Ibis (2006), **148**, 468–476

Reduced nestling growth of East African Stonechats *Saxicola torquata axillaris* in the presence of a predator

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We investigated nestling growth of tropical East African Stonechats *Saxicola torquata axillaris* to evaluate the effects of nest predation, predator presence and food availability. We provided some Stonechat pairs with supplemental food, while others in a similar habitat served as a control. Concomitantly, we assessed the presence of Fiscal Shrikes *Lanius collaris* in supplemental fed and unsupplemented territories. Fiscal Shrikes prey on adult Stonechats and nestlings. We found that nestling growth was considerably reduced in Stonechat pairs that shared their territory with a Shrike. This effect was greater in nestlings of pairs that did not receive supplemental food. The reduction in nestling growth rates was significantly correlated with a reduced rate of visiting by the parents. Behavioural observations further suggested that parents reduced their feeding visits to the nest presumably to minimize their own predation risk, rather than predation risk of their brood. Our experiments show that the lower reproductive investment in tropical Stonechats can be attributed to risk-sensitive behaviour of the parents, especially when food is in limited supply.

Lack (1968) hypothesized that the optimal growth rate of nestlings is determined by the interaction between the age-dependent mortality of nestlings (predation) and the ability of the parents to supply energy to the growing chick. Bosque and Bosque (1995) tested this hypothesis by comparing island species that experience little or no nestling predation with taxonomically related mainland species that are subject to higher predation intensity. They found that hole-nesting species on the predator-rich mainland had longer incubation and nestling periods than did their open-nesting relatives. By contrast, on predator-free islands, incubation and nestling periods were about as long in the open-nesters as in the hole-nesters. These findings are consistent with the idea that predation at least in some cases selects for faster development. In addition, direct competition between members of a brood will select for an increase in growth rate of all siblings (Werschkul & Jackson 1979, Ricklefs 1993). But why do bird chicks not grow at a maximum rate, and why are there profound differences in rates of nestling growth among taxa (Ricklefs *et al.* 1998)?

One possible answer to these questions is that postnatal growth is limited by physiological constraints on the chick, such as the capacity to utilize available resources, and a trade-off between growth and mature function at the cellular level (Ricklefs *et al.* 1998). These constraints probably account for variation in nestling growth rates at deeper phylogenetic levels (Starck & Ricklefs 1998).

Alternatively, constraints outside the chick's physiological capacity, such as the availability of food resources to chicks or parents, might affect growth rate. For example, tropical species have fewer hours to forage during the breeding season than do temperate species (Lack 1968), and parental time must be allocated between foraging and provisioning of the nestlings (Martin 1992). In addition, clutch size affects rates of nestling growth: parents have a choice to feed a small brood at a high rate per chick or a large brood at a lower rate (Ricklefs 1984). This ultimately implies a trade-off between nestling growth rate, clutch size and the number of broods reared per season (Williams 1966). Moreover, as Skutch (1949) pointed out, predation risk of the young in the nest might also affect the number of parental nest visits, provisioning rates and nestling growth. Furthermore,

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†Ebo Gwinner was involved in the planning stage, the experimental realization and the writing of a draft manuscript of this project. Unfortunately, he died before the manuscript was completed.

parental predation risk has been shown to determine reproductive effort in a variety of circumstances (Abrams 1983, Houston & McNamara 1986, Lima & Dill 1990), so that parents should adjust their foraging effort devoted to offspring according to their individual assessment of predation risk (Lima 1987). Recently, Zanette *et al.* (2003) have shown that the combined effects of food availability and predation risk affect the annual reproductive success of Song Sparrows *Melospiza melodia* in a synergistic manner.

Stonechats *Saxicola torquata* offer an excellent model to examine the effects of food availability and predation risk on nestling growth: a Stonechat territory is used exclusively by both members of a pair for feeding and breeding, whereas conspecific intruders are aggressively expelled by both sexes (Greig-Smith 1980). It is therefore possible to provide supplemental food exclusively for a specific pair, while a neighbouring pair in a territory of similar quality can serve as a control. Moreover, Stonechats are vigilant birds that respond with alarm calls to both mammalian and avian predators (Greig-Smith 1980). Stonechats of the East African subspecies *Saxicola torquata axillaris* are common year-round residents throughout open shrubby habitat in the highlands of Tanzania, Kenya and Uganda (Mackworth-Praed & Grant 1960). Breeding is seasonal, occurs in all years and lasts from 4 to 6 months (Scheuerlein & Gwinner 2002). At lower elevations, they share their territories with Fiscal Shrikes *Lanius collaris* (Scheuerlein *et al.* 2001), which prey on both adult and nestling Stonechats (Mackworth-Praed & Grant 1960, MacLean 1988).

