

# Element repetition rates encode functionally distinct information in pied babbler ‘clucks’ and ‘purrs’

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**Abstract** Human language is a recombinant system that achieves its productivity through the combination of a limited set of sounds. Research investigating the evolutionary origin of this generative capacity has generally focused on the capacity of non-human animals to combine different types of discrete sounds to encode new meaning, with less emphasis on meaning-differentiating mechanisms achieved through potentially simpler temporal modifications within a sequence of repeated sounds. Here we show that pied babblers (*Turdoides bicolor*) generate two functionally distinct vocalisations composed of the same sound type, which can only be distinguished by the number of

repeated elements. Specifically, babblers produce extended ‘purrs’ composed of, on average, around 17 element repetitions when drawing young offspring to a food source and truncated ‘clucks’ composed of a fixed number of 2–3 elements when collectively mediating imminent changes in foraging site. We propose that meaning-differentiating temporal structuring might be a much more widespread combinatorial mechanism than currently recognised and is likely of particular value for species with limited vocal repertoires in order to increase their communicative output.

**Keywords** Element repetition · Temporal structure · Animal communication · Combinatoriality · Language evolution · *Turdoides bicolor*

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## Introduction

Animals employ various mechanisms to communicate and transfer information (Marler 1977). Combinatorial operations, whereby animals combine discrete sounds together into larger meaningful structures, have received particular recent interest in part due to their similarities to the combinatorial layers, phonology and syntax, in language (Collier et al. 2014). Animals, including birds and mammals, further encode information through modifying the temporal arrangement of repeated elements within a sequence (Kershenbaum et al. 2014). Such temporal structuring has been shown to convey information on motivation or threat-levels experienced by an individual during aggressive or predatory encounters (DuBois et al. 2009; Rek and Osiejuk 2012; Kershenbaum et al. 2014; Wheatcroft 2015; though see also Antunes et al. 2011). Yellow-bellied marmots (*Marmota flaviventris*), for example, decrease the inter-call interval between alarm

calls with increasing proximity to a threat (Blumstein 2007). Accordingly, temporal modifications generally constitute a graded system correlating with a signaller's arousal level and typically take the form of changes in the number/rate of repeated elements or in inter-element intervals (DuBois et al. 2009; Rek and Osiejuk 2012; Kershenbaum et al. 2014; Wheatcroft 2015). However, work on the alarm calls of colobus monkeys (*Colobus guereza* and *polykomos*) and the social vocalisations of Mexican free-tailed bats (*Tadarida brasiliensis*) have shown temporal changes can also encode both discrete predator-specific (i.e. aerial versus terrestrial predator) and behaviour-specific information (Bohn et al. 2008; Schel et al. 2009, 2010). These results suggest that, besides transferring graded information, temporal modifications can encode more discrete, categorical information; a feature more commonly associated with the combination of different sound types (Zuberbühler 2015).

Here we investigate whether similar temporally induced meaning-differentiation also exists outside of mammals, in the discrete vocal system of the pied babbler (*Turdoides bicolor*). Babblers are social passerines, which live in stable, territorial groups of up to 15 individuals (Radford and Ridley 2006). They are weak flyers and spend most of their time on the ground searching for invertebrate prey by probing the substrate and excavating the soil using their bill (Radford and Ridley 2006). Given their limited visual contact with conspecifics, babblers rely on vocal signals to keep track of changes in their social and ecological environment (Radford and Ridley 2007; Hollén et al. 2008; Radford and Ridley 2008; Bell et al. 2009; Engesser et al. 2016). During the day, group members forage closely together (~2 m) and move cohesively between foraging sites (Thompson 2012). Babblers typically forage below and around vegetation as well as in open areas (Ridley et al. 2014). Foraging sites are therefore abundant and distributed unevenly throughout a group's territory (average territory size 0.75 km<sup>2</sup> (Humphries 2012)). Overnight, group members roost huddled together in the same tree with an average of 53 roost trees (range 34–76) being used across a group's territory (Raihani and Ridley 2007b; Golabek 2010).

