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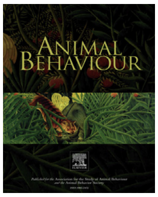

Plastic territoriality in group-living chestnut-crowned babblers: roles of resource value, holding potential and predation risk

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The factors selecting for territoriality and their relative importance are poorly resolved. Theoretical models predict that territoriality will be selected when resources of intermediate abundance are distributed variably and predictably in time and space, but can be selected against if the resource-holding potential of individuals is low or the risk of predation is high. Here we used a model averaging approach in a mixed modelling framework to analyse 5 years of observational and experimental data collected on group responses to actual and perceived intruders in the cooperatively breeding chestnut-crowned babbler, *Pomatostomus ruficeps*, in order to provide a rare test of the relative importance of resource value, resource-holding potential and predation risk in territorial behaviour. We found that babblers were highly plastic in their responses to actual and simulated intruders: on average, approaches occurred on 55% of occasions, and aggression ensued in 55% of approaches (observational and experimental results combined). Whether or not babbler groups approached, and if so were aggressive towards, actual or simulated intrusions was explained by time of day, location, group sizes, predator encounter rate and habitat characteristics, but not by reproductive status. Consideration of each of these effects regarding the three hypotheses above suggested comparable roles of group competitive advantage and predation risk on approach probability, whereas ensuing aggression was mostly explained by correlates of resource value. Our study provides compelling evidence to suggest that the risk of predation can affect the incidence of territorial and agonistic behaviour between social groups of animals by moderating the effects of resource value and group competitiveness, and might partly explain the high plasticity in group responses to intrusions.

Territoriality has defining effects on population phenotype and structure, but underlying selection pressures remain contentious (Brown, 1969; Clutton-Brock, Green, Hiraiwa-Hasegawa, & Albon, 1988; Gordon, 1997; Newton, 1992; Packer et al., 2005). Early theory proposed that the incidence of territoriality can be understood in economic terms, with individuals being territorial when the payoffs of defending an exclusive area exceed the sum of costs involved (Brown, 1964; Davies, 1980; Davies & Houston, 1981; Kodric-Brown & Brown, 1978). Classic studies of territorial behaviour in wintering golden-winged sunbirds, *Drepanorhynchus reichenowi* (Gill & Wolf, 1975) and pied wagtails, *Motacilla alba* (Davies, 1976) are testament to the fruits of this approach. Nevertheless, for year-round residents with contiguous territories in which the benefits and costs of territoriality can be varied (Adams, 2001; Lima, 1984; Maher & Lott, 2000), identifying the salient correlates of territorial behaviour and integrating them into a unifying economic currency becomes increasingly challenging, and risks misinterpretation of the relative importance of constituent parameters (Maher & Lott, 2000).

The most commonly reported associates of territorial behaviour are spatiotemporal aspects of resource distribution (Maher & Lott, 2000). Chief among these is a common positive association between the spatiotemporal predictability of resources (particularly food) and the incidence of territorial behaviour (Maher & Lott,

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2000). By contrast, the relationships between territoriality and either resource abundance or its distribution appear to be more variable. For example, in the two studies outlined above, Gill and Wolf (1975) and Davies (1976) reported a positive and negative relationship, respectively, between food abundance and territoriality. Similarly, while Davies (1976) reported a positive relationship between food clumping and territoriality, Krebs (1974) found a negative relationship in the great blue heron, *Ardea herodias*. One possible explanation for these apparently inconsistent results is that the relationship between resource value and food abundance/distribution is generally an inverted ‘U-shape’ (Grant, 1993; Maher & Lott, 2000), with evidence reported for the left-hand or right-hand sections of the distribution, but seldom both (Maher & Lott, 2000; Toobaie & Grant, 2013). Nevertheless, this does not easily explain why other studies have failed to detect any relationship between food availability and territoriality (Armstrong, 1992; Hofer & East, 1993), unless variation in food availability is unusually limiting. One possibility is that food abundance/distribution can be poorly correlated with resource value because its effects are mediated, modified or swamped by other factors (Stamps, 1994).

For example, given that territorial contests are likely to be physiologically and physically costly (Briffa & Sneddon, 2007), differences in resource-holding potential between ‘resident’ and ‘intruder’ are likely to have a significant bearing on territorial behaviour (Hammerstein, 1981; Parker, 1974; Tobias, 1997). For species living in invariant group sizes (e.g. individuals or pairs) differences in resource-holding potential will be correlated with differences in body size or condition (Jennings, Gammell, Carlin, & Hayden, 2004; Lindström, 1992), while in social species that live in group territories, group size asymmetries are likely to have additional or overriding effects on fighting ability (Clutton-Brock, 2002; Radford & du Plessis, 2004). Additionally, the threat of predation might modify the benefits of territoriality and enforce tolerance of intruding conspecifics (Jakobsson, Brick, & Kullberg, 1995) because territorial disputes inevitably lead to reduced vigilance and increased visibility to predators (Kim, Wood, Grant, & Brown, 2011; Lima & Dill, 1990). Nevertheless, no study to our knowledge has simultaneously tested the relative roles of resource value, resource-holding potential and predation risk in predicting territorial behaviour.

