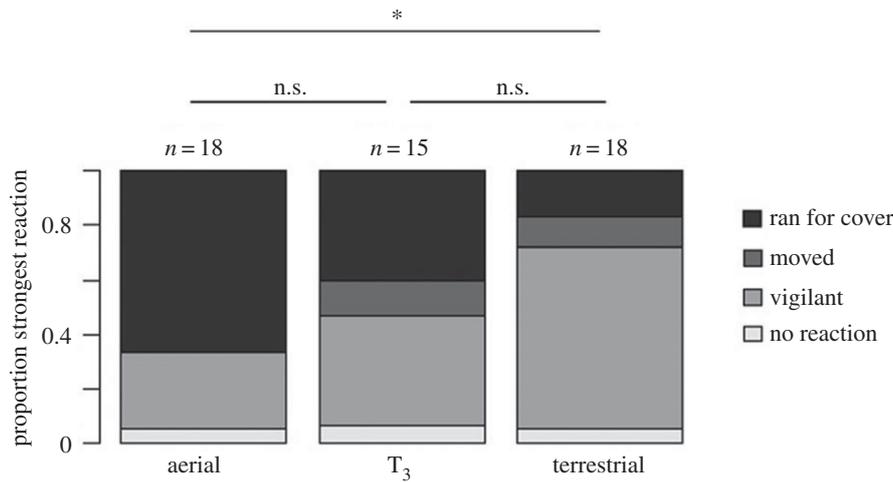


Figure 2. Frequency of the different types of reaction by focal individuals to the playbacks of natural alarm calls. * $p < 0.05$ [39]; n.s.: non-significant.

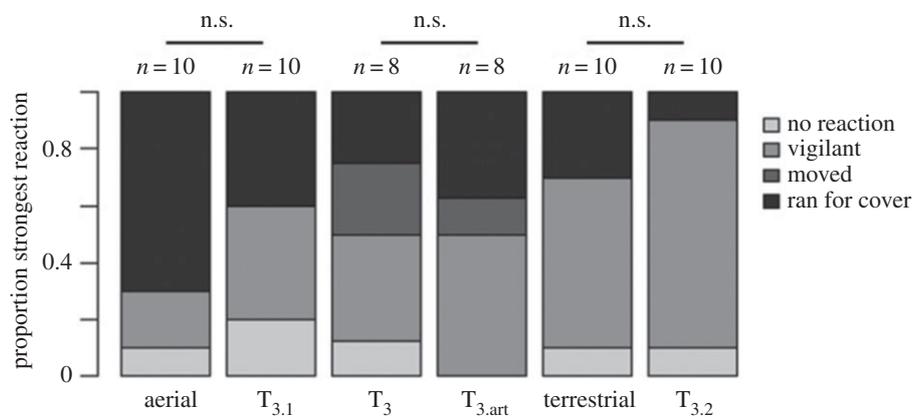


Figure 3. Pairwise comparisons of the relative frequency of different types of reaction by focal individuals in response to playbacks of natural alarm calls and their artificial counterparts. CLMMs: T_3 and $T_{3.art}$: $\chi^2_1 = 0.22$, $p = 0.26$; aerial and $T_{3.1}$: $\chi^2_1 = 3.06$, $p = 0.08$; terrestrial and $T_{3.2}$: $\chi^2_1 = 1.25$, $p = 0.26$. n.s.: non-significant.

