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Variable fledging age according to group size: trade-offs in a cooperatively breeding bird

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Group living can provide individuals with several benefits, including cooperative vigilance and lower predation rates. Individuals in larger groups may be less vulnerable to predation due to dilution effects, efficient detection or greater ability to repel predators. Individuals in smaller groups may consequently employ alternative behavioural tactics to compensate for their greater vulnerability to predators. Here, we describe how pied babbler (*Turdoides bicolor*) fledging age varies with group size and the associated risk of nestling predation. Nestling predation is highest in smaller groups, but there is no effect of group size on fledgling predation. Consequently, small groups fledge young earlier, thereby reducing the risk of predation. However, there is a cost to this behaviour as younger fledglings are less mobile than older fledglings: they move shorter distances and are less likely to successfully reach the communal roost tree. The optimal age to fledge young appears to depend on the trade-off between reduced nestling predation and increased fledgling mobility. We suggest that such trade-offs may be common in species where group size critically affects individual survival and reproductive success.

Keywords: group size; predation; fledging age; nestling development; trade-off; pied babbler

1. INTRODUCTION

In social species, group size can have important consequences for both individual and group survival (Courchamp *et al.* 1999; Kokko *et al.* 2001). Additional group members may reduce predation rates via dilution effects (Foster & Treherne 1981), increased predator detection or greater ability to repel predators (Hass & Valenzuela 2002), and group productivity may increase as a result (Williams & Hale 2006). Cooperative breeders, where multiple group members assist in the production of young (Koenig & Dickinson 2004), have been shown to be particularly vulnerable to the negative effects of small group size. For example, the mutually exclusive tasks of hunting and pup-guarding render African wild dog (*Lycaon pictus*) packs with fewer than

five members particularly vulnerable to extinction (Courchamp *et al.* 2002). Similarly, the combined effects of predation pressure and limited food availability mean that meerkat (*Suricata suricatta*) groups with fewer than nine members typically go extinct (Clutton-Brock *et al.* 1999). To mitigate the negative effects of small group size, members of smaller groups might employ compensatory behavioural tactics. However, this often represents a trade-off. For example, small groups of pied babblers (*Turdoides bicolor*) do not have enough members to invest the same amount of time in vigilance as large groups. Consequently, small groups are more likely to tolerate fork-tailed drongos (*Dicrurus adsimilis*) that provide extra predator vigilance (Ridley & Raihani 2007a). However, drongos often steal food items from foraging babblers. Thus, small babbler groups trade-off the cost of kleptoparasitism against the benefits of increased predator detection.

Similar cost–benefit trade-offs may occur in other aspects of cooperative behaviour. For example, many cooperatively breeding birds feed young both in the nest and post-fledging (Langen 2000; Ridley & Raihani 2007b). Since begging calls risk attracting predators to the nest area, nestlings may be particularly vulnerable to predation (Haskell 1994). Thus, smaller groups, which may be less able to defend the nest area, may benefit from fledging young earlier. However, since fledging mass is often a good predictor of survival (Magrath 1991; Monrós *et al.* 2002), fledging early may be traded-off against allowing young a longer period to develop in the nest. In this study we describe the effect of group size on nestling predation and subsequent fledging age in the cooperatively breeding pied babbler. In this species, adults use purr calls to encourage young to leave the nest (Raihani & Ridley *in press a*). We hypothesized that nestling predation would be higher in smaller groups and that small groups would fledge young earlier as a result. Evidence on the trade-off that groups face between vacating the nest early to reduce predation, and the impaired mobility of young that fledge early are presented.

2. MATERIAL AND METHODS

Data were collected from September 2003 to May 2007 on 18 habituated babbler groups in the southern Kalahari (26°58' S, 20°49' E; see Raihani & Ridley (*in press a*) for a detailed site description). Pied babblers are medium sized (75–95 g) cooperatively breeding passerines. See electronic supplementary material for additional background information on pied babblers.

Linear mixed models and generalized linear mixed models ((G)LMMs) were used to assess the terms affecting (i) fledging age (days post-hatching), (ii) nestling provisioning rate, (iii) nestling predation and (iv) fledgling mobility. We investigated the effect of group size and nestling weight on fledging age. Mean nestling weight (g) was included in the model to control for the effect of nestling condition on fledging age. Since previous studies have found that young fledge in response to reduced parental provisioning (Ydenberg *et al.* 1995; Gjerdrum 2004; but see Harfenist 1995), we tested whether this occurred in pied babblers by comparing provisioning rates (g per chick h⁻¹) on fledging day to the days immediately before and after (see electronic supplementary material for feeding rate calculations). We recorded nestling and fledgling predation during the period that young could potentially fledge (13–19 days post-hatching). As fledgling predation was extremely rare during this period, we investigated the effects of group size (number of adults) and rainfall (as a proxy for food availability, see Cumming & Bernard (1997)) on nestling predation rate from day 13 to day 19 post-hatching. See electronic supplementary material for further methods and a list of common predators at this study site.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2007.0435> or via <http://www.journals.royalsoc.ac.uk>. Both authors contributed equally to this study.

