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

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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.

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

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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 ± SE annual rainfall of 285 ± 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 ± SD = 6.1 ± 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