During nestling provisioning and when attracting fledglings towards food sources, babblers produce soft 'purr' vocalisations, composed of an extended number of up to ~40 repetitions of the same acoustic element. They are generally produced by a single individual providing a food item or foraging at a sharable food patch and are directed to dependent or inexperienced offspring resulting in only the offspring approaching the caller, with adults not responding (Radford and Ridley 2006; Raihani and Ridley 2007a, 2008). Purrs are typically emitted until the caller is approached by the recipient, resulting in purrs of varying length. Preliminary work indicated that babblers also

produce truncated variants of purrs with a considerably reduced, finite number of 2–3 elements, named here as 'clucks' (Fig. 1). Initial observations indicated that, in contrast to purrs, clucks are jointly produced by multiple group members (usually over several minutes) before groups cohesively move to the first foraging site in the morning, or generally before switching between foraging sites. Crucially, the number of clucking individuals seems to impact a group's decision to move between foraging sites, with the number of callers appearing to correlate with the distance a group eventually moves to a new site. Accordingly, clucks may represent an egalitarian decision-making mechanism, linking individual preferences to group travel processes.

In order to investigate the temporal features of clucks and purrs, we used acoustic analyses to examine whether the same element is used within and across the two call types, and whether their temporal distinctiveness is determined by the number of repeated elements. To support previous work indicating purrs function to recruit offspring to a food source, and to verify the functional specificity of clucks, behavioural observations were conducted where the context in which both calls were produced, and responses of receivers were recorded. Specifically, in line with earlier findings, we expected purrs to only be produced by a single individual and lead to a single recipient approaching the caller with the remaining group members not moving, while for clucks we expected the number of individuals calling prior to movement to impact the subsequent distance moved by the whole group.

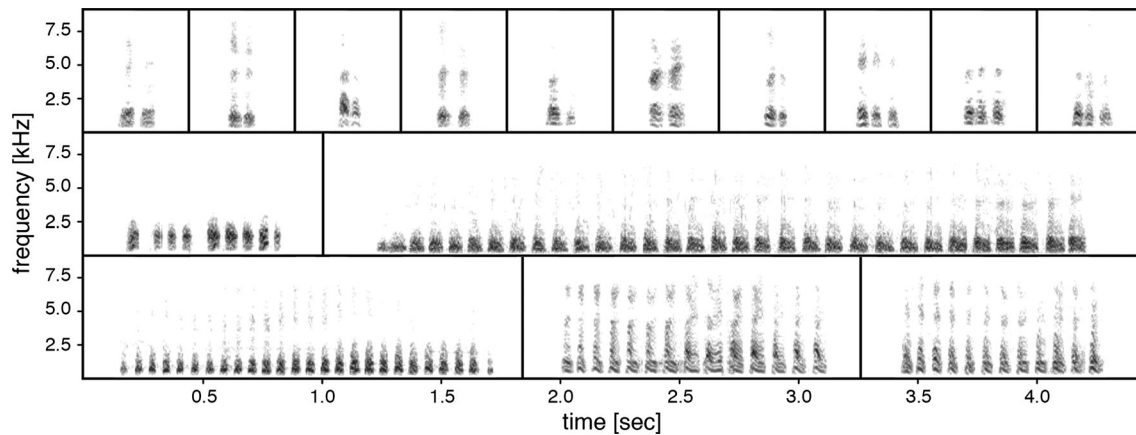
## Methods

### Study site and species

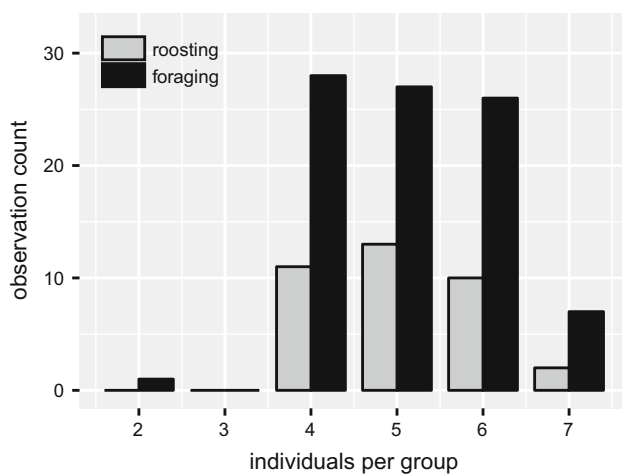
The study was conducted on a population of free-living, habituated pied babblers at the Kuruman River Reserve, South Africa (26°58'S, 21°49'E; for details on the habitat, see Raihani and Ridley 2007a and Hollén et al. 2011). All birds in the study population are individually recognisable through the combination of three coloured rings and one numbered metal leg ring (Radford and Ridley 2008). During the data collection period, mean group size ranged between 2 and 7 individuals (mean ± SD = 5 ± 1, Fig. 2).

