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Predators as stressors? Physiological and reproductive consequences of predation risk in tropical stonechats (*Saxicola torquata axillaris*)

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Tropical birds usually lay smaller clutches and are less likely to initiate a second brood than their temperate-zone relatives. This reduction in annual fecundity is generally explained as an adaptation either to higher rates of nest predation or to a more limited food supply concurrent with higher adult survival in the tropics. However, the physiological parameters associated with lower annual fecundity in tropical birds have not been well investigated. We compared the annual fecundity, behaviour and a number of physiological parameters of stonechat parents feeding fledged juveniles in territories with and without fiscal shrikes, a predator on adult and fledged birds. Stonechat pairs in territories with shrikes were less likely to initiate a second brood and delayed successive broods compared to pairs in territories without shrikes. After fledging of their young, males showed a greater propensity than females to initiate distraction calls after a human intrusion into their territory and, therefore, invested more in the defence of their young. In territories with shrikes stonechat males had higher initial plasma corticosterone levels and lower body conditions than males in territories without shrikes, suggesting that they were chronically stressed. In contrast, the females from both types of territory had low initial plasma corticosterone levels. We conclude that shrike presence might account for the delay in initiation of a second brood and the reduction in the tendency to initiate a second brood. Whether these effects are mediated by the elevated levels of corticosterone remains to be demonstrated.

Keywords: tropical birds; predation corticosterone; stress response; life history; *Saxicola torquata*

1. INTRODUCTION

Predators, apart from directly affecting prey populations through mortality and thus influencing prey dynamics (Sinclair & Pech 1996), exert indirect effects on their prey by influencing behaviour, reproduction and foraging patterns (Lima & Dill 1990). Indirect effects of predator presence on reproduction and survivorship have been found to be the major factors controlling the population cycle of the snowshoe hare in North America (Krebs *et al.* 1986), and have also been described in several studies on birds (Arcese & Smith 1988; Lima & Dill 1990). Studies on tropical bird species have provided evidence that various reproductive parameters can be shaped by predation on adults or nests (Young 1994; Woodworth 1997; Martin *et al.* 2000). However, the physiological correlates of the interactions between predator presence and various reproductive parameters have not been investigated.

Stonechats are widely distributed in several subspecies throughout the Palaearctic and Palaeotropic (Cramp 1988) and, therefore, provide a useful model to investigate interactions between environmental parameters and life history. One of the many life-history traits in which stonechats of the Eastern African subspecies (*Saxicola torquata axillaris*) differ from birds of the European subspecies

(*Saxicola torquata rubicola*) is the timing of successive broods. In the field, females of the European subspecies initiate second or third clutches while still feeding nestlings, i.e. when the young are less than two weeks old (the nestlings are then taken care of by the male; Frankevoort & Hubatsch 1966). In contrast, Eastern African stonechats initiate follow-up clutches only after the fledged juveniles of the first brood have begun their post-juvenile moult at an age of at least six weeks. In the aviary, however, Eastern African stonechats were found regularly to initiate a second brood while young were still in the nest, just like their European conspecifics (Koenig & Gwinner 1995). Therefore, the considerably longer inter-brood interval found in field studies in the Eastern African subspecies as compared to the European subspecies must be due to environmental factors rather than genetic differences between the subspecies.

Extended parental care for the offspring involves delayed initiation of a second brood (Lack 1968; Verboven & Verhulst 1996), and parents should extend parental care if the fitness gain of caring for fledged juveniles is higher than the fitness gain of initiating a second clutch (Williams 1966). Correspondingly, birds nesting in tropical environments where there is high nest predation (Martin 1992) tend to invest more time in fledged young than do temperate-zone species, and consequently raise fewer broods per year than birds in temperate environments (Ricklefs 2000).

At the proximate level, several studies have found that within a population the re-nesting interval covaries with

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predation pressure and ecological factors (Burley 1980; Verhulst 1998; Sullivan *et al.* 1999). However, the physiological correlates of this covariance are largely unknown.

