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

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Abstract

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.

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 to 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 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, *Hylobates 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 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 vocalisations (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 information about the eliciting context [40]), and can occur in ambiguous predation contexts [39], potentially suggesting that the meaning of T_3 is related to the meaning of its parts. However, an experimental demonstration that the T_3 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 T_3 alarm calls and to determine the extent to which the overall meaning of the combination is derived from its parts. First, if T_3 serves as a general alarm call, we expected to observe general anti-predator behaviours in response to its playback. Second, if T_3 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 T_3's component parts should be similar to the acoustic structures of the corresponding alarm call types; and ii) playbacks of the different parts of T_3 in isolation should reveal similar responses to the aerial and terrestrial alarm calls.

Methods

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 (>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 1–3 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].

Alarm call collection and acoustic analysis

Alarm calls for acoustic analysis were collected through 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 T_3 is structurally a combination of an aerial and a terrestrial alarm. We first visualized the calls using Praat version 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 (Table 1). We did this for each of the natural alarm call types (aerial, terrestrial and T_3) but also for the first and second halves of T_3 ($T_{3.1}$ and $T_{3.2}$), respectively resembling an aerial and a terrestrial alarm call.

Playbacks

Following on from previous work investigating the contexts in which the different dwarf mongoose alarm-call types are produced [39] (results summarised in Table 2), we aimed to clarify T_3's status as a general alarm call by considering the responses to playbacks of three natural alarm calls: aerial, terrestrial and T_3. 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 T_3 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 T_3 alarm call as a combination of aerial and terrestrial alarms, we carried out paired playbacks of three sets of stimuli: i) T_3 and artificial T_3 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 nine of T_3 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.

Statistical analysis

a) 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 (Table 1). 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 permutated 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 version 3.2.1 [47] with the packages usdm [48] and MASS [49].

b) 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 group as a random effect. When a significant result was returned, we carried out post-hoc pairwise CLMMs between the treatments (aerial vs terrestrial, aerial vs T_3, terrestrial vs 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 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 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].

Results

Acoustic analysis

The three natural alarm call types were distinguishable by the measured acoustic parameters (pDFA: $N_{calls}=105$, 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 ($N_{calls}=70$, p=0.091, percentage correctly cross-classified=68%), whereas terrestrial alarms and the second element of T_3 ($T_{3.2}$) could be discriminated ($N_{calls}=100$, p=0.026, percentage correctly cross-classified=94%).

Function of T_3 alarm calls

The strength of reaction by dwarf mongooses to playbacks of natural alarm calls depended on alarm-call type (CLMM: $\chi^2_2=6.88$, p=0.03; Figure 2). Whilst 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 ($\chi^2_1=1.27$, $p_{adj}=0.78$) and to terrestrial and T_3 alarm calls ($\chi^2_1=2.01$, $p_{adj}=0.48$). 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: $\chi^2_2=4.98$, $p=0.083$).

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 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_{3art}: 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_{3art}: $\chi^2_1=0$, p=1; aerial and $T_{3.1}$: $\chi^2_1=0$, p=1) or in sentinel behaviour (GLMM, T_3 and T_{3art}: $\chi^2_1=0.40$, 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 vs aerial alarm calls (See Electronic Supplemental Material for details).

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 generalised, way: they respond with a mix of behaviours, compared to 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 mongoose are capable of communicating related, yet subtly different information [26,30,31]. Decomposing 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 sciences. 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". Whilst 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 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.

Whilst 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 whilst 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 to 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.

Conclusions

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 phenomena. 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.

Ethical statement

Competing interests

Author contributions

Conceptualization, K.C., S.S., M.B.M., B.B., and S.W.T.; Methodology, K.C., M.B.M., A.N.R., B.B. and S.W.T; Investigation, K.C.; Formal Analysis, K.C., B.B., S.S., S.K.W. and S.W.T; Writing, K.C., A.N.R., S.S., M.B.M., B.B. and S.W.T.

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Figure 1: Spectrograms of dwarf mongoose alarm calls. 1) Aerial alarm call; 2) Terrestrial alarm call; 3) Type 3 or T_3 alarm call composed of two parts: 3.1) pulsed first segment ($T_{3.1}$) and 3.2) noisy second segment ($T_{3.2}$). Window length = 0.05 s, dynamic range = 70 dB.

Figure 2: Frequency of the different types of reaction by focal individuals to the playbacks of natural alarm calls. *: P<0.05 [39]; NS: 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_{3art}: χ^2_1=0.22, p=0.26; aerial and $T_{3.1}$: χ^2_1=3.06, p=0.08; terrestrial and $T_{3.2}$: χ^2_1=1.25, p=0.26. NS: non-significant.

Table 1: Measured acoustic parameters and their definitions. Values presented are mean ± SD. *Used for the pDFA comparing the acoustic structure of aerial, terrestrial and T_3 calls. # used to compare aerial and $T_{3.1}$ calls. ¤ used to compare terrestrial and $T_{3.2}$ calls.

