

Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species

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There is a divergence between models examining the evolution of group living in species in which groups are largely based on families and those based on fluid aggregations of nonrelatives. In the former, the onus has been on ecological and demographic factors that select for offspring philopatry; in the latter, the importance of factors such as foraging success and predation risk are more typically emphasized. We examined the association between predation risk and both group size and foraging behaviour in the chestnut-crowned babbler, *Pomatostomus ruficeps*, a family-living cooperatively breeding bird that does not appear to face classic ecological or demographic constraints on dispersal and breeding. Groups were more likely to encounter, and be attacked by, avian predators when dependent young were present. Large groups were also more likely to encounter a predator, but less likely to be attacked by it, consistent with a benefit of group living through early predator detection or confusion effects. In addition, the average risk of predation for a given individual was reduced in large groups compared to small ones, owing to the dilution effect. That predation might partly select for group living in this species is boosted by findings showing reductions in ground foraging and increases in sentinel behaviour when predation risk was higher. We conclude that predation might represent an important force selecting for sociality in chestnut-crowned babblers, and highlight the need for future studies to consider more explicitly inherent benefits to group living in the evolution of vertebrate cooperative breeding systems.

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Many animals live in social groups at some stage in their lives. While grouping can be costly, for example because of increased parasite transmission (Brown & Brown 1986), foraging competition (Milinski & Parker 1991) or probability of detection and attack by predators (Vine 1973; Lindström 1989; Cresswell 1994), it is also associated with numerous benefits (Krause & Ruxton 2002; Clutton-Brock 2009). For example, groups might be more adept than individuals at finding and foraging for food (Clark & Mangel 1986; Giraldeau & Beauchamp 1999; Krause & Ruxton 2002), as well as at detecting or evading predators (Pulliam 1973; Neill & Cullen 1974; Elgar 1989; Roberts 1996; Caro 2005; Sridhar et al. 2009). Despite this, models addressing the evolution of cooperative breeding systems, in which animals live in groups but group members provide care to the offspring of others, seldom consider such generalized benefits of grouping (Brown 1987; Stacey & Ligon 1987; Koenig et al. 1992; Du Plessis 2004; Ekman et al. 2004; Doerr

& Doerr 2006). Instead, sociality in such species is generally regarded as being a function of the relative costs of offspring dispersal to positions of independent reproduction rather than relative benefits of group living per se (Emlen 1982, 1994; Koenig et al. 1992; Hatchwell & Komdeur 2000). These differences in theoretical perspective have some biological grounding: grouping in cooperative species tends to arise through natal philopatry and is commonly associated with lost reproductive opportunities, while in noncooperative species it arises mainly through coalescences of unrelated adults and has little influence on reproductive skew. Nevertheless, classic ideas of ecological constraints on offspring dispersal and breeding appear limited in their application to a growing number of cooperative vertebrates, leading to a need to consider additional selective forces (Brown 1987; Koenig et al. 1992; Clutton-Brock 2002, 2009).

In cooperative birds, in which most of the research on the factors selecting for group living has been conducted (Ekman et al. 2004; Russell 2004), group size is generally predicted to increase with the relative costs of dispersing to breed independently owing to a lack of mates or territories of sufficient quality (Emlen 1982, 1995; Stacey & Ligon 1987; Koenig et al. 1992; Covas & Griesser 2007). In

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some cases, elegant experiments have upheld predictions of such models by showing that the relaxation of a constraint on dispersal and independent breeding leads to offspring dispersal and reduced group sizes. For example, the removal of territorial birds in superb fairy-wrens, *Malurus cyaneus*, caused dispersal of helpers from neighbouring groups when females were present to pair with (Pruett-Jones & Lewis 1990). Similarly, experimental creation of limiting roosting (Du Plessis 1992) or nesting (Walters et al. 1992) holes led to increased dispersal in green woodhoopoes, *Phoeniculus purpureus*, and red-cockaded woodpeckers, *Picoides borealis*, respectively. Finally, translocation of families to previously unoccupied islands led to family dissolution in Seychelles warblers, *Acrocephalus sechellensis*, until habitat of equivalent quality to the natal one again became limiting (Komdeur 1992; Komdeur et al. 1995). While these studies provide compelling evidence to support the idea that constraints on dispersal promote group living, in a significant number of other species the existence and extent of constraints on dispersal are unclear (Hatchwell & Komdeur 2000; Cockburn 2003).

More recently, the idea that more generalized group benefits can favour philopatry and lead to group living has been invoked in a number of cooperative species for which classic explanations of habitat saturation and mate limitation appear unlikely (Clutton-Brock 2002). For example, benefits of cooperation in a foraging context have been suggested to account for the evolution of eusociality within mole-rats (Bathyergidae, Jarvis et al. 1994), while thermodynamic benefits of huddling have been highlighted as a largely overlooked benefit of group living in many cooperative birds (Du Plessis 2004). Nepotistic access to food resources and protection from predators provided by parents have also been suggested as mechanisms selecting for delayed dispersal in several family-living bird species (e.g. Griesser et al. 2006; Dickinson et al. 2009). In addition, predation risk has been invoked as an important mechanism selecting for group living in cooperative meerkats, *Suricata suricatta* (Clutton-Brock et al. 1999a), and has been shown experimentally to influence dispersal propensity of helpers in the cooperative cichlid *Neolamprologus pulcher* (Heg et al. 2004). That predation risk might constitute an important selection pressure on group living in cooperative species is further supported by the fact that some species have evolved sentinel systems, where group members stand guard from an elevated position to scan for predators while the rest of the group forages (McGowan & Woolfenden 1989; Clutton-Brock et al. 1999b; Wright et al. 2001; Bell et al. 2009). While predation risk is known to influence individual behaviours, including sentinel behaviour (e.g. Bell et al. 2009; Hollén et al. 2011), foraging (Hollén et al. 2008; Bell et al. 2009) and dispersal (Heg et al. 2004), whether it influences group size is currently untested. This current paucity of information on the interplay between predation risk and group size in cooperative vertebrates presumably arises because of the difficulty of assessing predation risk through direct observations, as well as complications involved with determining whether group size is a consequence or cause of predation risk when it is ethically and logistically impractical to tease apart cause and consequence experimentally through the long-term removal of predators or group members (Cockburn 1998; Clutton-Brock et al. 1999a).

We investigated the association between group size and predation risk using the cooperatively breeding chestnut-crowned babbler, *Pomatostomus ruficeps*, a species that does not seem to be constrained by a lack of potential breeding sites and mates. For example, chestnut-crowned babblers have no specific habitat requirement other than trees for nesting/roosting, and appear not to be constrained through a lack of potential mates, as most social groups contain both males and females that do not breed (Rollins et al. 2012). Evidence over the past 8 years from our study population shows that habitat in which successful breeding has

occurred in some years commonly remains unoccupied (A. F. Russell, unpublished data), and analysis of the effects of known ecological correlates of breeding success (Portelli et al. 2009) has failed to identify any ecological or demographic factors that might account for vacant habitat patches apparently suitable for breeding. In contrast, predation might have some explanatory power for group living in this species, because the openness of the arid habitat, and frequent digging in the ground during foraging (Portelli et al. 2009), might make chestnut-crowned babblers particularly vulnerable to aerial predators (as has been suggested for other cooperative species: see Ford et al. 1988; Clutton-Brock et al. 1999a, b).