In this study we measured variation in nestling growth rate and observed parental behaviour dependent on both predator presence and experimentally manipulated food availability. Specifically, we attempted to investigate whether predator presence or food availability had a greater effect on nestling growth. Moreover, we were interested in the behavioural mechanisms of the parents that precipitate this effect. A specific aim of the study was to test whether increased co-operation between members of a pair may help to alleviate the adverse effects of predators or food shortage.

METHODS

Study species

East African Stonechats are small insectivorous birds that weigh 13–18 g as adults. The number of broods fledged depends on the length of the breeding season, but never exceeds two broods (Scheuerlein 2000). Their cup-shaped, sometimes domed, nest consists of fine plant material and animal hair, and is generally well hidden on or just above the ground. Clutches of this subspecies contain three eggs, sometimes two or four.

Study area

The study was conducted in the lowlands of Arusha National Park, Tanzania (between latitude 3°12′S and 3°18′S, and longitude 36°45′E and 36°56′E). In total, 74 adult birds were caught with spring traps and then colour-ringed. During two breeding seasons nest-building Stonechat pairs were located and nests were searched. In total, 58 Stonechat pairs were monitored every week until fledging. These pairs initiated 76 nests between October and November of 1995, and 98 nests in 1996. The fate of the fledglings was monitored every other week until independence, which occurs at an age of 2 months (Scheuerlein *et al.* 2001). Dates of nest-loss or fledgling-loss were estimated as the mean date between the last check with nests or young still present and the first check when nests or young had disappeared. The number of clutches lost during the incubation stage did not differ from the number of broods lost during the nestling stage (Fisher's exact test, $P > 0.1$). Nest visits, however, were more frequent in the nestling stage (up to 20 nest-visits per hour, $n = 15$) than during incubation with only four nest visits per hour ($n = 10$) (Wilcoxon's $Z = -3.94$, $P < 0.001$).

Assessment of predator frequency

Fiscal Shrikes are the most frequently recorded predators of Stonechats in the study area (Scheuerlein 2000). They are conspicuous birds that perch in the open on trees or bushes, and elicit frequent alarm calls from Stonechats. The presence of Shrikes was assessed during each monitoring visit. Territories in which Shrikes were observed were classified as 'Shrike' territories, and territories where no Shrike was observed as 'no-Shrike' territories. Territories whose status was unclear, as well as territories that changed status during our observations, were excluded from our study. We selected 12 Stonechat pairs with nestlings in Shrike territories and 13 pairs in no-Shrike territories as focal pairs and assessed their fate daily until the nestlings had fledged.

Supplemental feeding

A Stonechat territory is used exclusively by one pair for feeding and breeding, whereas conspecific intruders are expelled aggressively by both sexes (Greig-Smith 1980). These facts enabled us to feed five pairs exclusively in the Shrike category (fed), and five pairs in the no-Shrike category (fed). The other pairs in similar habitat served as unfed controls (termed 'unfed').

Birds were given the food supplement by placing a plastic dish containing daily rations of 30 g live mealworms (*Tenebrio molitor* larvae, $n = 150$, dry mass = 10 g) between 08:00 and 10:00 h in the territory's centre. This amount corresponds to approximately 110 kJ of food for each bird [= (10 g dry mass × 5500 cal × 4.1833 J)/2] using average values for energy contents of arthropods from Golley (1961) and Robel *et al.* (1995). Feeding was initiated a month before the onset of egg-laying. The mealworms were fed on a diet of carrots and oats, enriched from time to time with VITIN (Chevita GmbH, Pfaffenhofen, Germany), a vitamin cocktail developed for birds. Birds started to take mealworms from the feeder after a short while and within 3 days made frequent use of the new food source (Scheuerlein & Gwinner 2002).

