**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 yr⁻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 d post-fledging (four times longer than is typical of European Great Tits) and remained with their parents for up to three 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

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 (c. 0.75; P. Shaw, unpublished) than is typical of adult Great Tits (c. 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 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 (29°46'E, 1°02'S) during 1998–2012 (Fig. 1). Bwindi is part of a chain of montane forests in the Albertine Rift, and covers c. 331 km² (Kasangaki et al. 2012). At c. 2330 m a.s.l. 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 1374 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 (c. 8 birds km⁻²) in the study area, mainly above c. 2080 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, pers. comm.), rising to 80 by 2008. The boxes were constructed using 1.8–2.0 cm hardwood, had a mean volume of 2760 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 2–3 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 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 2–3 day intervals, mainly at ages 3–19 d ($n = 15$ –22 broods weighed d⁻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 2008–12, 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 (Yatuha 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, during 07:00–19:00 ($n = 5047$ 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 ($n = 16323$ items, 68 nests), and the latter identified broadly as caterpillar/larva; adult Lepidoptera; 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 S.E., 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 S.E., 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 19:04 h) and sunrise (mean 06:57 h; 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 hours of daylight, between 07:00 and 19:00, 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), British Isles; and Tokyo (35° 39' N) or Mt Gongenyama (33° 22' N), Japan. Sources used are listed in Tables 1 and 2, and Figs 3–5. 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*, Carp's Tit *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, two 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 d and 8–22 d, 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 Inc., Chicago, IL, USA) and R (3.0.1; R Development Core Team 2009). All probabilities are quoted as two-tailed.

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 S.E., range = 2–5), producing 1.62 fledged offspring clutch⁻¹ (± 0.140 S.E., range = 0–5, $n = 18$ females, 63 clutches; ESM Table 1). A mean of 1.72 clutches were laid yr⁻¹ (maximum: 4), yielding 3.10 fledged offspring yr⁻¹ (± 0.511 S.E., range = 0–14, $n = 11$ females, 50 clutches). The results for males were slightly lower; a mean of 1.50 breeding attempts yr⁻¹, yielding 2.42 fledged offspring yr⁻¹ (± 0.407 S.E., range = 0–14, $n = 11$ males, 47 clutches). These figures suggest that 1.21–1.55 offspring were fledged breeding adult⁻¹ yr⁻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 S.E.), individual productivity was correspondingly lower: c. 0.82–1.04 fledglings participant⁻¹ yr⁻¹.

The daily nest survival rate was lower during the brood stage (0.988 ± 0.003 S.E., $n = 60$ nests, 15 failed, 1133.5 exposure d) than the egg stage (0.996 ± 0.002 S.E., $n = 71$ nests, 5 failed, 1069.5 exposure d) ($t = 2.082$, $P < 0.05$). 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% ($\pm 3.4\%$ S.E., $n = 16$ 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-yr). Although the median interval between first and second breeding

attempts was shorter if the first attempt failed (failure date to clutch initiation = 11 d, $n = 6$ female-yrs) than if it was successful (fledging date to clutch initiation = 67 d, $n = 11$ female-yrs), this difference was only marginally significant (Kruskal-Wallis = 3.28, 1 d.f., $P = 0.070$).

Between-year differences in breeding parameters were significant in 15 out of 19 LME models (ESM Table 3). Over a 10-yr period (2002–03 to 2011–12), during which c. 50–80 nestboxes were available and checked at least monthly, the number and productivity of breeding attempts yr^{-1} varied substantially. From three to 19 clutches were laid yr^{-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 yr^{-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% ($\pm 0.23\%$ S.E.) of daylight time on the nest; equivalent to 84% of each 24 h period ($n = 14$ females, 46 clutches, 1223 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%; $n = 16323$ items, 68 nests). Each nestling received a mean of 2.04 feeds h^{-1} (± 0.011 S.E., $n = 2626$ 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 $\text{nestling}^{-1} \text{h}^{-1}$). 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 $\text{nestling}^{-1} \text{h}^{-1}$, ± 0.013 S.E., 27 broods) did not differ significantly from the main sample, and showed a similar increase throughout the nestling period. Each parent delivered a mean of 2.27 feeds $\text{brood}^{-1} \text{h}^{-1}$ (± 0.014 S.E., 49 broods); equivalent to just c. 28 feeds $\text{parent}^{-1} \text{d}^{-1}$. At nests where helpers were present they collectively contributed 26.0% of feeds (28 nests, 9117 feeds).

