

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



Enrico Sorato <sup>a, b, \*</sup>, Philippa R. Gullett <sup>a, c</sup>, Matthew J. S. Creasey <sup>d</sup>, Simon C. Griffith <sup>a, e</sup>, Andrew F. Russell <sup>d</sup>

<sup>a</sup> Department of Biological Sciences, Macquarie University, Sydney, NSW, Australia

<sup>b</sup> Station d'Ecologie Expérimentale du CNRS, Moulis, France

<sup>c</sup> Department of Animal and Plant Sciences, University of Sheffield, Sheffield, U.K.

<sup>d</sup> Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, U.K.

<sup>e</sup> School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia

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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 babbblers 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.

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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,

\* Correspondence: E. Sorato, Department of Biological Sciences, Macquarie University, Sydney NSW 2109, Australia.

E-mail address: [enrico.srt@gmail.com](mailto:enrico.srt@gmail.com) (E. Sorato).

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<sup>2</sup> 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.

Wales, Australia (31°05'S, 141°43'E) (Sorato, Gullett, Griffith, & Russell, 2012). The site is dominated by open chenopod shrubland characteristic of this region of low and unpredictable annual rainfall (median = ca. 220 mm/year), but the species composition, size and abundance of vegetation vary between babbler home ranges owing to variation in the topography and the extent of creeks and drainage channels where most of the sparse vegetation is found (Portelli et al., 2009). Although babblers forage primarily on the ground, shrubs and arboreal vegetation represent further foraging substrate and provide cover from aerial predators (Portelli et al., 2009; Sorato et al., 2012), as well as critical resources for roosting and breeding (Russell et al., 2010). Aerial predators constitute a major source of mortality for most species of birds (Griesser, Nystrand, & Ekman, 2006; Valcu, Dale, Griesser, Nakagawa, & Kempenaers, 2014). Raptors (*Falco* spp. and *Accipiter* spp.; see Sorato et al., 2012 for further details) can be spotted daily throughout much of the study site, and pose a considerable threat to babblers. Babblers react to the detection of aerial predators in flight by uttering loud, specific alarm calls that induce other group members to seek cover. The population has been monitored since 2004 and individual-specific colour ring combinations permit group identity to be readily determined in the field. Details on ringing procedures have been provided elsewhere (Sorato et al., 2012).

#### *Natural Intergroup Encounters, Approaches and Fights*

Overall, 43 groups were followed for 495 h (mean  $\pm$  SE = 11.2  $\pm$  1.2 h/group) at a distance of 30–50 m, encompassing the various habitat types throughout the field site (Fig. A1a, b). During tracking sessions, we recorded all focal group encounters with other groups, the identity of encountered groups, whether or not the focal group approached the encountered groups, and whether, after approaching, they engaged in aggression (Fig. A1a, c). Group encounters were defined when the focal group of babblers travelled within observable or audible distance of another group. An approach was defined when the focal group changed their travel direction to coincide with that of the encountered group and/or flew directly towards the encountered group. We appreciate that focal group responses to encountered groups also depend on the behaviour of the encountered group. However, for logistical and analytical reasons, we could not simultaneously evaluate how the behaviour of the encountered group influenced the outcome of an encounter, but point out that measured outcomes of focal groups to natural versus simulated encounters were comparable (see below). Babbler approaches during natural encounters can be readily categorized into two main outcomes based on presence or absence of physical aggression ('fights'). Fights were characterized by extensive chasing and counter-chasing (one or more individuals running or flying after another from the other groups) which always occurred in association with loud repetitive chatter vocalizations uttered by most or all group members.

#### *Playback Experiments*

We simulated group encounters by using playbacks of group vocalization recorded at dawn within 10 m of roost sites. Babblers habitually roost in dome-shaped nests throughout their foraging range and engage in short periods of intense chattering on first light (total time = 15–40 s). This chattering can be heard hundreds of metres away and is presumably audible to close neighbouring groups, suggesting that roost calls themselves might function as indicators of territory occupancy (e.g. Reyer & Schimdl, 1988). Comparisons of the spectrograms of these calls with those of 'chatter' calls uttered by foraging groups during periods of

intergroup conflict revealed no obvious differences. Vocalizations were recorded at known roost sites using a Marantz PMD660 solid-state recorder (sampling rate of 44.100 Hz at 16-bit precision) connected to a Sennheiser ME 66/K6 directional microphone. Recording equipment was set predawn, with the observer retreating >50 m to avoid disturbance ( $N = 50$  calls from 35 groups).

Using Wavepad sound editor (NCH software, Greenwood Village, CO, U.S.A.), we created playbacks by selecting the 10–15 s of intense calling and repeating it to create bouts of 30 s. Calls were standardized for loudness so that each playback had the same sound intensity, comparable to natural vocalizations, background noise was removed using a cutoff filter of 300 Hz, and 30 s of silence was added at the end of the vocalization. The entire 60 s track was then looped nine times to give a 10 min playback, in which bouts of vocalizations alternated with periods of silence (30 s each), and a further 60 s of silence was added at the beginning to allow the observer to retreat to >50 m from the speaker before playback initiation. The total playback duration and structure were devised to mimic patterns and durations of vocalizations observed during natural intergroup conflicts, which can last for several minutes and in which territorial conflict is often observed in bouts. Playback experiments were conducted using an iPod nano (Apple, Cupertino, CA, U.S.A.) connected to a Logitech im207 loudspeaker. Focal groups were never played their own vocalizations, but most (70%) received playbacks of both neighbouring and non-neighbouring groups (see below).

Two sets of playback experiment were conducted. In the first set, we performed 126 playbacks throughout the study site (Fig. A1b) during May–October 2008 (48 trials), July–November 2009 (63 trials) and in February 2010 (15 trials), while the second set were conducted in a random subset of areas in October and November 2012 (16 trials). In both sets, playback calls were recorded from groups of varying size, and the speaker was concealed in an area of low shrubs, to ensure that the playback source was out of direct sight. In the first set, playbacks were performed throughout the day in areas with scant or no tree cover, during periods of breeding and nonbreeding and at various locations relative to the focal group's home range centroid (20–1900 m, mean = 413 m; Fig. A1d), encompassing the entire range of distances from centroids observed in natural encounters (Fig. A1c). The key aim of the first set of playbacks was to test the effects of group size (focal and playback size), location within the home range, habitat characteristics (vegetation cover and type) and predator encounter rates within the home range on focal group responses to simulated intrusions. By contrast, the second set was designed specifically to investigate the effects of local vegetation cover (i.e. between the initial position of the group and the location of the playback), and hence potential predation risk (Sorato et al., 2012), on group responses to playbacks. As such, the second set of playbacks was conducted in areas of either scant (no or isolated trees;  $N = 6$ ) or extensive ( $N = 10$ ) tree cover, and in the mornings (0600–1045 hours) within the core area of the group's home range. The group–speaker distance at the start of the experiment averaged 42 m for the first set of experiments (range 20–100 m) and 73 m for the second set (range 40–110 m).

During all trials, we verified that the group had registered the playback recording: in all cases birds stopped their current activity and looked in the direction of the speaker. We then recorded whether the focal group made any effort to advance towards the playback source, and if so, their approach distance from the speaker and behaviour. We considered an approach in two ways, which were consistent with the observational data described above (encounters). First, we considered whether or not group members showed any sign of changing their previous direction of movement

towards the playback source, with an approach defined as movement of >10 m in the source's direction. Second, aggression was characterized by whether or not group members approached to within 5 m and mimicked observed behaviours during escalating natural encounters, including tail fanning and spread-wing displays, loud chattering and running on the ground.