and $T_{3.1}$ ($\chi^2_1 = 3.06$, $p = 0.08$). Furthermore, despite differences in acoustic structure between $T_{3.2}$ and terrestrial alarm calls, we also found no difference in strength of response between these calls ($\chi^2_1 = 1.25$, $p = 0.26$; figure 3). One possible explanation for $T_{3.2}$'s differing acoustic structure could therefore be a co-articulation mechanism, in which the properties of a sound are modified by the influences of adjacent sounds [52]. There was, in addition, no significant difference in latency to relax (Wilcoxon, T_3 and $T_{3.art}$: $v = 16.5$, $n = 8$, $p = 0.51$; aerial and $T_{3.1}$: $v = 21$, $n = 10$, $p = 0.73$; terrestrial and $T_{3.2}$: $v = 12$, $n = 10$, $p = 0.83$), in looking-up behaviour (GLMM, T_3 and $T_{3.art}$: $\chi^2_1 = 0$, $p = 1$; aerial and $T_{3.1}$: $\chi^2_1 = 0$, $p = 1$) or in sentinel behaviour (GLMM, T_3 and $T_{3.art}$: $\chi^2_1 = 0.40$, $p = 0.53$; aerial and $T_{3.1}$: $\chi^2_1 = 1.41$, $p = 0.23$; terrestrial and $T_{3.2}$: $\chi^2_1 = 0.43$, $p = 0.51$) between the pairs of playbacks.

Given the nature of p-values and the relatively small sample sizes, we wished to exercise caution when inferring a lack of effect from non-significant results. We therefore reran our analyses using Bayesian mixed-effects models, which are able to estimate parameters more accurately from smaller sample sizes than maximum-likelihood approaches [53]. This analysis supported the outcomes of our original frequentist analysis in that there was no strong evidence of an effect of playback type on any behavioural response except

terrestrial versus aerial alarm calls (see electronic supplementary material for details).

4. Discussion

Our observational and experimental results indicate that dwarf mongooses produce a complex call type (T_3) that, at least at the surface level, seems to comprise units that are not clearly functionally different from two meaningful alarm calls (aerial and terrestrial). Furthermore, the strength of reaction to playbacks suggests that the structure of the T_3 call appears meaningful to dwarf mongooses, with subjects reacting to it in an intermediary, or generalized, way: they respond with a mix of behaviours, compared with the two distinct alarm calls, rather than with a novel qualitatively different response as in [15]. We consider both combinatorial and non-combinatorial hypotheses for the origin of T_3 .

One possible interpretation of the T_3 alarm call is that it represents a combination of two different alarm calls and that by recombining existing meaningful calls from the repertoire in transparent ways, dwarf mongooses are capable of communicating related, yet subtly different information [26,30,31]. Analysing how the precise information content of two predator-specific alarm calls gives rise to a more

general alarm call is, however, non-trivial. Here, we analyse the calls within a linguistic framework, adopting technical notions from language science. It is important to highlight that in doing so, we do not mean to imply the same cognitive mechanisms are at play as when combinations are processed in human language. Rather, it represents one method to assess the precise use conditions of animal calls. Specifically, we considered different possible interpretations of the T_3 alarm call depending on the potential contexts of use and the associated informational content of the distinct aerial and terrestrial alarm calls and the ways in which they could be combined. For example, in line with previous findings in two bird species [30,31], one potential interpretation would be that the alarm components denote their respective predator type and T_3 would act as a 'conjunction' [54], denoting the presence of both predators simultaneously. This interpretation, however, is incongruent with the data because this conjunction of events was never observed, yet T_3 was commonly emitted (20% of all alarm calls recorded) [39]. Moreover, we would expect a stronger reaction to an alarm call denoting the presence of two types of predator instead of one, which was not the case.

Several other interpretations can be considered. In the first, the alarm components could indicate the behaviour that receivers should perform (run for cover; vigilance). In which case, T_3 would convey something akin to 'run for cover and be vigilant'. While possible, this interpretation of the individual calls is problematic, which in turn makes this interpretation of T_3 unlikely. That is because the experimental data suggest dwarf mongooses sometimes become vigilant in response to an aerial alarm or run for cover when hearing a terrestrial alarm (figure 2), implying that these calls do not denote the behaviour receivers should perform. Furthermore, an additional cognitive step would be required on the caller's part as, once the caller has identified the type of threat (e.g. aerial or terrestrial predator), it would then have to convert predator type into the appropriate reaction for receivers to perform (e.g. run for cover, be vigilant) before emitting the alarm call.