Growth

During days 3–11 inclusive, nestlings showed an approximately linear increase in mass, gaining a mean of 1.32 g day^{-1} ($\pm 0.136 \text{ S.E.}$, 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 (d)), was fitted to the mean mass brood⁻¹ at ages 13–23 d ($n = 44$ 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 d ($n = 46$ 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 d⁻¹, at least one laying interval of 2+ days was recorded in 18% 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, n.s.). 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 one (22%) two (72%) or three days (6%; $n = 46$ broods). The mean and modal nestling periods were 23.5 d and 24 d (19–26 d, $n = 12$ females, 37 broods) respectively, while the developmental period (clutch completion to fledging) spanned 38.8 d ($n = 11$ females, 31 broods) (ESM Table 1). Juveniles were last recorded receiving care from a parent or helper at a mean of 81 d post-fledging ($\pm 19.04 \text{ S.E.}$, $n = 16$ broods) (Fig. 4), and were last seen in association with their parents or helpers at a mean of 408 days post-fledging ($\pm 60.1 \text{ S.E.}$, max = 1111 d, $n = 28$ 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 yr⁻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 yr⁻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 yr⁻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 yr⁻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- 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 c. 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 *c.* 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 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 d 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 *c.* 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 yrs (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 yrs, 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 d 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, pers. comm. 2009, based on Charmantier 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 c. 18–24%.

The period from clutch initiation to the termination of care by Stripe-breasted Tit parents (124 d) was approximately twice that recorded in European Great Tit populations (61–63 d), 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 c. 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 d 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 just 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 Stripe-breasted Tit, whose offspring remained with their parents for up to three 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, pers. comm.; 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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Table 1 Stripe-breasted Tit breeding productivity and duration, compared with three north temperate subspecies of the Great Tit. Detailed breeding parameters for Stripe-breasted Tit are given in ESM Table 1

Attribute	Stripe-breasted Tit	Great Tit			Sources	Details
	<i>P. f. fasciiventer</i> Uganda	<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	1,2,3,4,5,6,7	
Relative egg mass	9.3%	9.0–10.2%	8.4–9.3%	-	8, 9,10	Egg mass as % of female mass
Incubation period (d)	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 & 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, d)	18.8 (19)	17.7 (15)	18.5 (14)	15.2	6,10,13,14	Mean asymptotic mass (g) and brood age (d)
Relative mass & wing length at fledging	91%, 90%	91%, 76%	-	-	15	Projected mass & wing length at fledging, as a % of adult value
Nestling period (d)	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 yr ⁻¹	1.7	1.4	1.0	1.4	7,16	Mean clutches female ⁻¹ yr ⁻¹
Mean eggs yr ⁻¹	6.4	11.8	8.7	11.0	7,16	Mean eggs female ⁻¹ yr ⁻¹
Annual fecundity	3.1	7.7	7.0	7.7	7,16	Mean fledglings female ⁻¹ yr ⁻¹

1 from Kluijver (1951), 2 de Heij et al. (2006), 3 van Balen et al. (1987), 4 from Perrins (1965, 1979), 5 Lack (1955), 6 Eguchi (1980), 7 Seki and Takano (1998), 8 from Cramp and Perrins (1993), 9 Lessells et al. (2002), 10 from Gibb (1950) and 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).

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

Parameter	Measure	Stripe-breasted Tit	Great Tit	Subspecies	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
	Feeds brood ⁻¹ parent ⁻¹ h ⁻¹	2.3	12.7	<i>P.m. major</i>	Spain	3
			17.1	<i>P.m. major</i>	Belgium	5
			19.9	<i>P.m. major</i>	Finland	3
			23.0	<i>P.m. major</i>	Netherlands	3
	Feeds brood ⁻¹ parent ⁻¹ d ⁻¹	28	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
			2499	<i>P.m. minor</i>	Japan	6
Nestling growth rate	g d ⁻¹ (d 2–9)	1.28	1.44–1.49	<i>P.m. major</i>	Finland, Netherlands	11,12
			1.54	<i>P.m. newtoni</i>	UK	13
	g d ⁻¹ (d 3–11)	1.32				

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 from Royama (1966), 7 Eguchi (1985), 8 Gibb (1950), 9 Sanz et al. (1998), 10 from Sanz et al. (1998) and Cramp and Perrins (1993), 11 van Balen (1973), 12 from Orell (1983), 13 from Gibb (1950) and Schifferli (1973).

