



## Food availability affects strength of seasonal territorial behaviour in a cooperatively breeding bird

K. A. Golabek<sup>a,\*</sup>, A. R. Ridley<sup>b</sup>, A. N. Radford<sup>a</sup>

<sup>a</sup>School of Biological Sciences, University of Bristol, Bristol, U.K.

<sup>b</sup>Department of Science and Technology/National Research Foundation Centre of Excellence, Percy FitzPatrick Institute, University of Cape Town, Cape Town, South Africa

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Seasonal patterns in territorial behaviour are common in many species, and are often attributed to the adaptive benefits of increased defence or the provision of information to potential competitors or mates during the breeding season. However, because defence behaviour is likely to be costly in terms of time and energy, an alternative possibility is that decreases in the nonbreeding season are a consequence of reduced food availability. We studied territoriality in the pied babbler, *Turdoides bicolor*, a cooperatively breeding bird species that defends permanent territories. Groups interacted with rivals less and responded less strongly to an experimentally simulated intrusion of neighbours in nonbreeding periods compared to the breeding season. Foraging efficiency and biomass intake were significantly lower in the nonbreeding season, which resulted in birds being significantly lighter at this time of year. Finally, a feeding experiment in the nonbreeding season showed that groups given supplementary food significantly increased their response to a simulated territorial intrusion. These results indicate that the reduction in territorial behaviour during the nonbreeding season may be attributed, at least in part, to a reduction in food availability. We suggest that future studies on seasonal variation in territorial behaviour, especially those investigating species in which two or more individuals combine their defence, should take this potential constraint into account.

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Individuals, pairs and groups of animals in a wide variety of taxa are territorial, defending a fixed area of land for exclusive access to critical resources such as food, mates and breeding sites (Kaufmann 1983). Defence can involve a range of different activities, beginning with suspension of other behaviours and movement towards intruders following their detection. The majority of disputes between territorial rivals tend to be resolved via signalling, including visual and vocal displays and scent marking (Gosling 1982; McGregor 1993; Bradbury & Vehrenkamp 1998), and can, in the case of social species, involve the combination of several individuals in a coordinated display (e.g. Reyer & Schimdl 1988; Radford 2005; Hall 2009). On some occasions, however, territorial disputes can escalate to physical fights, although this tends to be a last resort (Maynard Smith & Parker 1976).

Many species only defend territories for part of the year, such as the breeding season (e.g. Krebs et al. 1978; Vinuela et al. 1995). The most obvious reason for this seasonality is that the relevant resources (e.g. nesting or mating sites) are only required during that

particular period. However, because defence results in lost foraging time (Erlinge 1968; Kruuk 1972; Gorman & Mills 1984) and displays are costly to produce (Taigen & Wells 1985; Vehrencamp et al. 1989; Eberhardt 1994), territorial behaviour may be restricted to certain times of the year. Annual breeding cycles tend to coincide with favourable conditions (see Zann et al. 1995), meaning that food is most abundant and energy for territorial defence is more readily available at such times. Moreover, several studies have demonstrated that individual investment in territorial signalling (e.g. song output) can be increased by the experimental provision of supplementary food (Cuthill & MacDonald 1990; Lucas et al. 1999; Berg et al. 2005). It seems clear, therefore, that energetic constraints are likely to explain at least some of the variation in defence behaviour exhibited by species that hold seasonal territories.

In some other species, permanent territories are defended all year, either because breeding occurs throughout the year (e.g. Waterman 1998) or, more commonly, because particular areas contain the necessary breeding sites and food resources for both reproductive success and year-round survival. Such all-purpose territories are frequent among cooperatively breeding species (e.g. Woodroffe & Lawton 1990; Radford & du Plessis 2004a; Jordan et al. 2007, 2010). Seasonal patterns in defence behaviour can also occur among permanent territory holders. Scent marking, for

\* Correspondence and present address: K. A. Golabek, Botswana Predator Conservation Trust, Private Bag 13, Maun, Botswana.

E-mail address: [kagolabek@gmail.com](mailto:kagolabek@gmail.com) (K. A. Golabek).

instance, often increases during the breeding period (e.g. Woodroffe & Lawton 1990; Gese & Ruff 1997; Jordan et al. 2007), while vocal signalling can similarly vary during the year (Reyer & Schimdl 1988; Wingfield & Lewis 1993; Topp & Mennill 2008).

Breeding-season peaks in the defence activities of year-round territory holders are commonly argued to be of adaptive benefit. This is the period when it is most important to defend mates (Jordan et al. 2007), and also to indicate reproductive condition (Gese & Ruff 1997) and to signal to possible partners (Eriksson & Wallin 1986); territorial displays can serve multiple functions, acting not just as signals of ownership but also of sex, status as a mated pair and reproductive state (reviewed in Hall 2009). However, seasonal differences in the behaviour of permanent territory holders might also be the consequence of variation in food availability, since food abundance is typically lower in the nonbreeding season (Beatley 1974; Cumming & Bernard 1997). This possibility has received little experimental consideration, especially in group-territorial species; such species have generally been the subject of far less empirical attention than individual territory holders (see Topp & Mennill 2008).