### Explanatory Variables

We considered six potential explanatory parameters to test the three hypotheses outlined (Table 1). These data were used in analyses of natural observations and responses to playbacks, and they were obtained principally during tracking sessions, with the exception of group reproductive status which was separately determined during nest checks as part of other work. For each tracking session, we recorded the reproductive status of focal groups ('nonbreeding', 'nesting', 'with dependent young'), number of independent (>4 months) group members in focal and encountered groups (group size = 3–23, mean = 11), and number of predator encounters with known aerial predators (Sorato et al. 2012). Such encounter rates (total encounters/total tracking duration) were highly variable across the field site (range 0–0.9, mean = 0.3 encounters/h). Almost all encounters (>90%) were with aerial predators in flight and were in most instances detected by the observer following an alarm call by the focal group. It is important to note that we do not use predator encounter rates as the sole measure of predation risk, since risk also depends on cover. In addition, GPS coordinates, with date and time, were automatically recorded every 50 m using a Garmin eTrex or a Geko 301 GPS, allowing group home range and locations relative to home range centroid to be determined. Chestnut crowned-babblers are year-round residents with relatively stable home ranges between years, although during breeding they contract significantly around the active nest owing to the constraints of nest attendance. Home ranges were estimated as 100% isopleths using the local convex hull algorithm in the R package *Adehabitat* (Calenge, 2006), a nonparametric method that is suitable for analysis of temporally autocorrelated coordinates and relatively robust to extreme locations (Getz et al., 2007), and were determined separately for the nonbreeding periods (October 2007–January 2008 and May–June 2008), breeding periods (August–October 2008) and combination periods in which breeding and nonbreeding were common (July–October 2009 and January–March 2010). Home ranges varied significantly between groups and between periods, ranging from 17 to 250 ha (2007–2008 prebreeding: mean = 104, range 33–204 ha; 2008 breeding: mean = 53, range 17–143 ha; 2009–2010: mean = 127, range 25–250 ha), while natural encounters were not limited to home range borders and occurred when focal groups were 80–2390 m (mean = 586 m) from their centroids (Fig. A1c).

Knowledge of each group's home range permitted an estimation of habitat characteristics present in each group's range. In babblers, habitat features are known to affect both prey availability (Portelli et al., 2009) and predation risk (Sorato et al., 2012). To quantify spatial variation in habitat structure (hence potential quality and predation risk), we used a 400x400 m grid design to frame the 64 km<sup>2</sup> study area ( $N = 268$  quadrants). The total amounts of arboreal and shrub vegetation cover were each scored 0–4 from the central point of each quadrant, as were the relative contributions of each of the main tree/tall shrub species and short shrub type to overall cover estimates (see Table A1 and Portelli et al., 2009 for details of vegetation taxa). Each group's home range was then overlaid onto the quadrants, and average tree and shrub cover values for the home range were calculated by weighting each quadrant cover value by its amount of overlap with the focal group

home range. Additionally, the main dimensions of variation in habitat type within home ranges were characterized using a nonlinear principal component analysis (R package *homals*; de Leeuw & Mair, 2009) conducted on the relative cover values of different tree and shrub species. Principal component analysis of habitat variables extracted two components: habitat PC1 represented the main axis of variation in vegetation type, and was in large agreement with previous categorizations of habitat types within different areas of the study site (see Sorato et al., 2012); high PC2 values, on the other hand, were mainly associated with the presence of large eucalyptus trees, and were mostly restricted to the proximity of large ephemeral creeks and artificial dams (Table A2, Figs. A1a, b, A2). Low levels of PC1 were associated with areas of high babbler density and presumably reflect preferred babbler habitat, whereas low PC2 values reflect more open habitat, offering reduced cover from predators, and were also associated with lower individual body mass (Table A2). To provide average values of vegetation type within group home ranges, the weighted average principal component scores for vegetation type were calculated from habitat quadrants overlapping with each home range polygon, similarly to that done for tree and shrub cover.

We did not include intergroup relatedness in our analyses. While relatedness of neighbouring groups can influence social interactions between groups (Hatchwell, Anderson, Ross, Fowlie, & Blackwell, 2001), there is no simple metric for intergroup relatedness in babblers. Rollins et al. (2012) reported significant kin structuring by distance for male babblers, but this effect was generated because immediate neighbours tended to include one or more closely related males, while more distant groups did not. That encounters occur with neighbours suggests that, in some cases, both the focal and encountered groups will contain a minority of close relatives in common. Identifying whether relatedness influences the outcome of intergroup encounters requires detailed further work that is beyond the scope of this current study.

We can rule out an effect of familiarity on group responses in both the observational and experimental data sets. In the observational data set, given that encounters habitually arise between neighbours, all should be familiar. Ruling out familiarity as a source of variation in responses to playbacks is more challenging because focal groups might perceive playback groups based on their vocalizations or the location in which the playback was conducted (Radford, 2005). Our first set of playback experiments involved the calls of 59 non-neighbours and 67 neighbours, while the second set ( $N = 16$ ) involved only non-neighbours. In the former, focal groups were not more likely to respond to calls of neighbours versus non-neighbours (45% versus 41%;  $\chi^2 = 0.22$ ,  $P = 0.72$ ), and when they did respond to playbacks, were not significantly more likely to approach either neighbours or non-neighbours more aggressively ('approach close': 70% versus 54%;  $\chi^2 = 1.43$ ,  $P = 0.27$ ). Additionally, groups are unlikely to use playback location to gauge group identity because groups share overlap zones with multiple groups, while core areas are seldom visited by other groups and so playbacks in such areas will offer little information as to potential group identity.

### Statistical Modelling

Statistical analyses were conducted in R version 2.13.0 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). Generalized linear mixed models (GLMMs) were conducted using the package *lme4* (Bates, Maechler, & Bolker, 2010). In such analyses, we used an information-theoretic approach to select a final set of best models from initial candidate model sets, based on the Akaike information criterion (Burnham & Anderson, 2002) with the Hurvich and Tsay correction for finite sample size (AICc). Sets of candidate models were defined to reflect

multiple working hypotheses (Burnham & Anderson, 2002), guided by knowledge of the study system and hypothesized predictors (Table 1). In all model sets, quadratic terms and two-way interactions were considered where specifically predicted by the hypotheses under investigation (Table 1). Model predictors were centred by subtraction of mean values, and continuous variables were further standardized by dividing them by twice their sample standard deviation, allowing direct comparison of effect sizes within and between models. Scatterplots of residuals and predicted values were generated to check model assumptions. Model selection yielded AICc scores with relative weights for candidate sets of models based on AICc values. Models with the lowest AICc scores constituted the best models within candidate sets, while models with AICc values differing more than two units from the top model were deemed unlikely and excluded from final best model sets. Model averaging was performed on best model sets to obtain, for predictors of interest, average estimates of effect sizes, with associated standard errors and confidence intervals. Model selection and averaging were performed using the R package *AICcmodavg* (Mazerolle, 2011). Repeatabilities of focal group responses for both natural encounters and playbacks (see below) were calculated using the *rptR* package (Nakagawa & Schielzeth, 2010).