^a Days 4–15 of incubation period.

Figure legends

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

Fig. 2 Nest attentiveness (percentage of time females 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 d^{-1}), 5047 h of observation). ■: laying period; ●: incubation; ○: nestling period. Error bars = ± 1 S.E.

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). ●: Stripe-breasted Tit, days 1–22; ± 1 S.E.; ●: single brood. □: Great Tit, days 0–16; data pooled from Gibb (1950) and Schifferli (1973)

Fig. 4 Mean age (days since fledging; ± 1 S.E.) 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. ●: Stripe-breasted Tit; ○: Great Tit (from Verhulst and Hut 1996)

Fig. 5 Proportional differences in life history traits. For each trait, the larger value has been divided by the smaller value (e.g. Great Tit/Stripe-breasted Tit clutch size), to show the degree to which the two species differ. ■: Great Tit value exceeds Stripe-breasted Tit; ■: 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. from Cramp and Perrins (1993), 7. Orell (1983), 8. Verhulst and Hut (1996)

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 5.

* Participants: parents and helpers

** Non-predated nests

*** Clutch completion to fledging

**** Wing length at fledging as a proportion of adult wing length

ESM Table 1. Stripe-breasted Tit biometrics and breeding parameters. Breeding parameters are presented as arithmetic means (by breeding attempt or female-yr), and as means derived from linear mixed-effects (LME) models, in which female identity was treated as a random factor

a. Biometrics

Group	Mass (g)				Wing length (mm)				Notes
	Mean	S.D.	Range	<i>n</i>	Mean	S.D.	Range	<i>n</i>	
Males	18.9	1.224	16.1–20.9	17	77.7	1.335	76.0–80.5	17	During nestling period only. Each individual is represented once only.
Females	18.7	0.945	17.0–20.2	13	73.6	1.418	72.0–77.5	14	
All adults	18.8	1.098	16.1–20.9	30	75.8	2.443	72.0–80.5	31	
Egg mass	1.76	0.181	1.37–2.03	29					Estimated mass at laying, from eggs that failed to hatch (<i>n</i> = eggs)
	1.78	0.151	-	10					Aggregated by individual female (<i>n</i> = females).

b. Productivity and breeding cycle

Parameter	By breeding attempt				LME models		Notes
	Mean	Mode (%) ^a	Range	<i>n</i>	Mean ± S.E.	<i>n</i> (females, nests)	
Breeding output							
Clutch size	3.74	4 (53%)	2–5	74 clutches	3.72 ±0.045	18,63	
Brood size at hatching	2.57	4 (35%)	0–5	77 broods	2.65 ±0.154	18,63	From all clutches laid
	3.19	4 (43%)	1–5	62 broods	3.11 ±0.100	15,55	Where 1+ egg(s) hatched
Brood size at fledging	1.80	0 (41%)	0–5	76 clutches	1.62 ±0.140	18,63	
Development							
Laying period (d)	3.9	4 (66%)	3–5	38 clutches	3.92 ±0.067	13,35	First laid to last laid, inclusive
Incubation period (d)	15.2	15 (57%)	14–18	44 clutches	15.13 ±0.087	11,41	First hatching date minus date last egg laid
Hatching period (d)	1.8	2 (67%)	1–3	49 clutches	1.72 ±0.042	12,45	First hatched to last hatched, inclusive
Nestling period (d)	23.5	24 (45%)	19–26	42 clutches	23.54 ±0.112	12,37	Fledging date minus date first egg hatched
Development (d)	38.7	39 (26%)	34–41	34 attempts	38.83 ±0.185	11,31	Fledging date minus date last egg laid
Annual fecundity						<i>n</i> (females, female-yrs)	
Clutches	1.79	2 (46%)	0–4	28 female-yrs	1.72 ±0.125	11,28	Clutches female ⁻¹ yr ⁻¹
Eggs laid	6.79	3 (21%)	0–20	28 female-yrs	6.38 ±0.562	11,28	Eggs laid female ⁻¹ yr ⁻¹
Offspring fledged	3.50	0 (29%)	0–14	28 female-yrs	3.10 ±0.511	11,28	Offspring fledged female ⁻¹ yr ⁻¹

^a Modal value as a percentage of sample.