Nestling growth rates

All eggs of a clutch hatched on the same day, creating broods of homogeneous ages. Different broods hatched on different days throughout the study period. We measured nestling mass daily from the day of hatching (day 0) until day 7, using a spring balance (Pesola) with ± 0.25 g accuracy. All measurements were taken around noon and each brood was measured at the same time each day. Although each nestling was weighed separately, only the average nestling mass per brood per day was used for further analysis.

Care was taken to avoid human-induced predation (East 1982). There was no effect of the above treatment on fledging success: 20 out of 125 experimental pairs fledged young successfully; this did not differ significantly from the equivalent figures for undisturbed control pairs of 57 out of 149 (Fisher's exact test, two-sided, $P = 1.0$).

Brood feeding rates of adults

When the nestlings were 5 days old, the behaviour of the parents at the nest in all 25 territories was observed from a concealed position. Observations of both fed and unfed parents were initiated around 10:00 h and lasted for 120 min. On observation days, fed pairs were fed at 08:00 h and observation started 2 h after they had received food. Parental behaviour was recorded on a programmable Psion hand-held computer and analysed with the Observer (Noldus, Wageningen, Netherlands) software. The behaviours recorded were: number of feeding visits to the nest by each sex; percentage of time the parents spent foraging (total time minus time seen carrying food); the number of alarm calls (recorded for males and females separately); and total time spent perching close to the nest, termed nest guarding. The time spent nest guarding without food was included in the foraging time because we observed the birds foraging around the nest.

Statistical methods

Data were tested for normality using the Shapiro–Wilk statistic (SAS 1999–2000). Growth data were analysed in a multivariate repeated measures analysis of covariance (ANCOVA) with nestling age as covariate and brood size (2, 3 or 4), experimental group (fed, unfed) and Shrike presence (Shrike, no-Shrike) as the main factors.

The durations of behavioural state variables (time spent foraging, nest guarding) were transformed into percentages of total observation time, and arcsine square root transformed to achieve normality before analyses. Behavioural events (feeding visits, alarm calls) entered the analysis as integers. All behavioural parameters were tested simultaneously in a multivariate ANOVA (proc glm in SAS) with behavioural variables and brood size as independent factors, and feeding treatment and Shrike presence/absence as dependent factors. As the rates of food provisioning between males and females were indistinguishable, nest visit rates of both sexes were pooled.

The expected number of nest visits made by a focal bird while the partner was present at the nest (NV_{exp}) was calculated as

$$NV_{exp} = (NV_{tot} \times t_{par})/t_{tot}$$

where NV_{tot} is the number of nest visits during the observation period, t_{par} is the time the focal bird spent in the vicinity of the nest while the partner was present and t_{tot} is the total observation time. We then calculated the difference between the expected number of nest visits and the observed number of

Table 1. The influence of environmental factors on nestling growth rate: results from a repeated-measures GLM ($n = 25$ nests); type III statistics are reported (unique contributions of each variable).

	df	Type III sum of squares	*F*-value	Significance of *F*
Fed/unfed	1	0.945	0.64	$P = 0.4334$
Shrike/no-Shrike	1	30.10	20.47	$P = 0.0003$
Fed/unfed × Shrike/no-Shrike	1	7.592	5.16	$P = 0.0356$
Brood size	1	4.045	2.75	$P = 0.1146$
Fed/unfed × brood size	1	0.234	0.16	$P = 0.6949$
Shrike/no-Shrike × brood size	1	3.632	2.47	$P = 0.1335$
Error	18	26.38		

nest visits and compared parents in Shrike and no-Shrike territories by using a Wilcoxon's rank sum test. All data were analysed using SAS version 8.01 (SAS_Institute 1999–2000).

RESULTS

Nestling growth rates

There was no effect of brood size on nestling growth, and there were no interactions between brood size and Shrike presence, or feeding treatment (Table 1). When Shrike presence and feeding treatment were entered as independent variables, only Shrike presence had a significant effect (Fig. 1), while feeding treatment had no effect (Fig. 2). However, when we entered the interaction Shrike presence × feeding treatment into a type III sum of squares General Linear Model (GLM) (unique contributions from each variable), it also became significant ($F_{1,24} = 5.16$, $P = 0.0356$; see Table 1), in addition to Shrike presence. Testing the effect of Shrike presence separately on fed and unfed pairs, we found that the negative effect of Shrikes on nestling growth was highly significant in territories that were unfed. However, we did not detect a significant effect in territories that were supplemented with food.