Table 1. Output of (G)LMMs investigating response terms (a)–(e). (χ^2 is the Wald statistic for each term. See §2 and electronic supplementary material for model details. Group identity was included as a random term in all models. Brood identity was included as an additional random term in model (b). Effect sizes for significant explanatory terms (bold) are presented.)

response term	explanatory terms	χ^2	<i>p</i> -value	effect \pm s.e.
(a) fledging age (days post-hatching) <i>N</i> = 40 broods (12 groups)	constant			16.3 \pm 0.21
	group size	15.6	< 0.001	0.34 \pm 0.09
	weight	0.07	0.793	
(b) feeding rate (g per chick h ⁻¹) <i>N</i> = 55 observation days (35 broods; 9 groups)	constant			0.28 \pm 0.04
	days post-fledging	8.41	0.015	-1: 0.0 \pm 0.0 0: -0.09 \pm 0.04 1: 0.02 \pm 0.05
	group size	0.46	0.50	
(c) nestling predation nestlings predated/total <i>N</i> = 60 broods (15 groups)	constant			-1.72 \pm 0.55
	group size	5.10	0.024	-0.64 \pm 0.28
	rainfall	2.32	0.098	
(d) distance moved (m from nest) <i>N</i> = 33 broods (11 groups)	constant			49.1 \pm 7.72
	fledging age	7.99	0.005	22.5 \pm 7.96
	group size	0.07	0.785	
(e) roosting success 1 = successful; 0 = failed to roost <i>N</i> = 27 broods (10 groups)	constant			-0.36 \pm 0.46
	fledging age	4.99	0.025	1.73 \pm 0.77
	group size	0.09	0.766	

To investigate the costs of fledging early, we used two measures of offspring mobility on fledging day. First, we used handheld GPS trackers (Garmin, UK) to measure the total distance (m) that young moved on the day of fledging (see electronic supplementary material for further details). Second, we investigated whether young successfully reached the overnight roost tree on the day of fledging. Roosting was termed successful if at least half the brood reached the roost. Additional information on explanatory terms and statistical methods provided in the electronic supplementary material; sample sizes presented in table 1.

3. RESULTS

Fledging age ranged from 13 to 19 (mean: 16.4 \pm 0.1) days post-hatching. Nestlings from small groups fledged significantly earlier than those in larger groups (table 1). Provisioning patterns suggested that adults, rather than young, determined fledging age: we found that adults provisioned young less on the day of fledging compared with the days immediately before and after (figure 1). Fledging age varied with nestling predation risk. During the variable fledging period (13–19 days post-hatching), 26 out of 145 (mean per group: 23.9 \pm 10.0%) nestlings were predated, compared with just 4 out of 120 (mean per group: 3.1 \pm 2.0%) fledglings (chi-squared test: $\chi^2_1 = 13.9$, $p < 0.001$). Further analysis revealed that smaller groups were more vulnerable to nestling predation during this time (figure 2).

Newly fledged offspring had poor motor skills and many (44 out of 77, 57.1%) did not reach the overnight roost tree on fledging day. The mean distance moved by fledglings on fledging day was 49.5 \pm 8.1 (0–151) m. Young that fledged earlier were less mobile than those that spent a longer period in the nest: younger fledglings moved shorter distances from the nest tree on fledging day and were less likely to reach the overnight roost tree (table 1). Fledglings that failed to roost with adults typically roosted alone in small trees or on the ground. Four of the 44 (9.1%) fledglings that failed to reach the roost died overnight compared with 0 out of 33