Pied babblers, *Turdoides bicolor*, are cooperatively breeding birds that live in stable, permanent groups and hold year-round territories in semiarid seasonal Kalahari scrubland. They only breed during part of the year, the timing of which greatly depends on rainfall (Ridley & Raihani 2007), but actively defend their territory throughout the year (Golabek 2010). Groups initiate defence behaviour when a rival group is detected within their territory or near the shared boundary; rivals are often detected from their raucous choruses, which are given all year and involve the combined vocalizations of several individuals. On hearing chorusing, group members suspend foraging, move towards the intruders and then engage in protracted visual and vocal displays (Golabek 2010). These intergroup interactions rarely escalate into physical fights (Raihani 2008).

In this study, we first compared the occurrence of natural intergroup interactions and the response to simulated territorial intrusions in the breeding and nonbreeding season. We then investigated whether the decreased investment in territorial defence activities during the nonbreeding season is related to patterns in food availability and thus potential energetic constraints. Specifically, we examined whether during the nonbreeding season there is less rainfall and lower foraging success, and whether individual birds are lighter in weight; rainfall is strongly linked to the onset of desert phenological events such as the emergence of insects (Beatley 1974; Cumming & Bernard 1997), and invertebrates are the primary food source for babblers (Ridley & Child 2009). Finally, we conducted a feeding experiment to enhance the energy potentially available to pied babblers in the nonbreeding season, and assessed whether this results in an increased investment in territorial defence behaviour.

## METHODS

### *Study Site and Population*

Data were collected between 2004 and 2009 from a colour-ringed pied babbler population on the Kuruman River Reserve, Northern Cape Province, South Africa (26°58'S, 21°49'E). Study groups were visited approximately three times a week, were habituated to human presence at a distance of <3 m, and were trained to stand on a flat-top balance scale for the reward of a mealworm. The study site consists of semiarid Kalahari scrubland with a mean  $\pm$  SE annual rainfall of 285  $\pm$  45 mm (2003–2009). The climate is warm and wet in the summer (September–April) and cold and dry in the winter (May–August). For a more detailed description of climate and vegetation see Raihani & Ridley (2007).

Pied babblers live in groups consisting of a dominant breeding pair, which produce ca. 95% of the offspring (Nelson-Flower et al. 2011), and a mixed number of adult subordinate helpers and immature offspring (<12 months); group size in this study period was 2–11 adults (mean  $\pm$  SD = 6.1  $\pm$  2.6). Members of the dominant breeding pair are clearly identifiable from agonistic interactions towards other group members, copulation behaviour, extended incubation periods and greater effort put into nest building (Ridley & Raihani 2008; Nelson-Flower 2010). Birds were sexed using DNA (for methodological details, see Griffiths et al. 1998) from blood collected when ringing (for trapping details, see Radford & Ridley 2008).

Group members move around their permanent territory as a tight unit throughout the day, foraging together and responding cohesively to threats from rivals. Intergroup interactions, stimulated by visual or vocal cues of another group, involve alternating choruses and parallel posturing displays in which birds extend their necks, flap their wings and fan their tails. Such displays can last for up to 35 min at a time (Golabek 2010) and are therefore likely to be costly, in terms of both performance energy and lost time for other vital activities. Intergroup interactions always involve neighbours and tend to occur on shared boundaries (Golabek 2010), suggesting that at least part of their function is in territorial defence.

### *Territorial Behaviour*

#### *Natural observations*

During observation sessions of known duration in the morning (starting at first light) and evening (starting approximately 2 h before sunset), from December 2006 to October 2007, we recorded the occurrence of all intergroup interactions and the time of year (breeding or nonbreeding season). The breeding season was defined as the period when groups in the study population were building successful nests (those in which eggs were subsequently laid), egg laying, incubating or feeding nestlings; the start date was the first day a successful nest was built and the end date was the last day on which any of these breeding behaviours was performed. We used dates from the study population as a whole because the breeding behaviour of neighbouring groups may influence the occurrence of territorial encounters and behaviour.

To investigate whether intergroup interaction occurrence in an observation session is affected by season, we ran a series of generalized linear mixed models (GLMMs) with a binomial error distribution (0 = no intergroup interaction, 1 = intergroup interaction occurred) and a logit link function. We included session duration as a fixed term and group identity as a random term to account for multiple data from the same groups, and analysed sessions that were greater than 15 min in duration and in which the group was observed continuously from start to finish ( $N = 52$  sessions in the breeding season, 35 sessions in the nonbreeding season). We used Akaike's second-order information criterion (AICc) for small sample sizes to select the most plausible model from a set of credible options. All terms, including breeding season, data session duration and their two-way interaction, were removed from a saturated model. Terms were retained only if their removal inflated AICc by more than two (Burnham & Anderson 2004), as lower AICc values correspond with better relative support for each model (Akaike 1974). To validate that there was no improvement to the minimal model, all original terms were returned to the model one by one, creating our model set together with the basic model, containing only the intercept and the random term. Akaike weights were then calculated to show relative importance (Akaike 1974) between these final models.

#### *Simulated intrusion*

To investigate experimentally the variation in territorial behaviour between breeding and nonbreeding seasons, we

simulated the intrusion of neighbouring groups using playbacks of chorus recordings. Chorus recordings were made during natural observation sessions using a Sennheiser ME66 directional microphone (frequency response 40 Hz–20 kHz  $\pm$  2.5 dB) with a K6 power module (2004 Sennheiser), and digitally transformed through a Marantz PMD660 solid-state recorder (frequency response 20 Hz–16 kHz,  $-0.5$  dB tolerance; D&M Holdings Inc., [www.dm-holdings.com](http://www.dm-holdings.com)). All recordings were made within 50 m of the group, typically closer, and only high-quality calls (low-noise-to-high-sound ratio) were used for playback.

