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Life history traits associated with low annual fecundity in a central African Parid: the Stripe-breasted Tit *Parus fasciiventer*

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Abstract Most *Parus* species live in the tropics or sub-tropics, and are likely to show life history traits associated with relatively high survival and low fecundity. Based on a 15-year study, we provide the first detailed account of the life history traits of an equatorial Parid, the Stripe-breasted Tit *P. fasciiventer*, which we contrast with published accounts of north temperate races of the Great Tit *P. major*. Stripe-breasted Tits fledged a mean of just 1.62 offspring clutch⁻¹, but laid up to four clutches year⁻¹ (mean 1.72) over 11 calendar months, raising their mean annual fecundity to 3.09 fledglings female⁻¹, less than half that of European Great Tits but double that of single-brooded southern African congeners. During incubation, Stripe-breasted and Great Tit females showed similar levels of nest attentiveness, spending 84 and 83–86 % of each 24-h period on the nest, respectively. In contrast, Stripe-breasted Tit parents provisioned at just 10–18 % of the rates recorded for European Great Tits, suggesting that parental investment or prey availability in their respective habitats

differed to a similar degree. Consequently, Stripe-breasted Tit nestlings grew more slowly, remained in the nest 4.6 days (20 %) longer, but fledged with proportionately longer wings, perhaps improving their ability to avoid predation. Offspring were last recorded receiving parental care at a mean of 81 days post-fledging (four times longer than is typical of European Great Tits) and remained with their parents for up to 3 years. Helpers were recorded at 61 % of Stripe-breasted Tit nests, and 76 % of breeding adults had helpers during at least one breeding attempt. While latitudinal comparisons often focus on clutch size, much greater disparities were thus evident in other traits, including brood provisioning, the duration of post-fledging care and the incidence of cooperative breeding.

Keywords *Parus fasciiventer* · Fecundity · Nest attentiveness · Provisioning · Cooperative breeding · Post-fledging care

Zusammenfassung

Biologische Eigenschaften im Zusammenhang mit niedriger Fortpflanzungsrate bei einer zentralafrikanischen Paridenart: der Schwarzbrustmeise *Parus fasciiventer*

Die meisten *Parus*-Arten leben in den Tropen oder Sub-tropen, daher liegt es nahe, dass sie biologische Eigenschaften zeigen, die mit vergleichsweise hohen Überlebensraten und niedriger Fortpflanzungsrate in Zusammenhang stehen. Auf der Grundlage einer 15-jährigen Studie geben wir hier die erste ausführliche Beschreibung der Biologie einer äquatorialen Paridenart, der Schwarzbrustmeise *P. fasciiventer*, der wir in der Literatur veröffentlichte Darstellungen von Unterarten der Kohlmeise *P. major* aus den nördlichen gemäßigten Breiten

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gegenüberstellen. Die Ausflugrate bei den Schwarzbrustmeisen betrug im Mittel nur 1,62 Junge pro Gelege, es wurden jedoch über einen Zeitraum von elf Kalendernaten bis zu vier Gelege im Jahr produziert (Mittelwert: 1,72), was die durchschnittliche jährliche Fruchtbarkeit auf 3,09 flügge Jungvögel pro Weibchen steigerte; weniger als die Hälfte des Wertes für die europäischen Kohlmeisen, aber doppelt so viel wie bei den nur einmal im Jahr brütenden südafrikanischen Gattungsgenossen. Während der Bebrütungsphase waren die Weibchen von Schwarzbrustmeisen und Kohlmeisen in ähnlichem Maße am Nest anwesend und verbrachten 84 % beziehungsweise 83–86 % eines jeden 24-Stunden-Zeitraums mit Brüten. Im Gegensatz dazu betrug die Fütterungsrate der Schwarzbrustmeisen nur 10–18 % des bei den Kohlmeisen festgestellten Wertes, was darauf hindeutet, dass sich entweder der elterliche Aufwand oder aber die Beuteverfügbarkeit im jeweiligen Habitat im entsprechenden Maße unterschied. Infolgedessen wuchsen die Schwarzbrustmeisen-Nestlinge langsamer und blieben 4,6 Tage (20 %) länger im Nest, hatten beim Ausfliegen aber proportional längere Flügel, was möglicherweise ihre Fähigkeit verbessert, Beutegreifern zu entgehen. Im Schnitt wurde der Nachwuchs noch 81 Tage nach dem Aufliegen von den Eltern weiter versorgt (viertel länger als bei europäischen Kohlmeisen typisch) und blieb bis zu drei Jahren mit den Elternvögeln zusammen. An 61 % der Schwarzbrustmeisen-Nester konnten Helfer beobachtet werden und 76 % der brütenden Altvögel hatten bei zumindest einem Brutversuch Hilfe. Während sich Vergleiche zwischen Breitengraden häufig auf die Gelegegröße beschränken, offenbarten sich viel deutlichere Unterschiede bezüglich anderer Merkmale, darunter die Versorgung der Jungen, die Dauer der elterlichen Zuwendung nach dem Ausfliegen sowie das Auftreten kooperativer Bruten.

Introduction

Many tropical and south temperate bird species lay smaller clutches and appear to live longer than their north temperate counterparts (Moreau 1944; Lack 1947; Skutch 1950; Ashmole 1963; Cody 1966). This observation has become a central paradigm in life history theory, and has been attributed mainly to regional variation in the balance struck between fecundity and survival, mediated through resource constraints (Lack 1947; Ricklefs 1976), predation pressure (Skutch 1949; Slagsvold 1982) or parental restraint: long-lived species restricting their current breeding effort to safeguard their future breeding potential (Moreau 1944; Williams 1966; Martin 2002). While these hypotheses have occasionally been tested experimentally, life history theory has

advanced mainly through comparative studies, contrasting the breeding performance and survival of closely related taxa at tropical and temperate latitudes (e.g. König and Gwinner 1995; Martin et al. 2000; Simmons 2000; Bennett and Owens 2002; Martin 2002; McGregor et al. 2007).

The genus *Parus* is a geographically widespread group, its 23 species dominated numerically by tropical and sub-tropical taxa, of which the majority are confined to sub-Saharan Africa (65 % of the genus; Gosler and Clement 2007). Life history theory would therefore predict that most *Parus* species are likely to be long-lived ‘slow’ breeders, in the sense that they rear small broods with long developmental periods over the course of a protracted breeding season, and may suffer high rates of nest failure. Although well-studied north temperate races of the Great Tit *P. major* are thus likely to prove atypical of the genus in many important respects, only three *Parus* species have been described in any detail outside of the Palearctic. All three occur at sub-tropical latitudes in southern Africa, where they have been shown to rear small broods, provision slowly and to suffer high rates of nest failure (Tarboton 1981; Fry et al. 2000; Wiggins 2001; Hockey et al. 2005).