ESM Table 1 continued.

c. Breeding success

Parameter	By breeding attempt		LME models		Notes
	Percentage	<i>n</i>	Mean percentage $\pm$ S.E.	<i>n</i> (females, nests)	
Hatching success	70.8%	274 eggs	69.5% $\pm$ 3.6%	17,62	Eggs laid that hatched
	76.1%	255 eggs	70.6% $\pm$ 3.4%	16,61	Excluding predated clutches
Egg losses	4.4%	274 eggs	-	-	Assumed predated
	2.6%	274 eggs	-	-	Abandoned
	23.9%	255 eggs	-	-	Survived incubation period but failed to hatch
Fledging success	70.6%	194 nestlings	62.2% $\pm$ 3.9%	15,55	Fledglings as a % of eggs hatched
	85.8%	155 nestlings	81.0% $\pm$ 4.5%	13,43	Excluding predated nestlings
Nestling losses	18.0%	194 nestlings	-	-	Assumed predated
	11.3%	194 nestlings	-	-	Starvation or other causes
Breeding success	50.7%	270 eggs	46.0% $\pm$ 3.4%	17,62	Fledglings as a % of eggs laid
	69.6%	191 eggs	61.7% $\pm$ 4.5%	14,47	Excluding predated nests
Successful attempts	60.5%	76 clutches	58.5% $\pm$ 4.0%	18,63	Clutches yielding 1+ fledgling

ESM Table 2. Nests from which measures of breeding performance, nestling biometrics and the duration of post-fledging care were drawn ('+'), ordered by year and by breeder identify.

Year	Nestbox ID	Female ID	Male ID	Eggs hatched	Nestling(s) weighed	Nestling(s) fledged	Brood resighted post-fledging
1998	8	-	-	+			
1998	6	-	-	+			
2000	4	-	-	+		+	
2001	4	-	-	+		+	
2002	9	4	3	+		+	
2003	9	4	3	+			
2003	47	9	-	+		+	
2003	46	-	-				
2004	9	4	3	+	+		
2004	21	9	28	+	+	+	+
2004	47	9	-	+	+	+	
2004	25	22	23	+	+	+	+
2004	21	-	-	+	+	+	+
2004	54	-	-	+	+	+	
2004	8	-	-	+	+	+	
2004	NC1 ¹	-	-	+		+	
2005	22	4	3	+	+	+	+
2005	1	4	3	+	+	+	
2005	32	22	23	+	+	+	+
2005	60	37	28	+	+	+	+
2006	9	4	3	+	+	+	+
2006	36	4	51	+	+	+	+
2006	20	4	-	+	+		
2006	47	37	28	+	+	+	
2006	21	50	27				
2006	NC2 ¹	-	-				
2007	58	-	-				
2008	22	4	51	+	+	+	+
2008	8/23	4	51	+	+	+	+
2008	32	22	23	+	+		
2008	43	22	23	+	+	+	+
2008	8/09	22	23	+	+	+	+
2008	47	50	11				
2008	34	50	11				
2008	21	59	27	+	+		
2008	48	59	27				
2008	8/12	59	27	+	+	+	+
2008	36	76	77	+	+	+	+
2009	8/09	22	23	+	+	+	+
2009	31	50	11				
2009	8/12	59	27	+	+	+	+
2009	44	76	77	+	+	+	+
2009	36	76	77	+	+	+	+