Exposure to predators has been found to be positively correlated with initial plasma levels of corticosterone, the principal biologically active avian glucocorticoid (Silverin 1989; Wingfield *et al.* 1998). An increase in plasma corticosterone levels is often used as a physiological indicator of stress (Siegel 1980). The ability to express this acute corticosterone stress response to an array of stressors has been demonstrated in a variety of bird species, including songbirds (Siegel 1980; Wingfield *et al.* 1982; Schwabl *et al.* 1991). Short-term increases in plasma corticosterone in response to unpredictable events (e.g. storms, predation risk) are believed to redirect behaviour away from ongoing activities such as reproduction and territoriality toward immediate life-saving responses (Sapolsky 1987; Wingfield *et al.* 2000). This is thought to be achieved in mammals by decreasing hypothalamic gonadotrophic releasing hormone release, reducing gonadal responsiveness to luteinizing hormone and decreasing concentrations of luteinizing hormone receptors (Sapolsky *et al.* 2000). After the perturbation has passed, corticosterone levels return to baseline and normal activities can be resumed.

While the corticosterone stress response may help to effect short-term adjustments during transient perturbations, high levels of the hormone over a prolonged time (chronic stress) may be deleterious. Chronic high levels of corticosterone can suppress the immune system, compromise growth and development and result in neuronal-cell death (Siegel 1980; Sapolsky 1987). In vertebrates, chronic high corticosterone levels are often incompatible with breeding (Wingfield & Silverin 1986).

We hypothesized that the delay in re-nesting in the Eastern African subspecies of stonechat is a direct consequence of stress-induced increased corticosterone levels caused by the presence of a predator of adults and fledgling birds. Previous studies indicate that the stress response is attenuated under certain circumstances, such as during the breeding season in female white-crowned sparrows but not in males (Wingfield *et al.* 1982), during moult (Astheimer *et al.* 1995) and during different migratory phases (Schwabl *et al.* 1991). These changes appear to be related to differences in the sensitivity of the hypothalamus–pituitary–adrenal axis under different conditions (Romero *et al.* 1998*a*,*b*). Thus, assessment of the stress response of males and females provides a measure of the sensitivity of the hypothalamus–pituitary–adrenal axis to perturbation. We therefore studied both initial levels of plasma corticosterone and changes in corticosterone levels during the stress response to obtain more information on the overall state of the individuals during the breeding season.

A conspicuous predator of small passerine birds in the African tropics is the fiscal shrike (*Lanius collaris*), a bird species that preys on adult and fledgling birds (Mackworth-Praed & Grant 1960). Pairs with fledged young in territories with and without fiscal shrikes were subjected to a capture–restraint protocol, during which plasma samples were taken. Pairs in the same breeding stage that had just lost their young served as controls.

2. MATERIAL AND METHODS

The study was conducted during the 1994/1995, 1995/1996 and 1996/1997 breeding seasons of stonechats in Arusha National Park. Arusha National Park is situated on the eastern side of Mount Meru in northeastern Tanzania and covers an area of 137 km^2 between latitudes 3° 2′ S and 3° 8′ S and longitudes 36° 45′ E and 36° 56′ E. Stonechat pairs with fledged young and pairs that had lost eggs, nestlings or fledged young were identified.

(a) *Behavioural observations and reproductive success*

Stonechats utter alarm calls in the presence of other animals. Observers can use these alarm calls and other antipredator behaviours, such as 'diving' into the vegetation, to identify the presence of potential predators (Greig-Smith 1980). In some areas stonechats share their territories, at least temporarily, with the fiscal shrike, a territorial predator on arthropods and vertebrates, including birds up to their own size (Emlen 1979). This species is 'devastating to young birds' (Mackworth-Praed & Grant 1960, p. 593) and is also reported to prey on nestlings (MacLean 1988). Territories were classified as 'shrike' and 'no-shrike' territories.

The onset of breeding and the breeding success were monitored in all pairs of the population throughout the study period. Each pair was visited in alternate weeks and its breeding status was assessed. Thus, every attempt to initiate a second brood could be recorded.

The survival of the fledged broods of 32 pairs in territories with shrikes and 40 pairs in territories without shrikes was monitored in all three years. Juvenile tropical stonechats leave their natal territories after completion of the post-juvenile moult at an age of between six and eight weeks. Parent stonechats utter alarm calls with a higher frequency in the presence of potential predators or human intruders (Greig-Smith 1980) when fledged young are present in the territory. Therefore, this behaviour provides a robust measure of the presence of juveniles, although the number of fledged juveniles present was difficult to assess. Fledged young were defined as absent when the parents no longer uttered alarm calls and no juveniles could be found in the territory. As the date of fledging was known, the absence of young in a territory could be attributed to either predation or dispersal.