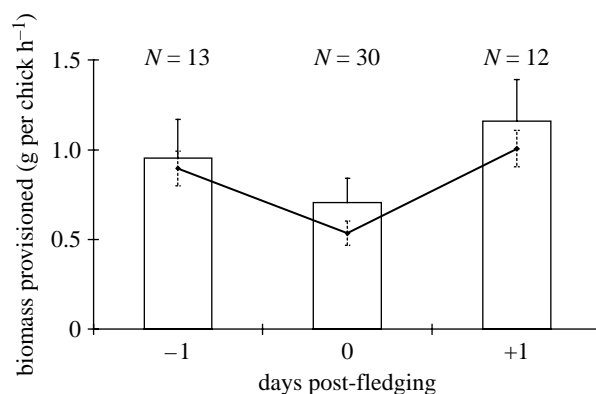


Figure 1. Biomass provisioned to young (g per chick h⁻¹) on the day before fledging, the day of fledging and the day after fledging. Sample sizes for each day are displayed on the graph. Mean values (\pm s.e.) from 35 broods (nine groups) are displayed as columns. The line of best fit was generated from the predictions of model (b) (table 1).

fledglings that succeeded to reach the roost tree, although this was not statistically significant (Fisher's exact test: $p = 0.20$).

4. DISCUSSION

In pied babblers, there seems to be a trade-off between fledging early and having a longer period to develop in the nest. Smaller groups are less likely to detect predators (Ridley & Raihani 2007a) and incur higher levels of nestling predation than larger groups during the period that young can potentially fledge (13–19 days post-hatching). As the risk of fledging predation during this period is comparatively low, selection acts on smaller groups to fledge young as early as possible in order to mitigate the risk of offspring predation. However, fledging early is likely to be costly: younger fledglings typically have worse motor skills than older fledglings. They did not move as far from the nest site and were less likely to make

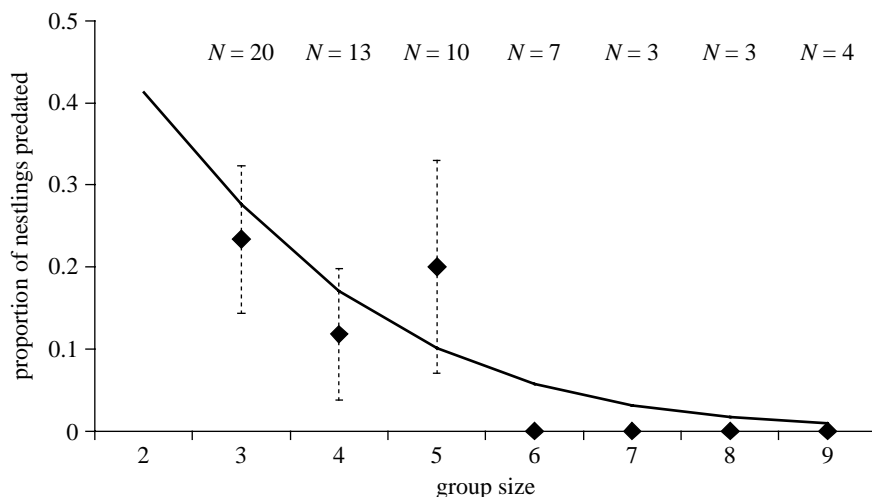


Figure 2. The relationship between group size and the proportion of all nestlings that were predated in the period 13–19 days post-hatching. Mean values (\pm s.e.) from 60 broods (from 15 groups) are displayed. The line of best fit was generated from the predictions of model (c) (table 1). Sample sizes for each group size are displayed on the graph.

it to the overnight roost. This is unlikely to be inconsequential: fledglings that failed to roost with adults sometimes died, perhaps due to the thermoregulatory costs of roosting alone (duPlessis & Williams 1994) or increased vulnerability to nocturnal predators. Given the potential costs of fledging early, we might expect nestlings to simply remain in the nest until adults signal that a predator is approaching. However, the poor motor skills of newly fledged young may preclude this as a viable strategy, as they cannot fly (Raihani & Ridley *in press a*) and are unlikely to be able to outrun predators.

Fledging seems to be precipitated by adults, rather than offspring in this species. It is unlikely that adults in smaller groups fledged young earlier in order to terminate investment in offspring, since young continue to receive food from adults for an extended period post-fledging (Ridley & Raihani 2007b). Previous work on pied babblers has shown that adults condition offspring to associate purr calls with food delivery, and that hungry offspring show stronger responses to purr calls (Raihani & Ridley *in press a,b*). Adults give purr calls most frequently on fledging day to lead young from the nest (Raihani & Ridley *in press a*). Here we show that adults provisioned offspring at a lower rate on fledging day, relative to the surrounding days. Previous research has predicted that reduced provisioning will precipitate fledging (Ydenberg *et al.* 1995). By feeding young less than normal, adult babblers may therefore have increased the chances that nestlings would leave the nest in response to purr calls.