### Acoustic analyses

Data for acoustic analyses were collected between January and May 2013, 2014 and 2015. To verify the acoustic similarity among cluck and purr elements, we acoustically analysed at least one purr and one cluck vocalisation of a given individual in 16 different groups and recorded the



**Fig. 1** Spectrograms of clucks (*top row*) and purrs (*lower two rows*) of different individuals. Spectrograms were drawn in a Hamming window (fast Fourier transformation, length 512, 75% overlap)



**Fig. 2** Group size distribution during observational data collection on clucks. Roosting context (*grey*): group size range 4–7, mean  $\pm$  SD =  $5 \pm 0.9$ . Foraging context (*black*): group size range 2–7, mean  $\pm$  SD =  $5 \pm 1.0$

number of element repetitions constituting the call. For each call, the first element and a further randomly chosen element [determined using a random number generator (R-Core-Team 2014)] were acoustically analysed resulting in the following 4 element categories: 1st cluck element,  $n$ th cluck element, 1st purr element,  $n$ th purr element. Only vocalisations of one individual per group were chosen to avoid including calls of genetically related individuals (i.e. group members) and to ensure assumptions regarding independence of the data were upheld (Sharp et al. 2005). While audio recordings were conducted during the breeding seasons of 3 consecutive years, in order to avoid age-related variations (Humphries et al. 2016), we only considered cluck-purr pairs of an individual recorded in the same season. This, in addition to the low amplitude nature of the vocalisations, making high signal-to-noise ratio calls difficult to obtain, resulted in only 7 individuals with more

than one example per specific element category (see supplementary dataset).

All vocalisations were recorded using a Rode NTG-2 directional microphone coupled with a Rode Blimp Suspension Windshield (Rode microphones) and a Roland R-26 portable recorder (Roland Corporation; sampling frequency 48 kHz, 24-bit accuracy). During vocal recordings, the identity of the caller was noted. The extracted elements for the acoustic analyses were analysed using Praat (version 5.3.55). Since the elements comprising clucks and purrs are often characterised by atonal, noisy structures, where a clear fundamental frequency (F0) cannot be resolved, we only extracted non-F0-related spectral parameters including: element duration, frequency value at the maximum amplitude, time-percentage to maximum amplitude, amplitude variation, as well as the frequency values at the first, second and third energy quartiles.

Statistical analyses were performed in R (version 3.2.3) (R-Core-Team 2014). Model assumptions were inspected visually, and potential multicollinearity among predictor variables was controlled by removing variables with variance inflation factors (VIF)  $>10$  (Filzmoser et al. 2005; Fox and Weisberg 2011; Frank 2011). Due to a high VIF, the frequency measurements at the second energy quartile were excluded from the acoustic analyses. To verify the acoustic similarity among the elements within, as well as across clucks and purrs, a permuted discriminant function analysis (pDFA) with 1000 permutations was conducted (script provided by R. Mundry). The pDFA tested the classification probability of element to element category, while at the same time controlling for repeated measurements from the same individuals (Venables and Ripley 2002; Mundry and Sommer 2007).

Lastly, a two-tailed, paired Wilcoxon signed-rank test was conducted to investigate whether clucks and purrs differed in the number of element repetitions (Venables

and Ripley 2002). For instances where more than one cluck or purr call were obtained for one individual, the average was used.

## Natural calling observations

### Purrs

To support previous research on purrs functioning to recruit offspring to a food source, observations on purring events in 11 groups from 2015 were analysed. We recorded the number of callers during a purring event, the context of calling, the recipient's behaviour and its status (fledgling, yearling, adult), as well as whether a group movement ensued.

### Clucks

To investigate whether and how clucks influence movement between foraging sites, we collected two sets of observational data on 14 babbler groups in 2015. The first set included natural observations conducted at dawn at a group's roost, before the birds started to forage. We recorded the number of individuals producing clucks (including cases when no clucks were produced) and the distance the group subsequently moved to their first foraging site. Additionally, we documented a group's overall clucking duration to rule out the possibility that longer calling durations might result in more calling individuals, in addition to the group's size to investigate whether the distance travelled is mediated by the absolute or relative number of clucking individuals. Foraging sites were classified as locations where at least half of the group collected to forage. Distances were measured using a handheld GPS data logger (eTrex 10, Garmin).