Feeding rates and parent behaviour at the nest

A multivariate analysis of variance using type III sums of squares (unique contributions from each variable) revealed that brood size did not differ with regard to feeding or Shrike status. As expected, fed pairs spent significantly less time foraging than unfed pairs (Table 2, Fig. 2; $F_{1,24} = 54.55$, $P = 0.0001$). However, fed and unfed pairs did not differ significantly with respect to the number of nest visits, time spent nest guarding or the number of alarm calls recorded during the observation (Table 2, Fig. 2). However, both fed and unfed birds in Shrike territories gave more alarm calls, and spent more time nest guarding. Interestingly, we found that parents in Shrike territories made fewer visits to the nest ($F_{1,24} = 11.73$, $P < 0.0025$; Table 2, Fig. 3). Because

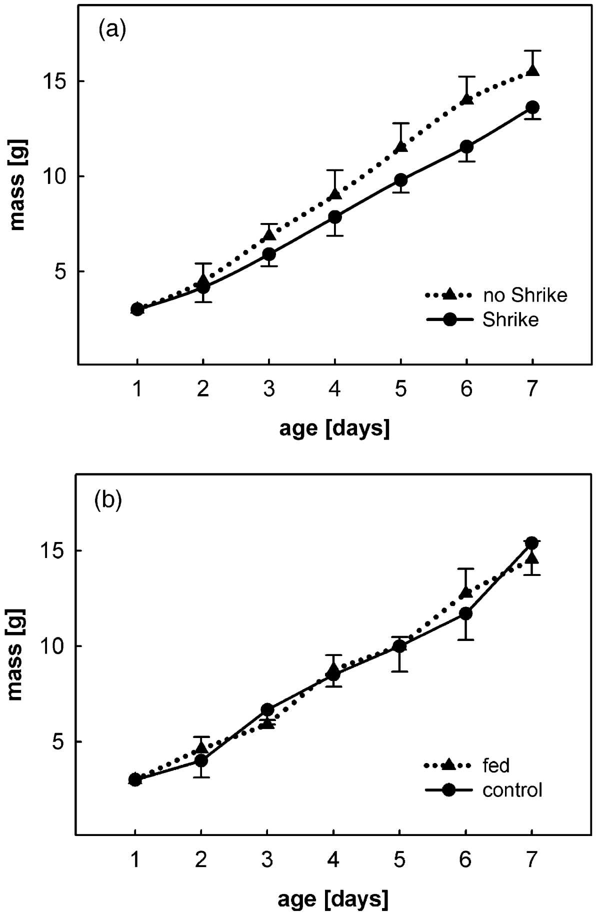

Figure 1. (a) Nestling growth of Stonechat nestlings in territories where a Fiscal Shrike was present (Shrike: circles = means; – minima; bold curve) and of nestlings in territories where no Fiscal Shrike was present (no-Shrike: triangles = means; + maxima; hatched curve). (b) Nestling growth of Stonechat nestlings in territories where parents were supplied with supplemental food (fed; triangles = means; + maxima; hatched curve) versus in territories where parents were not fed (control; circles = means; – minima; bold curve).