In another possible interpretation, the aerial and terrestrial alarm calls could refer, respectively, to aerial and terrestrial predators, and T_3 refers to an aerial *or* a terrestrial predator. This interpretation would represent a 'disjunction', in which two units are combined with at least one context being appropriate or 'true', but not necessarily both (e.g. 'turn left *or* right') [54]. This interpretation of T_3 would be very inefficient, indicating two very distinct forms that a threat could take, leaving receivers uncertain as to the exact nature of the danger. In these circumstances, as a disjunction does not provide specific information on the type of threat but only that danger is present, we would predict that mongooses would alternate between vigilance (to detect a terrestrial threat) and looking-up at the sky (to detect an aerial threat) to establish first what the probable threat is before engaging in any potentially dangerous anti-predator behaviour that might be detrimental to survival. Yet this is not what we observed: mongooses only occasionally looked at the sky after hearing a T_3 alarm call (2/15 trials) and this was always after running for cover. Nevertheless, the disjunction analysis does seem to capture something genuine about the function of this combination and its use as a general alarm call: enumerating the alternatives (here: raptor, terrestrial predator) as a way of generalizing across them (danger).

Following on from this, an additional potential interpretation is that T_3 calls would have a similar structure to what are termed 'listing compounds' in human language. Listing compounds also define a context by enumerating the possible alternatives. An example from English is 'pass-fail', as in a 'pass-fail exam', which details all possible contexts or outcomes of this type of exam. The critical difference between a listing compound (a pass-fail exam) and an explicit disjunction (an exam in which you can pass or in which you can fail) in language is that a compound is interpreted as a whole and points to a single specific context, in this case an established type of exam, while the disjunction rests on interpreting each statement on its own (you can pass it, you can fail it) followed by the complex logical operation that combines the two by 'or'. Under this analogy with listing compounds in language, T_3 calls would signal a more general danger context, defined by listing its alternatives. This interpretation reflects the fact that the component calls indeed signal disjoint contexts, but it is at the same time consistent with the fact that a combination refers to a single context and is not ambiguous between two contexts.

While general alarm calls are common in non-human animals [55], it is unclear why dwarf mongooses use a combination of independently occurring calls, rather than a single call to fulfil this general alarm function. Interestingly, a similar phenomenon also exists in Campbell monkeys who have been demonstrated to use call combinations (e.g. 'krak-oo') in more general threat situations, as opposed to the single calls (e.g. 'krak') used in response to a specific predator type [26]. In line with theoretical modelling work, it is possible that in dwarf mongooses, each of the individual alarms accomplishes a specific function, leading to the compounding of calls to communicate additional information [35]. It is worth noting that while aerial and terrestrial calls are primarily associated with a specific behavioural response (run for cover and vigilance, respectively), this is more of a probabilistic rather than a deterministic relationship. It could be, therefore, that the intermediate response elicited by T_3 is, instead, a result of receivers probabilistically inferring the referent of two separate alarm calls sequentially leading to a more noisy behavioural response.

Alternatively, rather than the T_3 call being a combination of two independently occurring calls, an equally plausible interpretation is that the T_3 call represents a stand-alone, holistically meaningful call from which the more specific aerial and terrestrial calls are derived. Such an analysis is particularly attractive as it is potentially simpler (in an evolutionary sense): if T_3 is in fact a single, albeit acoustically complex, call, then there is no need to explain why a combination of calls, rather than a single-call type, would be used to signal a general threat. This alternative scenario also has important evolutionary implications. To date, the majority of work focusing on combinatoriality in animal communication has posited that it serves to expand the vocal repertoire, particularly in species that are constrained in their vocal production [15,30]. However, it may well be that repertoire size is expanded, not through combinatoriality, but instead by decomposing complex calls into smaller, more specific parts.