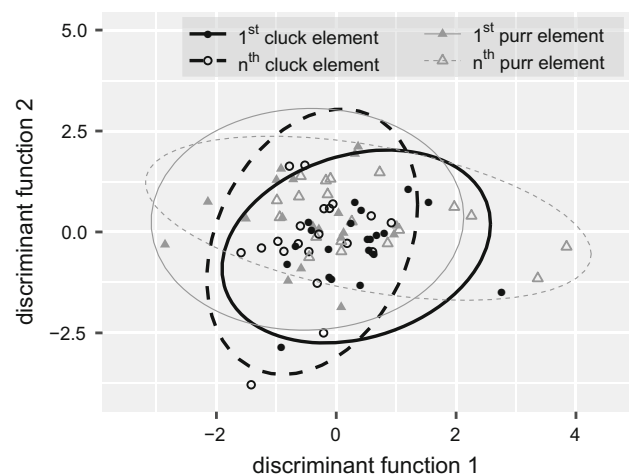
The second set of observations were conducted later in the morning or in the early evening when groups were continuously foraging. We collected the same behavioural data as for the first set of observations, but only considered events when clucks were produced. While data on foraging site-switches which have not been preceded by clucking would have been feasible to collect, similar data on non-clucking events that did not result in a site-switch cannot be determined and thus could not be collected. Such non-clucking/non-movement events could only be detected in the roosting context due to clear change in the group's behaviour from roosting to initiating foraging. Finally, since group movements are often lead by the group's dominant male (Engesser et al. in prep), we additionally investigated whether the dominant male's call contribution influenced the distance travelled by the group. Because individual ring combinations enabling dominant male identification were not visible at the roost tree, these data could only be collected during daylight hours.

Linear mixed models were fitted in R and model selection based on Akaike's information criterion corrected for small sample sizes (AICc) were applied (Barto'n 2014; Bates et al. 2015). Specifically, we investigated the effect of the predictor variables on the distance a group moved (1) from the roost to the first foraging site and (2) between two foraging sites. Response variables were transformed when necessary. Since multiple observations per group were used, group identity was fitted as random term. The best model was selected based on the Akaike's information criterion corrected for small sample sizes (AICc), with a threshold difference ( $\Delta$ AIC) of one (Burnham and Anderson 2002). Parametric bootstrapping was applied to assess the significance of the fixed effects (pbkrtest using 10,000 iterations which provides *PBtest* as test statistic (Halekoh and Højsgaard 2014)).

## Results

### Acoustic analyses

The results of the pDFA revealed that cluck and purr elements could not be discriminated based on their spectral features (correctly cross-classified elements = 5.37 (=35.80%), expected number correctly cross-classified elements = 4.29 (=28.62%),  $P = 0.228$ ,  $N = 79$  elements of 16 individuals; Fig. 3). However, both call types could clearly be distinguished by the number of element repetitions (paired, two-tailed Wilcoxon signed-rank test:  $V = 136$ ,  $P < 0.001$ ,  $N = 16$ ). Specifically, clucks were composed of 2–3 repeated elements (mean  $\pm$  SD =  $2.3 \pm 0.4$ ), and purrs of 5–38 (mean  $\pm$  SD =  $17.4 \pm 9.7$ ).



**Fig. 3** DFA output on cluck and purr elements. Circles represent clusters assuming a multivariate normal distribution with a 95% confidence level.  $N$  1st cluck element = 21,  $N$  nth cluck element = 20,  $N$  1st purr element = 19,  $N$  nth purr element = 19