Where nest failure rates are high adults are under greater pressure to shorten incubation and nestling periods (Lack 1968; Slagsvold 1982; Skutch 1985), through increased nest attentiveness (Moreno 1989) and more rapid provisioning. Yet, paradoxically, many tropical and south temperate passerines appear to show lower levels of nest attentiveness and to provision their nestlings more slowly (Skutch 1949; but see Martin et al. 2000), perhaps reducing their daily energy expenditure on incubation, and its impact on their own survival (Martin 2002). Low attentiveness might also explain a tendency for tropical species to lay relatively large eggs, since these cool more slowly when left unattended (Martin et al. 2006; Martin 2008).

Here, we provide the first detailed account of the life history of an equatorial Parid, the Stripe-breasted Tit *P. fasciiventer*. Confined to montane rain forests of the Albertine Rift, the species’ restricted global range straddles the equator in central Africa (Harrap and Quinn 1996), where it experiences limited seasonal variation in temperature and day length, and rainfall in all months. Provisional findings have shown that Stripe-breasted Tits lay smaller clutches than north temperate Great Tits, have slower provisioning rates, sometimes breed cooperatively (Shaw 2003; Yatuha and Dranzoa 2010), and may have a higher annual survival rate (ca. 0.75; P. Shaw, unpublished) than is typical of adult Great Tits (ca. 0.50; Perrins 1979). Contrary to expectations, the two species show similar levels of nest attentiveness (Shaw and Cresswell 2014).

Based on a 15-year study, we contrast life history traits of the Stripe-breasted Tit with published estimates for three sub-tropical and one north temperate congener, and

examine the following life history predictions. First, that the clutch size, breeding success and annual fecundity of this equatorial Parid should be lower than those of its sub-tropical and north temperate congeners. Second, that latitudinal variation in *Parus* clutch and brood sizes are partly offset by differences in breeding frequency. Third, that the Stripe-breasted Tit has slower provisioning and growth rates than its temperate congener, despite brood size differences. Fourth, that it has a longer breeding season and developmental period, with extended post-fledging care. We assess the degree to which life history traits of this species and those of its north temperate congener have diverged, identifying those traits showing the greatest proportional disparity.

Methods

Study area and species

This study was conducted at the Institute of Tropical Forest Conservation (ITFC) field station at Ruhija, Bwindi Impenetrable Forest, SW Uganda (1°02'S, 29°46'E) during 1998–2012 (Fig. 1). Bwindi is part of a chain of montane forests in the Albertine Rift, and covers ca. 331 km² (Kasangaki et al. 2012). At ca. 2,330 m asl, the study area consists of steep ridges and hills with a mosaic of closed- and open canopy forest. Rain falls in all months of the year,

averaging 1,374 mm p.a. during 1987–2012 (ITFC, unpublished), and there is limited seasonal variation in temperature (Kasangaki et al. 2012) or day length (USNO 2012). Stripe-breasted Tits occur at low densities (ca. 8 birds km⁻²) in the study area, mainly above ca. 2,080 m (Shaw 2010). Adults are very similar in size to Great Tits *P. m. newtoni* in the British Isles, which are reportedly larger than *P. m. major* in Continental Europe and *P. m. minor* in Japan (Cramp and Perrins 1993; Harrap and Quinn 1996). For mean mass and wing lengths, see ESM Table 1.

Data collection

Twenty-five nestboxes were erected at Ruhija in 1995 (C.M. Perrins, D. Pomeroy, personal communication), rising to 80 by 2008. The boxes were constructed using 1.8–2.0 cm hardwood, had a mean volume of 2,760 cm³ and a 32-mm entrance hole, protected by a metal plate. Each box was inspected in most months during 1998–2000, and in all months during 2001–2012. Occupied nestboxes were checked at 2- to 3-day intervals, and daily at around anticipated laying, hatching and fledging dates. We defined the incubation period as the hatching date minus the date of clutch completion (day 0), and the nestling period as the fledging date minus the date of first hatching (day 0). Since no eggs were handled prior to completion of the incubation period (to avoid breakage), egg mass at laying was

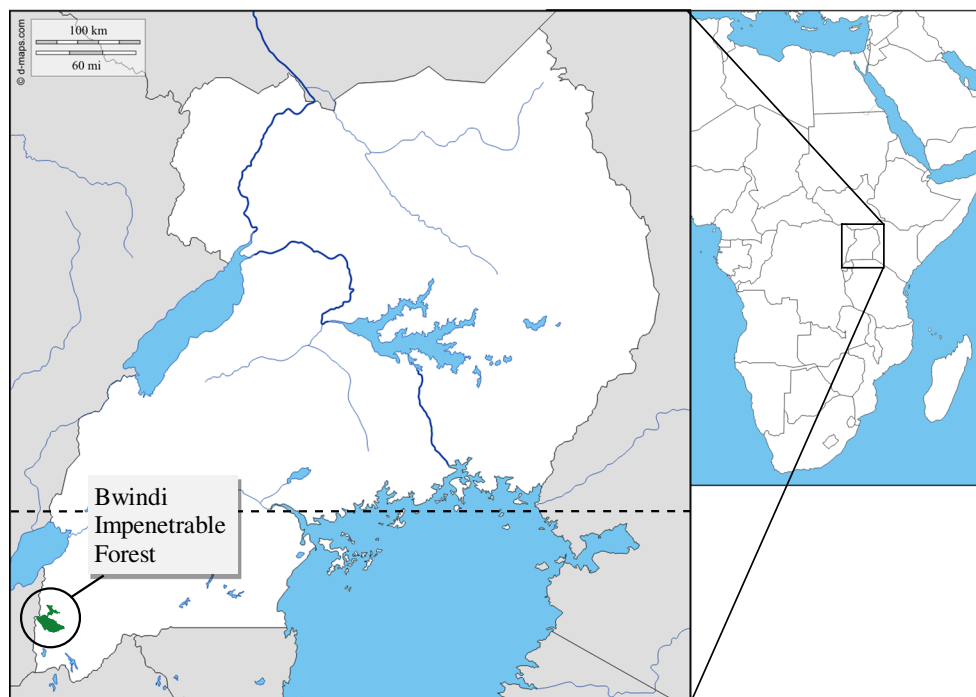


Fig. 1 Location of study area, Bwindi Impenetrable Forest, in SW Uganda. Dashed line equator

estimated from eggs that failed to hatch, using the formula $0.527(L \times B^2)$ (where L and B are measured in cm; after Schifferli 1973). We determined egg mass as a proportion of female body mass, the latter being measured just once during the nestling period, to minimise disturbance.