It is evident that more research is ultimately needed. Though reanalysis of our data within a Bayesian framework broadly corroborates our findings, increasing the power with a larger sample size would be important. Furthermore,

additional playback experiments, in particular, could be a fruitful way to begin to disentangle the competing hypotheses regarding T_3 's origins and meaning. For example, in line with the proposal that T_3 represents a third distinct call type (as opposed to a combination of individual calls), a playback experiment reversing the order of units structurally equivalent to aerial and terrestrial calls should lead to a loss in behavioural response, as the call is never produced in this way. If, on the other hand, T_3 is a combination of independent alarm calls and derives its meaning, in some way, from these individual parts, dwarf mongoose should still be able to process the meaning of T_3 , irrespective of the order of its components. Moreover, manipulations of the duration between calls, or indeed simulating T_3 from callers in two different locations, could shed additional light on whether T_3 is a bona fide, simple, syntactic structure, as opposed to an unrelated sequence of two calls that happen to fall adjacent to each other.

5. Conclusion

Our study offers a new example of a complex call structure (T_3) in mammals that superficially resembles a combination of two individual calls (aerial and terrestrial alarm calls). This research in dwarf mongooses not only complements previous research on combinatoriality in animal communication but also helps shed light on the phylogenetic distribution of this phenomenon. This, in turn, will ultimately help inform our knowledge about the social and environmental factors promoting such vocal complexity and, more specifically, the exact type of combinatoriality employed by a species (e.g. compounding, disjunction, conjunction). Further work is still necessary to rule out other potential explanations—namely that T_3 is actually the source of the individual calls, rather than being a product of combining two calls. Such an analysis represents an intriguing avenue for future research in dwarf mongoose communication but also in animal combinatoriality in general. Lastly, to our knowledge,

this is the first attempt at analysing a non-human animal call combination based on the possible meanings of the combination's individual components and the different ways in which they can be combined. Such an approach is key to unpacking not only the similarities and differences between combinations in various animal communication systems, but also between such combinations and those found in human language.

Ethics. Our work was carried out under permission from the Limpopo Department of Economic Development, Environment and Tourism (permit no.: 001-CPM403-00013) and the Ethical Committee of Pretoria University, South Africa (permit no.: EC049-16).

Data accessibility. The data used for this research is available as electronic supplementary material.

Authors' contributions. K.C., S.S., M.B.M., B.B. and S.W.T. were involved in conceptualization; K.C., M.B.M., A.N.R., B.B. and S.W.T. were involved in methodology; K.C. was involved in investigation; K.C., B.B., S.S., S.K.W. and S.W.T. were involved in formal analysis; K.C., A.N.R., S.S., M.B.M., B.B. and S.W.T. were involved in writing.

Competing interests. We declare we have no competing interests.

Funding. This work was funded by a collaborative University of Zurich Research Priority Program grant (University Research Priority Programs: Evolution in Action), grant no. URPP U-702-06. A.N.R. was funded by the University of Bristol; S.W.T. by the University of Zurich, the University of Warwick and the Swiss National Science Foundation (PP003_163850); M.B.M. by the University of Zurich. We also acknowledge NCCR Evolving Language, Swiss National Science Foundation Agreement no. 51NF40_180888.

Acknowledgements. We thank H. Yeates for allowing us to work on Sorabi Rock Lodge, and C. Esterhuizen for logistical support in the field. We are much obliged to J. Kern for creating and running the Dwarf Mongoose Research Project, as well as for her help. We also thank L. Sharpe for lending us Magic, the dog. We thank the research assistants who helped with data collection and group habituation: E. Ackerley, A. Bracken, F. Carr, C. Christensen, B. Davison, S. Edwards, H. McElliott, A. Morris-Drake and K. Rogerson. We thank P. Collier for blind coding part of the data and Andri Manser for help with statistical analyses. Finally, we thank B. Ehmann for her help labelling alarm calls and C. van Schaik, P. Schlenker, E. Chemla, S. Kita for discussions and Loeske Kruuk and two anonymous reviewers for extensive comments on previous versions of the manuscript.