Our aims in the present study were thus two-fold. First, we examined the potential risks of predation by measuring both the probability that groups encountered known avian predators as well as their probability of being attacked by them. In both cases, our primary terms of interest were effects of group size (both total size and numbers of independent individuals), reproductive stage (nonbreeding, nesting and fledgling/juvenile) and habitat characteristics (primarily based on shrub and tree availability). Second, we analysed foraging responses to our measures of predation risk, including choice of foraging substrate (ground versus tall shrubs and trees) and whether or not individuals more commonly chose to go on sentinel activity. In this case, in addition to the explanatory terms of interest above, we included whether or not a predator was encountered or whether it attacked, and, for the analysis of sentinel behaviour, the relative amount of time babblers spent foraging on the ground. Based on previous evidence, we predicted that if predation risk constitutes an important element in understanding group living in chestnut-crowned babblers, it would drive behaviours aimed at reducing the risks of being depredated, including increasing group size, foraging in safer areas and employment of a sentinel (Lima & Dill 1990; Nystrand 2006, 2007; Bell et al. 2009; Griesser & Nystrand 2009).

Although we were unable to conduct experiments for the reasons outlined above, the characteristics of the study system, in conjunction with our methodology, made it possible to elucidate whether group size might represent a behavioural strategy aimed at reducing predation risk. First, babblers can be tracked and all avian predators identified relatively easily over long periods of time throughout the year in their open habitat. Second, multiple (one to four) breeding units of 2–15 individuals can be found within social groups (Russell et al. 2010; this study); such breeding units can forage together or apart, meaning that a foraging group can vary significantly in size even within the same day (Portelli et al. 2009). Third, our study area is large, encompassing four distinct habitat types (Mabbutt 1973; see Methods) and observations were conducted over multiple years and life history phases. Finally, we assessed whether individuals changed their sentinel or foraging behaviour in response to predation risk. As such, we were able to obtain a meaningful estimate of what is a rare, but potentially life-altering event, predation, and examine whether estimates of predation risk in chestnut-crowned babblers are associated with group size and indicative aspects of foraging ecology (foraging substrate and sentinel behaviour). Thus, we used the unusually labile nature of babbler foraging groups in conjunction with an intense longitudinal study to elucidate whether babblers respond to increases in predation risk by elevating group size.

METHODS

Study Site

The study was conducted from October 2007 to March 2010 in an area of 64 km² at the University of New South Wales (UNSW), Arid Zone Research Station at Fowlers Gap, in western New South Wales, Australia (31°05'S, 141°43'E). A comprehensive account of the climate and habitat of the study site is presented elsewhere

(Portelli et al. 2009). We categorized habitat throughout the field site into four types based on the density and species identity of the dominant trees and shrubs, as well as underlying soil type, depth and geology (Mabbutt 1973). The most prevalent habitat encompassed areas of low relief in the centre of the field site and was characterized by a medium density of *belah*, *Casuarina pauper*, and bluebush, *Maireana* spp., on thin clay soils with commonly exposed bedrock ('Zone 1'). The second habitat zone was distinguished as having low numbers of both trees and bluebush, but a deeper soil layer including sand/loam ('Zone 2'). The third type of habitat ('Zone 3') had overlapping soil and rock characters as Zones 1 and 2, but differed because of a locally high tree density, coupled with a low density of bluebush. Finally, Zone 4 was characterized by flood plain areas, with a deep sandy soil layer, and was largely devoid of trees, with the exception of tall river red gum trees, *Eucalyptus camaldulensis*, bordering large ephemeral creeks, but had abundant tall shrubs, dominated by prickly wattle, *Acacia victoriae*, as well as short shrubs in the form of both bluebush and saltbush, *Rhagodia* and *Atriplex* spp. Habitat type was assigned to babbler groups on the basis of overlap between zones and group home ranges (see below).

Aerial predators can be spotted on a daily basis throughout most of the study site, and are likely to pose a considerable threat to babblers, as testified by our witnessing of three successful predation events (two during this study) and multiple unsuccessful attempts. Among falcons, nankeen kestrel, *Falco cenchroides*, is abundant, brown falcon, *Falco berigora*, is common, peregrine falcon, *Falco peregrinus*, and Australian hobby, *Falco longipennis*, are seen occasionally, while black falcon, *Falco subniger*, is rarely seen. Among accipiter hawks, both brown goshawk, *Accipiter fasciatus*, and collared sparrowhawk, *Accipiter cirrocephalus*, are common. All species are known to hunt birds of babbler size (Marchant et al. 1994) and all elicit pronounced aerial alarm calls and evasive actions from babblers when flying in obvious proximity (E. Sorato & A. F. Russell, personal observations).

Data Collection

Data were collected during five periods between October 2007 and March 2010. Reproductive phase differed between these five periods as follows: October 2007–January 2008: largely post-breeding; May–July 2008: prebreeding; August–October 2008: extensive breeding; July–October 2009 and January–March 2010: predominantly nonbreeding, but with occasional breeding (<40% of groups attempted to breed during 2009, probably owing to prolonged drought conditions, and a minority delayed attempts to early 2010).

Babbler groups were located by extensively searching throughout the study site, aided by their loud and distinctive calls (group chatter calls and individual long-distance contact calls), or by visiting known roost nests predawn. Groups were identified in the field using the distinctive ring-band combinations of individual birds, and were typically followed for up to 4 h (follows of <1 h were omitted from the analysis). Field research was approved by the Macquarie University Animal Ethics Committee (no. 2010/032); young and adult birds were caught by mist netting, while nestlings were ringed in the nest (Australian Bird and Bat Banding Scheme project no. 026). Care was taken to minimize disturbance to groups, and tracking in the hottest part of the day during summer months was avoided; individual birds were commonly observed foraging and interacting with other group members, suggesting that any disturbance from the observer did not have any significant adverse effect on group activity. We conducted a total of 256 tracking sessions across 53 social groups (average number sessions/group \pm SE = 4.7 ± 0.5 ; range 1–25; total tracking time = 610 h; average total tracking time/group \pm SE = 11.2 ± 1.2 h;

range 1.5–51.5 h), mainly during early to mid-mornings (0600–1100 hours, $N = 198$ sessions), and, to a lesser extent, during the middle of the day (1100–1600 hours, $N = 32$ sessions) and late afternoon (1600–1900 hours, $N = 26$ sessions). We generally tried to follow groups for about 3 h per session, on different days, but this was not always possible, either because focal groups were lost, or became less active when tracked during midday and in the evening (average tracking session duration \pm SE = 2.3 ± 0.05 h; range 1–4.5 h). Track duration did not covary with group size (Kendall's tau = -0.07 , $N = 256$, $P = 0.36$), or with habitat type (generalized linear mixed model, GLMM: Zone \pm SE: Zone 1 = 131 ± 4.3 min, Zone 2 = 146 ± 7.4 min, Zone 3 = 134 ± 8.4 min, Zone 4 = 137 ± 8.3 min).

For each tracking session, the following general information was recorded: (1) start and end times, to control for potential diurnal variation in behaviour; (2) location on a Garmin GPS, which was used to determine the primary zone over which babblers foraged; (3) total number of group members that were either independent (aged > 4 months, with full adult plumage) or dependent (fledglings aged < 1 month, or juveniles aged 1–4 months) group members; and (4) reproductive phase, categorized as nesting (incubation and nestling phases), young-with-group (fledglings or juveniles present) and nonbreeding (all other times).