The probabilities that focal groups approached an encountered neighbouring group and attacked an approached group during a given tracking session were modelled using two separate sets of GLMMs with binomial error structures, denominators of 1 and logit-link functions. The following fixed effects were considered in each set: time of day; focal group reproductive stage; distance from home range centroid; focal group size, focal-encountered size difference and combined size; predator encounter rate; and aspects of habitat, including amount of arboreal cover and shrub cover within the home range and within the 400 m habitat quadrant in which the encounter occurred, as well as habitat principal components PC1 and PC2 at each spatial scale. Both focal and encountered group identities were fitted as random terms to account for repeated, and any nonrandom, sampling.

In the first playback set, we used two GLMMs as outlined above for natural encounters to investigate whether or not focal group members approached the speaker ('Approach'), and, if so, whether or not the approach appeared aggressive ('Approach Close'). Explanatory variables tested were the same as in the analyses of natural encounters, except that encountered group size was replaced by the playback group size (number of adults in the group) and initial distance of the focal group from the playback was fitted as a confounding term. Random terms were constituted by focal and playback group identities. In the second experiment set, we used a GLM with normal error structure (following a square-root transformation) to investigate the shortest distance from the speaker attained by the focal group. In this case, the primary fixed effect of interest was whether or not the speaker was placed in an area with contiguous tree cover, and start time was fitted as a covariate.

## RESULTS

### *Natural Intergroup Encounters, Approaches and Fights*

Focal groups encountered other foraging groups on 123 occasions, leading to an encounter rate of 0.25 groups/h of observation (ca. 3 encounters/day). Focal group approach probability showed low repeatability ( $R = 0.14$ , 95% CI [0,0.37],  $P = 0.10$ ). Overall, 67% of encounters resulted in an approach, with the probability of approach being best explained by models including time of day, distance from centroid, competitive advantage (group size asymmetry), tree cover and predation risk (Table A3). Approach

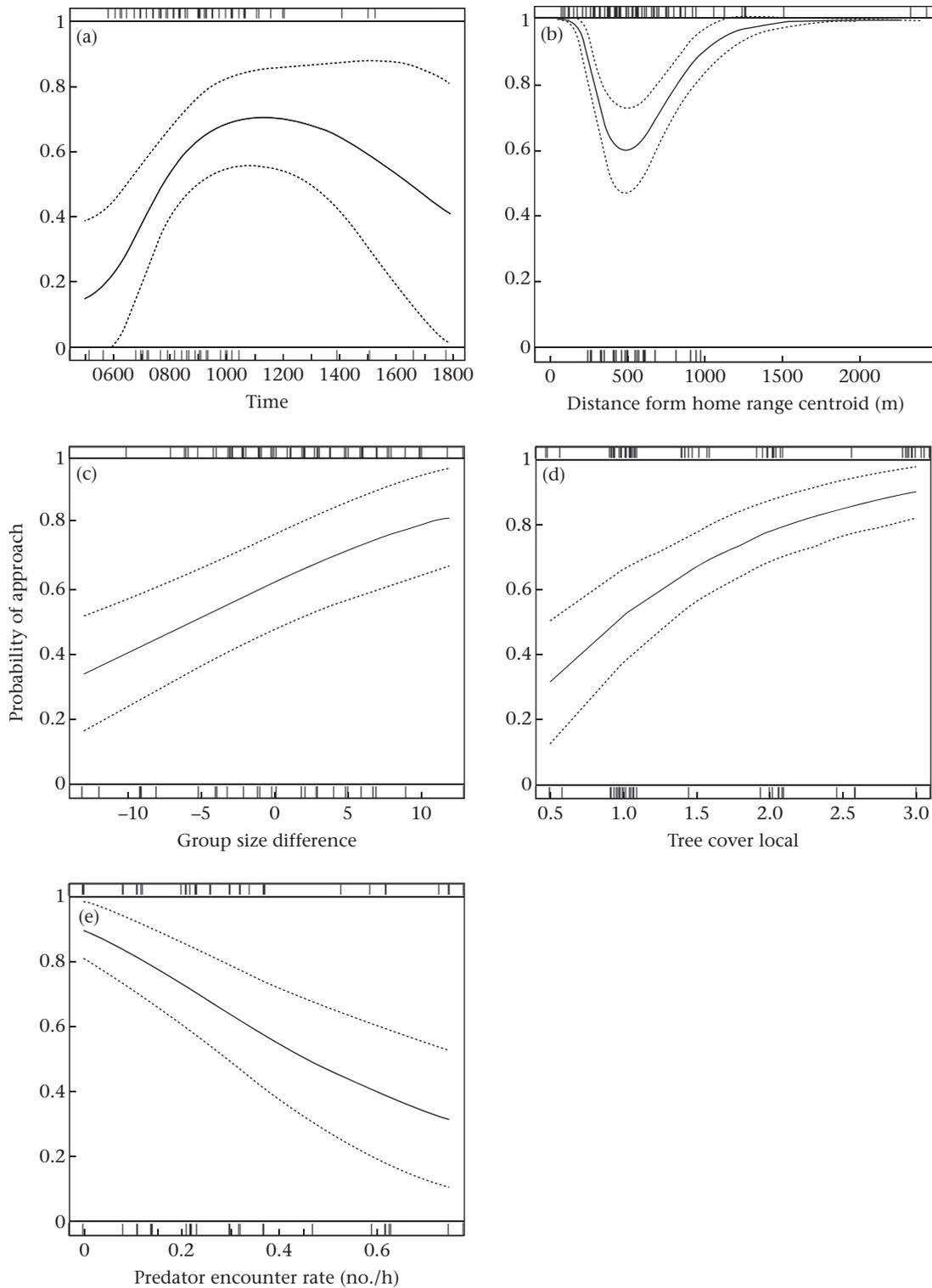
probability increased from dawn to late morning, before declining towards late afternoon (Fig. 1a) and showed a U-shaped relationship with distance from the focal group's home range centroid (Fig. 1b). Groups were also more likely to approach those they encountered as their size advantage increased from its minimum (size disadvantage) to its maximum value (Fig. 1c). Approach probabilities increased with amount of tree cover, with this effect being stronger for local cover (400 m quadrant) than for average home range tree cover (Fig. 1d). Finally, groups were increasingly more likely to approach as their encounter rate with predators declined (Fig. 1e). By contrast, we found no evidence to suggest that approach probability was influenced by the reproductive status of the group, and no evidence for an effect of habitat measures associated with shrub cover or habitat type (PC1, PC2; Table A3).

Fights ensued in 48% of encounters that led to an approach; in the remainder of cases, approaching groups were either observed foraging together without obvious signs of aggression (17%), or were seen displaying and vocalizing to each other without physical confrontation (34%). Again, the probability that groups engaged in fights showed low repeatability ( $R = 0.08$ , 95% CI [0,0.39],  $P = 0.20$ ), and there was also no effect of encounter rates (number of encounters/total tracking time) on the probability of groups attacking following approach (GLM:  $\chi^2_{28} 24.5$ ,  $P = 0.35$ ). There was little evidence to suggest that distance from home range centroid influenced the probability that fights would ensue from approaches, suggesting that babblers do not simply protect a core area (Fig. A1c). The factors most associated with physical aggression showed little congruence with the factors most associated with an approach. The main predictor of escalation to conflict was local (quadrant) habitat type (PC1), followed by time of day and average tree cover within the home range (Table A4). Encounters were more likely to escalate into a fight with increasing time of day (Fig. 2a), within habitat associated with high babbler density (Fig. 2b), and within home ranges with dense tree cover (Fig. 2c). By contrast, the likelihood of groups engaging in fights was not influenced by reproductive phase, measures of group size, the distance of the focal group from its home range centroid, habitat PC2, shrub cover, or predator encounter rate.