A powerful way of addressing these shortcomings is to analyse observational and experimental data within a mixed modelling framework which permits an estimation of effects within and between models. These methods should be particularly fruitful when conducted within a species characterized by plasticity in territoriality, since methodological and phylogenetic biases are removed (Maher & Lott, 2000). The aim of our study was to use the approaches described above to test the relative importance of resource value, resource-holding potential and predation risk hypotheses for explaining territorial behaviour in the chestnut-crowned babbler, *Pomatostomus ruficeps*, a 50 g insectivorous, obligate cooperative breeder from inland regions of southeastern Australia (Russell, Portelli, Russell, & Barclay, 2010). That our study was conducted in a cooperative breeder, in which offspring typically delay dispersal from their natal territory, adds further importance because territoriality is surprisingly poorly understood in such systems (Baglione et al. 2005; Furrer, Kyabulima, Willems, Cant, & Manser, 2011; Golabek, Ridley, & Radford, 2012), but is hypothesized to be integral to the benefits offspring derive from waiting for an opportunity to breed in high-quality habitat (Emlen, 1982; Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992). Indeed, neglecting intergroup competitive/territorial dynamics in cooperative societies might hinder our understanding of variation in social organization and optimal group sizes in such systems (Cockburn, 1998).

We used up to 5 years of detailed observational and experimental data to investigate the factors associated with the probability that groups would: (1) approach those groups they encountered during foraging; (2) fight with those they approached; (3) approach simulated intrusions achieved through playback experiments; and (4) within the latter, show evidence of escalation into a territorial confrontation. We used a mixed modelling framework to determine the significant contributors and their relative support. The explanatory terms fitted included time of day, reproductive phase, distance from home range centroid, group sizes, predator encounter rate, and habitat characteristics known to be associated with food availability and other critical resources for breeding, roosting and providing cover from predators (Portelli, Barclay, Russell, Griffith, & Russell, 2009). Although our statistical models include the factors most likely to encapsulate resource value, group resource-holding potential and predation risk, definitive support for a given hypothesis can be challenging because predictions are seldom mutually exclusive (see Table 1, the Discussion and the Appendix). Overriding support for hypotheses of resource value and resource-holding potential will be upheld by evidence of positive relationships between territoriality and home range quality and group size advantage, respectively. By contrast, predation risk is expected to have defining effects on territoriality if group responses to intrusions are governed by predator encounter rates and/or local arboreal cover.

METHODS

The study was conducted from October 2007 to March 2010, and October–November 2012, on a population of chestnut-crowned babblers in an area of 64 km^2 at the University of New South Wales Arid Zone Research Station, Fowlers Gap, western New South

Table 1
Expected effects of examined predictors on group territorial behaviour during naturally occurring intergroup encounters (O) and experimental group playbacks (P), under each of the three hypotheses tested

	Method	Predation risk	Resource value	Resource holding
Time of day	O,P	U	−	+
Reproductive phase				
Nesting	O,P	0	++	+
Postfledging	O,P	−	+	NP
Distance from home range centroid	O	0	U	0
	P	0	−	0
Group size parameters				
Group size focal	O,P	+	0	++
Group size encounters/playbacks	O,P	+	0	−−
Combined group size	O,P	+	0	0
Group size asymmetry	O,P	−	0	++
Predator encounter frequency	O,P	−	0	0
Habitat parameters	Spatial scale	Fine	Medium	Broad
Tree cover	O,P	++	+	0
Shrub cover	O,P	0	∩	0
Habitat PC1 (habitat type)	O,P	0	−	0
Habitat PC2 (eucalypt wood)	O,P	+	+	+

‘NP’ denotes cases with no obvious prediction due to insufficient background information or theoretically complex effects, while ‘0’ symbolizes no predicted effect; ‘+’ and ‘−’ denote linear positive and negative effects, respectively, and with double signs (‘++’ and ‘−−’) indicating expected strong effects; ‘U’ symbolizes U-shaped relationships. ‘Spatial scale’ indicates the main spatial resolution at which ecological effects (habitat type and cover) should become apparent (e.g. ‘broad’ for overall home range, ‘fine’ for local habitat in close proximity of encounters/playbacks). The rationales behind each predicted effect are provided in the Appendix.