Scan sampling (Martin & Bateson 2007) of group behaviour was conducted continuously, and relevant behaviours were recorded every 5 min throughout tracking sessions, since the often cryptic and flighty nature of the birds generally precluded instantaneous or individual sampling. For each 5 min period, the general behaviour of the birds (e.g. foraging, resting) and their location were noted; location was categorized as ground, tall shrubs (vegetation 0.5–2 m high) or trees (vegetation > 2 m high). Data on predator encounters and sentinel behaviour were collected on an ad libitum basis every time either was observed; because sentinel activity was recorded for only a subset of the tracking sessions, sample size for this behaviour was smaller than for encounters. Predator encounters were further categorized as those that reflected a predation attempt versus those that did not, based on whether or not the predator actively attempted to catch a group member; further to this, we were not able to distinguish between predator encounters arising through predators detecting babblers, babblers detecting predators or chance. Sentinel behaviour was defined as a single bird perching and being vigilant in an exposed prominent position, usually a tall shrub (1–2 m high), while the rest of the group was typically foraging on the ground (see Clutton-Brock et al. 1999b; Wright et al. 2001 for similar definitions). Sentinel bouts were recorded qualitatively and were not timed, as they were generally short (<3 min), presumably owing to the rapid pace at which babblers move through their habitat.

Statistical Analysis

All statistical analyses were performed in R version 2.11.1 (R Development Core Team, 2010). GLMMs were run using the R package lme4 (Bates & Maechler 2010). Group identity was fitted as a random intercept in all GLMM analyses to account for statistical nonindependence of multiple observation sessions on focal groups, and to model appropriately the random sampling of social groups from the study population. All model predictors were centred by subtraction of mean values, and continuous variables were further standardized by dividing them by their sample standard deviation (Schielzeth 2010), to facilitate direct comparison of estimates of effect sizes within and between models. Scatterplots of residuals and predicted values were generated to check model assumptions. To separate within-group effects from between-group effects, group size measures were further dissected into a 'within-subject' and a 'between-subject' component using a within-subject centring procedure (van de Pol & Wright 2009).

The factors affecting the probability of a group encountering a predator, the probability of attack during encounters and the proportion of time groups spent foraging on the ground (henceforth termed 'substrate use') were analysed using GLMMs with binomial error structure and logit link function. For encounter and attack models, predator met (0,1) and predator attack (0,1) were fitted as the response terms in two separate sets of GLMM models and 1 was fitted as the binomial denominator in each. For the substrate use analysis, the number of 5 min observations during which the focal group was located mainly on the ground was fitted as the binomial numerator and the total number of 5 min scans was fitted as the binomial denominator. Habitat type ('Zone'), reproductive stage and group size (either total group size, including both independent and dependent foraging group members, or number of independent members in the group) were fitted as primary explanatory terms of interest, while track duration and time of day were fitted as covariates to control for variation between tracking sessions. In the substrate use analysis, whether or not a predator was encountered, or alternatively whether or not it attacked during the tracking session, was included as a further explanatory term of interest. For models of predator attack, reproductive stage was categorized as a simpler binary variable ('young in the group' versus 'no young') owing to lack of observations of predator attacks during nesting phases.

Factors associated with sentinel behaviour were analysed using GLMMs with Poisson error structure and log link function. The number of sentinel bouts observed during each group follow constituted the dependent variable in the analysis. Habitat zone, group size,

reproductive phase, substrate use and whether or not a predator was encountered or attacked were entered as primary fixed effects of interest, while track duration and start time were again included as potentially confounding covariates. Finally, we performed a one-tailed binomial test to assess whether sentinel behaviour was more common after a predator encounter than before.

We used an information-theoretic approach to select the best explanatory models from candidate model sets, based on the Akaike information criterion (AICc with the Hurvich and Tsay correction for finite sample size, Burnham & Anderson 2002). Sets of candidate models were defined to reflect multiple working hypotheses (Burnham & Anderson 2002), guided by knowledge of the study system and hypothesized relevant predictors. We started by defining the simplest models including the intercept and random effects only, followed by models with confounding terms (e.g. track start time and duration) and then by more complex models featuring combinations of ecological and sociobehavioural predictors of interest (e.g. group size, breeding stage, habitat; see [Supplementary Table S1](#) for a full list of initial candidate model sets). Model selection was performed with the R package AICcmodavg (Mazerolle 2011), which yielded relative weights for candidate sets of models based on AICc scores. The best model was defined as the one with the lowest AIC score, while models with $\Delta\text{AICc} > 5$ were deemed as unlikely and excluded from final candidate model sets (Burnham & Anderson 2002). Inference was based on the single top-ranking model if this yielded a relative Akaike weight > 0.9 , otherwise lower-ranking models, with $\Delta\text{AICc} \leq 5$, were also considered as relatively plausible, in proportion to their relative weights; as an aid

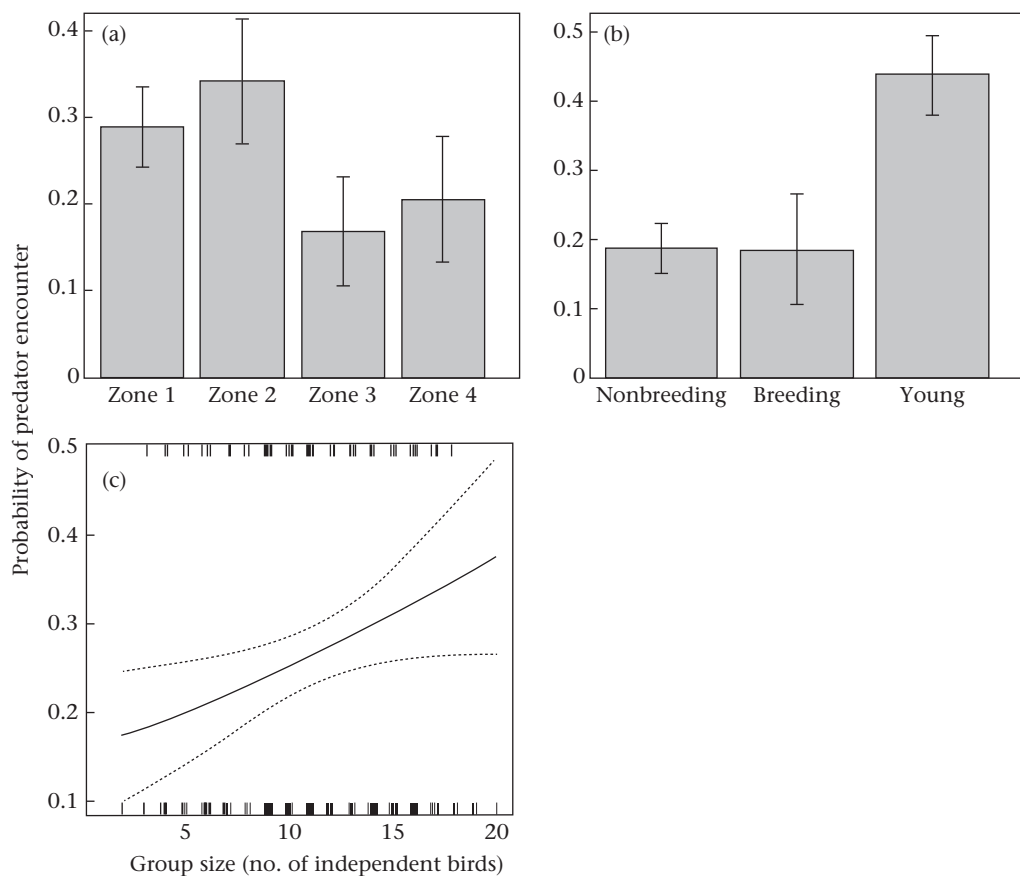


Figure 1. Relationship between probability of predator encounter (0–1) and (a) habitat zone, (b) reproductive phase and (c) number of independent birds in the group (within-subject effect). Standard errors are represented by bars in (a) and (b), and by dotted lines in (c). Rugs in (c) indicate distribution of raw observations of group encounters (top: encounter recorded; bottom: no encounter recorded).