References

- Bousquet CAH, Sumpter DJT, Manser MB. 2010 Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proc. R. Soc. B* **278**, 1482–1488. (doi:10.1098/rspb.2010.1739)
- Blumstein DT. 1995 Golden marmot alarm calls: I. The production of situationally—specific vocalizations. *Ethology* **100**, 113–125.
- Tomasello M. 1999 *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.
- Byers BE, Kroodsma DE. 2009 Female mate choice and songbird song repertoires. *Anim. Behav.* **77**, 13–22. (doi:10.1016/j.anbehav.2008.10.003)
- Pika S. 2017 Unpeeling the layers of communicative complexity. *Anim. Behav.* **134**, 223–227. (doi:10.1016/j.anbehav.2017.07.002)
- Freeberg TM, Dunbar RIM, Ord TJ. 2012 Social complexity as a proximate and ultimate factor in communicative complexity. *Phil. Trans. R. Soc. Lond. B* **367**, 1785–1801. (doi:10.1098/rstb.2011.0213)
- Pellegrino F, Coupé C, Marsico E. 2011 Across-language perspective on speech information rate. *Language* **87**, 539–558. (doi:10.1353/lan.2011.0057)
- Jackendoff R. 1999 Possible stages in the evolution of the language capacity. *Trends Cogn. Sci.* **3**, 272–279. (doi:10.1016/S1364-6613(99)01333-9)
- Nowak MA. 2000 Evolutionary biology of language. *Phil. Trans. R. Soc. B* **355**, 1615–1622. (doi:10.1098/rstb.2000.0723)
- Nowak MA, Krakauer DC, Dress A. 1999 An error limit for the evolution of language. *Proc. R. Soc. Lond. B* **266**, 2131–2136. (doi:10.1098/rspb.1999.0898)
- Nowak MA, Krakauer DC. 1999 The evolution of language. *Proc. Natl Acad. Sci. USA* **96**, 8028–8033. (doi:10.1073/pnas.96.14.8028)
- Cäsar C, Zuberbühler K, Young RJ, Byrne RW. 2013 Titi monkey call sequences vary with predator location and type. *Biol. Lett.* **9**, 20130535. (doi:10.1098/rsbl.2013.0535)
- Cäsar C, Byrne RW, Young RJ, Zuberbühler K. 2012 The alarm call system of wild black-fronted titi monkeys, *Callicebus nigrifrons*. *Behav. Ecol. Sociobiol.* **66**, 653–667. (doi:10.1007/s00265-011-1313-0)
- Spillmann B, Dunkel LP, van Noordwijk MA, Amda RNA, Lameira AR, Wich SA, van Schaik CP. 2010 Acoustic properties of long calls given by flanged male orang-utans (*Pongo pygmaeus wurmbii*) reflect both individual identity and context. *Ethology* **116**, 385–395. (doi:10.1111/j.1439-0310.2010.01744.x)
- Arnold K, Zuberbühler K. 2006 Language evolution: semantic combinations in primate calls. *Nature* **441**, 303. (doi:10.1038/441303a)
- Arnold K, Zuberbühler K. 2012 Call combinations in monkeys: compositional or idiomatic expressions?