The data presented here suggest that pied babblers trade-off the cost of fledging young early against the risk of nestling predation, which is higher in smaller groups. Adjusting behavioural tactics according to group size may be a beneficial aspect of many cooperative breeding behaviours and future work on the trade-offs faced by individuals in groups of sub-optimal sizes may be rewarding.

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- Clutton-Brock, T. H., Gaynor, D., McIlrath, G. M., Maccoll, A. D. C., Kansky, R., Chadwick, P., Manser, M., Skinner, J. D. & Brotherton, P. N. M. 1999 Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* **68**, 672–683. (doi:10.1046/j.1365-2656.1999.00317.x)
- Courchamp, F., Clutton-Brock, T. & Grenfell, B. 1999 Inverse density dependence and the Allee effect. *Trends Ecol. Evol.* **14**, 405–410. (doi:10.1016/S0169-5347(99)01683-3)
- Courchamp, F., Rasmussen, G. S. A. & Macdonald, D. W. 2002 Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog *Lycaon pictus*. *Behav. Ecol.* **13**, 20–27. (doi:10.1093/beheco/13.1.20)
- Cumming, G. S. & Bernard, R. T. F. 1997 Rainfall, food abundance and timing of parturition in African bats. *Oecologia* **111**, 309–317. (doi:10.1007/s004420050240)
- duPlessis, M. A. & Williams, J. B. 1994 Communal cavity-roosting in cooperatively-breeding green woodhoopoes: consequences for energy expenditure and the seasonal pattern of mortality. *Auk* **111**, 292–299.
- Foster, W. J. & Treherne, J. E. 1981 Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**, 466–467. (doi:10.1038/293466a0)
- Gjerdrum, C. 2004 Parental provisioning and nestling departure decisions: a supplementary feeding experiment in tufted puffins (*Fratercula cirrhata*) on Triangle Island, British Columbia. *Auk* **121**, 463–472. (doi:10.1642/0004-8038(2004)121[0463:PPANDD]2.0.CO;2)
- Harfenist, A. 1995 Effects of growth-rate variation on fledging of Rhinoceros Auklets *Cerorhinca monocerata*. *Auk* **112**, 60–66.
- Haskell, D. 1994 Experimental evidence that nestling begging behaviour incurs a cost due to nest predation. *Proc. R. Soc. B* **257**, 161–164. (doi:10.1098/rspb.1994.0110)

- Hass, C. C. & Valenzuela, D. 2002 Anti-predator benefits of group living in white-nosed coatis (*Nasua narica*). *Behav. Ecol. Sociobiol.* **51**, 570–578. (doi:10.1007/s00265-002-0463-5)
- Koenig, W. & Dickinson, J. 2004 *Ecology and evolution of cooperative breeding in birds*. Cambridge, UK: Cambridge University Press.
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. B* **268**, 187–196.
- Langen, T. A. 2000 Prolonged offspring dependence and cooperative breeding in birds. *Behav. Ecol.* **11**, 367–377. (doi:10.1093/beheco/11.4.367)
- Magrath, R. D. 1991 Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *J. Anim. Ecol.* **60**, 335–351. (doi:10.2307/5464)
- Monrós, J. S., Belda, E. J. & Barba, E. 2002 Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos* **99**, 481–488. (doi:10.1034/j.1600-0706.2002.11909.x)
- Raihani, N. J. & Ridley, A. R. In press *a*. Adult vocalizations during provisioning: offspring response and post-fledging benefits in wild pied babblers. *Anim. Behav.* (doi:10.1016/j.anbehav.2007.02.025)
- Raihani, N. J. & Ridley, A. R. In press *b*. Experimental evidence for teaching in wild pied babblers. *Anim. Behav.*
- Ridley, A. R. & Raihani, N. J. 2007 *a* Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behav. Ecol.* **18**, 324–330. (doi:10.1093/beheco/arl092)
- Ridley, A. R. & Raihani, N. J. 2007 *b* Variable post-fledging care in a cooperative bird: causes and consequences. *Behav. Ecol.* (doi:10.1093/beheco/arm074)
- Williams, D. A. & Hale, A. M. 2006 Helper effects on offspring production in cooperatively breeding brown jays (*Cyanocorax morio*). *Auk* **123**, 847–857. (doi:10.1642/0004-8038(2006)123[847:HEOOPI]2.0.CO;2)
- Ydenberg, R. C., Clark, C. W. & Harfeinst, A. 1995 Intraspecific fledging mass variation in the *Alcidae*, with special reference to the seasonal fledging mass decline. *Am. Nat.* **145**, 412–433. (doi:10.1086/285747)