Table 1
Model selection for the probability of predator encounter by focal groups

Model	K	AICc	Δ AICc	Weight	Cumulative weight	Deviance
*+N.adults WS+N.adults BS	7	292.6	0.0	0.26	0.26	278.2
*	5	292.9	0.3	0.22	0.48	282.7
*+N.adults	6	293.7	1.1	0.15	0.63	281.4
*+Group size	6	294.0	1.4	0.13	0.76	281.7
*+Group size WS+Group size BS	7	295.0	2.4	0.08	0.84	280.6
*+N.adults WS+N.adults BS+Zone	10	295.3	2.6	0.07	0.90	274.3
*+N.adults+Zone	9	296.8	4.1	0.03	0.94	278.0
*+Group size+Zone	9	296.9	4.3	0.03	0.97	278.2
*+Group size WS+Group size BS+Zone	10	297.3	4.7	0.02	0.99	276.4
Predictor	Sum of Akaike weights					
Duration	0.99					
Reproductive phase	0.99					
N.adults	0.18 ^a					
N.adults WS,BS	0.33 ^b	0.51 ^{a+b}				
Group size	0.16 ^c					
Group size WS,BS	0.10 ^d	0.26 ^{c+d}	0.77 ^{a+b+c+d}			
Zone	0.15					

All models with Δ AICc ≤ 5 are shown. Sum of Akaike weights (0–1) for putative predictors featuring in the final candidate model set are also presented. Predictors include: track duration ('duration'), reproductive phase ('nonbreeding', 'breeding', 'young' in the group), group size measures (number of independents in the group: 'N.adults'; total group size: 'group size') and habitat zone ('zone'). All models include the following terms (*): 'Group + duration + reproductive phase'. 'WS' and 'BS' identify within-subject and between-subject effects, respectively. 'K' is the number of parameters in the model; 'AICc' represents the Akaike information criterion corrected for sample size; Δ 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; 'deviance' is calculated as $-2\log$ likelihood of the model. Sum of Akaike weights is obtained by summing the Akaike weights of final models that included the predictor of interest. The superscripts a–d mark 'hierarchical' sums of Akaike weights (e.g. 0.51^{a+b} is the sum of 0.18^a and 0.33^b and represents the sum of Akaike weights of all models featuring N.adults as a predictor, either simply N.adults or dissected into within- and between-subject effects; similarly, 0.77^{a+b+c+d} represents the sum of Akaike weights of all models featuring measures of group size, be it N.adults or total group size).

for further evaluating the relative importance of putative predictors, we calculated the sums of Akaike weights of final candidate models featuring the predictor of interest (Burnham & Anderson 2002).

RESULTS

Predator Encounters and Attacks

Avian predators were encountered on a total of 66 of 256 tracking sessions (26%); of these, 14 resulted in an attack (21%) and two had fatal outcomes (3%). The most common predators encountered were large falcons (brown and peregrine; 65% of all predator encounters), with the remainder of encounters comprising small falcons (nankeen kestrels; 32% of encounters) and accipiter hawks (collared sparrowhawk and brown goshawk; 9% of encounters). Large falcons also accounted for the majority of attacks (11 of 14 attacks, of which one was fatal), with the

remainder of attacks being by accipiter hawks (3 of 14 attacks, one fatal); no attacks by small falcons were observed.

Associations with Group Size

Groups appeared to differ in their probability of encountering a predator (Group ID random variance component \pm SE = 0.14 ± 0.05 , with SE calculated using the minimum possible sample size of numbers of groups included, i.e. 53). At one extreme, one group never met a predator in the course of 15 h of observation (spread over 7 days), while at the other extreme, another group met predators on five out of six tracking sessions (4 days), over the course of 13 h. The top-ranking models suggested that the probability of a predator being encountered during a tracking session increased with the duration of the session, in habitat zones 1 and 2 compared with 3 and 4 (Fig. 1a), and when dependent young were present in the foraging group (Fig. 1b). After accounting for such

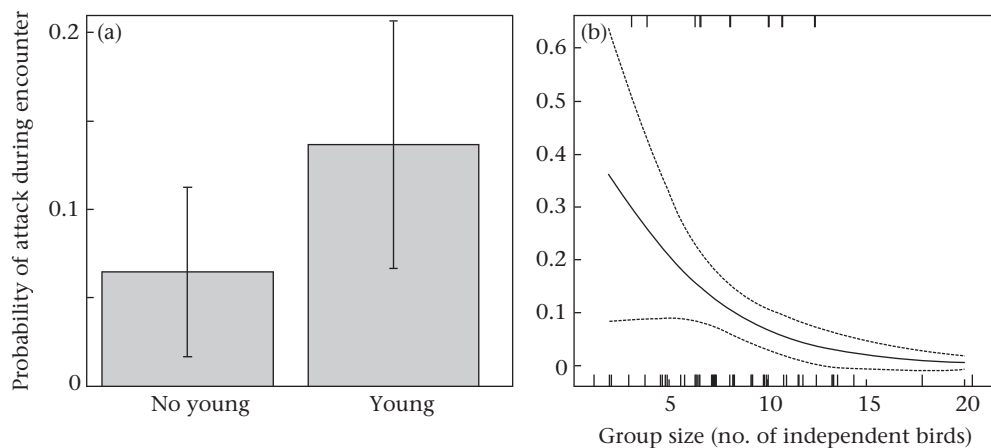


Figure 2. Relationship between probability of predator attack following encounter (0–1) and (a) reproductive phase, and (b) number of independent birds in the group (within-subject effect). Standard errors are shown by bars in (a), and by dotted lines in (b). Rugs in (b) represent distribution of raw observations of predator attacks (top: attack; bottom: no attack).