- Brain Lang.* **120**, 303–309. (doi:10.1016/j.bandl.2011.10.001)
17. Clarke E, Reichard UH, Zuberbühler K. 2006 The syntax and meaning of wild gibbon songs. *PLoS ONE* **1**, e73. (doi:10.1371/journal.pone.0000073)
 18. Crockford C, Boesch C. 2005 Call combinations in wild chimpanzees. *Behaviour* **142**, 397–421. (doi:10.1163/1568539054012047)
 19. Clay Z, Zuberbühler K. 2009 Food-associated calling sequences in bonobos. *Anim. Behav.* **77**, 1387–1396. (doi:10.1016/j.anbehav.2009.02.016)
 20. Clay Z, Zuberbühler K. 2011 Bonobos extract meaning from call sequences. *PLoS ONE* **6**, e18786. (doi:10.1371/journal.pone.0018786)
 21. Bouchet H, Pellier A-S, Blois-Heulin C, Lemasson A. 2010 Sex differences in the vocal repertoire of adult red-capped mangabeys (*Cercocebus torquatus*): a multi-level acoustic analysis. *Am. J. Primatol.* **72**, 360–375. (doi:10.1002/ajp.20791)
 22. Candiotti A, Zuberbühler K, Lemasson A. 2012 Context-related call combinations in female Diana monkeys. *Anim. Cogn.* **15**, 327–339. (doi:10.1007/s10071-011-0456-8)
 23. Hurford JR. 2011 *The origins of grammar: language in the light of evolution II*. Oxford, UK: Oxford University Press.
 24. Suzuki TN, Zuberbühler K. 2019 Animal syntax. *Curr. Biol.* **29**, R669–R671. (doi:10.1016/j.cub.2019.05.045)
 25. Ouattara K, Lemasson A, Zuberbühler K. 2009 Campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proc. Natl Acad. Sci.* **106**, 22 026–22 031. (doi:10.1073/pnas.0908118106)
 26. Ouattara K, Lemasson A, Zuberbühler K. 2009 Campbell's monkeys use affixation to alter call meaning. *PLoS ONE* **4**, e7808. (doi:10.1371/journal.pone.0007808)
 27. Collier K, Bickel B, van Schaik CP, Manser MB, Townsend SW. 2014 Language evolution: syntax before phonology? *Proc. R. Soc. B* **281**, 20140263. (doi:10.1098/rspb.2014.0263)
 28. Coye C, Ouattara K, Zuberbühler K, Lemasson A. 2015 Suffixation influences receivers' behaviour in non-human primates. *Proc. R. Soc. B* **282**, 20150265. (doi:10.1098/rspb.2015.0265)
 29. Schlenker P *et al.* 2016 Formal monkey linguistics. *Theor. Linguist.* **42**, 1–90. (doi:10.1515/tl-2016-0001)
 30. Engesser S, Ridley AR, Townsend SW. 2016 Meaningful call combinations and compositional processing in the southern pied babbler. *Proc. Natl Acad. Sci. USA* **113**, 5976–5981. (doi:10.1073/pnas.1600970113)
 31. Suzuki TN, Wheatcroft D, Griesser M. 2016 Experimental evidence for compositional syntax in bird calls. *Nat. Commun.* **7**, 10986. (doi:10.1038/ncomms10986)
 32. Jansen DAWAM, Cant MA, Manser MB. 2012 Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. *BMC Biol.* **10**, 97. (doi:10.1186/1741-7007-10-97)
 33. Manser MB, Jansen DAWAM, Graw B, Hollén LJ, Bousquet CAH, Furrer RD, le Roux A. 2014 Vocal complexity in meerkats and other mongoose species. In *Advances in the study of behavior* (eds M Naguib, L Barrett, HJ Brockmann, S Healy, JC Mitani, TJ Roper, LW Simmons), pp. 281–310. Oxford, UK: Elsevier.
 34. Déaux EC, Allen AP, Clarke JA, Charrier I. 2016 Concatenation of 'alert' and 'identity' segments in dingoes' alarm calls. *Sci. Rep.* **6**, 30556. (doi:10.1038/srep30556)
 35. Nowak MA, Plotkin JB, Jansen VAA. 2000 The evolution of syntactic communication. *Nature* **404**, 495–498. (doi:10.1038/35006635)
