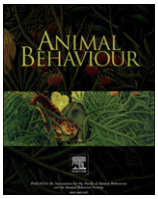
Animal Behaviour 82 (2011) 861–867

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Helped ground tit parents in poor foraging environments reduce provisioning effort despite nestling starvation

Xin Lu*, Tonglei Yu, Dianhua Ke

Department of Zoology, College of Life Sciences, Wuhan University

ARTICLE INFO

Article history:
Received 22 November 2010
Initial acceptance 4 January 2011
Final acceptance 6 July 2011
Available online 11 August 2011
MS. number: 10-00814R

Keywords:
environmental variability
ground tit
helping behaviour
kin selection
life history
Parus humilis

Life history theory views parental effort as a dynamic response to current productivity benefits and personal survival costs. Classical provisioning models specific to avian cooperative breeding systems predict that nestling starvation caused by local food limitation will induce helped parents to maintain their effort to ensure fledging success. Yet, food shortages may impose such a high provisioning cost that selection favours parents that lighten their workload at the expense of offspring productivity. We tested this alternative prediction with the ground tit, *Parus humilis*, which is an insectivorous, facultative cooperative breeder; helpers are mostly philopatric male offspring. Our study was based on data from three breeding seasons over which rainfall, and hence food resources, varied greatly. Total amount of food delivered to the young was highest for group-fed broods in food-rich environments, although helped male and female parents invested less than their counterparts with no helpers, and provisioning rate of the latter in both types of environmental conditions was similar to that of group-fed broods in food-poor environments. The variation in care level was mirrored by the observed pattern of partial brood loss, the single largest cause limiting productivity. The lowered effort in association with increased brood reduction under poor foraging conditions suggests ground tit parents with helpers trade future fitness against current reproduction to cope with harsh, unpredictable environments. This finding broadens our understanding of interspecific variability of parental response to the presence of helpers across ecological gradients.

In most avian cooperative breeding systems, philopatric offspring assist their parents in raising subsequent broods (Emlen 1997). Inclusive fitness benefits deriving from kin selection, which may arise through either increasing the group's productivity or lightening the breeders' workload, are assumed to be the major force driving helpers to help (Cockburn 1998). Which of these two sources of inclusive fitness is provided by a specific cooperative system depends largely on the investment strategies of parents that receive help. If parents maintain their care level in response to the presence of helpers, the total amount of food delivered to the nest, compared with those receiving no help, will be higher, potentially allowing parents to produce more or higher-quality offspring (Heinsohn 1992; Dickinson et al. 1996; Hatchwell et al. 2004; Blackmore & Heinsohn 2007). Alternatively, if parents reduce their own effort in response to help, they may save energy and thus enjoy a greater probability of surviving and breeding again in subsequent years (Crick 1992; Cockburn 1998; Khan & Walters 2002; Meade et al. 2010). The former parental strategy has been described as additive and the latter compensatory (Hatchwell 1999).

Based on an interspecific comparative approach, Hatchwell (1999) proposed a proximate cause behind the two care strategies: where nestling starvation is common, parental reactions tend to be additive so that partial brood loss (brood reduction) can be avoided; by contrast, if nestlings experience no starvation, compensatory responses will prevail and allow parents to allocate more energy towards self-maintenance at low risks of brood reduction. The availability of food in environments is a key predictor of nestling starvation (Magrath 1990; Emlen & Wrege 1991). Therefore, parents should adopt the additive strategy in food-poor habitats and the compensatory one when food resources are rich. This prediction was fulfilled in a study on the rufous treecreeper, *Climacteris rufa* (Luck 2002). Circumstantial evidence for it also comes from several other studies, which showed a significant positive helper effect on reproductive success in adverse environments but a less obvious effect in favourable environments (reviewed in Covas et al. 2008).

Life history theory argues that parental effort is a dynamic response to the benefits and costs of feeding offspring (Williams 1966; Roff 1992). Provisioning young is energetically expensive for birds if performed at high levels (Clutton-Brock 1991), as indicated by a negative relationship between individual feeding effort and both

---

* Correspondence: X. Lu, Department of Zoology, College of Life Sciences, Wuhan University, Wuhan 430072, China.
E-mail address: luxinwh@gmail.com (X. Lu).

0003-3472/$38.00 © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
doi:10.1016/j.anbehav.2011.07.024

body condition (Heinsohn & Cockburn 1994; Canestrari et al. 2007) and survival of care-givers (Reyer 1984; Rabenold 1990; Khan & Walters 2002; Davis et al. 2005). Hence, a trade-off of future reproduction against current provisioning investment should be particularly critical for parents that breed where resources are scarce or unpredictable; in such cases costs of parental care will increase so that the prospects for survival would further be biased towards adults relative to young (Lindén & Møller 1989; Erikstad et al. 1998). A theoretical approach with respect to cooperative breeding behaviour proposed that helped breeders tend to compensate for any help they receive when poor foraging conditions lead to a steep cost curve that overrides potential benefits from producing more offspring (Heinsohn 2004). In a cooperative species, the laughing kookaburra, *Dacelo novaeguineae*, Legge (2000) found that helpers failed to increase the overall feeding rates to a brood, although nestling starvation was the single largest source of lost productivity in this species. The same pattern has been reported in two other species: the rufous vanga, *Schetba rufa* (Eguchi et al. 2002) and the white-browed scrubwren, *Sericornis frontalis* (Magrath & Yezerinac 1997). Legge (2000) suggested that feeding young may be so costly that load lightening would be more beneficial to lifetime fitness than increasing investment in current offspring. These theoretical and empirical results contrast with the traditional provisioning models that emphasize the benefit of increasing care for current offspring in stressful environments (Hatchwell 1999). Nevertheless, the idea that the importance of load lightening is mediated by food shortage needs to be strengthened through more empirical studies on species that experience much more food stress.