To test the alertness of males, females and fledged juveniles, family groups with fledged juveniles were visited before noon. While approaching a family group the observer noted the sex and age of the bird initiating the alarm calls. In total, 60 family groups were tested in the course of the study.

(b) *Sampling*

We randomly chose 37 pairs from the population as focal pairs (nine pairs with young in 'shrike' territories, nine pairs with young in 'no-shrike' territories, ten pairs without fledged young in 'shrike' territories and nine pairs without fledged young in 'no-shrike' territories). All adult birds were caught between December and February, before the onset of the postnuptial moult. Birds were captured between 09.00 and 12.00 using spring traps baited with meal-worms. After capture the birds were subjected to the stressors of capture and restraint.

The stress paradigm was identical for all birds. At the time of capture a stopwatch was started and within 3 min *ca.* 50 μl of blood was taken from the ulnar vein. No correlation was found

between corticosterone levels and the timepoint when blood sampling was completed within the first 3 min (Spearman's rank; males: $r_{36} = -0.471$, $p = 0.805$; females: $r_{37} = 0.1659$, $p = 0.381$). Therefore, all samples taken within 3 min were considered to reflect initial levels. Blood was collected in heparinized microhaematocrit capillary tubes (75 mm long, inner diameter 1.1–1.2 mm); cotton stanched the blood flow. After sampling, and between subsequent bleeds, the birds were placed in opaque cloth bags. Further blood samples were taken 10, 20, 30 and 50 min after capture.

After collection of the last blood sample, birds were colour ringed, weighed, measured for tarsus length and scored for fat (Kaiser 1993) and moult (after Newton 1966). Birds were then released in their original territories.

The body condition of each bird was estimated, according to Linden *et al.* (1992), as the non-standardized residual of a regression of body mass on tarsus length.

Immediately after collection, the blood was centrifuged in the field and the plasma was transferred to cryotubes. These tubes were stored on ice in a thermos flask. In the evening, they were transferred into a liquid-nitrogen container. At the end of the field season in March the samples were transported on dry ice to Andechs (under permission of the Tanzanian and German authorities), where they were kept in a freezer at $-70\,^{\circ}$C until assayed.

(c) *Radioimmunoassay*

Corticosterone was measured after extraction by radioimmunoassay. Briefly, corticosterone was extracted from 10–50 µl of plasma with 3 ml dichloromethane (redistilled) on Extralut (Merck, Whitehouse Station, NJ, USA) columns to remove lipids. Before extraction, 3000 disintegrations per minute of tritiated corticosterone (NET 399 New England, Boston, MA, USA) was added to each sample and allowed to equilibrate for at least 30 min to estimate recovery and efficiency. Mean extraction recovery was mean $\pm$ s.e.m. $= 82 \pm 7\%$ and the efficiency of recovery of spiked samples was 97%. The eluate was dried under nitrogen at 37 °C, and dried extracts were reconstituted overnight in 0.05 M borate assay buffer. The reconstituted samples were then assayed using corticosterone antiserum (B3-163 Endocrine Sciences, Tarzana, CA). Briefly, duplicate 100 µl aliquots of reconstituted eluate were incubated first with corticosterone antibody solution at 37 °C for 30 min and then together with tritiated corticosterone at 4 °C for 20 h. Finally, a dextran-coated charcoal solution was used to separate the free from the bound fractions. The lower detection limit was $0.2\ \text{ng ml}^{-1}$. Inter- and intra-assay variations were 9.6% and 6.1%, respectively. Serial dilution of both extracted and unextracted pooled stonechat plasma exhibited parallel displacement to the standard curve.

(d) *Statistics*

Frequencies were tested using Fisher's exact test (Sokal & Rohlf 1998). Data were tested for normal distribution using a Kolmogorov–Smirnov test. Two-way analyses of variance (ANOVA) (procedure general linear model) were used to analyse the effects on initial corticosterone levels, and a two-way repeated-measures ANOVA (procedure general linear model) was performed to analyse the patterns of corticosterone increase during the capture–restraint protocol. In case the data were not normally distributed because of the occurrence of corticosterone levels below the detection limit, differences were tested using a Mann–Whitney U-test. All data were analysed using the Statistical Analysis System, Release 6.12 (SAS Institute, Cary, NC).