 36. Rasa OAE. 1977 The Ethology and Sociology of the dwarf mongoose (*Helogale undulata rufula*). *Z. Für Tierpsychol.* **43**, 337–406. (doi:10.1111/j.1439-0310.1977.tb00487.x)
 37. Keane B, Waser PM, Creel SR, Creel NM, Elliott LF, Minchella DJ. 1994 Subordinate reproduction in dwarf mongooses. *Anim. Behav.* **47**, 65–75. (doi:10.1006/anbe.1994.1008)
 38. Rasa OAE. 1986 Coordinated vigilance in dwarf mongoose family groups: the 'watchman's song' hypothesis and the costs of guarding. *Ethology* **71**, 340–344. (doi:10.1111/j.1439-0310.1986.tb00598.x)
 39. Collier K, Radford AN, Townsend SW, Manser MB. 2017 Wild dwarf mongooses produce general alert and predator-specific alarm calls. *Behav. Ecol.* **28**, 1293–1301. (doi:10.1093/beheco/axx091)
 40. Fichtel C, Perry S, Gros-Louis J. 2005 Alarm calls of white-faced capuchin monkeys: an acoustic analysis. *Anim. Behav.* **70**, 165–176. (doi:10.1016/j.anbehav.2004.09.020)
 41. Kern JM, Radford AN. 2013 Call of duty? Variation in use of the watchman's song by sentinel dwarf mongooses, *Helogale parvula*. *Anim. Behav.* **85**, 967–975. (doi:10.1016/j.anbehav.2013.02.020)
 42. Lachlan RF. 2007 *Luscinia: a bioacoustics analysis computer program*. See luscinia.sourceforge.net.
 43. Byrt T, Bishop J, Carlin JB. 1993 Bias, prevalence and kappa. *J. Clin. Epidemiol.* **46**, 423–429. (doi:10.1016/0895-4356(93)90018-v)
 44. Sim J, Wright CC. 2005 The kappa statistic in reliability studies: use, interpretation, and sample size requirements. *Phys. Ther.* **85**, 257–268. (doi:10.1093/ptj/85.3.257)
 45. Belsley DA, Kuh E, Welsch RE. 2005 *Regression diagnostics: identifying influential data and sources of collinearity*. New York, NY: John Wiley & Sons.
 46. Mundry R, Sommer C. 2007 Discriminant function analysis with nonindependent data: consequences and an alternative. *Anim. Behav.* **74**, 965–976. (doi:10.1016/j.anbehav.2006.12.028)
 47. R Core Team. 2015 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org/>.
 48. Naimi B. 2013 usdm package. See <https://cran.r-project.org/web/packages/usdm/usdm.pdf>.
 49. Venables WN, Ripley BD. 2002 *Modern applied statistics with S*, 4th edn. New York, NY: Springer.
 50. Christensen RHB. 2015 Ordinal: regression models for ordinal data. See <https://cran.r-project.org/web/packages/ordinal/index.html>.
 51. Bates D, Meachler M, Bolker BM, Walker S. 2015 lme4: linear mixed-effects models using Eigen and S4. See <https://cran.r-project.org/web/packages/lme4/index.html>.
 52. Flash T, Hochner B. 2005 Motor primitives in vertebrates and invertebrates. *Curr. Opin. Neurobiol.* **15**, 660–666. (doi:10.1016/j.conb.2005.10.011)
 53. Lee S-Y, Song X-Y. 2004 Evaluation of the Bayesian and maximum likelihood approaches in analyzing structural equation models with small sample sizes. *Multivar. Behav. Res.* **39**, 653–686. (doi:10.1207/s15327906mbr3904_4)
 54. Haspelmath M. 2007 Coordination. In *Language typology and syntactic description* (ed. T Shopen), pp. 1–51. Cambridge, UK: Cambridge University Press.
 55. Bradbury JW, Vehrencamp SL. 1998 *Principles of animal communication*. Sunderland, MA: Sinauer Associates.