Moreover, provisioning efforts often differ between cooperative group members (e.g. Wright 1998; Legge 2000; Doerr & Doerr 2007). Males and females may not follow the same provisioning rule when responding to the presence of helpers (Hatchwell 1999). For example, males of the Seychelles warbler, *Acrocephalus sechellensis*, reduced whereas females maintained their feeding rate with increased alloparental care (Komdeur 1994). This was the case for the long-tailed tit, *Aegithalos caudatus*, at larger brood sizes and the opposite was true at smaller brood sizes (Meade et al. 2010). Helpers that help relatives are expected to respond to the needs of nestlings, as the parents do, to gain inclusive fitness from enhanced production of offspring (Wright 1998; MacColl & Hatchwell 2003). On the other hand, helpers can gain direct fitness benefits from territory inheritance (Woolfenden & Fitzpatrick 1978). Therefore, care decisions made by helpers should also depend on trade-offs between current investment in helping and future reproduction of their own. Exploring individual provisioning strategies will provide further insight into the adaptive nature of helping behaviour (Heinsohn 2004).

We assessed provisioning strategies of the cooperatively breeding ground tit, *Parus humilis*, a burrow-nesting passerine endemic to alpine tundra on the Tibetan plateau. The birds live in all-purpose family territories year round. Pairs form monogamously and 28% (19–39%) of pairs have helpers at the nest. Almost all helpers are the breeders' male offspring from the last breeding season. These sexually mature 1-year-old individuals stay home probably because of their failure to meet a mate dispersing from other territories (Ke 2009). Ground tits feed almost exclusively on soil arthropods. As in the case of other insectivorous birds, including cooperative breeders (Emlen & Wrege 1991; Cockburn et al. 2008; Covas et al. 2008), rainfall during the breeding season is a key factor limiting their food availability. Rainfall in the study area varies considerably from year to year, and the quality of territories occupied by different ground tit pairs differs in terms of food abundance associated with soil moisture and vegetation condition (Ke 2009). This provided a good opportunity for us to investigate provisioning efforts in relation to local food availability.

In addition to their monogamous mating and facultative cooperative breeding, the following features of ground tit groups in our study area allowed us to control for some potential factors interacting with provisioning effort. (1) Extragroup paternity is very rare (0.3% of 363 young) and the helpers, as the helped breeders' first-order male relatives, never share group paternity; there is as yet no case of intraspecific brood parasitism (Johannessen et al. 2011). This contrasts with the social system of another ground tit population in northeastern Tibet (Du & Lu 2009; Wang & Lu 2011). (2) Annual breeding of the ground tits is restricted to a short time window during which a pair produces a single brood (double-brooded cases are noted sporadically, 1% of 208 nests); renesting occurs rarely owing to the low rate of complete nesting failure (1% of 188 nests). (3) Nest predation seems to be of little importance in our study system, as the birds nest in cavities and visually hunting predators are almost absent during daytime.

METHODS

Study Area and Study Population

Field work was carried out at Dangxiong (30°28′N, 91°05′E, elevation 4300 m), northern Tibet. This study area is open and flat, with a river running across it. It has an annual mean temperature of 1.7 °C (minimum: −9.3 °C in January; maximum: 10.9 °C in July) and annual total precipitation 441 mm, 78% of which falls between May and August (records over the period 1980–2009 were obtained from a weather station situated in the area). Almost no snow cover accumulates as a result of the low winter precipitation and the strong solar radiation (2911 h per year).

We have monitored the ground tit population since 2005 within a study plot of 480 ha in which 36–51 pairs nest. During the nonbreeding season, the birds live on permanent territories of 2.2–17.2 ha (mean ± SE = 5.7 ± 0.6, $N = 42$) in social groups consisting of parents, philopatric young males and immigrants (mostly yearling females) from other territories, with group size ranging from two to eight birds (4.2 ± 0.2, $N = 58$). When breeding, the groups break up. The original pairs, if both the male and female members survive between years (35% of 161 between-year pairs), persist on their initial territories as nesters, whereas widowed males (21% of 161 pairs) and females (11%) acquire a new mate, staying in or leaving the previous territories. No divorce has been recorded (all the remaining 32% of 161 pairs disappeared from the study plot). Breeding territories are slightly smaller (4.9 ± 0.3 ha, range 1.4–17.1 ha, $N = 98$) than winter territories. Yearlings of both sexes are capable of reproducing in their first spring, but some males remain on their natal territories acting as helpers, which participate in all parental activities including burrow building, feeding the incubating female and nestlings and defending territory. Most helpers (91% of 52) help only once, and then they acquire breeding status through either inheriting or budding off part of the natal territories, or filling the neighbouring vacancies (Ke 2009). The breeding period (measured as first-egg date) lasts from early May to mid-July, during which a breeding pair usually produces one brood. Clutch size varies between four and eight eggs (mean ± SE = 6.3 ± 0.8, $N = 56$) and brood size at hatching ranges from three to eight nestlings (5.5 ± 1.1, $N = 47$). Incubation is undertaken by females alone for 15–16 days, and nestlings are fed by both parents and helpers, if any, for 24–26 days. After fledging, juveniles continue to be reliant on adults for food for up to 1 month (Peng 2007).

Collecting General Data

Every year, all ground tit nests within the study plot were located. Ground tits excavate one burrow in spring for reproduction and