Recorded choruses were edited to a standard amplitude and duration (16 s, mean of natural choruses; see Golabek 2010), using Edit Pro 2.00 (Syntrillium Software Corporation, Scottsdale, AZ, U.S.A.). Playbacks were performed as a group foraged within its territory, at least 1 h after any natural intergroup contact. Playback was conducted from a joined pair of Creative TravelSound 200 speakers (frequency response 150 Hz–20 kHz; Creative Technology Ltd., Singapore), within 15 m of the foraging group, hidden in the branches of the nearest tree. This reflects a natural situation because chorusing babblers tend to sit close to one another in the same tree. Playback levels were normalized using AVISOFT-SAS Lab Pro 4.52 (R. Specht, Berlin, Germany), and played back using a palm TX (Palm Inc., Sunnyvale, CA, U.S.A.) at a volume to mimic the sounds of a group calling in the distance (ca. 100 m away).

We recorded three measures: (1) latency to the first response (time from the start of the audio playback to the first movement); (2) distance moved by the group (assessed from a GPS track (Garmin etrex, Garmin International Inc., Olathe, KS, U.S.A.) taken at the centre of the group from the start of playback until the group returned to foraging); and (3) total response duration (time from first movement to return to foraging). A response constituted any interruption in foraging behaviour including vigilance, short movement to a perch or actual flight. Groups were considered to be responding until all individuals, with the exception of a sentinel (an individual perched at least 1 m above ground and scanning the surrounding for predators; Ridley & Raihani 2007; Hollén et al. 2008), had begun foraging again. Each group received the playback of two different neighbouring groups (mean  $\pm$  SE =  $16 \pm 4.3$  days apart, range 1–43) in a given season (breeding or nonbreeding), and the response of each group was averaged for each season. Our sample included the average response of six groups in the breeding season (April–June 2008) and eight groups in the nonbreeding season (July–August 2007); originally the same groups were targeted for a paired comparison, but two groups disappeared between seasons.

#### *Energetic Constraints*

##### *Rainfall*

Rainwater was collected at the field site in a standard rain gauge, which was checked each day at dawn. We compared average daily rate (total rainfall/no. of days) for seven breeding and subsequent nonbreeding seasons, from August 2003 to August 2009.

##### *Foraging success*

Focal foraging watches, involving 5 min of continuous monitoring, were conducted on adult group members from March to June 2004, October to December 2004 and May to June 2005. Watches were conducted opportunistically, leaving at least 1 h between those on the same individual to enhance the independence of sampling (mean  $\pm$  SE =  $48 \pm 3$  watches per adult, range 11–93,  $N = 48$  individuals). Watches were abandoned if there was an alarm call, or the focal individual flew off or became engaged in activities other than foraging (e.g. became a sentinel or started preening). During a watch, we recorded onto a Dictaphone each: (1) foraging attempt (probe or peck); (2) foraging success; (3) prey

size; and (4) occurrence of nonforaging behaviour (e.g. vigilance, movement to a new patch, preening). Prey items were classified as follows: tiny = barely visible; small = visible in the bill; medium = hanging out the side of the bill; large = size of the bill; items larger than this were scored as multiples of 'large'. Fifty prey items representative of each size category were weighed and prey sizes were subsequently converted to biomass values as follows: tiny = 0.02 g; small = 0.11 g; medium = 0.45 g; large = 0.84 g (Radford & Ridley 2006). These values were used for the calculation of both biomass capture rate (food caught per minute of observation time) and foraging efficiency (biomass caught per minute of foraging time). To investigate seasonal variation in foraging success, we used data from individuals for which at least three focal watches were conducted in both the breeding and the nonbreeding season ( $N = 22$ ).

##### *Weight*

Groups were joined at dawn, before they left the roost tree, and individuals were weighed as soon as possible once they came down to the ground. To investigate seasonal variation, we compared the average morning weights of individuals in consecutive breeding and nonbreeding seasons. To remove any potential bias from increasing age, breeding season preceded nonbreeding season for half of the analysed individuals and for the other half this order was reversed. We used weight data from 32 adults, none of them egg-bound females, for which more than three weights were available for each season (mean  $\pm$  SD number of weights =  $40 \pm 29$  in the breeding season;  $12 \pm 6$  in the nonbreeding season).

##### *Food Supplementation Experiment*

To test whether the reduced investment in territorial defence behaviour in the nonbreeding season (see Results) is a consequence of reduced food availability, we conducted an experiment that combined food supplementation and chorus playbacks to simulate the intrusion of a neighbouring group. Six different resident groups received two 'feeding' treatments in August 2009: in one, all group members were fed hardboiled egg yolk until they were satiated (assessed as the point at which they would eat no more and moved to cover to allopreen); in the other, no egg yolk was provided (as a control).

Groups were joined off roost at dawn to ensure no previous intergroup interactions and no foraging had occurred that day, and the experiment was conducted straight after the morning weighing session (see above). Feeding treatments to the same group were performed a mean  $\pm$  SD of  $4.7 \pm 2.6$  days apart and the order of feeding treatments was counterbalanced across groups. Immediately after the feeding treatment, the group received a playback of the chorus of a neighbouring group; the same playback was used in both trials to the same group. The playback protocol followed that in the experiment above, with the speaker positioned so as to project the chorus from the direction of that particular neighbour. As in the previous simulated intrusion, we recorded latency to the first response, distance moved by the group and total response duration. We also recorded any vocal response given, measuring the latency to chorus (time from the start of the playback to the first chorus call made) and the chorus duration (time from the start to the end of the first chorus).