Table 2
Model selection for the probability of predator attack once a predator is met

Model	K	AICc	Δ AICc	Weight	Cumulative weight	Deviance
Group	2	72.9	0.0	0.2	0.20	69.1
Group+start time	3	73.2	0.4	0.17	0.37	66.9
Group+young	3	74.0	1.1	0.12	0.48	67.6
Group+start time+young	4	74.2	1.3	0.11	0.59	65.6
Group+start time+start time-2	4	75.0	2.1	0.07	0.66	66.4
Group+start time+N.adults	4	75.2	2.3	0.06	0.72	66.6
Group+start time+group size	4	75.4	2.5	0.06	0.78	66.8
Group+start time+N.adults WS+N.adults BS	5	76.0	3.1	0.04	0.82	65.1
Group+start time+young+N.adults	5	76.1	3.2	0.04	0.86	65.2
Group+start time+young+N.adults WS+N.adults BS	6	76.4	3.6	0.03	0.90	63.1
Group+start time+young+group size	5	76.4	3.6	0.03	0.93	65.5
Group+start time+group size WS+group size BS	5	76.5	3.6	0.03	0.96	65.6
Predictor	Sum of Akaike weights					
Start time	0.64					
Young	0.33					
N.adults	0.10 ^a					
N.adults WS,BS	0.07 ^b	0.17 ^{a+b}				
Group size	0.09 ^c					
Group size WS,BS	0.03 ^d	0.12 ^{c+d}	0.29 ^{a+b+c+d}			

All models with Δ AICc ≤ 5 are shown. Sum of Akaike weights (0–1) for putative predictors featuring in the final candidate model set are also presented. Predictors include: tracking start time ('start time'), reproductive phase ('young' present in the group versus 'no young' in the group), group size measures (number of independents in the group: 'N.adults'; total group size: 'group size'). 'WS' and 'BS' identify within-subject and between-subject effects, respectively; '^2' and '^3' refer to squared and cubic predictors, respectively. The superscripts a–d mark 'hierarchical' sums of Akaike weights. For further details see Table 1 legend.

effects, models that included either the number of independent birds or total group size featured in the final candidate model set, with the former contributing a slightly superior AICc score than the latter (Table 1). In addition, models separating number of independents into between-subject and within-subject effects were superior to corresponding models that did not separate the two contributions, with within-subject effects having greater effect size than between-subject effects (best model estimate of within-subject effect \pm SE = 0.26 ± 0.22 ; between-subject estimate \pm SE = 0.05 ± 0.22). The magnitude of the within-subject effect indicated that predators were 6.5% more likely to be recorded for every additional independent bird in the group (Fig. 1c).

The probability that a babbler group was attacked also varied with group identity (Group ID random variance component \pm SE = 1.74 ± 0.18 , N Groups = 53). The final candidate model set for the probability of predator attack suggested that, although attacks were not systematically biased across habitat zones (Table 1), they appeared to be two to three times more likely to occur when groups had dependent young (Fig. 2a, Table 2). In addition, measures of group size, particularly the number of independent group members, also featured in some models of the final candidate set, and again there was some support for distinguishing between within-subject and between-subject differences (Table 2). Accordingly, the probability of a predator attacking following an encounter with babblers was characterized by a roughly exponential decrease with increasing number of independents in the group (nested model estimate of within-subject effect \pm SE = -0.90 ± 0.66), while the between-subject effect was weaker and the direction appeared positive (nested model: estimate of between-subject effect \pm SE = 0.24 ± 0.61). The magnitude of the within-subject effect suggests that the probability of being attacked decreased rapidly when groups changed from the smallest to the average size, but declines thereafter were less pronounced (Fig. 2b).

Associations with Foraging Substrate

Babblers spent between 0% and 100% (mean \pm SE = $41 \pm 1.2\%$) of their time on the ground or in small shrubs, between 0% and 83% (mean \pm SE = $25 \pm 1\%$) in tall shrubs, and 0% to 95% (mean \pm SE = $33 \pm 1.4\%$) of their time in trees. Although the actual behaviour of birds was not always known, babblers are known to

spend most of their time foraging (Portelli et al. 2009), particularly in the early and late parts of the day when most of these data were collected. Thus, that babblers spent a large proportion of their time on the ground suggests that this represents the most profitable foraging substrate (see also Portelli et al. 2009). This suggestion is also supported further here because time of day featured in the final candidate models (see Table 3), and babblers spent most time on the ground in the early and late parts of the day when foraging is most intensive (Fig. 3a). Nevertheless, foraging on the ground might be more costly if it increases susceptibility to predation. In accordance, after controlling for the finding that ground foraging was unsurprisingly more common in habitat zones where trees were most lacking (zones 2 and 4; Fig. 3b), we found that the ground foraging strategy was less frequent when dependent young were travelling in the group (Fig. 3c), when group size was smaller (Fig. 3d) and in groups that commonly encountered predators (Fig. 3e).

Associations with Sentinel Behaviour

Sentinel behaviour was observed during 44 of 166 tracking sessions (26% of follows with sentinel information available; mean number of sentinel bouts per average tracking period = 0.5). According to the best model (Table 4), after we controlled for track duration, the frequency of observed sentinel behaviour increased from early to late morning, decreased slightly between midday and early afternoon and increased again in late afternoon (Fig. 4a). In addition, sentinel behaviour was more common in zones in which predators were frequently encountered (i.e. zones 1 and 2; Fig. 4b), and when babblers were foraging on the ground (Fig. 4c). The frequency of sentinel behaviour showed a 64% decrease between nonbreeding and breeding phases, and a seven-fold increase when fledglings or juveniles were present in the group (Fig. 4d). Group size, in terms of either the number of independents or total group size, did not feature in any model within the final candidate model set. Finally, although there seemed to be no clear effect of predator encounter on probability of observing sentinel behaviour (Table 4), within those tracking sessions during which a predator was met and sentinel activity was also observed, sentinel behaviour was more likely to be observed after the