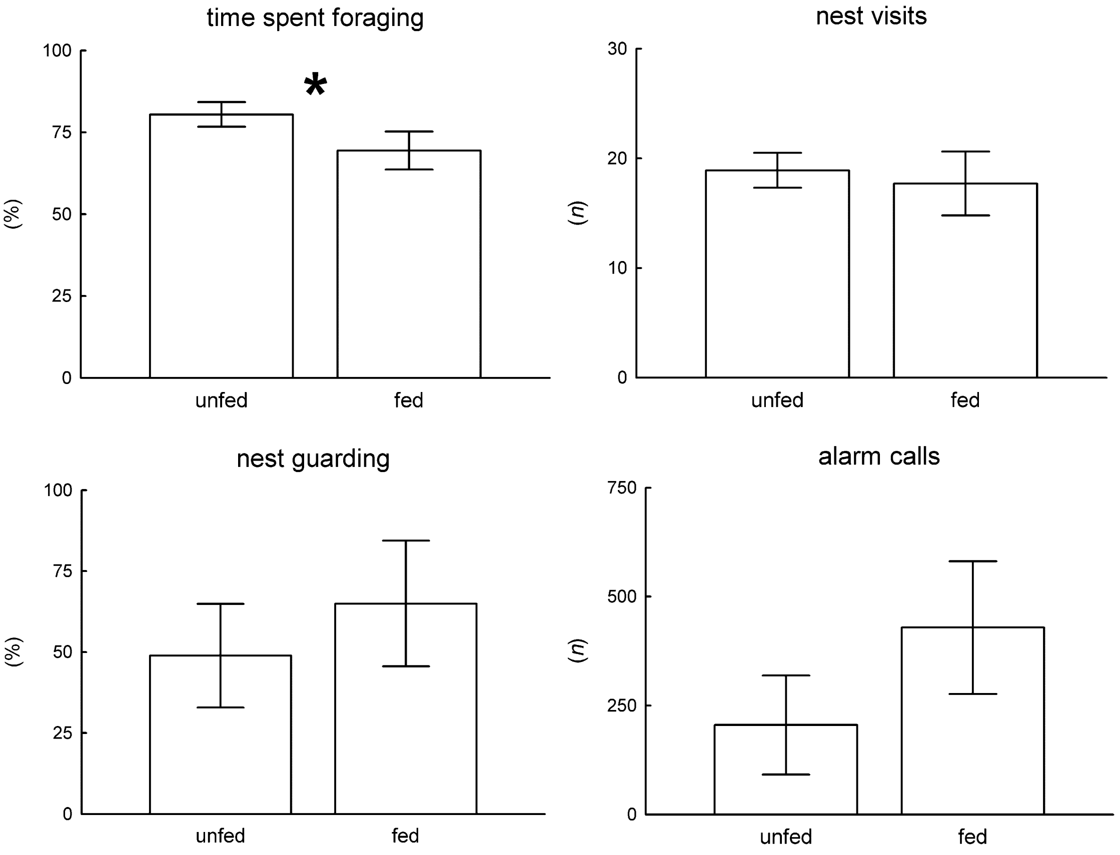

Figure 2. Time spent foraging and nest guarding, as percentage of total observation time, and number of nest visits and alarm calls during 120 min observation time of fed and unfed Stonechat pairs feeding 5-day-old nestlings (means ± se). $^*P < 0.05$.

Table 2. Effects of brood size and four behavioural traits in Shrike/no-Shrike and fed/unfed territories. Type III statistics are reported (unique contributions of each variable).

	Fed/unfed	Shrike/no-Shrike	Shrike/no-Shrike × fed/unfed
Brood size	$F_{1,24} = 1.27$ $P = 0.2721$	$F_{1,24} = 0.29$ $P = 0.5730$	$F_{1,24} = 0.16$ $P = 0.6939$
Time spent foraging	$F_{1,24} = 54.55$ $P = 0.0001$	$F_{1,24} = 0.42$ $P = 0.5250$	$F_{1,24} = 3.45$ $P = 0.0774$
Nest guarding	$F_{1,24} = 0.07$ $P = 0.7950$	$F_{1,24} = 34.52$ $P = 0.0001$	$F_{1,24} = 0.16$ $P = 0.6937$
Nest visits	$F_{1,24} = 0.08$ $P = 0.7819$	$F_{1,24} = 11.73$ $P = 0.0025$	$F_{1,24} = 4.32$ $P = 0.0502$
Alarm calls	$F_{1,24} = 2.30$ $P = 0.1446$	$F_{1,24} = 15.20$ $P = 0.0008$	$F_{1,24} = 3.71$ $P = 0.0676$

the interaction between feeding status and Shrike presence/absence bordered on significance ($P = 0.0502$), we calculated contrasts for nest visits in fed and unfed territories. We found that only parents in fed territories reduced the number of nest visits in the presence of Shrikes.

In order to test whether parents are able to alleviate the adverse effect of Shrike presence on growth of their nestlings by increasing co-operation, we analysed nest guarding behaviour. We found that parents in Shrike territories increased the frequency of nest visits while the partner was nest guarding. However, no such effect was found in territories without Shrikes (Wilcoxon's $Z = -2.86$, $P < 0.005$; Fig. 4).