## RESULTS

### *Territorial Behaviour*

The likelihood of an intergroup interaction being recorded in an observation session was significantly influenced by the interaction

**Table 1**

GLMMs with binomial error distribution and logit link function investigating the factors that predict the likelihood of an intergroup interaction occurring in an observation session ( $N = 87$ )

| Model                     | Description             | Estimate            | AICc  | k | $\Delta i$ | $w_i$ |
|---------------------------|-------------------------|---------------------|-------|---|------------|-------|
| 1                         | Basic                   | –                   | 102.5 | 2 | 8.2        | 0.011 |
|                           | Session duration        | 0.0044              |       |   |            |       |
|                           | +Season                 | Nonbreeding –5.8969 | 94.3  | 5 | 0          | 0.713 |
|                           |                         | Breeding 0.0000     |       |   |            |       |
|                           | +Session*Season         | Nonbreeding 0.0445  |       |   |            |       |
|                           | Breeding 0.0000         |                     |       |   |            |       |
| <b>Alternative models</b> |                         |                     |       |   |            |       |
| 2                         | Session duration        |                     | 100.5 | 3 | 6.2        | 0.032 |
| 3                         | Season                  |                     | 98.2  | 3 | 3.9        | 0.097 |
| 4                         | Session duration+Season |                     | 97.4  | 4 | 3.1        | 0.147 |

Group identity was included as a random term ( $N = 16$ ). Model 1 best fits the data with the fewest explanatory parameters and lowest AICc.  $k$  = parameters,  $\Delta i = AICc_i - AICc_{min}$ ,  $w_i$  = Akaike weights.

between session duration and season (Table 1): intergroup interactions were less likely in the nonbreeding season (mean  $\pm$  SE =  $0.17 \pm 0.07/h$ ), when session duration had little impact, compared to the breeding season ( $2.82 \pm 1.19/h$ ), when there was a positive effect of time spent with a group (Fig. 1).

In response to the simulated intrusion of a neighbour, there was no significant difference in latency of first response between breeding and nonbreeding seasons (two-sample  $t$  test:  $t_{12} = 0.20$ ,  $N = 13$ ,  $P = 0.847$ ). However, groups moved significantly less far ( $t_{12} = 3.85$ ,  $N = 13$ ,  $P = 0.002$ ) and responded for significantly less time ( $t_{12} = 2.96$ ,  $N = 13$ ,  $P = 0.012$ ) during the nonbreeding than the breeding season (Fig. 2).

#### Energetic Constraints

Average daily rainfall was significantly lower in the nonbreeding than the breeding season (Wilcoxon signed-ranks test:  $Z = 2.36$ ,  $N = 7$ ,  $P = 0.018$ ; Fig. 3a). This is likely to result in a lower abundance of invertebrate food and, indeed, babblers had a significantly lower foraging efficiency (that is, they caught less food per unit time spent foraging) in the nonbreeding season (paired  $t$  test:  $t_{21} = 5.91$ ,  $N = 22$ ,  $P < 0.001$ ; Fig. 3b). This resulted in foragers having a significantly lower biomass intake rate (that is, amount of food consumed per unit time) in the nonbreeding season ( $t_{21} = 6.40$ ,  $N = 22$ ,  $P < 0.001$ ; Fig. 3c) which, in turn, is likely to have contributed to the significantly lower weight of individuals in the nonbreeding than the breeding season ( $t_{31} = 3.91$ ,  $N = 32$ ,  $P < 0.001$ ; Fig. 3d).

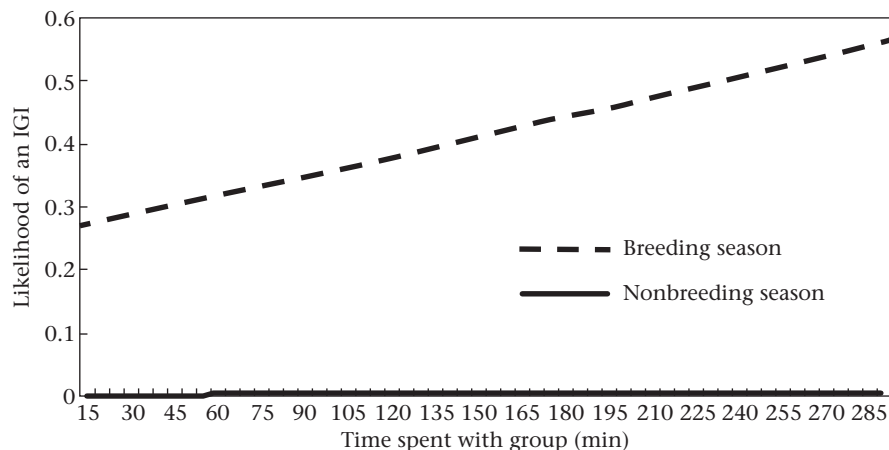
#### Food Supplementation Experiment

In response to the simulated intrusion of a neighbouring group in the nonbreeding season, food-supplemented groups moved significantly further (Wilcoxon signed-ranks test:  $Z = 2.20$ ,  $N = 6$ ,  $P = 0.027$ ), were significantly quicker to respond ( $Z = 2.02$ ,  $N = 6$ ,  $P = 0.043$ ), and showed a strong tendency to respond for longer ( $Z = 1.78$ ,  $N = 6$ ,  $P = 0.075$ ) compared to unfed groups (Fig. 4). However, vocal responses did not differ significantly between treatments, with fed groups calling no sooner after playbacks ( $Z = 0.94$ ,  $N = 6$ ,  $P = 0.345$ ) nor for longer ( $Z = 0.73$ ,  $N = 6$ ,  $P = 0.463$ ) than unfed groups.