Acoustic parameter	Description	Aerial	Terrestrial	T3	T3.1	T3.2
Call duration (ms) ¤	Time elapsed between the beginning and the end of the call.	374±200	598±169	912±263	370±155	498±198
Overall peak frequency (Hz)*, #, ¤	Peak frequency is the frequency of maximum amplitude within one spectrum of the spectrogram. Overall peak frequency is the frequency of maximum amplitude within the call.	6086±1007	4284±1066	5326±789	5660±861	3891±524
Mean peak frequency (Hz)	Mean of all peak frequencies within the call.	5837±870	3631±527	4315±496	5483±749	3835±400
Maximum peak frequency (Hz)	Peak frequency of highest peak frequency within the call.	7641±1020	5891±1098	7146±1007	7116±1002	4651±722
Minimum peak frequency (Hz)	Peak frequency of the lowest peak frequency within the call.	3526±721	2456±619	3095±481	3567±630	3132±429
Peak frequency start (Hz) *, ¤	Peak frequency at the beginning of the call	4203±704	4141±1094	3850±542	4226±719	3717±530

Peak frequency end (Hz) ¤	Peak frequency at the end of the call	6122±850	3419±522	4399±582	5903±914	3527±394
Mean fundamental frequency (Hz)	Fundamental frequency is the lowest frequency of a periodic waveform.	5838±857	3591±619	4313±495	5495±729	3826±401
Maximum fundamental frequency (Hz)	Fundamental frequency of highest frequency within the call.	7586±993	5830±1136	7113±985	7071±997	4563±733
Minimum fundamental frequency (Hz)	Fundamental frequency of lowest frequency within the call.	3604±749	2434±868	3173±524	3643±632	3238±433
Mean change in peak frequency (Hz)	Mean change in peak frequency over time.	0.63±0.06	0.50±0.01	0.53±0.02	0.61±0.04	0.50±0.01
Change in peak frequency end (Hz) ¤	Change in peak frequency at the end of the call	0.50±0.10	0.51±0.03	0.53±0.02	0.59±0.05	0.49±0.02
Mean change in fundamental frequency (Hz)	Mean change in fundamental frequency over time.	0.63±0.06	0.50±0.01	0.53±0.02	0.61±0.04	0.50±0.01
Minimum change in fundamental frequency (Hz) *	Smallest change in fundamental frequency	0.50±0.11	0.40±0.08	0.46±0.03	0.52±0.07	0.46±0.03
Change in fundamental frequency start (Hz)	Change in the fundamental frequency at the start of the call	0.71±0.04	0.53±0.08	0.55±0.03	0.61±0.05	0.49±0.02

Change in fundamental frequency end (Hz) *, #	Change in the fundamental frequency at the end of the call	0.57±0.10	0.52±0.05	0.52±0.02	0.59±0.05	0.49±0.02
Maximum absolute fundamental frequency change (Hz) #	Highest absolute change in fundamental frequency	0.22±0.06	0.14±0.09	0.19±0.06	0.18±0.06	0.05±0.03
Minimum absolute fundamental frequency change (Hz) ¤	Smallest absolute change in fundamental frequency	0.45±0.06	0.0002±0.0008	$9.90e^{-5}±9.5e^{-5}$	0.05±0.04	0.0002±0.001
Absolute change in fundamental frequency start (Hz) *, ¤	Absolute change in fundamental frequency at the start of the call	0.17±0.06	0.06±0.05	0.06±0.03	0.12±0.04	0.03±0.03
Absolute change in fundamental frequency end (Hz) ¤	Absolute change in fundamental frequency at the end of the call	0.11±0.06	0.03±0.05	0.04±0.02	0.10±0.05	0.01±0.01
Mean Wiener entropy	A measure of noisiness: Ratio of the geometric mean to the arithmetic mean of the power spectrum.	212±3	208±7	215±2	214±2	215±2
Maximum Wiener entropy #, ¤	Highest measure of Wiener entropy	222±1.35	220±2.73	223±0.89	222±1.17	221±1.53

Start Wiener entropy *, #, ¤	Wiener entropy at the beginning of the call	213±3.08	213±6.27	214±3.61	213±3.15	216±3.40
Mean frequency bandwidth (Hz)	Frequency difference between the first and final maximum intensity in the signal.	778±330	1266±688	582±257	621±265	558±213
Maximum frequency bandwidth *, #	Highest frequency bandwidth	2517±851	2400±933	2320±722	2190±729	1279±382
Minimum frequency bandwidth *, #, ¤	Lowest frequency bandwidth	8±60	44±164	0±0	0±0	0±0
End frequency bandwidth *, #, ¤	Frequency bandwidth at the end of the call	250±206	369±588	164±202	228±193	102±208
Number of elements	Number of continuous traces on the spectrogram that compose the call.	4.9±2.4	1.6±0.8	5.9±1.9	4.9±1.9	1.0±0.1
Within syllable gap (ms) *, #, ¤	Total duration of silence between the elements of a call.	202±118	24±38	244±101	197±94	0

Table 2: 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**