Assessment of breeding success

There were no partial brood losses throughout the study; predators either took all eggs or the whole brood from a nest. Overall, only 38% of 174 monitored breeding attempts yielded offspring that survived until fledging. Nineteen per cent of all clutches were predated during incubation, whereas 24% were lost during the nestling period (Table 3).

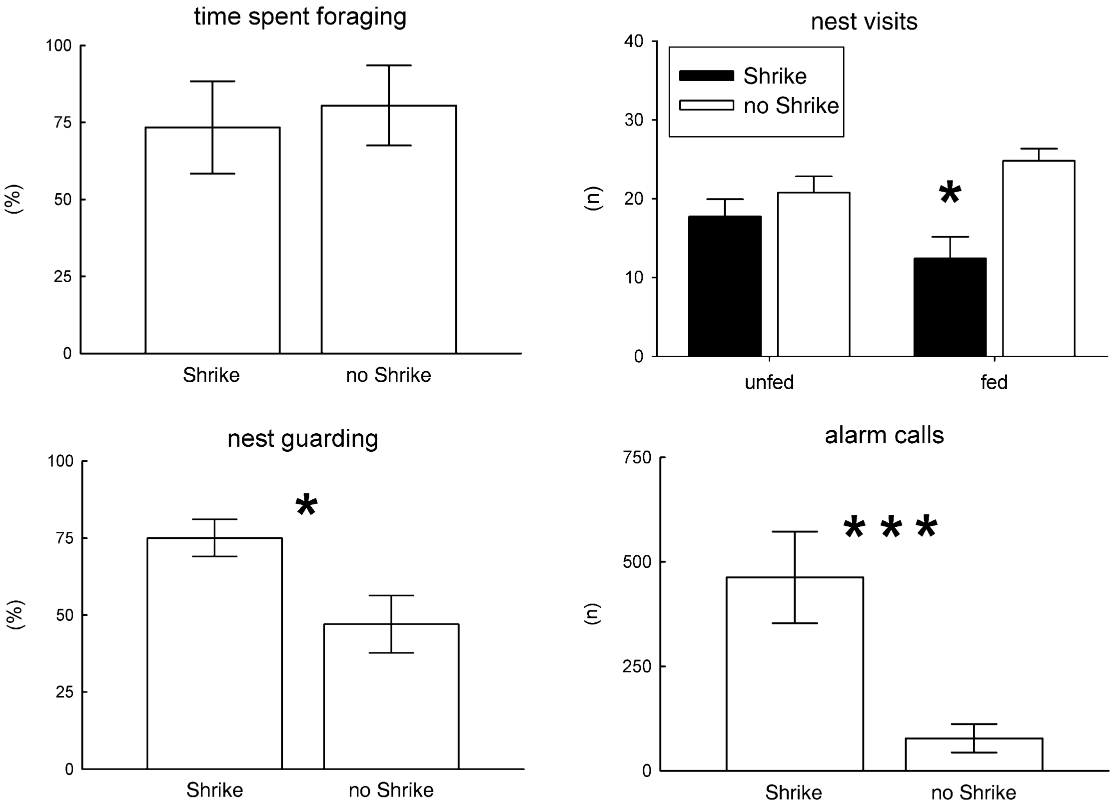

Figure 3. Time spent foraging and nest guarding, as a percentage of total observation time, and number of nest visits and alarm calls during 120 min observation time of Stonechat pairs in Shrike and no-Shrike territories, feeding 5-day-old nestlings (means ± se). As we found a significant interaction between feeding status and Shrike presence/absence in the number of nest visits, data are shown for each category separately. $^{*}P < 0.05$, $^{***}P < 0.001$.

Table 3. Fate of 174 Stonechat clutches found in 1995–97 in Arusha National Park.