3. RESULTS

(a) *Reproductive success*

Stonechat pairs that shared their territory with a shrike initiated laying later than pairs in territories without shrikes when all years were pooled (Mann–Whitney $U_{1,111} = 15.0$, $p < 0.005$; figure 1). The reproductive success of pairs in 'shrike' territories was reduced (figure 2): only eight out of 32 pairs in 'shrike' territories (25%) were able to raise their young to the post-juvenile moult, whereas 33 out of 40 pairs in 'no-shrike' territories (83%) were successful (Fisher's exact test using original data, $p < 0.001$).

Second broods were initiated by a total of 13 pairs in the 1994/1995 and the 1995/1996 breeding seasons. Only pairs that succeeded in fledging at least one chick from their first brood before 28 October eventually initiated a second brood. In 'shrike' territories only 32% of the pairs with fledged juveniles before 28 October initiated a second brood, whereas in 'no-shrike' territories 75% initiated a second brood (Fisher's exact test, $p < 0.05$). The interval between the first and second broods was longer in 'shrike' territories (67–108 days) than in 'no-shrike' territories (48–76 days) (Mann–Whitney U-test, $U_{7,7} = 24.5$, $p < 0.05$).

(b) *Behavioural observations*

When a human observer approached a family group of stonechats, in 60% of all cases the male initiated alarm calls and distraction behaviour; alarm calls were initiated in 34% of all cases by the females and in 6% of all cases by the juveniles. After a short time all members of the family group responded and each member uttered alarm calls. The male, however, was the only member of the family group to approach the intruder; the female and the young withdrew.

(c) *Body condition and fat levels of captured birds*

Males with fledged young in 'shrike' territories had a lower body condition than males in 'no-shrike' territories (two-way ANOVA, shrike $\times$ status, $F_{1,36} = 5.67$, $p < 0.05$; contrast: 'with shrike' in category 'with fledged' $F_{1,17} = 13.79$, $p < 0.001$; figure 3a). Conversely, the body condition of females with fledged young was the same, regardless of whether or not they had fledged young or were in 'shrike' or 'no-shrike' territories (two-way ANOVA, no significant classes, no significant interactions; figure 3b).

When no fledged juveniles were present, the body conditions of both males and females did not differ between 'shrike' and 'no-shrike' territories.

Eight out of 18 males had a visible amount of body fat, whereas only one female out of 18 with visible body fat was caught during the course of this study.

(d) *Plasma corticosterone levels*

Over the period sampled (between 09.00 and 12.00), there was no influence of the time of day on initial levels of corticosterone (Spearman's rank, $r_{58} = 0.1794$, $p > 0.1$).

When fledged young were present, males in 'shrike' territories had higher initial corticosterone levels than males in 'no-shrike' territories (two-way ANOVA, shrike $\times$ status, $F_{1,36} = 5.37$, $p < 0.05$; contrast: 'with shrike'
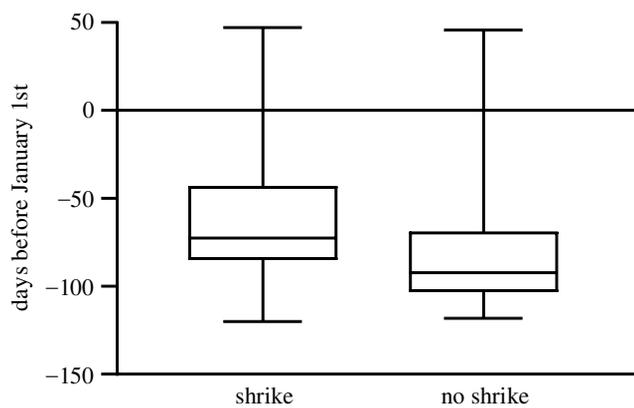
Figure 1. The onset of laying of pairs in 'shrike' ($n = 69$) and 'no-shrike' ($n = 42$) territories (median, quartiles, range; Mann–Whitney U-test, $U_{1,111} = 15.0$, $p < 0.005$).
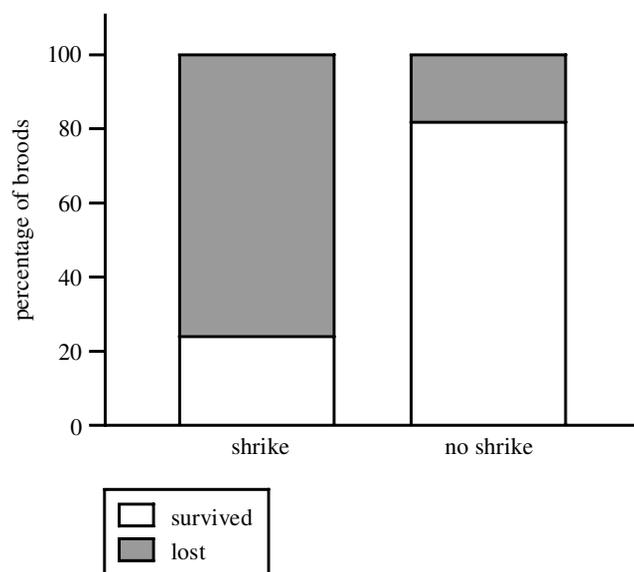

