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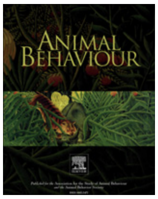

Effects of predation risk on foraging behaviour and group size: adaptations in a social cooperative species

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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.

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 km^2 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