Infertile	Eggs lost	Nestlings lost	Fledglings lost	Successful
7%	19%	24%	12%	38%

DISCUSSION

No effect of supplemented food on nestling growth

Nestling growth is a life history trait that exhibits little variation between species within genera, as suggested by Ricklefs (1984). Moreover, it appears that nestling growth in *Saxicola* has been pushed to its physiological maximum, as nestling East African Stonechats in an aviary provided with food *ad libitum* (Starck *et al.* 1995) had similar growth rates to nestlings in no-Shrike territories. In addition, Greig-Smith (1985) showed that nestling Stonechats that were lighter in mass than their siblings incurred a higher mortality risk before fledging. As Stonechat nestlings hatch synchronously, growth rates should be under

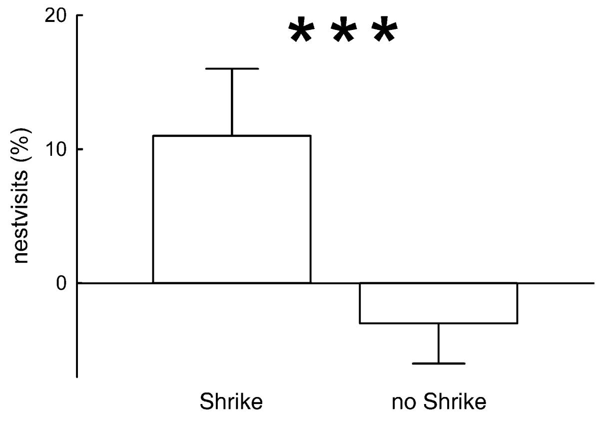

Figure 4. The difference between observed and expected proportions of nest visits made while a partner was present and vigilant in Shrike or no-Shrike territories (means ± se). $^{***}P < 0.001$.

strong selection (Ricklefs 1993). Furthermore, Ricklefs (1969) and Martin (1992) suggested that because open-habitat ground-nesting bird species generally incur a high rate of nest predation, selection should favour fast growth to minimize nest exposure time, both in tropical and in temperate environments. As a result, small clutches rather than slow nestling growth should be favoured in the face of limited food availability at high population density levels while minimizing nest exposure (Stearns 1992, Ricklefs 1993, Roff 2002). This was confirmed by the investigation of Gwinner *et al.* (1995), who found that clutch size in the East African Stonechat subspecies is genetically fixed at a smaller number than in the European subspecies.

Effect of supplemental feeding on parental behaviour

Although supplemental food had a positive effect only in pairs that shared their territory with a Shrike, it nevertheless affected the time budget of the feeding parents. We found that fed pairs spent less time away from the nest than unfed pairs. As most of the food is gathered far from the nest, the amount of time spent away from the nest can be interpreted as a measure of foraging time (Ydenberg 1994, Andersson 1981). In our study, supplemental feeding reduced the time the parents had to spend foraging in their territory. However, the naturally available food in their territories, even without supplementation, may have been sufficient to sustain the same maximal growth rate as East African Stonechats in an aviary provided with food *ad libitum*, as the growth curves did not differ significantly (our data compared with aviary data from Starck *et al.* 1995).

Reduced nestling growth in the presence of Shrikes

Both Stonechat parents paid fewer feeding visits to the nest in Shrike than in no-Shrike territories when they were supplemented with food. This effect was not seen in 'unfed' territories. However, as nestling growth was also reduced in unfed territories with Shrikes, we assume that the nestling food gathered by parents in the presence of Shrikes must have been of poorer quality. Along these lines, a similar synergistic effect between predator presence and food availability was reported by Zanette *et al.* (2003) in Song Sparrows.

The reduction of nestling growth rate in Shrike territories is most apparent between days 3 and 7. Importantly, nestling growth during this time interval has been shown to predict nestling mortality (Greig-Smith 1979) and fitness (Perrins 1965, Linden *et al.* 1992, Horak *et al.* 1999). Why did parent Stonechats reduce their nest visit rate in the presence of Shrikes, or deliver food of inferior quality? Two non-exclusive hypotheses must be considered: **(1)** Nest visits are reduced to minimize the predation risk of nestlings.

Skutch (1949) suggested that predation on the brood increases with increasing activity of parents at the nest. As predators may detect the nest by the begging calls of nestlings and by observing feeding adults, parents should reduce nest visit rates and lower nestling feeding rates to avoid nest predation. This proposition has been confirmed in hole- and cavity-nesting birds (Perrins 1965, Young 1996). However, these results may not apply to open-nesters: hole- and cavity-nesting species are characterized by large clutch sizes and intense sibling competition as a result of the synchronous hatching of the nestlings (Martin 1995). This sets the stage for the evolution of loud nestling begging calls, as the brood is protected by the nest-site against predators (Martin 1992, Mock & Forbes 1994). However, loud begging calls of nestlings would be fatal in ground-nesting species. In a study on the tropical Western Slaty Antshrike *Thamnophilus atrinucha* in Panama, Roper and Goldstein (1997) found that nest predation did not increase during the nestling stage, when activity at the nest was highest. A similar result was obtained in our study, in which predation rates of nests with eggs and nests with nestlings did not differ.