Nestlings were weighed (to the nearest 0.5 g) at 2- to 3-day intervals, mainly at ages 3–19 days ($n = 15$ –22 broods weighed day⁻¹). Wing length (maximum chord) was measured to the nearest mm, by either of three observers. Since these measurements can vary consistently between observers (e.g. Jenni and Winkler 1989), we compared the mass and wing lengths recorded for adults of known sex, but found no significant observer effects (Kruskal–Wallis test; $n = 39$ adults). Nestling deaths were attributed to predation if all nestlings disappeared between inspections or if body parts were found in the nestbox. Otherwise, deaths were attributed to starvation if preceded by weight loss, or if individual nestlings died on different days. From 2003, all nestlings were given a unique combination of four colour rings, and a mean of 80 % of breeders and helpers at each nest were thus identifiable ($n = 74$ nests). The duration of post-fledging care was estimated from sightings of ringed birds made opportunistically and, during 2008–2012, in the course of monthly nestbox inspections. Due to logistical constraints, it was not possible to allocate equal time to searching each territory. Of 127 fledglings ringed, 72 % were sighted at least 10 days post-fledging, and 58 % at least 50 days post-fledging. Juveniles were said to be receiving care if they were seen begging from or being fed by a parent or helper (after Verhulst and Hut 1996), and to be associating with their parents or helpers if seen foraging in the same or an adjacent tree.

Stripe-breasted Tits are multi-brooded (Yatuhia and Dranzoa 2010), with clutches laid in October to August inclusive (P. Shaw, unpublished). During the study period, egg laying peaked in December–January (50 % of clutches) and May–June (17 %; $n = 81$ clutches), each peak coinciding with one of the two dry seasons at Bwindi. Consequently, 1 October was taken as the start of the breeding year. Annual fecundity was estimated from the productivity of 22 marked breeding adults. Data for a given adult and breeding year were included only if the individual concerned was known to have survived from October to August of that year. Three bird-years were excluded because the individual was seen with unringed dependent juveniles, indicating that a breeding attempt had been missed, and a further 10 bird-years were excluded because the individuals concerned were unrecorded for most of the year in question, leaving a sample of 58 bird-years. During the laying, incubation and nestling periods, occupied nestboxes were watched from a discrete distance (up to 30 m) for periods of 1–7 h, between 0700 and 1900

hours ($n = 5,047$ h, 59 nests). All visits and the identity (and hence breeding status) of the individual concerned were recorded. Where possible, any food items brought were also recorded ($n = 16,323$ items, 68 nests), and the latter identified broadly as caterpillar/larva, adult Lepidoptera, and other adult invertebrate.

To estimate the proportion of nests at which helpers were present, we determined the mean number of hours of observation (following clutch completion) at which the first helper was detected, at all nests where helpers were ultimately recorded, and at which both parents were colour ringed (15.4 h, ± 2.991 SE, 36 nests). The incidence of cooperative breeding was then estimated for nests observed for ≥ 21.2 h (15.4 h + CL). Similarly, we determined the mean number of hours of observation required to detect all of the helpers ultimately recorded (21.6 h, ± 3.489 SE, 36 helped nests), and estimated the mean number of helpers nest⁻¹ from all nests observed for at least 28.5 h (21.6 h + CL; 47 nests).

Nest attentiveness was defined as the percentage of time spent inside the nestbox over a 24-h period (after Shaw and Cresswell 2014). Since the period of twilight is very short at 1°S, darkness lifts and falls rapidly, precluding any significant activity before or after sunrise and sunset. Hence, we assumed that incubating female Stripe-breasted Tits remain inside the nestbox between sunset (mean 1904 hours) and sunrise (mean 0657 hours; from USNO 2012). Using a linear mixed-effect model (see below), we calculated the mean proportion of time spent inside the box during the 12 h of daylight, between 0700 and 1900 hours, over days 4–15 of the incubation period. We multiplied the mean proportion of time spent incubating in each hour by mean day length (727 min) to estimate the amount of time spent on the nest during daylight hours, and hence throughout the 24-h period.

Published sources

Great Tit life history traits were extracted from published results for sites in continental Europe (*P. m. major*), the British Isles (*P. m. newtoni*) and Japan (*P. m. minor*). Where multiple published estimates were available for a given region, we used results from studies with the largest nest samples or spanning the longest time period. For most parameters, these were at Hoge Veluwe (52°05'N) or Vlieland (53°18'N), The Netherlands; Wytham Woods, Oxford (51°46'N), United Kingdom; and Tokyo (35°39'N) or Mt Gongenyama (33°22'N), Japan. Sources used are listed in Tables 1 and 2 and Figs. 3, 4 and 5. Life history traits of three southern African congeners were drawn from studies in the Transvaal, South Africa (24°29'S; Southern Black Tit *P. niger*; Tarboton 1981) and Daan Viljoen, Namibia (22° 30'S; Ashy Tit *P. cinerascens* and Carp's Tit

Table 1 Stripe-breasted Tit breeding productivity and duration, compared with three north temperate races of the Great Tit

Attribute	Stripe-breasted Tit <i>P. f. fasciiventer</i> Uganda	Great Tit			Sources	Details
		<i>P. m. major</i> Continental Europe	<i>P. m. newtoni</i> UK	<i>P. m. minor</i> Japan		
Mean clutch size	3.7	8.4–9.3	8.6–10.2	7.5–8.4	1–7	
Relative egg mass	9.3 %	9.0–10.2 %	8.4–9.3 %	–	8, 9, 10	Egg mass as % of female mass
Incubation period (days)	15.1	13.9	13.9	–	8, 11	Date 1st egg hatched minus date last laid
Hatching success	71 %	91 %	92–95 %	86–89 %	2, 4, 5, 6, 7	Excluding predated and deserted clutches
Brood size at hatching	2.6	8.2	9.1	7.1–8.0	5, 7, 12, 13	Where at least 1 egg hatched
Asymptotic mass (age, days)	18.8 (19)	17.7 (15)	18.5 (14)	15.2	6, 10, 13, 14	Mean asymptotic mass (g) and brood age (days)
Relative mass and wing length at fledging	91 %, 90 %	91 %, 76 %	–	–	15	Projected mass and wing length at fledging, as a % of adult value
Nestling period (days)	23.5	18.8	18.9	17.8–18.4	7, 8, 11, 12	Mean age at which broods fledged
Fledging success	81 %	90–92 %	90–96 %	81–100 %	2, 4, 5, 6, 7, 14	Excluding predated broods
Fledglings clutch ⁻¹	1.6	5.0–5.6	7.0	5.6	3, 7, 16	Fledglings per clutch laid (including failed nests)
Breeding success	46 %	65 %	80 %	61 %	7, 16, 17, 18	Fledglings as a % of eggs laid
	59 %	72–80 %	67 %	–	17, 18	% Clutches yielding 1+ fledgling
Mean clutches year ⁻¹	1.7	1.4	1.0	1.4	7, 16	Mean clutches female ⁻¹ year ⁻¹
Mean eggs year ⁻¹	6.4	11.8	8.7	11.0	7, 16	Mean eggs female ⁻¹ year ⁻¹
Annual fecundity	3.1	7.7	7.0	7.7	7, 16	Mean fledglings female ⁻¹ year ⁻¹