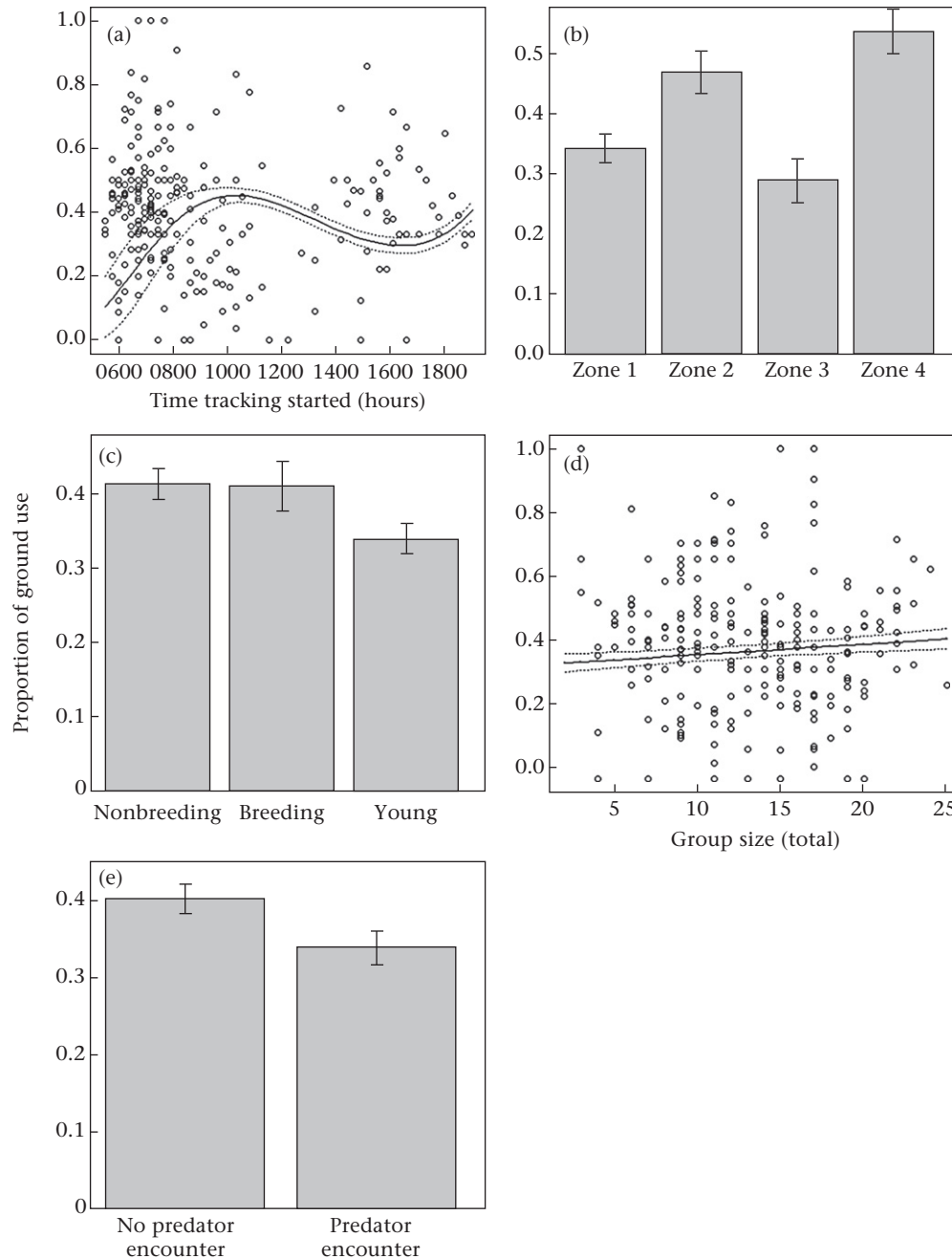


Figure 3. Proportion of ground substrate use (0–1) as a function of (a) time of day, (b) habitat zone, (c) reproductive phase, (d) total group size and (e) predator encounter. Standard errors are represented by dotted lines in (a) and (d), and by bars in (b), (c), (e). Open circles in (a) and (d) represent raw observations.

encounter with the predator rather than before (one-tailed binomial test: $P = 0.03$; Fig. 4e).

DISCUSSION

As far as we are aware, while previous investigations on other cooperatively breeding animals have considered interplays between perceived predation risk, sentinel behaviour, social foraging and local ecology (e.g. Manser 1999; Hollén et al. 2008, 2011; Bell et al. 2009; Ridley et al. 2010), this study is the first that simultaneously addressed the effects of actual predation risk on foraging behaviour and group size in a social cooperative vertebrate. Indeed very few studies of any species have been able to

evaluate predator encounter and risk of predation to individuals as they conduct their normal lives (but see for example Cresswell & Quinn 2011). Our results are therefore of broad interest in the context of predation threats in birds versus social aggregation, in addition to being specifically applicable to selection on group size in highly social cooperative breeders.

Our findings provide evidence that group behaviour is risk sensitive in an open habitat in which aerial predators are commonly encountered, and further suggest that both group size and other aspects of social organization may be adaptively fine-tuned to match local predation risk. There was some suggestion that predators were more likely to be encountered in some habitat zones than others, and groups were substantially more likely to

Table 3
Model selection for the amount of ground substrate use

Model	K	AICc	Δ AICc	Weight	Cumulative weight	Deviance
*+N.adults	13	425.7	0.0	0.26	0.26	398.1
WS+N.adults BS						
+group size	12	425.9	0.2	0.24	0.51	400.6
*	11	426.3	0.5	0.2	0.71	403.1
*+N.adults	12	426.4	0.6	0.19	0.90	401.0
*+group size	13	428.0	2.2	0.09	0.99	400.4
WS+group size BS						
Predictor	Sum of Akaike weights					
Start time	0.98					
Reproductive phase	0.98					
N.adults	0.19 ^a					
N.adults WS,BS	0.26 ^b					
Group size	0.24 ^c					
Group size WS,BS	0.09 ^d					
Zone	0.98					
Predator encounter	0.98					

All models with Δ AICc ≤ 5 are shown. Sum of Akaike weights (0–1) for putative predictors featuring in the final candidate model set are also presented. Predictors include: tracking start time ('start time'), reproductive phase ('nonbreeding', 'breeding', 'young' present in the group), group size measures (number of independents in the group: 'N.adults'; total group size: 'group size'), habitat zone ('zone') and whether a predator was encountered ('predator encounter'). 'WS' and 'BS' identify within-subject and between-subject effects, respectively; '^2' and '^3' refer to squared and cubic predictors, respectively. All models include the following terms (*): 'Group + start time + start time^2 + start time^3 + reproductive phase + zone + predator encounter'. The superscripts a–d mark 'hierarchical' sums of Akaike weights. For further details see Table 1 legend.

encounter predators and be attacked when foraging with dependent young. Accordingly, groups spent less time on the ground when foraging in areas where predator encounters were common and when dependent young were travelling with the group. Similarly, groups more often employed a sentinel when foraging on the ground and in zones where predator encounters were common, as well as when dependent young were present and following an encounter with a predator. In addition, although groups with large numbers of independent birds were more likely to encounter predators, we also found some evidence to suggest that such groups were less likely to be attacked. Therefore, the higher encounter rate for larger groups appeared to some extent to be compensated by a reduced probability of attack. Taken together with the expected exponential reduction in individual predation risk with increasing group size, owing to the dilution effect (Foster & Treherne 1981), these results suggest that living in large groups may bear significant antipredator benefits for chestnut-crowned babblers, and represent, at least in part, a behavioural strategy aimed at reducing the risk of predation.

One of the key problems with correlative research is disentangling cause from effect. Most notably for this study is whether or not apparent evidence of sensitivity to predation risk is an adaptive behavioural modification aimed at reducing risk, as suggested above, or whether perceived predation risk arises as a consequence of behavioural differences. This problem is most acute in relationships with group size (see below), but it may also be relevant for foraging substrate use and sentinel behaviour. For example, the negative association between ground foraging and predator encounters can be explained by babblers being less likely to feed on the ground following a predator encounter (as suggested above) or because when babblers forage on the ground, they are less likely to encounter a predator. We can reject the latter as a likely explanation because, if this were the case, we would expect groups to forage on the ground more frequently in the presence of dependent young, not less commonly. Similarly, in the case of sentinel behaviour, we can be confident that such behaviour was a response to predation risk, not

a cause, because sentinels were more common following, not preceding, predator encounters. Thus, our results suggest that both changes in foraging substrate use and sentinel behaviour occur as a direct consequence of predator encounters, and highlight that chestnut-crowned babblers are sensitive to the risk of predation, as is the case for many species (Lima & Dill 1990; Lima & Bednekoff 1999; Rodríguez et al. 2001; Caro 2005; Verdolin 2006; Griesser & Nystrand 2009; Ridley et al. 2010).