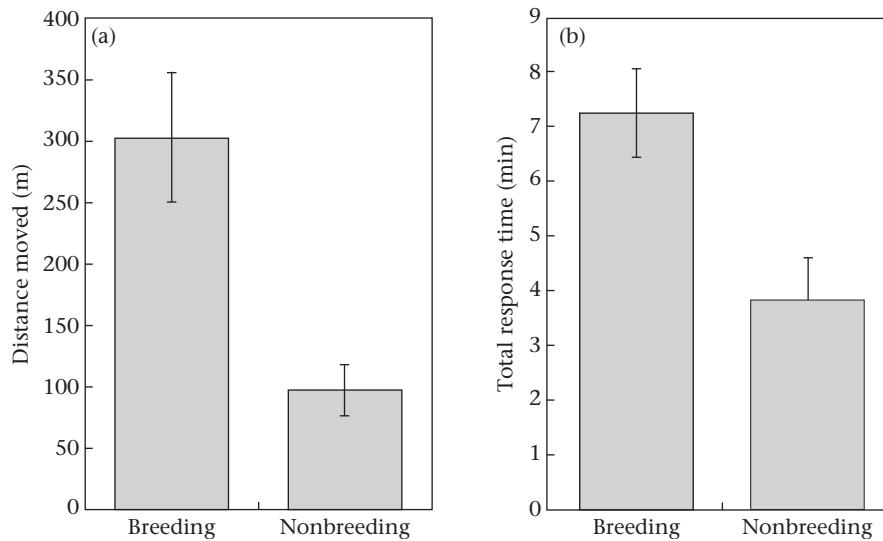
#### DISCUSSION

Previous work, focusing on species in which individuals hold seasonal territories, has demonstrated that defence behaviour can be affected by energetic constraints (e.g. Cuthill & MacDonald 1990; Lucas et al. 1999; Berg et al. 2005). Our results indicate that seasonal variation in year-round territorial behaviour may be similarly affected by food availability, and provide the first experimental evidence that group-territorial species can be influenced in this way. Pied babbler intergroup interactions occurred less frequently and groups responded less intensively to simulated intrusions of neighbouring groups in the nonbreeding season than the breeding season. In the nonbreeding season, individuals were lighter, potentially because of their reduced foraging success; rainfall is lower at this time of year, negatively affecting the emergence of invertebrate species (see Beatley 1974; Cumming & Bernard 1997). The importance of this decreased prey availability was shown by our supplementary feeding experiment: when additional food was provided in the nonbreeding season, investment in territorial behaviour increased.

As with other cooperatively breeding species (see Radford & du Plessis 2004b), pied babblers can spend considerable amounts of time on territory defence: individual intergroup interactions can last for up to 35 min (Golabek 2010), which does not include time spent flying around locating intruders. This reduces time available for other vital activities, such as foraging (Erlinge 1968; Kruuk 1972; Gorman & Mills 1984). Moreover, the choruses and visual posturing displays that form an integral part of intergroup interactions are likely to be energetically costly to produce (see Taigen & Wells 1985; Vehrencamp et al. 1989; Eberhardt 1994). Such a major investment in territorial defence may only be feasible at times of year when food is readily available and when energetic demands of other activities can be easily met.



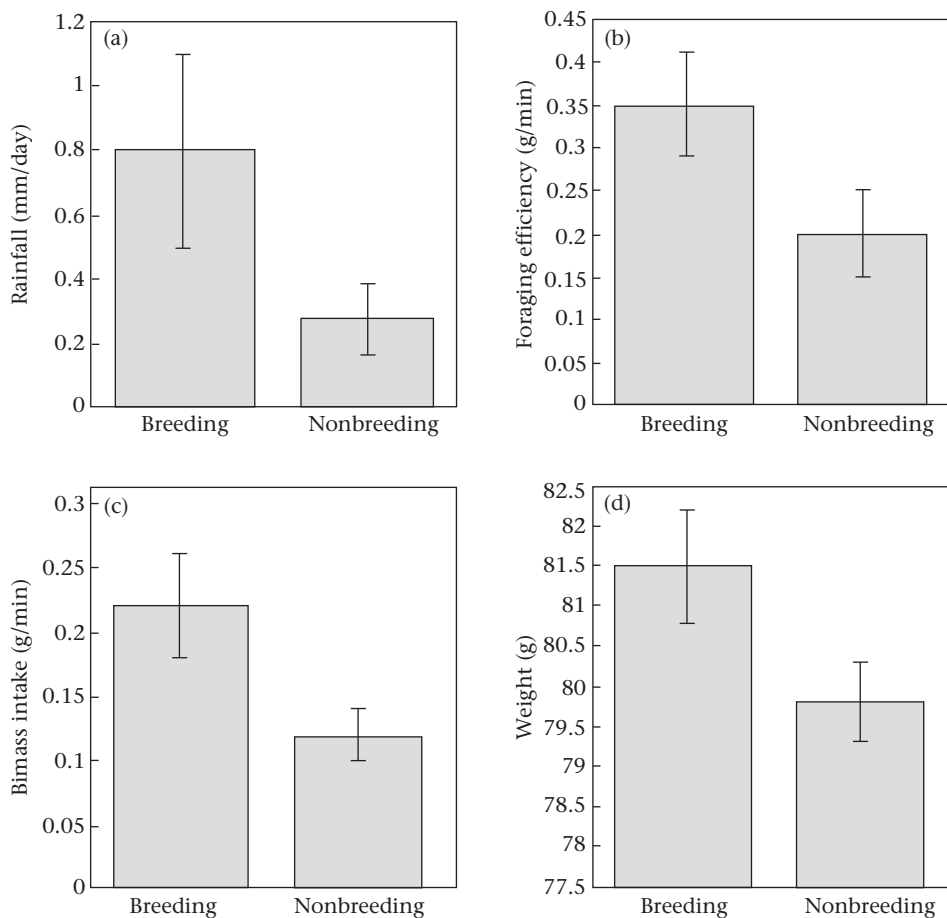
**Figure 1.** Predicted effect of season and session duration on intergroup interaction (IGI) occurrence, from model 1, Table 1.