Many authors agree that a reduction in nest visits would not be an appropriate strategy to avoid nest predators such as snakes or nocturnal animals. Some snakes use non-visual cues to detect their prey, and egg-predators such as *Bitis arietans*, *Dendroaspis angusticeps* and *Dasypeltis scabra* are common in Arusha National Park (Razzetti & Msuya 2002). Most nocturnal mammalian predators that were identified as the main cause of nest predation in other studies of tropical bird species (Woodworth 1997, Sloan *et al.* 1998, Degraaf *et al.* 1999) use non-visual cues. We conclude therefore that a reduction in the number of nest visits is ineffective in reducing nest predation rate. In agreement with this, Martin *et al.* (2000) showed in a comparative study on nest feeding rates and predation in birds in Arizona and Argentina that nest predation alone could not explain differences in clutch size between birds of sibling species in the two study areas, although nest predation covaried with nest visit rates within species.

(2) Nest visit rates are reduced to minimize predation on adults.

Considerable evidence suggests that the parents themselves incur a higher predation risk during their frequent nest visits: Stonechat parents approach their nest flying low over the ground for some distance, with very little space for escape manoeuvres (Greig-Smith 1985). Shrikes and sparrowhawks *Accipiter* spp. usually attack when their prey flies low between bushes or trees (Newton 1986). Correspondingly, Roedl (1999) found in Stonechat wintering grounds in Israel that Mourning Wheatears *Oenanthe lugens*, a competitor for food and a kleptoparasite, were more likely to attack Stonechats that were on the ground. Tye (1984) observed that Fiscal Shrikes usually attacked birds that flew low during foraging flights or feeding flights to the nest.

In our case, Stonechats in Shrike territories increased the frequency of nest guarding and distraction behaviour (Greig-Smith 1980) while the partner was away foraging. In addition, we found that a parent Stonechat in a Shrike territory was more likely to visit the nest when the partner was close. Clearly, this behaviour does little to reduce the risk of nest predation, but rather reduces the predation risk on the parent while provisioning a brood, as a partner could alert to approaching predators, or distract them. A similar case was reported by Ricklefs (1980) in a co-operatively breeding species, the Rusty-margined Flycatcher *Myiozetes cayanensis* in Panama, which visited the nest only when a helper or a parent was in the vicinity. These observations suggest that parents may not so much guard their offspring as protect themselves or their partner for future nesting attempts. Consequently, density-dependent selection in a risky environment would lead to either increased vigilance of parents and reduced reproductive effort (Ricklefs 1991, 2000, Both *et al.* 2000), or increasingly differential parental responses towards adult vs. nestling predators (Ghalambor & Martin 2001).

In summary, our data suggest that parents reduce nest-feeding rates due to positively selected risk-sensitive behaviour rather than an evolutionary response to limited environmental resources. We understand ‘risk-sensitive’ in this context to mean the adjustment of foraging effort with respect to the acute or perceived risk of being predated. In this sense, risk-sensitive behaviour is intended to promote ‘own’ survival as well as benefit the partner of the current and future breeding attempts, both at the expense of current reproductive effort. Ultimately, this evolutionary scenario might lead to a reduction in current reproductive investment, and constitute one of the reasons for the occurrence of lower clutch sizes in most tropical bird species.

We thank the Tanzanian Commission for Science and Technology (CoSTech) and the Tanzania National Parks Authorities (TaNaPa) for permitting us to conduct our project in Arusha National Park, Tanzania. Professors Kim Howell and Charles Mlingwa from the University of Dar es Salaam were our local sponsors. The manuscript was considerably improved by the Animal Behaviour Discussion Group at University of Missouri at St Louis, notably Stan Braude, Zuleyma Tang-Martinez and George Taylor. We would like to thank Dr Marion East, in particular, for directing our attention to the provisioning rates of tropical birds in the field. This project was supported by the Max-Planck-Society and a grant by the National Geographic Society.

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Received 21 February 2005; revision accepted 31 January 2006.