Whether group sizes are a cause or a consequence of predation risk, however, is more difficult to answer definitively in a correlational study. On the one hand, larger groups are more likely to be detected, either visually or acoustically, and provide by definition more potential targets during attacks. As a consequence, predators are known to locate and attack large groups of prey (Krause & Godin 1995; Krause & Ruxton 2002; Cresswell & Quinn 2011). On the other hand, despite the above costs of group living for prey species, there are also numerous benefits associated with grouping, even with regard to avoiding predation (Krause & Ruxton 2002; Caro 2005), leading to the possibility that sociality is, at least in part, an adaptive response to predation pressure in babblers. Distinguishing between these two alternative possibilities is compounded by the fact that the degree to which predator encounters arose through the detection of babblers by predators or the detection of predators by babblers is unclear. Nevertheless, we can make some testable predictions, the combination of which can elucidate the relative importance of the two possibilities. For example, if it were the case that relationships between group size and predation were due to predators targeting larger groups of babblers, we would predict: (1) greater between- than within-group effects on predator encounters and attacks; (2) a positive relationship between group size and attack probability; (3) large groups forage on substrates providing more cover from predators (i.e. tall shrubs and trees) and employ a sentinel more often (Bell et al. 2009; Ridley et al. 2010); and (4) group size is a superior predictor of predator encounters and attacks than the number of adult birds.

Overall, we found more evidence against rather than in support of these predictions. First, if predators simply preferred large groups, we would expect these to be targeted more than small groups (i.e. strong between-subject effects). That this was not the case raises the possibility that the within-subject association between group size and predator encounters arose because groups modify their size depending on the current threats of predation. There are two ways babblers may achieve this: in the short-term, through amalgamation of breeding units into social groups for foraging, a behaviour that is common (Portelli et al. 2009); or over the longer term, through a differential retention of group members and acceptance of immigrants. Second, the probability that groups experienced a predator attack following an encounter declined (not increased) with increasing group size, suggesting that predators do not specifically target large groups. Third, group size showed a positive relationship with ground foraging (not negative) and was not associated with sentinel frequency, despite the fact that both behaviours are apparently indicative of predation threat (see above). Fourth, the effects of number of independent group members and total group size on predator encounters/attacks were similar in all models, and if anything the former was a superior predictor than the latter. Together, these results suggest that the association between group size and predator encounter rate may have been, at least partly, driven by an adjustment of group size to the perceived (or actual) local threat of predation, and hence reflect an adaptive behavioural response to predation risk (van Schaik & Hörstermann 1994; Hill & Lee 1998; Banks 2001; Krause & Ruxton 2002; Caro 2005; Cresswell & Quinn 2011).

For predation risk to exercise an important selection pressure on group living, individuals must experience a decreasing risk of

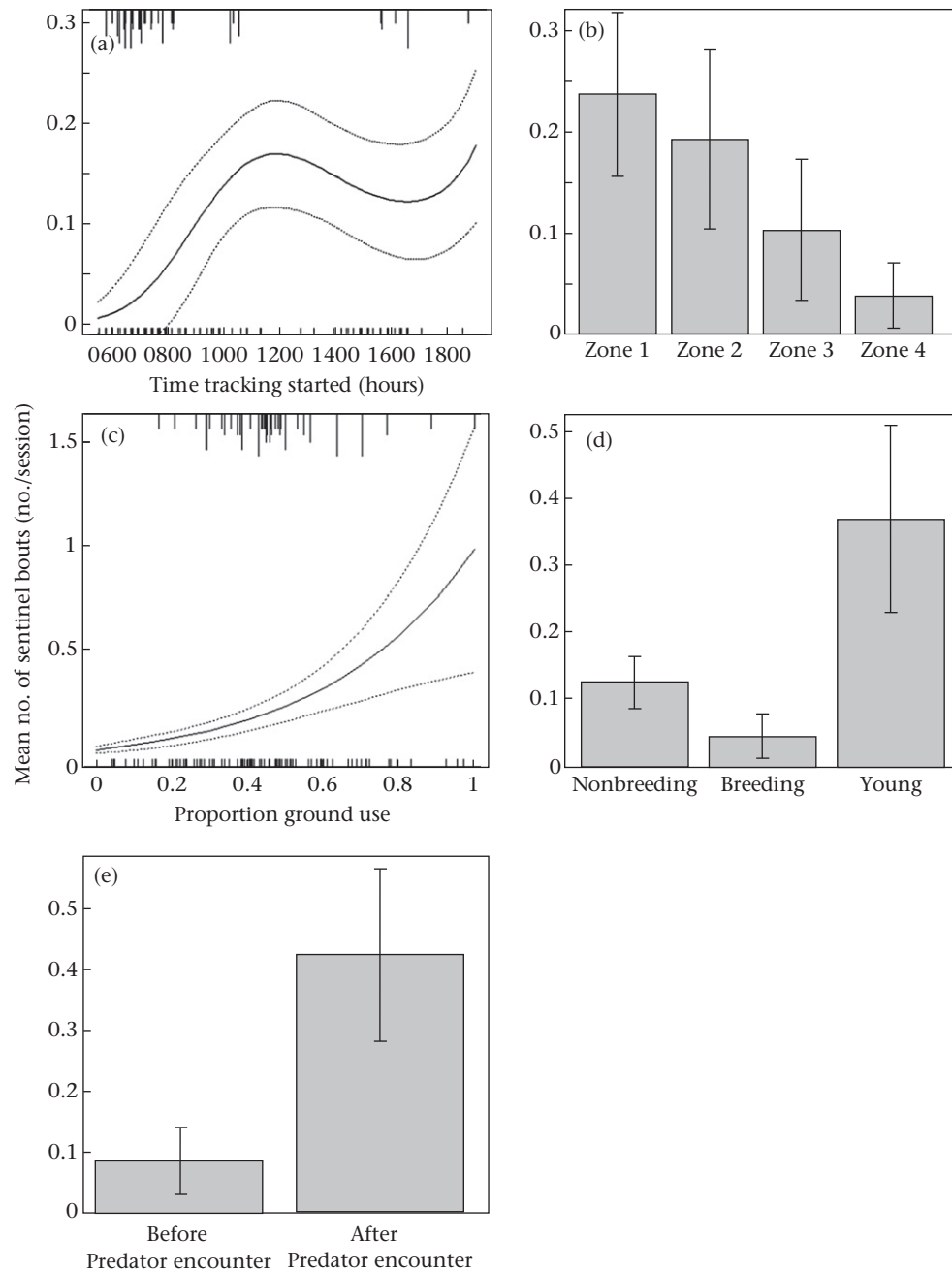


Figure 4. Relationship between number of instances of sentinel behaviour during tracking sessions and (a) time of day, (b) habitat zone, (c) proportion of ground substrate use and (d) reproductive phase. In (e), the mean number of observed sentinel instances before and after predator encounters is shown. Standard errors are represented by dotted lines in (a) and (c), and by bars in (b), (d), (e). Rugs in (a) and (c) represent distributions of raw observations of predator attacks (top: sentinel observed; bottom: no sentinel); length of top vertical lines is proportional to the observed number of sentinel instances (range 1–5).

predation with increasing group size (Krause & Ruxton 2002; Caro 2005). This raises the question of what are the likely antipredator benefits of group living for chestnut-crowned babblers. Active predator deterrence (Curio 1978; Caro 2005; Graw & Manser 2007) can be ruled out because babblers were never observed to mob aerial predators and always fled to cover. More probably, larger groups of babblers are more efficient at detecting predators early (Pulliam 1973; Elgar 1989; Krause & Ruxton 2002) and/or confusing predators during their escape (Landeau & Terborgh 1986; Cresswell & Quinn 2011) which involves diving into the nearest appropriate bush for cover. The association between group size and predator encounters may itself be driven, in part, by the superior predator

detection of large babbler groups (see above). In addition, that predators were less likely to attack large groups of babblers (both measures of group size) is consistent with a lower probability of success with such groups, presumably following early detection and/or confusion effects. Furthermore, group members can also benefit from selfish herd mechanisms (Hamilton 1971; Quinn & Cresswell 2006) or dilution effects (Foster & Treherne 1981; Whitfield 2003; Beauchamp & Ruxton 2008; Cresswell & Quinn 2011).