Figure 2. Percentage of broods where at least one fledged chick survived until the post-juvenile moult in 'shrike' and 'no-shrike' territories ($n = 72$; Fisher's exact test using original data, $p < 0.001$).

in category 'with fledged' $F_{1,17} = 11.03$, $p < 0.005$; figure 4a); when no fledged young were present, males in 'shrike' and 'no-shrike' territories had similar initial corticosterone levels. There was no significant correlation between initial corticosterone levels in males and the age of their fledged young (Spearman's rank, $r_8 = 0.59$, $p > 0.1$), indicating that the males had elevated corticosterone levels throughout the time that they tended fledged juveniles.

When the same analysis was applied to females, the initial levels of corticosterone were found to be similar in all groups (two-way ANOVA, shrike × status, $F_{1,36} = 0.50$, $p > 0.1$; figure 4b).

Males and females, regardless of whether they were with or without young, or in 'shrike' or 'no-shrike' territories, responded to the protocol of capture and restraint with a pronounced rise in corticosterone levels.

The corticosterone responses of males and females were found to be different (two-way repeated-measures ANOVA, with plasma corticosterone levels at different time points during the capture–restraint protocol as the dependent variable and sex and predator presence as classes; table 1). We also tested specifically whether males
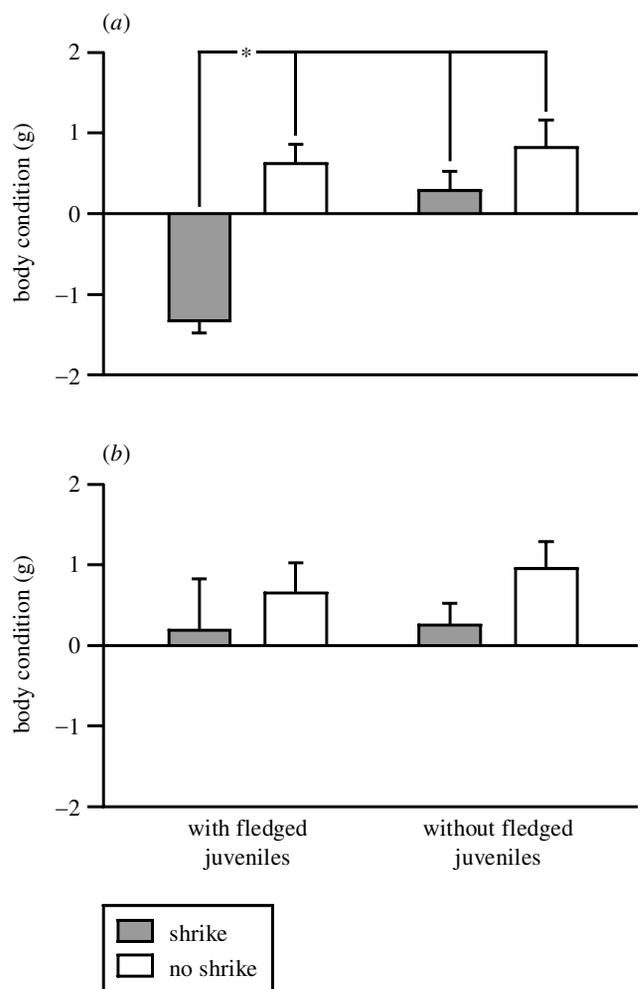
Figure 3. Body condition (residuals of a regression of body mass on tarsus length) of (a) male and (b) female stonechats with and without fledged juveniles in 'shrike' (shaded bars) and 'no-shrike' (open bars) territories (mean+s.e.m.). Males with fledged young in 'shrike' territories had a lower body condition than males in 'no-shrike' territories (two-way ANOVA, shrike × status, $F_{1,36} = 5.67$, $p < 0.05$; contrast: 'with shrike' in category 'with fledged', $F_{1,17} = 13.79$, $p < 0.001$).