### *Experimental Playbacks*

Of the 126 experimental playbacks conducted throughout group home ranges, only 56 (44%) elicited an approach response towards the speaker. Groups that failed to approach stopped their previous activity and either vocalized back (67%) or became silent and inconspicuous (33%); in the latter case, the entire group generally responded by hiding under the cover of shrubs and trees for the playback duration (22%). The repeatability of group approach responses was relatively low, but significant ( $R = 0.17$ , 95% CI [0,0.32],  $P = 0.01$ ). The probability that the focal group approached the speaker was explained by time of day and average habitat PC2 within the focal home range (Table A5). Approaches declined by approximately 60% from dawn to midday, before increasing by more than 100% towards late afternoon (Fig. 3a). In addition, approaches increased more than six-fold across the range of PC2 scores measured, with PC2 being associated with increasing eucalypt woodland associated with main creek beds and dams (Fig. 3b). By contrast, there were no effects of reproductive status, distance from home range centroid, group size, predation risk, habitat PC1 and tree or shrub cover.

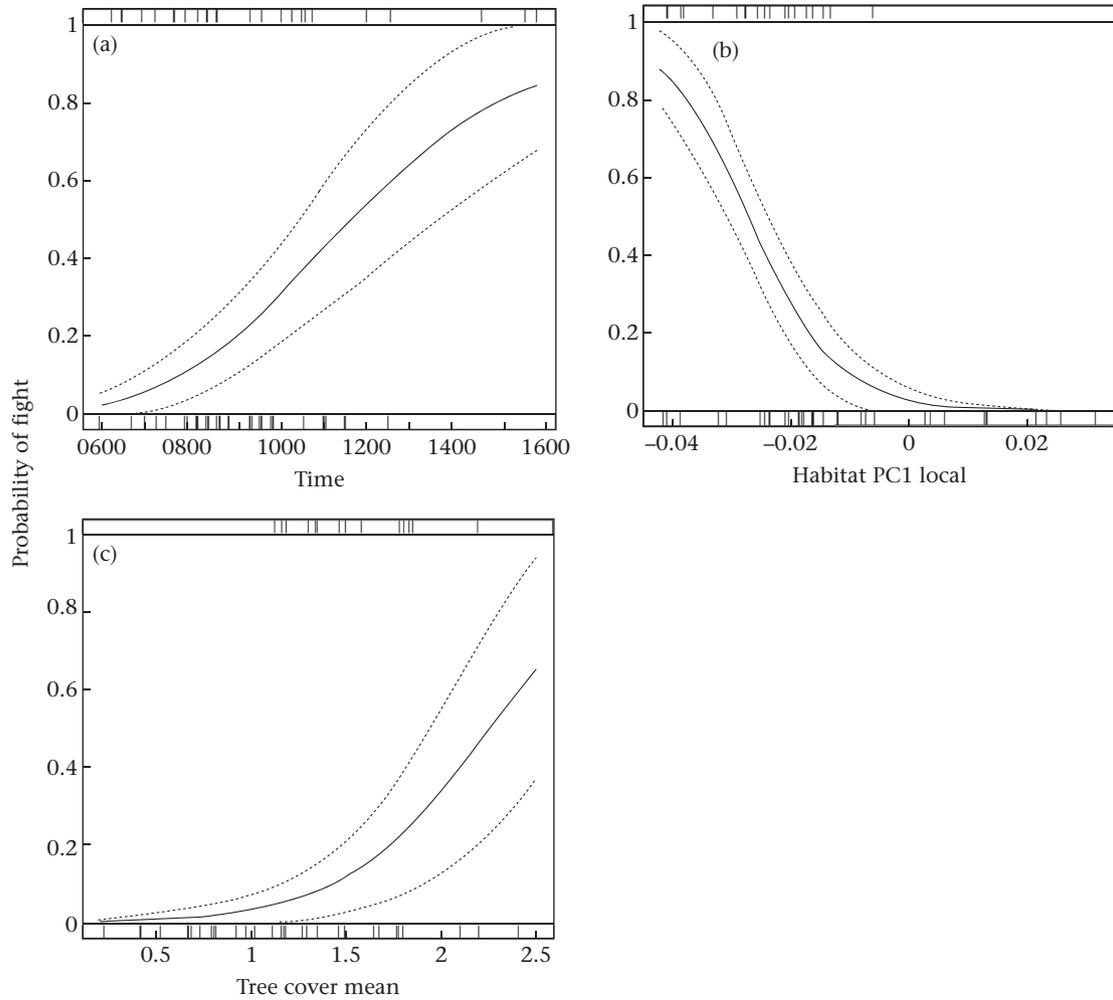
As was the case in natural encounters, not all approaches were aggressive. Of the 56 playback experiments that resulted in focal group approaches, 62% involved a close/aggressive approach ( $\leq 5$  m from the speaker) on the part of the responding group. Groups were not consistent in their probability of engaging in a close approach ( $R = 0.00$ , 95% CI [0,0.35],  $P = 0.81$ ). There was no



**Fig. 1.** Relationships between probability of approach during intergroup encounters and (a) time of day, (b) distance from home range centroid, (c) group size difference, (d) local tree cover and (e) predator encounter rate. Standard errors are represented by dotted lines. Vertical lines indicate distribution of raw observations of responses (top: response; bottom: no response).

correspondence with the factors affecting fighting probability in natural approaches, but some congruence with playback approaches (Table A6). Namely, the only predictor of aggressive approaches to playbacks was average habitat PC2 within the home range, with increasing probability of close approach with increasing eucalypt cover (Fig. 4a).

Finally, there was a significant effect of local vegetation cover on the approach distance in the second set of playback experiments. When we controlled for closer approaches with increasing time of morning (GLM:  $F_{1,14} = 6.98$ ,  $P = 0.02$ ), approach distances were 2.6 times closer when playbacks were conducted in areas with substantial arboreal cover versus open zones ( $F_{1,14} = 5.16$ ,  $P = 0.04$ ,

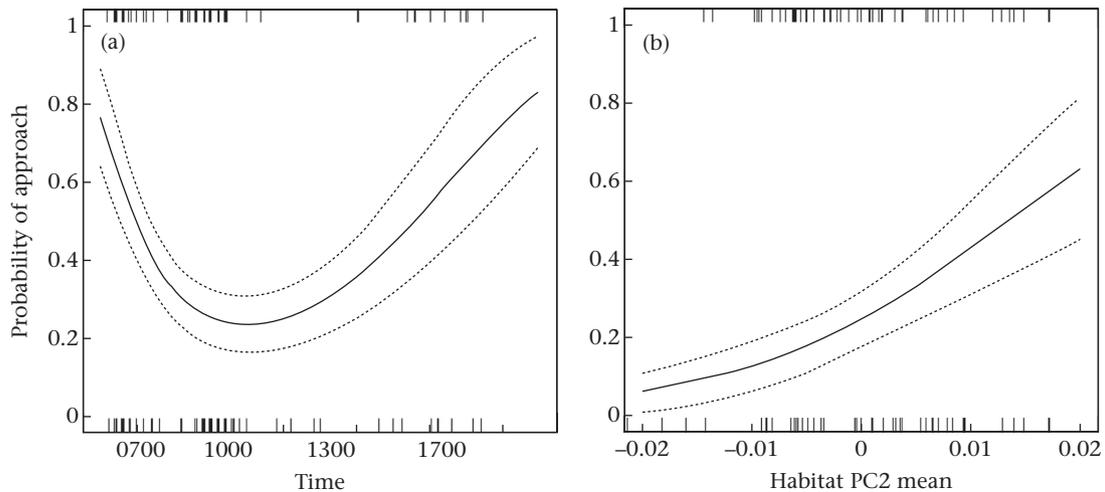


**Fig. 2.** Relationships between probability of escalation to a fight during intergroup encounters and (a) time of day, (b) local habitat PC1 and (c) average tree cover. Standard errors and vertical lines as for Fig. 1.