We provide a tentative estimate of the individual benefits of group living for chestnut-crowned babblers by calculating individual predation risk as a function of total group size. This

Table 4
Model selection for number of sentinel bouts observed within tracking sessions

Model	K	AICc	Δ AICc	Weight	Cumulative weight	Deviance
*+ground use	12	170.2	0.0	0.44	0.44	144.1
*+ground use+predator encounter	13	171.8	1.6	0.2	0.64	143.3
*+ground use+predator attack	13	171.9	1.7	0.19	0.83	143.4
*+tree use	12	172.3	2.2	0.15	0.98	146.3
Predictor	Sum of Akaike weights					
Start time	0.98					
Duration	0.98					
Reproductive phase	0.98					
Zone	0.98					
Predator encounter	0.20 ^a					
Predator attack	0.19 ^b 0.39 ^{a+b}					
Ground use	0.83 ^c					
Tree use	0.15 ^d 0.98 ^{c+d}					

All models with Δ AICc ≤ 5 are shown. Sum of Akaike weights (0–1) for putative predictors featuring in the final candidate model set are also presented. Predictors include: tracking start time ('start time'), reproductive phase ('nonbreeding', 'breeding', 'young' present in the group), group size measures (number of independents in the group: 'N.adults'; total group size: 'group size'), habitat zone ('zone'), whether a predator was encountered or attacked ('predator encounter' and 'predator attack'), proportion of ground substrate use and proportion of tree use ('ground use', 'tree use'). 'WS' and 'BS' identify within-subject and between-subject effects, respectively; '^2' and '^3' refer to squared and cubic predictors, respectively. 'WS' and 'BS' identify within-subject and between-subject effects, respectively. All models include the following terms (*): 'Group + start time + start time^2 + start time^3 + duration + reproductive phase + zone'. The superscripts a–d mark 'hierarchical' sums of Akaike weights. For further details see Table 1 legend.

calculation shows that individual risk of predation was characterized by a roughly exponential decrease with increasing group size (Fig. 5a). These results were not modified substantially by inclusion of the increased probability of being attacked when foraging dependent young were in the group, because their presence partially compensated for these additional costs through an increased dilution effect (Fig. 5b). Indeed, it is conceivable that less related group members benefit from the presence of juveniles, since they might be expected to constitute preferential targets of attack, although further research is required to examine this potential benefit. Our calculations show that, all else being equal, an individual babbler was, on average, increasingly less likely to be

the target of an attack until group size reached approximately 10 individuals, after which the probability declined only slightly, to level off at a size of roughly 20 individuals. While breeding units in chestnut-crowned babblers average six individuals (range 2–15), and the majority of these comprise fewer than 10 birds (Russell et al. 2010), units within social groups commonly forage together (Portelli et al. 2009). Accordingly, one possible explanation for joint foraging of breeding units is that it constitutes a strategy to reduce the risks of predation during breeding. Reassembly of social groups, through the amalgamation of breeding units and their new juveniles following reproduction, might represent a further adaptation to reduce predation risk.

In conclusion, we propose that predation risk is likely to promote group living in chestnut-crowned babblers, and in particular might represent an important factor for group size selection. Our tentative calculations suggest that being in groups of between 10 and 20 individuals would minimize individual predation risk. Such sizes are relatively large, yet they match reasonably closely the group sizes of both amalgamated foraging units during the breeding season and of social groups throughout periods of nonbreeding. Predation risk is commonly invoked to explain grouping in noncooperative species across a broad range of taxa (Caro 2005; Beauchamp 2010), but seldom in cooperative species (but see Clutton-Brock et al. 1999a; Heg et al. 2004; Doerr & Doerr 2006). This might be because in cooperative vertebrates helping is an inferior strategy to breeding, leading to suggestions that helpers must be constrained from dispersal (Emlen 1982; Koenig et al. 1992). Nevertheless, this does not imply that inherent benefits of grouping are always irrelevant to selection on delayed dispersal and group living in cooperative breeders (Brown 1987; Stacey & Ligon 1987; Koenig et al. 1992; Emlen 1994). In fact, inherent benefits of grouping might be particularly likely for species, such as chestnut-crowned babblers, where individuals live in challenging habitats and forage primarily by digging in the ground (Ford et al. 1988; Clutton-Brock et al. 1999a). We therefore hope that this study will stimulate a more in-depth examination of the potential benefits of group living through reduced predation in cooperative vertebrates. It is likely that both extrinsic constraints on dispersal and intrinsic benefits of grouping will be required to understand intraspecific and interspecific variation in group sizes, and to arrive at a single all-encompassing theoretical framework for understanding the evolution of cooperative breeding.

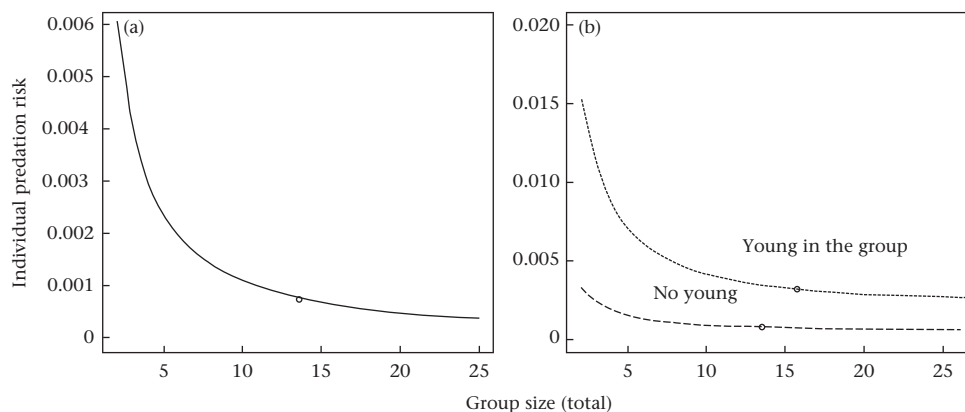


Figure 5. Estimated individual risk of predation as a function of group size: (a) overall individual risk, (b) individual risk when young are present in the group (top curve) versus not present (bottom curve). Open circles show estimated individual predation risk in correspondence of mean observed group size values. Individual risk was derived from model predictions of probability of predator attack during foraging as a function of total group size, divided by associated group size. For the purpose of this calculation, an 'overall predator attack' binomial variable was fitted as the response term in GLMM models ('0' = no attack during a tracking session; '1' = attack observed). Hence the predator attack function here differs from the one previously presented (attack within encounters) in that it is not limited to tracking sessions with predator encounters, but instead integrates probability of encounter with subsequent probability of attack.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2012.07.003>.

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