with elevated initial levels of corticosterone had a lower response, but no significant effects were found (Spearman's rank $r_{17} = 0.267$, $p > 0.1$). When males with fledged young were analysed separately, higher maximal levels of plasma corticosterone were found in males with visible body fat than in males without visible body fat, irrespective of shrike presence (two-way repeated-measures ANOVA, factor fat level, $F_{1,17} = 6.5$, $p < 0.05$; factor shrike not significant, no significant interactions found; figure 5). No relationships were found in males without fledged young between maximal plasma corticosterone levels and the amount of visible body fat or body condition. Furthermore, no correlation between the amount of visible body fat and body condition was detected in the females.

4. DISCUSSION

(a) *The initiation of a second brood in the field: bet-hedging between parental care and breeding*

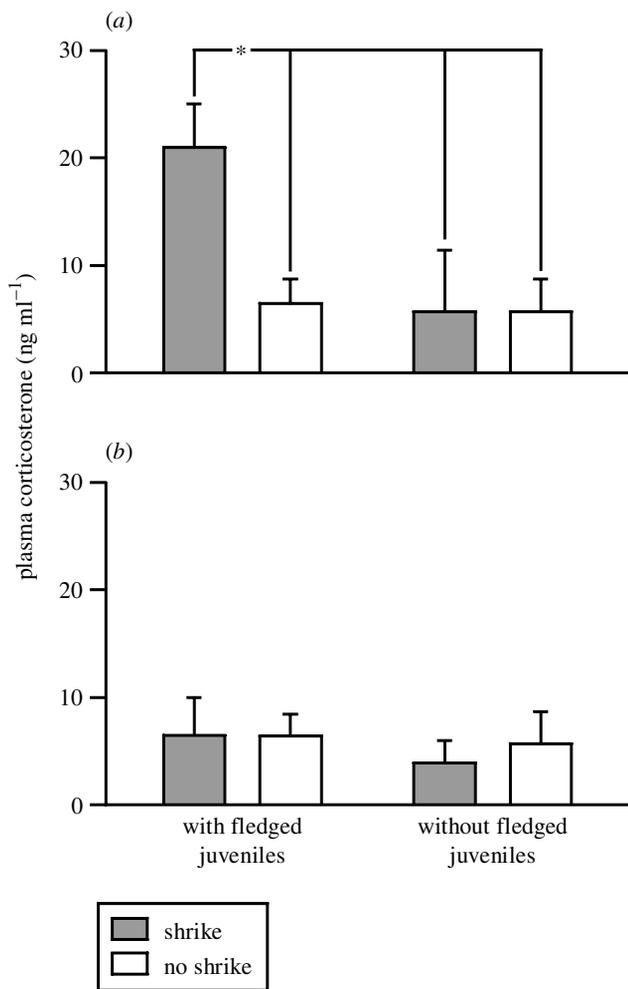Fledged stonechat juveniles in territories with fiscal shrikes are at high mortality risk. Fiscal shrikes are a

Figure 4. Initial plasma corticosterone concentrations of (*a*) male and (*b*) female stonechats with and without fledged juveniles in 'shrike' (shaded bars) and 'no-shrike' (open bars) territories (mean+s.e.m.). Males with fledged young in 'shrike' territories had higher initial levels of corticosterone than males in 'no-shrike' territories (two-way ANOVA, shrike × status, $F_{1,36} = 5.37$; $p < 0.05$; contrast: 'with shrike' in category 'with fledged', $F_{1,17} = 11.03$, $p < 0.005$). Initial plasma corticosterone levels in females were not different.

Table 1. Two-way repeated-measures ANOVA of plasma corticosterone levels during the capture–restraint protocol with the factors sex and shrike presence.