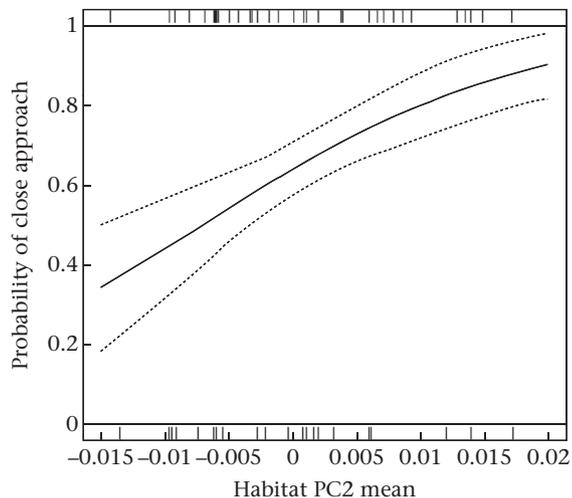
explaining 19% of the variance in approach distance). In areas of habitat with contiguous tree cover, babblers approached to within 17 m of the speaker on average ( $\pm$ SE = 5 m), while in areas of isolated vegetation, the average distance was 44 m ( $\pm$ SE = 10 m).

**DISCUSSION**

Chestnut-crowned babbler groups were highly variable in their responses to actual and perceived intrusions. Natural observations



**Fig. 3.** Relationship between probability of approach during playbacks and (a) time of day and (b) average habitat PC2. Standard errors and vertical lines as for Fig. 1.



**Fig. 4.** Relationship between probability of a close approach ( $\leq 5$  m) within approaches to playbacks and average habitat PC2. Standard errors and vertical lines as for Fig. 1.

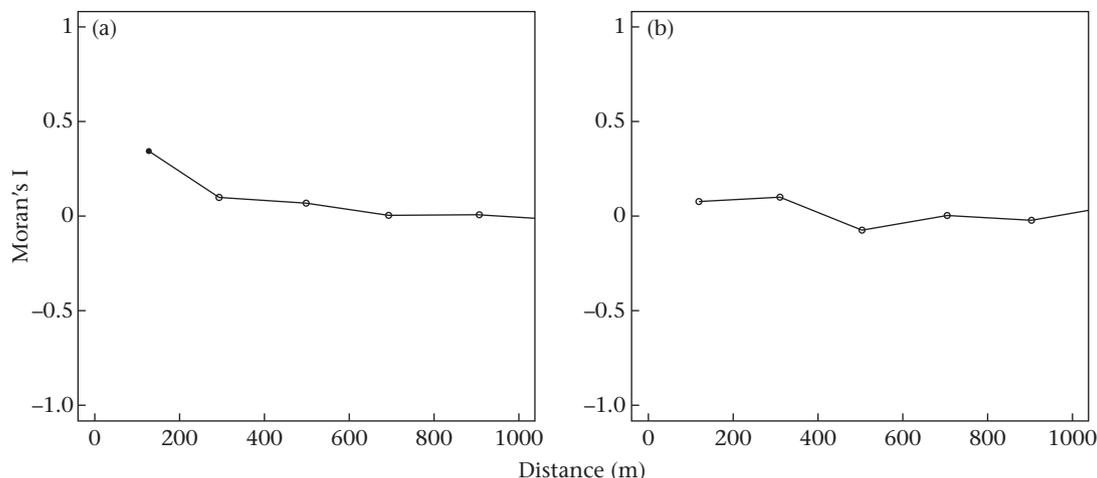
showed that babblers commonly encountered other groups during their daily forays, but only approached groups on 67% of occasions, with overt aggression ensuing in 48% of approaches. In the main playback experiment, 44% of playbacks resulted in approaches, and 62% of these were apparently aggressive ('close approach'). Thus, in both natural and experimentally simulated intrusions, only about 30% of encounters resulted in overt aggression. The congruence of factors affecting responses to natural encounters versus simulated intrusions was relatively poor. One explanation is that natural encounters usually involved known neighbours (e.g. dear enemy effect), with focal group responses being a product of previous interactions with those encountered groups. By contrast, playbacks included unknown groups and might be more often construed as escalated aggressive intrusions. Overall, our results suggest that the effects of predation risk on territorial behaviour are at least comparable with those of resource value and resource-holding potential, and might even lessen the selective advantages of territorial defence.

Resource value can vary in the short term within a territory as a function of resource depletion (Brown, 1982), in the medium term within and between territories as a function of reproductive status (Krebs & Davies, 1993), and in the long term between territories as a function of differing quality (Maher & Lott, 2000). We found no evidence that territorial behaviour declined over the course of a day in a manner consistent with resource value, suggesting either that resources do not decline during the day or that any declines are insufficient to influence territoriality. In addition, territorial behaviour was not influenced by reproductive status, despite clear predictions that the value of a resource should be positively associated with nesting and the presence of fledglings (Table 1, Appendix), or by shrub cover which is positively associated with prey availability (Portelli et al., 2009). By contrast, approaches during encounters were more frequent within the core area of home ranges, and the probability that natural approaches led to conflict decreased as habitat type transformed from high babbler density (low PC1 scores) to low babbler density areas (high PC1), and as tree cover in the home range declined, suggesting that aggression declined with decreasing habitat quality. However, whether or not these habitat results provide convincing evidence for a role of resource value in territorial behaviour is unclear, because only general habitat PC2 (and not PC1) influenced playback responses (see below) and tree cover was associated with predation risk too (see below). Additionally, if resource value was the dominant force

accounting for habitat correlates of territoriality, we would expect moderate to high repeatability in group responses, since such correlates are largely invariant over time, but this was not the case in any analysis.

The pattern of territorial behaviour is also predicted to be influenced by the ability of groups to defend their resources. Prohibitively high intrusion rates (Hinsch & Komdeur, 2010) or insufficient asymmetries among competitors (Persson, 1985) can select against investment in territorial behaviour. While intrusions in the study population were relatively common, the effect of encounter rates on the probability of groups attacking following approach was nonsignificant, contrary to what would be predicted under an intrusion effect. We also found limited evidence to suggest that group resource-holding potential overwhelmingly explained observed patterns of territoriality. Group size advantage predicted the probability of approach following natural encounters, but did not influence whether or not aggression ensued following approach, possibly because the size asymmetry of approaching groups was sufficient in conferring a large enough competitive advantage should a fight have ensued. However, large groups were no more likely to approach or show aggression during experimental playbacks. Thus, either group resource-holding potential may have a limited effect on territorial behaviour or its effects may be modified by other factors, especially under high perceived threat from contestants (i.e. playback of group vocalizations associated with escalated encounters). Collective action problems have been recently invoked to explain the lack of group size advantage during contests in some social animals (Crofoot & Gilby, 2012; Willems, Hellriegel and Schaik, 2013) and may be exacerbated as costs of individual investment in communal territorial defence increase. Under this scenario, group size advantage may be replaced in importance by individual body condition (Golabek et al., 2012). The strong effect of average habitat PC2 on the probability of approach towards playbacks is consistent with condition dependence, as the amount of eucalypt woodland associated with major creek systems was also a strong predictor of individual body mass (Table A2). Further research is required to disentangle interplays and relative effects of group size, collective action problem and individual condition on group territorial behaviour. None the less, as for resource value, the low repeatability of group responses to both actual and simulated encounters does not appear to support a dominant role of resource-holding potential in babbler territorial behaviour.