Detailed breeding parameters for Stripe-breasted Tit are given in ESM Table 1

Sources: 1, Kluijver (1951); 2, de Heij et al. (2006); 3, van Balen et al. (1987); 4, Perrins (1965, 1979); 5, Lack (1955); 6, Eguchi (1980); 7, Seki and Takano (1998); 8, Cramp and Perrins (1993); 9, Lessells et al. (2002); 10, Gibb (1950); Schifferli (1973); 11, Gibb (1950); 12, Royama (1966); 13, Nour et al. (1998); 14, van Balen (1973); 15, Orell (1983); 16, Bouwhuis et al. (2010); 17, McCleery and Perrins (1989); 18, Talloen et al. (2010)

P. carpi; Wiggins 2001). Those of other congeners were extracted from Harrap and Quinn (1996), Fry et al. (2000), Hockey et al. (2005) and Gosler and Clement (2007).

Data analysis

Breeding parameters were estimated from all 78 clutches or broods found, 2 of which were in natural cavities, the remainder in nestboxes. At 64 nests, one or both breeders were colour ringed ($n = 18$ breeding females, 15 breeding males), most breeders making multiple breeding attempts (ESM Table 2). To control for the effects of repeated measures from the same individuals, we estimated breeding parameters, nest attentiveness and provisioning rates from linear mixed-effects models (LMEs), using the *lme* function in R (R Development Core Team 2009). In each model, individual identity was entered as a random factor, and year, brood size, brood age and hour as fixed factors, as appropriate (ESM Table 3). Separate models were used to estimate breeding parameters for males and females. We

used a natural log transformation to normalise dependent variables, and obtained predicted values (controlling for the effects of individual identity and of each fixed factor) using the R *fitted* function. These values were then back-transformed. Residual plots were inspected for any obvious deviations from homoscedasticity or normality (Crawley 2013).

Daily nest survival rates were estimated for 71 nests, using a maximum-likelihood estimator based on Mayfield (1975), available in the program MARK (Cooch and White 2008). Peak nestling mass and projected wing-length at fledging were determined by fitting linear and quadratic regression models to mass and wing measurements from broods aged 13–23 and 8–22 days, respectively. Quadratic models were selected where they provided a significantly better fit than an equivalent linear model, based on an *F*-test of the residual sum of squares. Statistical tests were made using PASW[®] Statistics 19 software (SPSS, Chicago, IL, USA) and R (3.0.1; R Development Core Team 2009). All probabilities are quoted as two-tailed.

Table 2 Nest attentiveness, provisioning and growth rates of Stripe-breasted Tits, compared with three north temperate races of the Great Tit

Parameter	Measure	Stripe-breasted Tit	Great Tit	Races	Location	Sources
Nest attentiveness	% Time on nest 24-h ⁻¹ during incubation	84 % ^a	83 %	<i>P. m. major</i>	Netherlands	1
			86 %	<i>P. m. newtoni</i>	UK	2
Provisioning rate	Feeds nestling ⁻¹ h ⁻¹	2.0	2.8–3.6	<i>P. m. major</i>	Spain	3, 4
			4.2	<i>P. m. major</i>	Belgium	5
			4.4	<i>P. m. major</i>	Finland	3
			5.6	<i>P. m. major</i>	Netherlands	3
			12.7	<i>P. m. major</i>	Spain	3
			17.1	<i>P. m. major</i>	Belgium	5
	Feeds brood ⁻¹ parent ⁻¹ h ⁻¹	2.3	19.9	<i>P. m. major</i>	Finland	3
			23.0	<i>P. m. major</i>	Netherlands	3
			52–132	<i>P. m. minor</i>	Japan	6, 7
			204	<i>P. m. newtoni</i>	UK	8
			247	<i>P. m. major</i>	Finland	9
			2,499	<i>P. m. minor</i>	Japan	6
Nestling growth rate	g day ⁻¹ (days 2–9)	1.28	3,874	<i>P. m. newtoni</i>	UK	8
			4,669	<i>P. m. major</i>	Finland	10
			1.44–1.49	<i>P. m. major</i>	Finland, Netherlands	11, 12
	g day ⁻¹ (days 3–11)	1.32	1.54	<i>P. m. newtoni</i>	UK	13

Sources: 1, de Heij et al. (2008); 2, Bryan and Bryant (1999); 3, Sanz et al. (2000); 4, broods of 3–4; Barba et al. (2009); 5, Nour et al. (1998); 6, Royama (1966); 7, Eguchi (1985); 8, Gibb (1950); 9, Sanz et al. (1998); 10, Sanz et al. (1998); Cramp and Perrins (1993); 11, van Balen (1973); 12, Orell (1983); 13, Gibb (1950); Schifferli (1973)

^a Days 4–15 of incubation period

The duration of post-fledging care was estimated from sightings of 84 individuals fledged from 32 broods. Since fledglings associate closely in family parties we used broods as the unit of measurement instead of individuals. Also, since some broods seen shortly after fledging may have subsequently died before the age at which care is normally terminated, we included only those broods in which at least one member was re-sighted after the date on which they or a sibling were last seen receiving care (after Verhulst and Hut 1996). Since Stripe-breasted Tits show extended parental care (see below), broods less than 1 year old at the time of the analysis were excluded, to avoid bias.