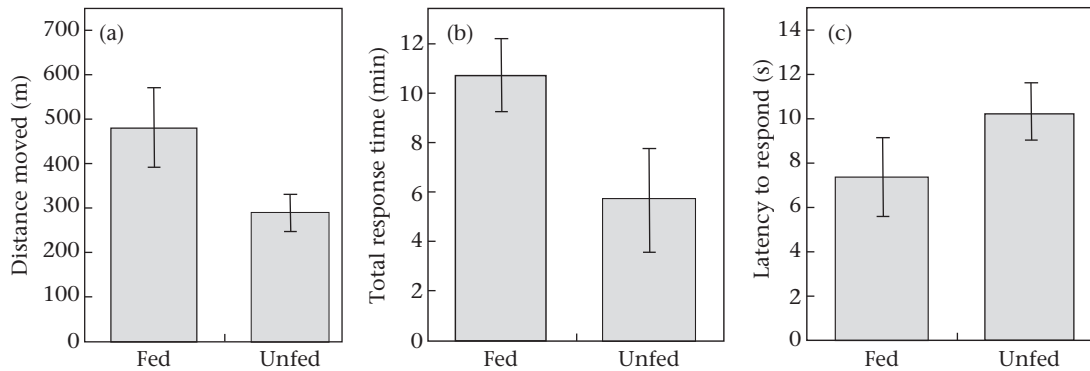
**Figure 2.** Mean  $\pm$  SE (a) distance moved and (b) total time spent responding by pied babbler groups following the playback of a neighbouring group chorus in different seasons.

While pied babblers engage in territorial behaviour all year round, the reduction in the nonbreeding season may potentially lead to the weakening of territory boundaries. More data are needed to investigate whether there are seasonal changes in territory size in the study population, but complete breakdown of territory boundaries may be prevented because pied babbler

choruses are loud: they are audible to the human ear at a minimum of 500 m (personal observation). As pied babbler territories average 775 m<sup>2</sup> in size (K. A. Golabek, unpublished data), choruses are likely to be heard by neighbours over much of their territory, and it is plausible that they alone act as a sufficient signal of presence to potential rivals. Visual interactions during intergroup interactions



**Figure 3.** Mean  $\pm$  SE (a) rainfall, (b) foraging efficiency, (c) biomass intake rate and (d) individual weight in different seasons.



**Figure 4.** Mean  $\pm$  SE (a) distance moved (b) total time spent responding and (c) latency to respond by pied babbler groups following the playback of a neighbouring group chorus in the nonbreeding season, having received either supplementary feeding (fed) or no additional food (unfed).

may provide additional benefits, however, such as clarifying group size and motivation or aiding in dispersal decisions (see Henzi et al. 1998; Hale et al. 2003).

While the results of our supplementary feeding experiment provided a strong indication that general territorial behaviour (movement to locate and engage potential intruders) might be influenced by energetic constraints, the situation with respect to vocal displays (i.e. choruses) was less clear cut. There was no significant difference in latency to chorus or duration of first chorus between the two feeding treatments, which could be because choruses are not as energetically costly as suspected. However, the lack of any discernable difference may more likely be the consequence of the measures recorded and the stimulus provided. We collected data on only the first chorus and natural intergroup interactions can involve multiple alternating choruses; the full impact of energetic constraints on vocal signalling may be apparent only when taking full-length contests into account. To stimulate such contests, though, would potentially entail the use of both visual models and interactive playbacks, neither of which were employed here. Further work is clearly needed to explore how vocal territorial behaviour is affected by energetic constraints in this species, especially given the link between food intake and vocal output found in several studies of individual territory holders (e.g. Cuthill & MacDonald 1990; Lucas et al. 1999; Berg et al. 2005).

A considerable body of previous work has detailed the adaptive reasons why territorial behaviour in general, and signalling in particular, might be most prevalent during the breeding season (see Hyman 2005; Erne & Amrhein 2008). For example, this is when there is the greatest need to defend breeding sites and resources for the raising of young, and thus the territory is of greatest reproductive value (Armstrong 1956; Jacot et al. 2009). Moreover, displays are likely to serve additional functions during the breeding season, such as the prevention of mate and paternity loss (Olendorf et al. 2004; Akcay et al. 2009), the attraction of potential new mates (Catchpole 1987; McComb 1991) and the strengthening of pair bonds to ensure the retention of current mates (Wickler 1980; Smith 1994); although group members signal together and there may be some joint functions, individual payoffs may differ (see Radford 2003). The prevalence of suitable nesting sites for pied babblers and the apparent lack of extragroup fertilization in the study population (Nelson-Flower et al. 2011) suggest some of these reasons may not apply to pied babblers, although further work is needed to confirm this. For now, the current study emphasises that in addition to adaptive reasons, seasonal variation in territorial behaviour can also be influenced by food availability and energetic constraints. We suggest that this possibility should be considered more regularly in studies of territorial signalling and defence,

especially when it involves the combined behaviour of pairs or groups.