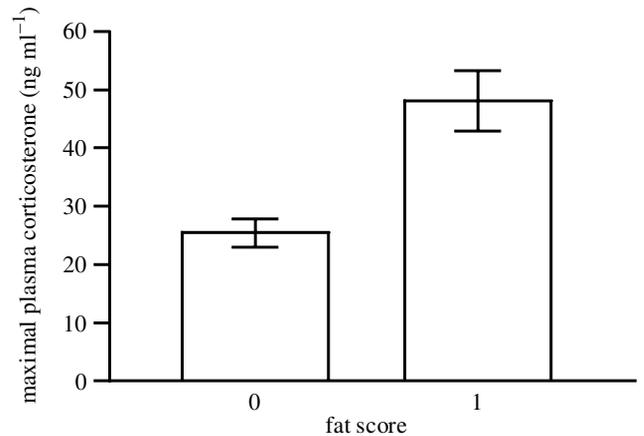| source	sum of squares	*F* value	p
sex	3996	10.38	< 0.01
shrike	353	0.92	> 0.1
sex × shrike	1758	3.52	> 0.1
error	6160		

Figure 5. Maximal plasma corticosterone levels in male stonechats guarding fledged juveniles with (fat score = 1) and without (fat score = 0) visible body fat (mean ± s.e.m.). Males with visible body fat had higher maximal levels of plasma corticosterone, irrespective of shrike presence in the territory (two-way analysis of covariance, factor fat level, $F_{1,36} = 7.4$, $p < 0.05$).

threat especially to recently fledged young, which are not yet capable of escaping by flying because of their increased weight after fledging and their reduced flying skills (Flinks 1999).

In this study population of the Eastern African sub-species of stonechat, the odds of successfully raising juveniles in 'shrike' territories were quite low: up to 70% of the nests and broods were lost. The mortality rate increased as the breeding season progressed, so that the chances of successfully raising a second brood were even lower. Therefore, if parental vigilance reduced juvenile mortality, selection should favour extended periods of parental care (Drent & Daan 1980).

Stonechats are among the species that use distraction calls and conspicuous behaviours to distract potential predators away from the nest (Greig-Smith 1982). Parental care and vigilance after fledging may, therefore, have immediate effects on the survival of fledged juveniles, until they become independent and leave their parental territory. Thus, parents in 'shrike' territories are likely to increase the survivorship of their offspring by providing parental care for a longer time. As a consequence, they should stay with their young for a prolonged period and delay a second brood even longer. The latter prediction was confirmed in our study: parents in 'shrike' territories were less likely to initiate a second brood and had longer intervals between consecutive broods than parents in territories without shrikes. Although pairs in 'shrike' territories initiated laying later than pairs in territories without shrikes, the above finding cannot be attributed to this effect, as even the early breeders in 'shrike' territories that fledged their young concomitantly with pairs in 'no-shrike' territories considerably delayed or even abandoned a successive brood. Thus, reproductive output is maximized in Eastern African stonechats that care for their fledged young over an extended period of time at the expense of the opportunity to initiate a second brood. In line with this, Koenig & Gwinner (1995) found that captive Eastern African stonechats in a predator-free aviary had very short re-nesting intervals, shorter than birds in the field in 'no-shrike' territories, and shorter than aviary birds of the European subspecies (*S.t.rubicola*).

(b) Gender differences in the attendance to fledged juveniles: the role of the males

Our results indicate that stonechat males respond to predators in their territory more frequently than do females and juveniles. Males are more conspicuous due to their exposed perching position (Roedl 1999) and their brighter colour, and, consequently, attract most attacks by predators. In line with this, it is in many cases the male that shows distraction displays (Greig-Smith 1980), while the female stays hidden with the juveniles and leads them away from the predator (A. Scheuerlein, personal observation). Indeed, male stonechats with fledged juveniles in 'shrike' territories had higher initial corticosterone levels and lower body conditions than males in 'no-shrike' territories. One of the major functions of corticosterone is to redirect behaviour towards the 'fight-or-flight' response and to initiate an emergency life-history stage (Wingfield *et al.* 1998). This response of elevated initial corticosterone levels has been documented as the immediate response of birds to stressful stimuli such as inclement weather (Wingfield *et al.* 1995). The fact that the initial corticosterone levels of male stonechats were elevated suggests chronic stress, possibly due to the frequent exposure to predation (Wingfield *et al.* 1998). As we did not detect a significant correlation between the age of the fledged juveniles and the initial corticosterone plasma levels in males, it can be inferred that male stonechats in 'shrike' territories have elevated corticosterone levels throughout the two-month fledgling period. Several deleterious effects associated with long-term elevated corticosterone levels have been described: total failure of reproductive function (Wingfield *et al.* 1998), increased susceptibility to disease owing to suppression of the immune system (Apanius 1998), neuronal-cell death (particularly in the hippocampus; Kimonides *et al.* 1999) and severe protein loss (Munck *et al.* 1984). In a study on social stress in tree shrews (*Tupaia berlangeri*) it was established that males that had lost social-interaction fights with conspecifics subsequently had serum glucocorticoid levels of up to six times normal, and frequently died due to renal failure (Von Holst 1972, 1998).