Results

Fecundity

Linear mixed-effects models yielded a mean clutch size of 3.72 eggs (± 0.045 SE, range 2–5), producing 1.62 fledged offspring clutch⁻¹ (± 0.140 SE, range = 0–5, $n = 18$ females, 63 clutches; ESM Table 1). A mean of 1.72 clutches were laid year⁻¹ (maximum: 4), yielding 3.10 fledged offspring year⁻¹ (± 0.511 SE, range = 0–14, $n = 11$ females, 50 clutches). The results for males were slightly

lower; a mean of 1.50 breeding attempts year⁻¹, yielding 2.42 fledged offspring year⁻¹ (± 0.407 SE, range = 0–14, $n = 11$ males, 47 clutches). These figures suggest that 1.21–1.55 offspring were fledged breeding adult⁻¹ year⁻¹. Note, however, that helpers were present at 61 % of nests ($n = 49$ nests), and 76 % of breeding adults received help during one or more breeding attempts. Since nests were attended by a mean of 2.96 participants (parents and helpers; ± 0.143 SE), individual productivity was correspondingly lower: ca. 0.82–1.04 fledglings participant⁻¹ year⁻¹.

The daily nest survival rate was lower during the brood stage (0.988 ± 0.003 SE, $n = 60$ nests, 15 failed, 1133.5 exposure days) than the egg stage (0.996 ± 0.002 SE, $n = 71$ nests, 5 failed, 1,069.5 exposure days) ($t = 2.082$, $P < 0.05$). Egg losses through predation were low (4.4 % of 274 eggs), as was the hatching success of eggs that survived the incubation period: 70.6 % (± 3.4 % SE, $n = 16$ females, 61 nests). Nestling mortality (29.4 % of 194 nestlings) was attributed to predation (61 % of deaths), starvation (30 %) or unknown causes (9 %). Predation accounted for partial clutch- or brood losses (11 % of 18 cases) as well as entire losses, and was attributed to attacks by ants (33 %) as well as vertebrates (67 %). Circumstantial evidence suggests that the latter included African Harrier Hawk *Polyboroides typus*.

The success or failure of a female's first breeding attempt in a given study year had no significant effect on the likelihood of her laying a second clutch in that year (Fisher's exact: $P = 1.00$, $n = 27$ female-years). Although the median interval between first and second breeding attempts was shorter if the first attempt failed (failure date to clutch initiation = 11 days, $n = 6$ female-years) than if it was successful (fledging date to clutch initiation = 67 days, $n = 11$ female-years), this difference was only marginally significant (Kruskal–Wallis = 3.28, 1 *df*, $P = 0.070$).

Between-year differences in breeding parameters were significant in 15 out of 19 LME models (ESM Table 3). Over a 10-year period (2002–2003 to 2011–2012), during which ca. 50–80 nestboxes were available and checked at least monthly, the number and productivity of breeding attempts year⁻¹ varied substantially. From three to 19 clutches were laid year⁻¹ (median 5.5), containing 11–73 eggs (median 20) and yielding 2–51 fledglings (median 7.5). When corrected for variation in the number of nestboxes deployed, the numbers of clutches, eggs and fledglings produced year⁻¹ varied by a factor of 4.8, 6.1 and 25.5, respectively. Mean clutch size (range 3.0–4.1) and the mean number of fledglings clutch⁻¹ (0.7–2.7) varied between years by a factor of 1.4 and 5.8, respectively. This difference was due to variation in hatching success (range 0.33–0.88; median 0.68) and fledging success (range 0.16–1.00; median 0.74), which varied by a factor of 2.7 and 6.2, respectively.

Nest attentiveness and provisioning rates

During the laying period, females spent 2–4 % of daylight time in the nestbox, rising to 37 % on day 0 (clutch completion). A linear mixed effects model indicated that females spent a mean of 68.0 % (± 0.23 % SE) of daylight time on the nest; equivalent to 84 % of each 24-h period ($n = 14$ females, 46 clutches, 1,223 h). Nest attentiveness declined post-hatching, to just 6 % of daylight time by day 11 (Fig. 2).

Caterpillars accounted for 72 % of identified items, the remainder comprising adult Lepidoptera (4 %) and other invertebrates (24 %; $n = 16,323$ items, 68 nests). Each nestling received a mean of 2.04 feeds h⁻¹ (± 0.011 SE, $n = 2,626$ h, 47 broods), this rate increasing by a factor of 1.7 between the first and last three days of the nestling period (from 1.67 to 2.80 feeds nestling⁻¹ h⁻¹). Since a rise in the mean provisioning rate could reflect a progressive shift in the quality of broods surviving, rates were recalculated for those broods in which all nestlings survived to fledge. The mean provisioning rate for these broods (2.05 feeds nestling⁻¹ h⁻¹, ± 0.013 SE, 27 broods) did not differ significantly from the main sample, and showed a similar

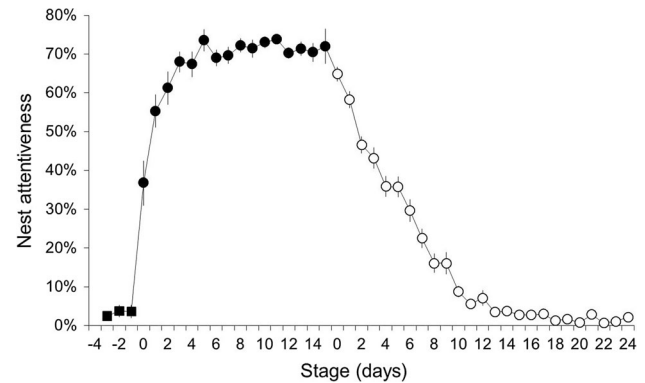


Fig. 2 Nest attentiveness (percentage of time female Stripe-breasted Tits spent inside the nestbox) during daylight hours, in relation to stage of breeding cycle. Day 0 = clutch completion or first hatching [$n = 59$ nests (7–35 nests day⁻¹), 5,047 h of observation]. Closed square laying period, closed circle incubation, open circle nestling period. Error bars ± 1 SE

increase throughout the nestling period. Each parent delivered a mean of 2.27 feeds brood⁻¹ h⁻¹ (± 0.014 SE, 49 broods); equivalent to just ca. 28 feeds parent⁻¹ days⁻¹. At nests where helpers were present they collectively contributed 26.0 % of feeds (28 nests, 9,117 feeds).