Year	Nestbox ID	Female ID	Male ID	Eggs hatched	Nestling(s) weighed	Nestling(s) fledged	Brood resighted post-fledging
2009	22	89	78	+	+	+	+
2010	42	59	27	+	+	+	+
2010	8/17	59	27	+	+	+	+
2010	28	59	27	+	+	+	+
2010	44	76	77	+	+	+	+
2010	50	76	77	+	+	+	+
2010	8/20	82	132	+	+	+	+
2010	8/04	89	78	+	+	+	+
2010	34	98	11	+	+	+	+
2010	21	98	65	+			
2010	K11	102	101	+		+	
2010	K58	107	114	+		+	
2010	8/06	108	110	+	+	+	
2010	48	108	110	+	+	+	+
2010	8/09	109	116	+	+	+	
2010	12	109	116	+	+		
2010	15	-	-				
2011	44	76	77				
2011	1	89	78	+	+	+	+
2011	48	89	110	+	+	+	+
2011	34	98	65	+	+		
2011	8/20	98	132	+	+		
2011	34	109	65	+			
2011	8/08	109	65	+			
2011	9	151	77				
2011	8/17	-	27				
2012	8/06	89	110	+	+	+	+
2012	8/08	109	65	+			
2012	34	109	65	+			
2012	14	159	132	+	+	+	+
2012	8/20	159	132	+			
2012	37	166	167	+			
2012	8/25	172	27				
2012	8/08	-	-				
2012	27	-	-				

¹ NC: Natural cavity

ESM Table 3. Linear mixed-effects models used to estimate measures of fecundity, provisioning rate and nest attentiveness. Female identity was entered as a random factor, to control for repeated measures of the same individuals. Year, hour of day and brood size were entered as fixed factors, and brood age as a covariate, where appropriate.

Dependent variable	Effect	<i>F</i>	d.f.	<i>P</i>
Clutch size	Constant	399.46	1,36	<0.001
	Year	1.57	9,36	0.162
Brood size at hatching	Constant	18.27	1,36	<0.001
	Year	3.32	9,36	0.005
Brood size at hatching (non-predated clutches)	Constant	87.86	1,31	<0.001
	Year	3.02	9,31	0.010
Brood size at fledging	Constant	4.86	1,36	0.034
	Year	2.73	9,36	0.016
Laying period	Constant	541.72	1,13	<0.001
	Year	1.54	9,13	0.233
Incubation period	Constant	14897.11	1,21	<0.001
	Year	2.83	9,21	0.024
Hatching period	Constant	13.96	1,25	0.001
	Year	1.79	8,25	0.125
Nestling period	Constant	10600.30	1,16	<0.001
	Year	1.61	9,16	0.194
Development	Constant	41134.98	1,11	<0.001
	Year	3.43	9,11	0.029
Clutches p.a.	Constant	9.34	1,10	0.012
	Year	4.00	8,9	0.027
Eggs laid p.a.	Constant	13.77	1,10	0.004
	Year	4.76	8,9	0.016
Fledglings p.a.	Constant	2.84	1,10	0.123
	Year	6.13	8,9	0.007
Hatching success	Constant	17.02	1,36	<0.001
	Year	3.42	9,36	0.004
Hatching success (non-predated clutches)	Constant	18.17	1,36	<0.001
	Year	3.19	9,36	0.006
Fledging success	Constant	12.22	1,31	0.001
	Year	2.58	9,31	0.024
Fledging success (non-predated broods)	Constant	71.45	1,21	<0.001
	Year	5.51	9,21	<0.001
Breeding success	Constant	4.83	1,36	0.035
	Year	2.58	9,36	0.021
Breeding success (non-predated nests)	Constant	18.35	1,24	<0.001
	Year	3.41	9,24	<0.008
Successful attempts	Constant	6.00	1,36	0.019
	Year	2.46	9,36	0.026

ESM Table 3 continued.

Dependent variable	Effect	<i>F</i>	d.f.	<i>P</i>
Nest attentiveness	Constant	191.03	1,1320	<0.001
	Hour	0.68	11,1310	0.755
Feeds nestling ⁻¹ hr ⁻¹	Constant	202.78	1,2796	<0.001
	Hour	13.98	11,2796	<0.001
	Brood size	16.24	4,2796	<0.001
	Brood age	254.38	1,2796	<0.001
Feeds brood ⁻¹ parent ⁻¹ hr ⁻¹	Constant	16.72	1,2796	<0.001
	Hour	20.16	11,2796	<0.001
	Brood size	81.59	4,2796	<0.001
	Brood age	183.86	1,2796	<0.001