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### References

- Akaike, H. 1974. New look at statistical-model identification. *IEEE Transactions on Automatic Control*, **AC19**, 716–723.
- Armstrong, E. A. 1956. Territory in the wren *Troglodytes troglodytes*. *Ibis*, **98**, 430–437.
- Akcay, C., Wood, W. E., Searcy, W. A., Templeton, C. N., Campbell, S. E. & Beecher, M. D. 2009. Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals. *Animal Behaviour*, **78**, 97–102.
- Beatty, J. C. 1974. Phenological events and their environmental triggers in Mojave desert ecosystems. *Ecology*, **55**, 856–863.
- Berg, M. L., Beintema, N. H., Welbergen, J. A. & Komdeur, J. 2005. Singing as a handicap: the effects of food availability and weather on song output in the Australian reed warbler *Acrocephalus australis*. *Journal of Avian Biology*, **36**, 102–109.
- Bradbury, J. W. & Vehrenkamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Burnham, K. P. & Anderson, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research*, **33**, 261–304.
- Catchpole, C. K. 1987. Bird song, sexual selection and female choice. *Trends in Ecology & Evolution*, **2**, 94–97.
- Cumming, G. S. & Bernard, R. T. F. 1997. Rainfall, food abundance and timing of parturition in African bats. *Oecologia*, **111**, 309–317.
- Cuthill, I. C. & MacDonald, W. A. 1990. Experimental manipulation of the dawn and dusk chorus in the blackbird *Turdus merula*. *Behavioral Ecology and Sociobiology*, **26**, 209–216.
- Eberhardt, L. S. 1994. Oxygen-consumption during singing by male Carolina wrens (*Thryothorus ludovicianus*). *Auk*, **111**, 124–130.
- Eriksson, D. & Wallin, L. 1986. Male bird song attracts females: a field experiment. *Behavioral Ecology and Sociobiology*, **19**, 297–299.
- Erlinge, S. 1968. Territoriality of the otter (*Lutra lutra*). *Oikos*, **19**, 81–98.
- Erne, N. & Amrhein, V. 2008. Long-term influence of simulated territorial intrusions on dawn and dusk singing in the winter wren: spring versus autumn. *Journal of Ornithology*, **149**, 479–486.
- Gese, E. M. & Ruff, R. L. 1997. Scent-marking by coyotes, *Canis latrans*: the influence of social and ecological factors. *Animal Behaviour*, **54**, 1155–1166.