Growth

During days 3–11 inclusive, nestlings showed an approximately linear increase in mass, gaining a mean of 1.32 g day⁻¹ (± 0.136 SE, 45 broods; Fig. 3a). To determine the asymptotic mass a quadratic regression model [$y = 2.109(x) - 0.057(x^2) - 0.730$; where x = brood age (days)], was fitted to the mean mass brood⁻¹ at ages 13–23 days ($n = 44$ broods, 136 brood-days). This provided an improved fit over a linear model ($F_{1,133} = 9.603$, $P < 0.001$). The quadratic model indicated a maximum mass of 18.8 g on day 19, and a mass of 17.1 g on day 24 (the modal fledging age); equivalent to 91 % of mean adult mass. From day 8 onwards, wing length showed an approximately linear rate of increase; this rate declined slightly after days 18–19. Again, a quadratic regression model [$y = 4.545(x) - 0.042(x^2) - 16.760$] provided a better fit than a linear model ($F_{1,196} = 8.789$, $P = 0.003$) when fitted to the mean wing length brood⁻¹ at ages 8–22 days ($n = 46$ broods, 199 brood-days). The model gave a projected wing length of 68.0 mm on day 24; equivalent to 90 % of mean adult wing length (88 % of male, 93 % of female).

Length of breeding cycle

While most clutches were laid at a rate of 1 egg day⁻¹, at least one laying interval of 2+ days was recorded in 18 %

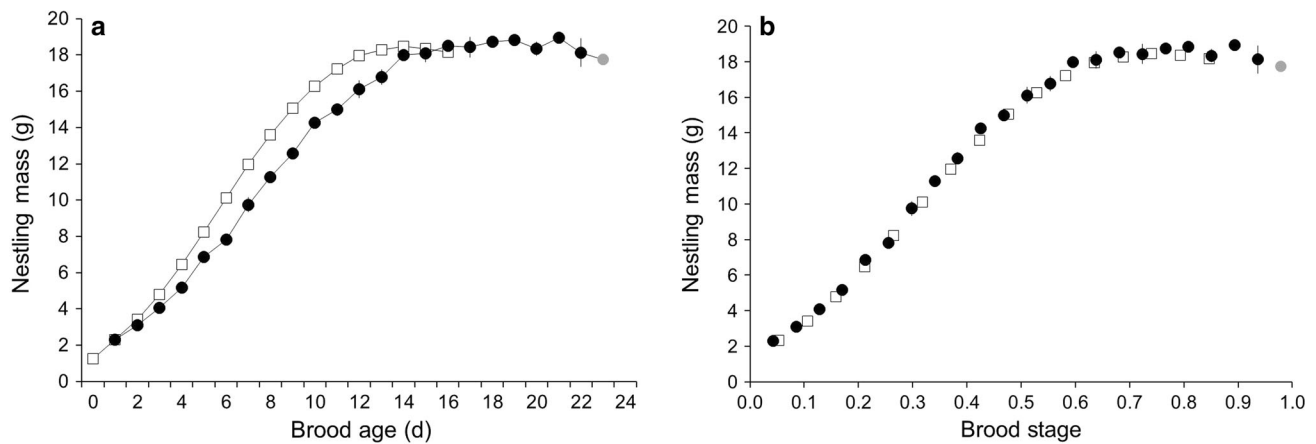


Fig. 3 Growth in mass of nestling Stripe-breasted and Great Tits. Mean mass is shown in relation to: **a** age, where day 0 = hatching day, **b** stage of nestling period (age as a proportion of mean fledging

age). Closed circle Stripe-breasted Tit, days 1–22, ± 1 SE, grey circle single brood, open square Great Tit, days 0–16; data pooled from Gibb (1950) and Schifferli (1973)

of clutches ($n = 39$). Laying gaps occurred in 46 % of 2–3 egg clutches and in just 4 % of 4–5 egg clutches (Fisher's exact: $P = 0.003$). In non-predated clutches, laying gaps were associated with slightly, though not significantly, lower hatching success (62 vs. 75 %; $n = 35$ clutches, ns). Laying averaged 3.9 days ($n = 13$ females, 35 clutches), while incubation averaged 15.1 days ($n = 11$ females, 41 clutches). In broods of two or more, hatching spanned 1 (22 %) 2 (72 %) or 3 days (6 %; $n = 46$ broods). The mean and modal nestling periods were 23.5 and 24 days (19–26 days, $n = 12$ females, 37 broods) respectively, while the developmental period (clutch completion to fledging) spanned 38.8 days ($n = 11$ females, 31 broods) (ESM Table 1). Juveniles were last recorded receiving care from a parent or helper at a mean of 81 days post-fledging (± 19.04 SE, $n = 16$ broods) (Fig. 4), and were last seen in association with their parents or helpers at a mean of 408 days post-fledging (± 60.1 SE, max = 1,111 days, $n = 28$ broods).

Comparisons with Great Tit

In most respects, the breeding performance of Stripe-breasted Tits differed markedly from that reported for north temperate Great Tit populations, in terms of productivity (Table 1), provisioning rates (Table 2), growth rates (Table 2; Fig. 3), length of breeding cycle and of post-fledging dependency (Fig. 4). To place these differences in context, we divided the higher value for each trait (e.g. Great Tit clutch size) by the lower value (Stripe-breasted Tit clutch size) (Fig. 5). Where possible, the Great Tit value used was drawn from the largest or longest study of *P. m. major* or *P. m. newtoni* for which published results were available. While clutch sizes of European Great Tits exceeded those of equatorial Stripe-breasted Tits, by a

factor of 2.3, brood sizes, provisioning rates, the duration of post-fledging care and of association between parents and offspring all showed a greater proportional disparity (Fig. 5).

Discussion

Breeding patterns within the genus *Parus* vary markedly; from multiple large broods (Great Tit *P. m. major*) through single large broods (Great Tit *P. m. newtoni*, in deciduous woodland), to multiple small broods (Stripe-breasted Tit) and single small broods (e.g. Southern Black, Carp's and Ashy Tit) (Tarboton 1981; Wiggins 2001; Gosler and Clement 2007). The annual fecundity of Stripe-breasted Tit pairs (3.1 fledglings pair⁻¹ year⁻¹) was less than half of that recorded in large-scale studies of European Great Tits (Table 1), but almost twice that of Southern Black Tits in southern Africa (1.6 fledglings pair⁻¹ year⁻¹; from Tarboton 1981; Vernon 1984). Although the latter were breeding in natural cavities, and may have suffered higher rates of nest failure, productivity was similarly low in a nestbox study of Carp's and Ashy Tit in Namibia (Wiggins 2001). Thus, Stripe-breasted Tits at 1°S, laying during 11 calendar months and raising up to four broods p.a., were much less fecund than Great Tits at 51–53°N, but more so than their congeners at 20–24°S in southern African, where breeding opportunities appear to be more tightly constrained by a longer, more arid dry season (Tarboton 1981; Wiggins 2001).