Increased risk of predation during intergroup conflict might be another significant parameter affecting territorial behaviour, since territorial disputes are conspicuous affairs that preclude scanning for predators (Jakobsson et al., 1995). Although seldom considered (Maher & Lott, 2000), predation risk might represent a salient impediment to territorial behaviour, particularly in species like chestnut-crowned babblers, which inhabit exceptionally open landscapes (Portelli et al., 2009), in which attacks from predators are common and have known consequences for foraging behaviour and group size (Sorato et al., 2012). Many of our findings are consistent with a predation risk hypothesis. Most importantly, the probability of approaching following natural encounters declined with increasing predator encounter rate and decreasing local tree cover. Additionally, our experiment, specifically designed to test the effects of local arboreal cover on responses to experimental playback, provides further compelling support, with groups approaching substantially closer to the speaker when it was placed within contiguous tree cover. Finally, as outlined above, we found low repeatability between group territorial responses to actual and perceived intrusions, which would not be anticipated under either the resource value or resource-holding potential hypotheses, but is



**Fig. 5.** Spatial correlograms (Moran's I) for type of focal group response during (a) encounters and (b) playbacks. Significant values are marked by solid symbols.

expected if local habitat in close proximity of the encounter has a significant bearing on the costs of engaging in territorial disputes.

We further tested the predation risk hypothesis by analysing the spatial autocorrelation in response type during natural encounters ('no approach', 'approach without overt aggression', 'approach with overt aggression') and during playback experiments ('no approach', 'approach not close', 'approach close'). We surmised that if group responses were mainly affected by local habitat features at the encounter/playback location, significant positive spatial autocorrelation should only be detected at distances below the average habitat patch size within the field site (ca. 100 m, e.g. patches of trees in proximity of creeks). To evaluate this prediction we implemented spatial correlograms, by plotting values of spatial autocorrelation in response type between pairs of encounters/playbacks as a function of their spatial distances (R package *ncf*; Bjornstad, 2013). In agreement with the local effect of tree cover on probability of approach, significant spatial autocorrelation in natural encounters was found only for distances below 200 m (Fig. 5). These results are consistent with the hypothesis that group behaviour during encounters is sensitive to local habitat features, supporting the idea that the risk of predation was a significant determinant of group responses. Although not all of our predictions of the predation risk hypothesis were upheld (see Table 1), overall our evidence suggests that predation risk plays a significant role in explaining variation in territorial behaviour in chestnut-crowned babbblers, and, more generally, upholds a rare test of this hypothesis (Jakobsson et al., 1995; Krebs & Davies, 1993; Maher & Lott, 2000).

In conclusion, unsurprisingly, we found evidence to suggest that correlates of resource value and resource-holding potential had significant effects on both the probability that groups would approach intruders and the probability that they would engage in fights. Nevertheless, our evidence for each was not as overwhelming as might be expected for a year-round resident cooperative breeder (Golabek et al., 2012; Radford & du Plessis, 2004). At least part of the reason for this appears to have been due to significant effects of predation risk. Predation risk, as judged by predator encounter rates and the degree of arboreal cover, significantly influenced approach probability in both observational and experimental data sets, independently of resource value and competitive advantage. In fact, high risk of predation may weaken selection pressures to defend valuable resources and moderate decisions to defend resources despite competitive advantages. Accordingly, elevated risks of predation might not only lead to

increased plasticity in territorial behaviour, but also contribute to the apparently low levels of territoriality found in this system. Although further studies are clearly required, the threat of predation appears to have tangible effects on territorial behaviour, a hitherto underappreciated factor in governing territoriality (Dunn, Copelston, & Workman, 2004; Kim et al., 2011), and adds to previous evidence suggesting that predation constitutes a significant selective force on foraging behaviour and group size in this species (Sorato et al., 2012).

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## Appendix

Here we describe the rationale behind the effects predicted for each parameter under hypotheses of resource value (RV), resource-holding potential (RHP) and predation risk (PR) (see Table 1).

### Time of day

RV: resource value is expected to be higher early in the day when the need to forage is highest and prey are replenished to some degree during the previous night. RHP: group resource-holding potential is predicted to increase over the day in parallel with increasing body condition of group members (see Table A2). PR: daily patterns of foraging, ground substrate use and sentinel behaviour suggest an increase in predation risk from early to late morning followed by a decrease until late afternoon (Sorato et al., 2012).

### Nesting phase (defined when eggs or chicks are present)

RV: resource value is expected to be significantly greater during the nesting phase than in the prenesting phase; this is because a brood itself becomes a valuable resource, coupled with the fact that the growing brood need more food resources (Birt, Goulet, Cairns, & Montevecchi, 1987). RHP: breeding is generally associated with

rainfall and ensuing increased prey availability which enhances individual condition (Golabek et al., 2012). PR: predation risk does not differ during nesting and prenesting periods (Sorato et al., 2012).

#### Fledgling/juvenile phases

RV: resource value is expected to increase in comparison to the prenesting phases due to the presence of juveniles. This is both because the juveniles themselves may be viewed as a resource and because the augmented group size (beyond what is accounted for by the 'No. of adults' predictor) increases the need for foraging resources compared to prebreeding levels. However, because juveniles are mobile, local resource depletion and the need to defend a restricted area are likely to decline compared to the nesting phase; accordingly we predicted resource value to be lower during the juvenile stage than during the nesting phase. RHP: it is unclear how group competitive potential may change with the presence of dependent young. PR: group predation risk increases with presence of young. This is because the presence of juveniles attracts predators, and their reduced escape responses might make them more vulnerable. Having said this, given that it is likely to be juveniles rather than adults that are taken by predators, how juvenile presence influences territorial behaviour through the predation risk hypothesis is difficult to determine (Sorato et al., 2012).

#### Distance from home range centre

RV: for natural encounters, a U-shaped relation is expected between resource value and distance from home range centre since group territoriality is predicted to decrease as the distance of the focal group from its home range core increases, but then to increase again due to territoriality of the encountered group closer to its core range. RHP: no effect predicted. PR: no effect predicted.

#### Number of independent individuals (No. of adults)

RV: there is no clear rationale to predict any effect of group size per se on resource value. RHP: resource-holding potential should increase with focal group size relative to the encountered/playback group. PR: individual predation risk is predicted to decrease with number of birds involved in a natural/simulated confrontation due to a dilution effect (Sorato et al., 2012); a positive group size asymmetry is also predicted to reduce focal territorial behaviour by increasing the odds of predation for the larger group.

#### Predator encounter rate

RV: no obvious effect on resource value. RHP: no rationale for an effect. PR: predation risk predicted to increase with rate of encounters with predators (Dubois & Giraldeau, 2005; Jakobsson et al., 1995).