- Golabek, K. A.** 2010. Vocal communication and the facilitation of social behaviour in the southern pied babbler (*Turdoides bicolor*). Ph.D. thesis, University of Bristol.
- Gorman, M. L. & Mills, M. G. L.** 1984. Scent marking strategies in hyaenas (Mammalia). *Journal of Zoology*, **202**, 535–547.
- Gosling, L. M.** 1982. A reassessment of the function of scent marking in territories. *Ethology*, **60**, 89–118.
- Griffiths, R., Double, M. C., Orr, K. & Dawson, R. J. G.** 1998. A DNA test to sex most birds. *Molecular Ecology*, **7**, 1071–1075.
- Hale, A. M., Williams, D. A. & Rabenold, K. N.** 2003. Territoriality and neighbour assessment in brown jays (*Cyanocorax morio*) in Costa Rica. *Auk*, **120**, 446–456.
- Hall, M. L.** 2009. A review of vocal duetting in birds. *Advances in the Study of Behavior*, **40**, 67–121.
- Henzi, S. P., Lycett, J. E. & Weingrill, T.** 1998. Mate guarding and risk assessment by male mountain baboons during inter-troop encounters. *Animal Behaviour*, **55**, 1421–1428.
- Hollén, L. L., Bell, M. B. V. & Radford, A. N.** 2008. Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology*, **18**, 576–579.
- Hyman, J.** 2005. Seasonal variation in response to neighbours and strangers by a territorial songbird. *Ethology*, **111**, 951–961.
- Jacot, A., Valcu, M., van Oers, K. & Kempenaers, B.** 2009. Experimental nest site limitation affects reproductive strategies and parental investment in a hole-nesting passerine. *Animal Behaviour*, **77**, 1075–1083.
- Jordan, N. R., Cherry, M. I. & Manser, M. B.** 2007. Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour*, **73**, 613–622.
- Jordan, N. R., Mwanguhya, F., Kyabulima, S., Ruedi, P. & Cant, M.** 2010. Scent marking within and between groups of wild banded mongooses. *Journal of Zoology*, **280**, 72–83.
- Kaufmann, J. H.** 1983. On the definitions and functions of dominance and territoriality. *Biological Reviews of the Cambridge Philosophical Society*, **58**, 1–20.
- Krebs, J., Ashcroft, R. & Webber, M.** 1978. Song repertoires and territory defence in great tits. *Nature*, **271**, 539–542.
- Kruuk, H.** 1972. *The Spotted Hyena; a Study of Predation and Social Behavior*. Chicago: University of Chicago Press.
- Lucas, J. R., Schraeder, A. & Jackson, C.** 1999. Carolina chickadee (Aves, Paridae, *Poecile carolinensis*) vocalisation rates: effects of body mass and food availability under aviary conditions. *Ethology*, **105**, 503–520.
- McComb, K.** 1991. Female choice for high roaring rates in red deer, *Cervus elaphus*. *Animal Behaviour*, **41**, 79–88.
- McGregor, P. K.** 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society B*, **340**, 237–244.
- Maynard Smith, J. & Parker, G. A.** 1976. Logic of asymmetric contest. *Animal Behaviour*, **24**, 159–175.
- Nelson-Flower, M. J.** 2010. Kinship and its consequences in the cooperatively breeding southern pied babbler *Turdoides bicolor*. Ph.D. thesis, University of Cape Town.
- Nelson-Flower, M. J., Hockey, P. A. R., O’Ryan, C., Raihani, N. J., du Plessis, M. A. & Ridley, A. R.** 2011. Monogamous dominant pairs monopolize reproduction in the cooperatively breeding pied babbler. *Behavioral Ecology*, **22**, 559–565.
- Olendorf, R., Getty, T., Scribner, K. & Robinson, S. K.** 2004. Male red-winged blackbirds distrust unreliable and sexually attractive neighbours. *Proceedings of the Royal Society B*, **271**, 1033–1038.
- Radford, A. N.** 2003. Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. *Animal Behaviour*, **66**, 1035–1044.
- Radford, A. N.** 2005. Group-specific vocal signatures and neighbour-stranger discrimination in the cooperatively breeding green woodhoopoe. *Animal Behaviour*, **70**, 1227–1234.
- Radford, A. N. & du Plessis, M. A.** 2004a. Green woodhoopoe *Phoeniculus purpureus* territories remain stable despite group-size fluctuations. *Journal of Avian Biology*, **35**, 262–268.
- Radford, A. N. & du Plessis, M. A.** 2004b. Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. *Animal Behaviour*, **68**, 803–810.
- Radford, A. N. & Ridley, A. R.** 2006. Recruitment calling: a novel form of extended parental care in an altricial species. *Current Biology*, **16**, 1700–1704.
- Radford, A. N. & Ridley, A. R.** 2008. Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal Behaviour*, **75**, 519–527.
- Raihani, N. J.** 2008. Cooperation and conflict in pied babblers. Ph.D. thesis, University of Cambridge.
- Raihani, N. J. & Ridley, A. R.** 2007. Adult vocalizations during provisioning: offspring response and postfledging benefits in wild pied babblers. *Animal Behaviour*, **74**, 1303–1309.
- Reyer, H. U. & Schmidl, D.** 1988. Helpers have little to laugh about: group-structure and vocalization in the laughing kookaburra *Dacelo-novaeguineae*. *Emu*, **88**, 150–160.
- Ridley, A. R. & Child, M. F.** 2009. Specific targeting of host individuals by a kleptoparasitic bird. *Behavioral Ecology and Sociobiology*, **63**, 1119–1126.
- Ridley, A. R. & Raihani, N. J.** 2007. Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology*, **18**, 324–330.
- Ridley, A. R. & Raihani, N. J.** 2008. Task partitioning increases reproductive output in a cooperative bird. *Behavioral Ecology*, **19**, 1136–1142.
- Smith, W. J.** 1994. Animal duets: forcing a mate to be attentive. *Journal of Theoretical Biology*, **166**, 221–223.
- Taigen, T. L. & Wells, K. D.** 1985. Energetics of vocalization by an anuran amphibian (*Hyla versicolor*). *Journal of Comparative Physiology B: Biochemical Systemic and Environmental Physiology*, **155**, 163–170.
- Topp, S. M. & Mennill, D. J.** 2008. Seasonal variation in the duetting behaviour of rufous-and-white wrens (*Thryothorus rufalbus*). *Behavioral Ecology and Sociobiology*, **62**, 1107–1117.
- Vehrencamp, S. L., Bradbury, J. W. & Gibson, R. M.** 1989. The energetic cost of display in male sage grouse. *Animal Behaviour*, **38**, 885–896.
- Vinuela, J., Amat, J. A. & Ferrer, M.** 1995. Nest defence of nesting chinstrap penguins (*Pygoscelis antarctica*) against intruders. *Ethology*, **99**, 323–331.
- Waterman, J. M.** 1998. Mating tactics of male Cape ground squirrels, *Xerus inauris*: consequences of year-round breeding. *Animal Behaviour*, **56**, 459–466.
- Wickler, W.** 1980. Vocal duetting and the pair bond. 1. Coyness and partner commitment: a hypothesis. *Journal of Comparative Ethology*, **52**, 201–209.
- Wingfield, J. C. & Lewis, D. M.** 1993. Hormonal and behavioural responses to simulated territorial intrusion in the cooperatively breeding white-browed sparrow weaver, *Plocepasser mahali*. *Animal Behaviour*, **45**, 1–11.
- Woodroffe, G. L. & Lawton, J. H.** 1990. Patterns in the production of latrines by water voles (*Arvicola terrestris*) and their use as indexes of abundance in population surveys. *Journal of Zoology*, **220**, 439–445.
- Zann, R. A., Morton, S. R., Jones, K. R. & Burley, N. T.** 1995. The timing of breeding by zebra finches in relation to rainfall in central Australia. *Emu*, **95**, 208–222.