In the case of stonechats, the increase in the initial corticosterone levels of males in 'shrike' territories was associated with a decrease in body condition. Since fat scores were not different from those of males in 'no-shrike' territories, this may indicate a reduction in the protein-rich component of the body, such as the muscle. Perhaps protein reserves were catabolized in response to chronic high corticosterone levels to augment energy for the defensive behaviour of the males. Wingfield & Silverin (1986) and Silverin (1986) experimentally demonstrated loss of protein from the flight muscles in both song sparrows (*Melospiza melodia*) and pied flycatchers (*Ficedula hypoleuca*) implanted with corticosterone. However, since fat deposits also increased markedly, the overall body mass was not affected.

The responsiveness of the hypothalamus–pituitary–adrenal axis during the capture–restraint protocol was positively correlated with the amount of visible body fat: males with visible body fat reached higher plasma corticosterone levels than males without visible body fat. The reduced stress response in the low-fat birds may protect lean birds from depleting their resources below a critical

level, as high levels of corticosterone have been shown to increase gluconeogenesis and promote lipolysis (Munck & Naray-Fejes-Toth 1995). Conversely, during migration, increased initial corticosterone levels are correlated with lower amounts of visible body fat (Holberton *et al.* 1996). Clearly, the relationship between fat score and initial corticosterone level is complex. Some populations of redpolls (*Carduelis flammea*) show a negative relationship between fat deposit size and corticosterone levels whereas others show no relationship (Romero *et al.* 1998*b*). In addition, the interaction between initial levels of corticosterone and lipid metabolism is not well understood because of the confusion between the pharmacological effects of corticosterone in implant studies and effects induced by physiological levels of corticosterone (Silverin 1998).

(c) The role of the females

When guarding the young, females play a different role from males: they take part in distraction displays only occasionally and their overall vigilance is lower (A. Scheuerlein, personal observation). Coincidentally, their initial plasma corticosterone levels were never as high as those of the males.

No difference in initial corticosterone levels was found between females with fledged young and females with no young. Therefore, the hypothesis that stress due to prolonged parental care or imminent predation suppresses the reproductive drive (Wingfield & Ramenofsky 1985) is not supported for female stonechats. Female white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) can initiate a second brood with initial corticosterone levels as high as 30–40 ng ml^{-1} (Wingfield & Ramenofsky 1997). It appears likely that stonechat females with relatively low initial levels of corticosterone are also able to initiate clutches. In this context it should be noted that females do not necessarily exhibit a plasma-corticosterone stress response. Wingfield *et al.* (1982) found an attenuated stress response in incubating female white-crowned sparrows concomitant with a reduction in the tendency of females to abandon the nest at critical times. Other studies have indicated that the release of corticosterone can be modulated (Astheimer *et al.* 1994, 1995; Romero *et al.* 1998). Finally, we measured only one parameter of a suite of responses to stress (Siegel 1980); other responses, such as the release of adrenaline and noradrenaline, could have revealed that females were indeed stressed but that the adrenal cortical response was suppressed.

Reproduction in 'shrike' territories may be inhibited or delayed because of the adverse effects of shrikes on male body condition. As a consequence, males may not reach a body condition suitable for breeding. Although there may be neighbouring males in reproductive condition, the female may not copulate with them as she may not be able to raise a brood alone. Moreover, because the male may no longer be able to distract predators, females themselves may not reach breeding condition. Detailed behavioural observations and physiological measurements are required to understand the effect of chronic stress on male reproductive performance.

In conclusion, we have demonstrated that the presence of a common predator, the fiscal shrike, increases plasma corticosterone levels in male stonechats attending fledged juveniles. This corresponds to a decreased propensity of

pairs in 'shrike' territories to initiate second broods and a delay in re-nesting. Whether and how these two sets of phenomena are functionally linked, i.e. whether it is the increased stress state that reduces reproductive performance, remains an open question.

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