#### Habitat

RV: resource value expected to decrease with habitat PC1 scores due to suboptimal habitat to increase with PC2 because large creeks provide high-quality foraging (Portelli et al., 2009), to increase with tree cover because trees provide nesting sites, extra foraging sub-

strate and cover from predators (Portelli et al., 2009; Sorato et al., 2012), and to show an inverse U-shape distribution with shrub cover, since babblers require both shrubs and bare ground for foraging (see also Brown & Balda, 1977, for evidence in the congener Hall's babbler, *Pomatostomus halli*). RHP: body condition increases with habitat PC2 (Table A2). PR: risk of predation should decrease with general amount of tree cover and availability of red gum eucalyptus trees (which decrease detectability and provide protective cover; Portelli et al., 2009; Sorato et al., 2012). The spatial scale at which habitat effects would manifest is predicted to be 'medium/broad' for resource value (habitat for the whole or a portion of home range that may be lost to other groups), 'broad' under resource-holding potential (i.e. condition is affected by habitat quality over the home range) and 'fine' for the risk of predation hypothesis (i.e. the risk of being predated is contingent upon the habitat structure in close proximity of the encounter/playback location).

**Table A1**  
Factor loadings for nonlinear principal component analysis on habitat variables

	PC1	PC2
Belah, <i>Casuarina pauper</i>	-0.22	-0.05
Mulga, <i>Acacia aneura</i>	-0.21	-0.06
Prickly wattle, <i>Acacia paradoxa</i>	0.17	0.16
Eucalyptus, <i>Eucalyptus</i> spp.	0.08	0.18
Other trees	-0.04	-0.03
Saltbush, <i>Rhagodia</i> and <i>Atriplex</i> spp.	0.23	-0.13
Bluebush, <i>Maireana</i> spp.	-0.21	0.20
Copperburr, <i>Sclerolaena</i> spp.	0.08	-0.22
Dead finish, <i>Acacia tetragonophylla</i>	-0.20	-0.07
Other shrubs	0.10	0.07

**Table A2**  
Averaged model of the effects of time, habitat and group size on individual body condition within babbler groups

Predictor	Estimate	SE	95% CI		
<sup>a</sup> Time of day	1.0	0.3	0.4, 1.5		
<sup>b</sup> Time of day <sup>2</sup>	-1.4	0.5	-2.4, -0.3		
<sup>c</sup> Habitat PC2	1.1	0.4	0.4, 1.8		
<sup>d</sup> No. of adults in group	-0.5	0.3	-1.2, 0.1		
Model	K	AICc	ΔAICc	Weight	
a+b+c+d	10	1715.6	0	0.6	
a+b+c	9	1716.5	0.9	0.4	

Condition was estimated using individual body mass values controlled for tarsus length (see below). In chestnut-crowned babblers body mass is higher in breeding males and females than in nonbreeders and decreases significantly in all group members during drought years when ecological conditions deteriorate and breeding is reduced. Individual body condition was analysed using GLMMs with a Gaussian-link function. Model specification and selection procedure follow methodology detailed in the Methods. Models were run on a data set of 401 ringing records of adult individuals, sampled during the breeding season (July–December), in 2007, 2008 and 2009. The following fixed-effect terms were considered: (1) time of day; (2) average habitat principal component scores (PC1, PC2) and vegetation cover (tree cover, shrub cover), including quadratic terms; (3) group size (no. of adults). In all models we controlled for body size (tarsus length) and year, with mass increasing with body size and decreasing in the drought year of 2009. Group and individual identity were fitted as random intercepts. Terms shown are those featured in the final model set ( $\Delta\text{AICc} \leq 2$ ). The superscript <sup>2</sup> indicates quadratic effects (squared predictor). K is the number of parameters in the model; AICc represents the Akaike information criterion corrected for sample size;  $\Delta\text{AICc}$  is the difference in AICc scores between focal models and the best candidate model (model with lowest AICc score); 'weight' measures the relative probability of each model within the full candidate model set.

**Table A3**

Averaged model of the probability of focal groups approaching during intergroup encounters

Predictor	Estimate	SE	95% CI	
<sup>a</sup> Time of day	1.5	0.9	−0.2, 3.3	
<sup>b</sup> Time of day <sup>2</sup>	−1.9	0.9	−3.7, 0.0	
<sup>c</sup> Distance from centroid	1.2	1.2	−1.3, 3.6	
<sup>d</sup> Distance from centroid <sup>2</sup>	7.1	3.1	1.1, 13.1	
<sup>e</sup> Group size difference	1.5	0.8	−0.1, 3.1	
<sup>f</sup> Predator encounter rate	−1.8	0.9	−3.5, −0.1	
<sup>g</sup> Tree cover quadrant	1.7	0.8	0.1, 3.4	
<sup>h</sup> Tree cover average	2.1	1.1	−0.1, 4.4	
Model	<i>K</i>	AICc	ΔAICc	Weight
a+b+c+d+e+f+g	14	82.3	0.0	0.4
a+b+c+d+e+f+h	14	83.0	0.7	0.3

Terms shown are those featured in the final model set ( $\Delta\text{AICc} \leq 2$ ). Excluded predictors are reproductive phase, habitat PC1, PC2 and combined group size. The superscript <sup>2</sup> indicates quadratic effects (squared predictor). All models included year as a confounding term and group identity as a random intercept. *K* is the number of parameters in the model; AICc represents the Akaike information criterion corrected for sample size;  $\Delta\text{AICc}$  is the difference in AICc scores between focal models and the best candidate model (model with lowest AICc score); 'weight' measures the relative probability of each model within the full candidate model set.

**Table A4**

Best model of the probability of escalation to a fight during intergroup encounters

Predictor	Estimate	SE	95% CI
Time of day	2.2	1.0	0.0, 4.5
Habitat PC1 quadrant	−4.8	1.7	−8.8, −0.8
Tree cover average	2.5	1.1	0.1, 5.0

Terms shown are those featured in the final model set ( $\Delta\text{AICc} \leq 2$ ). Excluded predictors are reproductive phase, distance from centroid, focal group size, number of adults encountered, group size difference and combined group size, predator encounter rate, habitat PC2 and shrub cover. All models included year as a confounding term and group identity as a random intercept.

**Table A5**

Best model of the probability of approaching playback vocalizations

Predictor	Estimate	SE	95% CI
Time of day	−0.9	0.5	−1.9, 0.1
Time of day <sup>2</sup>	2.4	0.8	0.8, 4.0
Habitat PC2 average	1.5	0.6	0.2, 2.7