Helpers were present at 61 % of Stripe-breasted Tit and at 58 % of Southern Black Tit nests (Tarboton 1981), raising the mean number of individuals participating in each breeding attempt to 3.0 and 2.7, respectively. Individual productivity was therefore correspondingly lower:

just 0.8–1.0 and 0.5 fledged offspring participant⁻¹ year⁻¹, respectively (Tarboton 1981). In contrast, Great Tits breeding in nestboxes in the UK and Netherlands reared a mean of 3.5–3.9 fledged offspring parent⁻¹ year⁻¹, and were thus approximately 3–5 times more productive than individual Stripe-breasted Tit participants, and 7–8 times more so than Southern Black Tits, the latter breeding in natural cavities.

The provision of nestboxes is likely to mask natural failure rates (e.g. Møller 1989) and may influence clutch size, since large broods in small boxes are at greater risk of hyperthermia (Karlsson and Nilsson 1977; van Balen 1984). The nestboxes used in this study, however, are unlikely to have accounted for the Stripe-breasted Tit's small clutch and brood sizes, being of a similar volume to those used in Europe. Moreover, despite its proximity to the Equator, temperatures at Ruhija (mean monthly maxima: 18–19 °C; Kasangaki et al. 2012) were similar to those recorded in a nestbox study of Great Tits in Spain (15–25 °C; Greño et al. 2008). Since Spanish Great Tit clutches (Cramp and Perrins 1993; Sanz et al. 2000) typically exceed those of the Stripe-breasted Tit, brood sizes in the latter would appear to be more tightly constrained by other factors.

Breeding failure

The daily nest failure rate was three times higher during the brood stage than the egg stage, a finding consistent with Skutch's hypothesis that increased parental activity raises the likelihood of nest detection by predators, and hence constrains brood sizes in the tropics (Skutch 1985). Although nestling mortality in non-predated broods was higher than that reported from European Great Tit study

sites (Table 1), starvation was not a major factor, despite the Stripe-breasted Tit's slow provisioning rate. Hatching failure by eggs that survived the incubation period (29 %) was higher than is typical at Great Tit study sites in Europe (5–9 %) or Japan (11–14 %; Table 1), suggesting that Stripe-breasted Tit eggs could have been at greater risk of over-heating (as noted above), or were less viable. The former explanation seems unlikely, however, in view of the moderate ambient temperatures experienced at Bwindi and the high thermal tolerance of most bird embryos (Webb 1987). Alternatively, energy constraints and calcium limitation during egg formation can lower egg volume and shell thickness, increase porosity and limit clutch sizes (Drent and Woldendorp 1989; Graveland and Drent 1997; Gosler et al. 2005). They may also retard skeletal development in nestlings, potentially extending the nestling period (Tilgar et al. 2004). Since soil calcium levels are typically low in central African forests (Patten 2007), including Kibale Forest in western Uganda (Mahaney et al. 1997), low calcium levels could partly explain the Stripe-breasted Tit's small clutch sizes, low hatching success and extended nestling period. Although inbreeding depression can also cause low egg viability, gene flow is likely to be adequate within the population at Bwindi, which is estimated at ca. 450 breeding pairs or groups (P. Shaw, unpublished).

Nest attentiveness

Shaw and Cresswell (2014) showed that Great Tits at Wytham Woods, UK, and Stripe-breasted Tits at Bwindi spent almost the same percentage of time on the nest during days 4–10 of the incubation period: 85 and 84 % 24 h⁻¹, respectively. A LME model, in which we controlled for female effects, produced the same estimate for female Stripe-breasted Tits over days 4–15 (84 % 24 h⁻¹), confirming that the two species show similar levels of nest attentiveness (Table 2), despite their wide latitudinal separation. They also produced eggs of a similar relative mass (Table 1), a finding consistent with the prediction that less attentive species should lay relatively large eggs (Martin et al. 2006; Martin 2008).

Provisioning and growth rates

Stripe-breasted and Great Tits mainly deliver single, large prey items to the nest (P. Shaw, unpublished; Perrins 1979), among which caterpillars account for ca. 72 and 80 % of items, respectively (this study; Gosler 1993). Stripe-breasted Tit nestlings each received just 2.0 feeds h⁻¹; the same rate as reported for Southern Black, Ashy and Carp's Tit (Tarboton 1981; Wiggins 2001), but just 36–48 % of that reported for Great Tit nestlings in much larger broods at

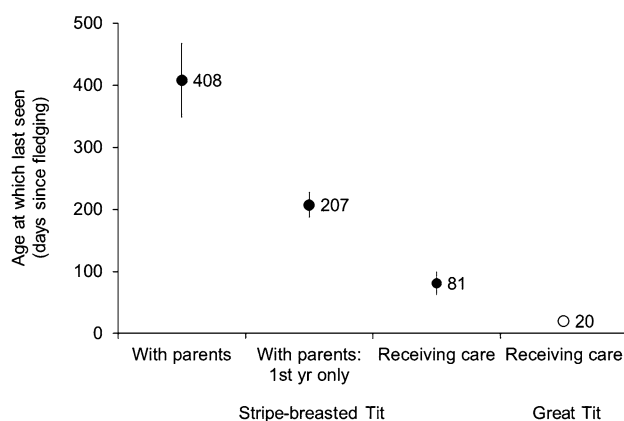


Fig. 4 Mean age (days since fledging; ± 1 SE) at which offspring were last seen associating with their parents or helpers (at all ages, or during their first year only), or receiving care from parents or helpers. See text for details. Closed circle Stripe-breasted Tit, open circle Great Tit (from Verhulst and Hut 1996)