## Natural calling observations

### Purrs

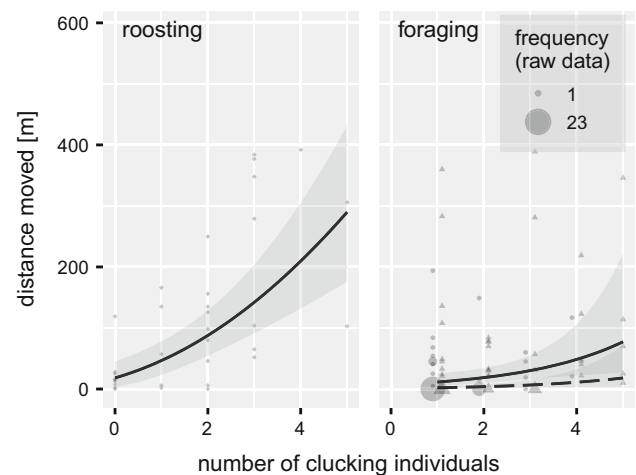
From a total of 40 purring events from 20 individuals of 11 groups, purrs were only ever produced by one adult individual. In 39 occasions (97.5%), the recipient approached the stationary caller, while the remaining group members did not approach or move. We only observed one instance where the caller moved 30 m to a new foraging site while purring and was followed by its group members (2.5%). Of the 39 cases where the birds approached the caller, the recipient had either been recruited to a sharable food source (17 cases, 44%), was provided with a prey item (20 cases, 51%) or was recruited without providing food (2 instances, 5%). Moreover, of these 39 recruitment events, in 32 cases fledglings were approaching (82%, in 3 cases a pair of fledglings and in the remaining a single fledgling), in 1 case, a yearling (3%), and in 6 cases, adults (15%, in 1 case a pair of adults in the remaining a single adult).

### Clucks

Behavioural observations on clucking events revealed groups travelled a greater distance to the first foraging site in the morning, and between foraging sites during the day when more individuals were clucking prior to movement (roosting:  $PB_{test} = 21.61$ ,  $P < 0.001$ ,  $N = 36$  observations from 13 groups; foraging:  $PB_{test} = 6.79$ ,  $P = 0.01$ ,  $N = 89$  observations from 11 groups; Fig. 4). Moreover, in the foraging context the distance a group moved was lower when the dominant male did not participate in clucking ( $PB_{test} = 10.33$ ,  $P < 0.01$ ,  $N = 89$  observations on 11 groups; Fig. 4). Group size and the overall clucking duration of a group did not affect subsequent movements in either of the two models (Table 1).

## Discussion

Acoustic analyses confirmed that babbler clucks and purrs are composed of the same acoustic elements, with only the number of element repetitions distinguishing the two calls. Our behavioural observations suggest, however, that, although composed of identical elements, clucks and purrs are produced in different contexts. In line with previous work, our findings on purrs demonstrate that purrs serve to primarily attract dependent or inexperienced offspring towards a food source, with one individual purring and the recipient approaching, while the rest of the group remains unresponsive (Radford and Ridley 2006; Raihani and Ridley 2007a, 2008). When clucks were produced at the roost tree in the morning, babblers flew further to a



**Fig. 4** Distance a group moved to a foraging site as a function of the number of clucking individuals, in the morning when leaving the roost and during foraging. Shaded areas illustrate the 95% CI. Dots show the raw data with the size corresponding to the frequency of occurrences. Within the foraging context specifically, the dominant male's contribution to clucking was further investigated. Solid line and triangular dots represent dominant male clucking events; dashed line and circular dots represent events when the dominant male did not cluck. Roosting context: conditional  $R^2 = 0.64$ ,  $N = 36$ ; foraging context: conditional  $R^2 = 0.25$ ,  $N = 89$

foraging site when more group members were clucking. In contrast, when no babblers were clucking, groups generally started to forage in the immediate vicinity of the roost tree. This result was supported by observations conducted during foraging, showing when more individuals were clucking prior to switching foraging sites, the distance moved between the two sites was larger. Besides the number of clucking individuals, the dominant male's clucking behaviour also appeared to impact a group's decision to move, with groups moving shorter distances if the dominant male did not participate in clucking. Since individual clucking contribution at dawn when groups left their night roost could not be determined, this effect could only be investigated specifically in the foraging context. Nevertheless, the result supports similar findings in babblers indicating dominant males play a central role in leading the group through their territory (Engesser et al. in prep).