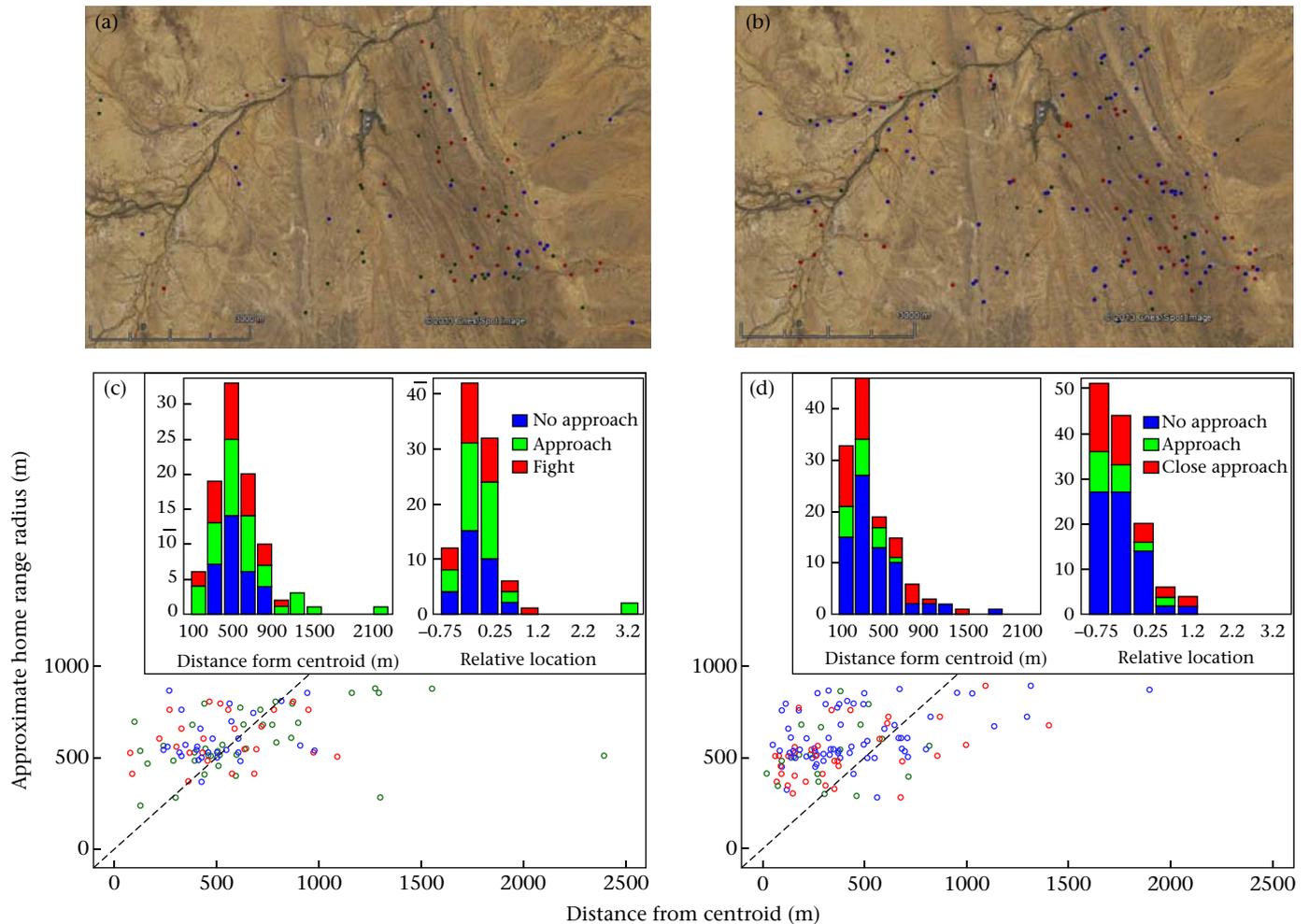
Terms shown are those featured in the final model set ( $\Delta\text{AICc} \leq 2$ ). Excluded predictors are reproductive phase, distance from centroid, focal and playback group size, group size difference and combined group size, predator encounter rate, habitat PC1, tree cover and shrub cover. The superscript <sup>2</sup> indicates quadratic effects. All models included year and start distance as confounding terms and group identity as a random intercept.

**Table A6**

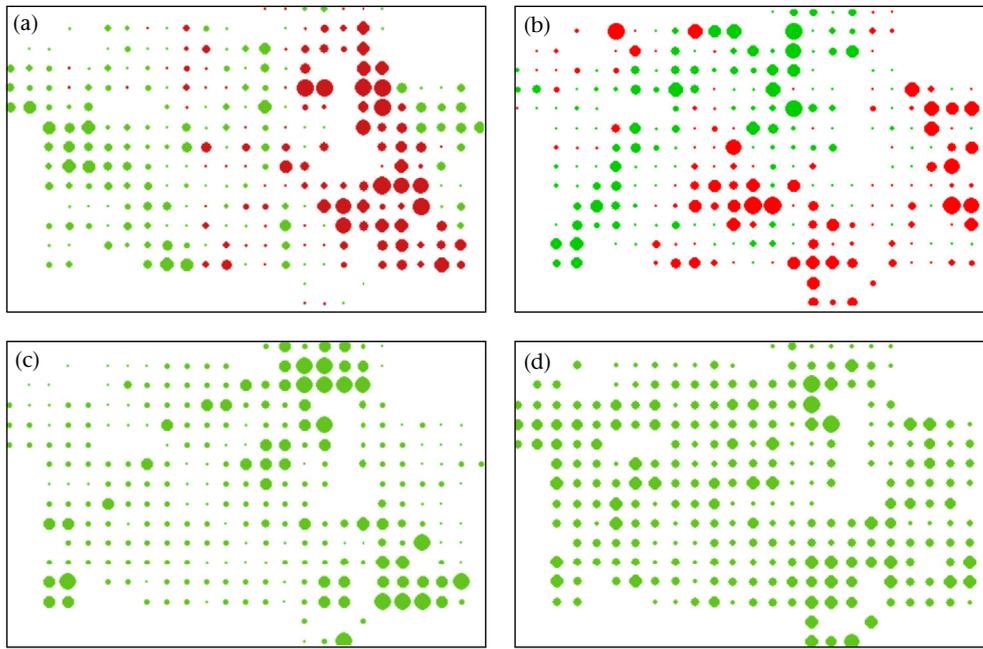
Best model of the probability of close approach to playback group vocalizations

Predictor	Estimate	SE	95% CI
Habitat PC2 average	1.3	0.7	−0.1, 2.7

Terms shown are those featured in the final model set ( $\Delta\text{AICc} \leq 2$ ). Excluded predictors are time of day, reproductive phase, distance from centroid, focal and playback group size, group size difference and combined group size, predator encounter rate, habitat PC1, tree cover and shrub cover. All models included year as a confounding term and group identity as a random intercept.



**Fig. A1.** (a) Locations of between-group encounters within the study site. Colours mark encounter type: encounter with no approach (blue), encounters leading to an approach but no fight (green) and encounters escalating to a fight (red). (b) Locations of playback experiments within the study site. Colours mark response type: playbacks with no approach (blue), playbacks leading to an approach but not within close distance (green) and playbacks leading to a close approach (red). (c) Scatterplot of encounter locations. Different colours indicate encounter type (see key). 'Distance from centroid' represents the distance between the encounter location and the home range centroid. 'Approximate home range radius' indicates the approximate position of the home range border (distance from the home range centre) calculated by assuming a circular home range and with the formula  $R = \sqrt{\text{area}/\pi}$  (mean  $\pm$  SE =  $594 \pm 15$  m). The dotted line separates encounters occurring within the focal group's home range (above) from those occurring outside (below). Inset: histograms of distances from centroid (left) and of relative encounter locations (right). Relative location is calculated as  $(D-R)/R$  with  $D$  = distance from centroid and  $R$  = approximate home range radius; values close to 0 indicate encounters occurring in proximity of the home range border, negative and positive values encounters within and outside the home range, respectively. (d) Scatterplot of playback locations. Different colours indicate playback type (see key). 'Distance from centroid' represents the distance between the playback location and the home range centroid. 'Approximate home range radius' indicates the approximate position of the home range border calculated as in (c) (mean  $\pm$  SE =  $574 \pm 14$  m). The dotted line separates playbacks occurring within the focal group's home range (above) from those occurring outside (below). Inset: histograms of distances from centroid (left) and of relative playback locations (right). Relative location is calculated as in (c); values close to 0 indicate playbacks occurring in proximity of the home range border, negative and positive values encounters within and outside the home range, respectively. (a, b) Copyright 2013 Cnes/Spot Image.



**Fig. A2.** Spatial distribution of habitat quadrant scores for (a) habitat PC1, (b) habitat PC2, (c) tree cover and (d) shrub cover. Each circle represents a sampling point on an equally spaced (400 m) grid; circle size is proportional to absolute score, 'red' and 'green' indicate negative and positive scores, respectively.