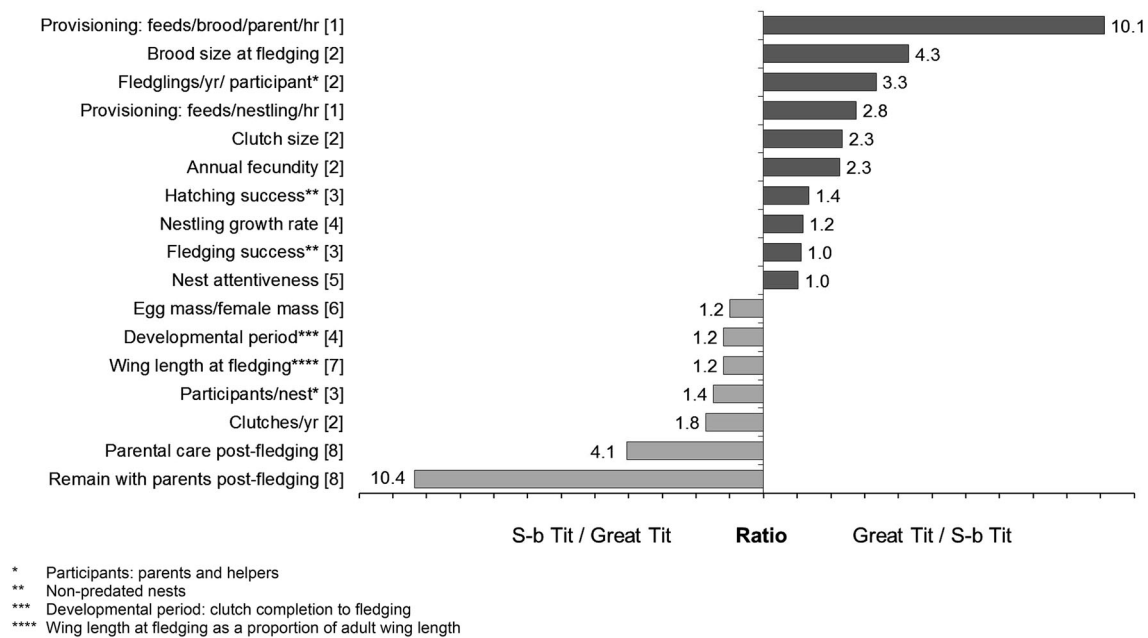


Fig. 5 Proportional differences in life history traits. For each trait, the larger value (e.g. Great Tit clutch size) has been divided by the smaller value, to show the degree to which the two species differ. *Closed square* Great Tit value exceeds Stripe-breasted Tit, *grey*

square Stripe-breasted Tit exceeds Great Tit. Sources: 1 Sanz et al. (2000), 2 Bouwhuis et al. (2010), 3 Perrins (1979), 4 Gibb (1950), 5 Bryan and Bryant (1999), 6 Cramp and Perrins (1993), 7 Orell (1983), 8 Verhulst and Hut (1996)

three northern European sites, and 55–71 % of that recorded at one site in Spain (Table 2), where broods were of a comparable size to those of Stripe-breasted Tits (3–4 nestlings). Accordingly, Stripe-breasted Tit nestlings grew more slowly than Great Tits, the two species achieving asymptotic mass at 19 and 14 days, respectively (Fig. 2a). Despite these differences, they showed near-identical growth curves when age was expressed as a proportion of the mean nestling period (Fig. 3b).

Since most Great Tit broods are larger, the number of feeds delivered throughout the nestling period by Great Tit parents in Europe is ca. 6–7 times that delivered by Stripe-breasted Tits, suggesting that prey availability is higher (and foraging effort correspondingly lower) in north temperate deciduous woodlands than in evergreen Afrotropical rain forest. An alternative explanation is that Stripe-breasted Tits exercise greater parental restraint, trading their current breeding effort against their future breeding potential. Stripe-breasted Tits at Bwindi have an estimated mean reproductive lifespan of 3.5 years (P. Shaw, unpublished), and are typically multi-brooded, while Great Tits in the UK and the Netherlands have a mean reproductive lifespan of just 1.9 years, and are mainly single-brooded (Bouwhuis et al. 2010). Consequently, Great Tit parents may be under greater selective pressure to invest more

heavily in their current brood than in their future survival and reproduction.

Extended development and post-fledging care

The Stripe-breasted Tit's developmental period (from clutch completion to fledging) averaged 6 days longer than is typical of north temperate Great Tits (Table 1), perhaps reflecting the strong selective advantages of early fledging in Great Tit populations. Although this is achieved primarily through early laying, our findings suggest that accelerated development might also contribute, but at a potential cost. While both species fledged at 91 % of adult mass, Great Tits fledging at 19 days have proportionally shorter wings (76 % fully grown; Orell 1983) than Stripe-breasted Tits fledging at 24 days (90 % fully grown). Great Tit fledglings thus appear to have a higher initial wing loading than their congener, perhaps placing them at increased risk from aerial predators, a major cause of mortality during the first few weeks post-fledging (Perrins 1979; Götmark 2002). But any such disadvantage is presumably offset by the competitive advantage gained through accelerated development. Great Tit broods at Wytham, Oxford, for example, are likely to experience a 3–4 % increase in relative fitness for each day that fledging

is advanced (B. Sheldon, personal communication, 2009, based on Charmanier et al. 2008). Hence, a 6-day advance in their fledging date, achieved by shortening the developmental period, is likely to raise their relative fitness by ca. 18–24 %.

The period from clutch initiation to the termination of care by Stripe-breasted Tit parents (124 days) was approximately twice that recorded in European Great Tit populations (61–63 days), due mainly to the provision of extended post-fledging care by Stripe-breasted Tit parents, for a mean of 81 days. Extended care has also been recorded in the Southern Black Tit (for ca. 49 days post-fledging; Tarboton 1981), and is consistent with the view that food is less abundant in tropical and sub-tropical habitats, such that fledglings are significantly more likely to survive if care is prolonged. In contrast, north temperate Great Tit parents typically terminate care at just 17–20 days post-fledging (Riddington 1992; Verhulst and Hut 1996; Seki and Takano 1998), suggesting that further parental investment is less likely to raise the survival chances of their offspring, or more likely to diminish the parent's own survival prospects, having reared a brood 2–3 times larger than is typical of the genus, and without helpers.

Extended post-fledging care and a continued association between parents and offspring are strongly linked with the evolution of cooperative breeding in birds (Russell et al. 2004), and may partly explain its occurrence in both the Southern Black Tit (Tarboton 1981) and the Stripe-breasted Tit, whose offspring remained with their parents for up to 3 years. Within the genus, cooperative breeding has been observed, or suspected, in nine species (Fry et al. 2000; Hockey et al. 2005; Gosler and Clement 2007; H. Kala, personal communication; P. Shaw, unpublished) and inferred in a further six (Cockburn 2006), suggesting that some 65 % of the genus may breed cooperatively. In this respect, non-cooperative races of the Great Tit may prove atypical, their high breeder turnover and high levels of promiscuity (Perrins 1979; Lubjuhn et al. 1999) tending to erode inter-brood relatedness, reducing any inclusive fitness gains that might otherwise accrue to putative helpers (Cornwallis et al. 2010). It follows that cooperative breeding *Parus* species should be expected to show a high degree of inter-brood relatedness, achieved through low breeder turnover or low levels of extra-pair paternity. Further work is required to confirm whether the Stripe-breasted Tit's low annual fecundity is balanced by relatively high survival rates, and to determine the fitness consequences of cooperative breeding in this species.

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