Our work suggests that clucks might function to mediate imminent movements. However, the factors that drive their production need further investigation. Clucks are potentially produced to initiate movement when individual foraging patches are depleted, or when the location of the roost tree is sub-optimal as a suitable foraging site. A similar mechanism is implemented by the socially foraging meerkat (*Suricata suricatta*), where 'move' calls produced by multiple individuals may indicate a depletion of the foraging site and induce group movement (Bousquet et al. 2011). In line with this, babbler clucks might function as a vocal tool to gather information on individual preferences



**Table 1** Summary of linear mixed models

Predictor variables	AICc	df
Roosting context		
Full model: clucking duration + group size * $\sum$ clucking individuals	218.8	7
Intercept model	232.0	3
Best model: $\sum$ clucking individuals	212.9	4
Foraging context		
Full model: clucking duration + group size * $\sum$ clucking individuals + dom. male clucking	376.6	8
Intercept model	393.2	3
Best model: $\sum$ clucking individuals + dom. male clucking	371.8	5

Full models included all fixed and random effects, intercept models included only the random effect, and best models included only the significant fixed effects based on AICc selection as well as the random effect

AICc Akaike information criterion corrected for small sample sizes, *df* degrees of freedom

or assessments of the group's current location (Bousquet et al. 2011). Specifically, cluck production might reflect the caller's independent assessment of the (decreasing) quality of the current foraging area. Therefore, an increasing number of clucking individuals might indicate a greater proportion of the group is motivated to switch foraging sites, with groups subsequently moving further when more individuals have signalled the motivation to switch sites. The more the individuals exhibiting a particular preference, the greater the magnitude of the particular behaviour. However, the magnitude might also be context specific, diminishing or changing under certain circumstances (Sueur and Deneubourg 2011). During foraging post-roosting, for example, babblers might have stronger tendencies to stay, or indeed switch sites, since individual foraging patches and needs might vary more in comparison with directly after roosting, where all group members are equally motivated to feed. Alternatively, decreased visibility at dawn (compared to in daylight) might require a tighter vocal coordination, constraining behavioural flexibility. This may explain the less pronounced relationship between clucking individuals and the distance moved during foraging compared to after roosting. Lastly, the absence of an interaction effect between group size and the number of clucking individuals on the distance a group subsequently moved suggests that babblers attend to the absolute rather than to the relative number of clucking individuals when mediating movements, though the small variation in observed group sizes might have obscured the detection of a potential effect (Fig. 2). Further systematic studies are now needed in order to determine how the production of clucks translates into the distance a group moves. Considering the effect the dominant male appears to have on his group's movement behaviour, investigating the contribution of individuals of different social or age categories to clucking events, as well as determining who

is initiating the clucking and who subsequently takes the lead to a new site, is one important avenue of investigation. Furthermore, playback experiments, where the number and indeed identity of individuals involved in clucking events can be manipulated, will be important to experimentally verify our observational findings. Central to this work is the demonstration that clucks and purrs convey sender-specific information to receivers, and receivers discriminate this, though preliminary acoustic analyses are indeed suggestive of this with clucks and purrs differing systematically between individuals (see supplementary material).

While future work is needed to help clarify the mechanisms underlying cluck-mediated group movements in pied babblers, our key advance is that we provide evidence suggesting babblers modify element repetition rates to generate two functionally distinct signals: the 'truncated' clucks and the 'extended' purrs. Recent work has begun to address non-human animal vocal combinatorial abilities, but the main focus has been on the ability to combine different sound types to encode new, discrete information (Marler 1977; Collier et al. 2014; Zuberbühler 2015). Temporal mechanisms have largely been neglected, potentially because they do not present an obvious analogue to language's combinatorial layers. In line with previous work in both primates and bats (Bohn et al. 2008; Schel et al. 2009, 2010), we show that, rather than encoding quantitative information related to arousal levels, modifications of temporal patterns can additionally transfer qualitatively different information and we provide evidence for this capacity in an avian system. Although such temporal modifications seem relatively simple and are likely less constrained by the vocal apparatus when compared with changes in frequency-related parameters (Janik and Slater 1997), we propose that they may still play an important role in increasing a species' vocal repertoire, and similarly to combinations of discrete sounds, temporal

operations might be a widespread mechanism applied by various animals to encode diverse information sets.

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**Author contributions** SE, ARR and SWT designed research; SE performed research and analysed data; SE and SWT wrote paper.

**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics statement** Permission was provided by the ethical committee for animal research of the University of Cape Town and the Northern Cape Conservation Authority, South Africa.

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