

Programmed patterns of territorial aggression in first-year European and African Stonechats (*Saxicola torquata rubicola* and *S. t. axillaris*)

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Programmierte Muster der territorialen Aggression von diesjährigen europäischen und afrikanischen Schwarzkehlchen (*Saxicola torquata rubicola* und *S. t. axillaris*).

– Im Alter von etwa fünf bis sechs Monaten etablieren Schwarzkehlchen aus den gemäßigten und tropischen Breiten ihre ersten Territorien: in der europäischen Unterart Winterterritorien, in der afrikanischen Unterart Ganzjahresterritorien. Somit sind die Vögel nach der sozialen Jugendperiode abrupt konfrontiert mit intensiver intraspezifischer Konkurrenz. Die Untersuchung von territorialer Aggression an Schwarzkehlchen in Volieren dient der Feststellung, welche Rolle interne Programme und Umweltfaktoren bei der Regulierung von Aggression spielen. Im Falle einer weitgehenden Regulierung durch endogene Faktoren und deren Interaktion mit Photoperiode würden wir erwarten, daß aggressives Verhalten auch in Abwesenheit der anderen normalerweise erfahrenen ökologischen und sozialen Veränderungen ansteigt, und zwar in etwa zu der Zeit, zu der im Freiland Territorien etabliert werden. Wenn aggressives Verhalten jedoch hauptsächlich von nicht-photischen Umweltveränderungen gesteuert wird sollten die Aggressionsraten in den Volieren konstant bleiben, denn der einzige veränderliche Umweltfaktor ist die Photoperiode.

Um zwischen diesen beiden Hypothesen unterscheiden zu können wurden 23 erstjährige europäische und 24 afrikanische Schwarzkehlchen in natürlicher Gruppengröße (drei europäische und sechs afrikanische Gruppen) unter unveränderten sozialen und lokalen Bedingungen und festem Nahrungsangebot gehalten. Die Vögel erfuhren ihre jeweiligen natürlichen photoperiodischen Bedingungen, d.h. die saisonal veränderliche europäische Tageslänge und die konstante afrikanische äquatoriale Tageslänge. Verhaltensdaten und Daten über Körpermasse, Jugendmauser, Testosteron und Zugunruhe wurden während des Sommers und der Zeit der Territorienbildung im Freiland erhoben solange die soziale Toleranz in den Gruppen anhält.

Mit Zeitserienanalysen überprüften wir, ob sich die Aggression vorhersagbar veränderte, und ob die Veränderungen speziell zum Ende des Experiments auftraten. Zusätzlich verglichen wir Aggressionswerte während und nach der Jugendmauser.

In allen Gruppen stiegen die aggressiven Interaktionen plötzlich an. In den drei europäischen Gruppen war der letzte notierte Aggressionswert signifikant höher als alle vorhergehenden Werte. In den afrikanischen Gruppen nahm die Aggression ebenfalls zu, der letzte Wert war jedoch nur in drei der sechs Gruppen signifikant höher als die vorangegangenen. In dieser Unterart war jedoch das Mauserende eng mit dem Anstieg der Aggression verbunden: in allen Gruppen waren die Aggressionsgesamtwerte nach der Mauser signifikant höher als während des Gefiederwechsels. Unterschiede in den Plasmakonzentrationen von Testosteron stimmten mit der Funktion der territorialen Aggression überein. In europäischen Schwarzkehlchen blieben die Testosteronwerte im Bereich der Grundlinie, wie zu erwarten für Vögel, die Winterterritorien verteidigen. Im Gegensatz dazu fanden wir bei afrikanischen Männchen, die prospektive Brutterritorien verteidigten, erhöhte Testosteronkonzentrationen.

Unsere Arbeit zeigt, daß der Anstieg von Aggression zeitgerecht abgestimmt war sowohl auf den Ablauf saisonaler Aktivitäten der Vögel als auch auf das Kalenderjahr. Die korrekte zeitliche Lage unter konstanten Sozial- und Umweltbedingungen deutet nachdrücklich darauf hin, daß für die Entwicklung des Territorialverhaltens in erstjährigen Schwarzkehlchen hauptsächlich ein Programm verantwortlich ist, das auf der Interaktion endogener Faktoren mit der Photoperiode basiert.

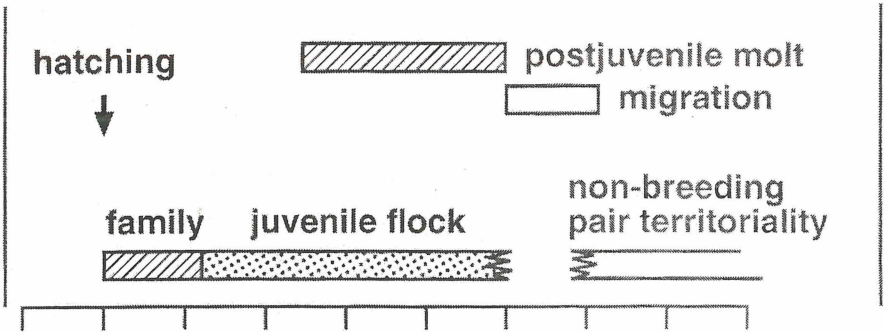
Key words: *Saxicola torquata*, Stonechat, aggression, territoriality, testosterone, time programs.

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Introduction

Young Stonechats of both the European and African subspecies experience their first season of territoriality at an age of about five to six months. The context in which territoriality is expressed is quite different between the two subspecies, and the same is true for the activities that precede territoriality (Fig. 1): *European* birds migrate to wintering grounds in the Mediterranean region (CRAMP et al. 1988, GLUTZ VON BLITZHEIM & BAUFER 1988). Between the time of fledging and the end of fall migration these birds tend to be social and are often found in loose aggregations. This is particularly true for the period of postjuvenile moult and the ensuing early stages of migration (FLINKS 1999). Upon arrival on their wintering grounds, however, males begin to aggressively defend a territory against male conspecifics. Shortly thereafter, usually a female joins the male and helps defend the territory

European Stonechats



African Stonechats

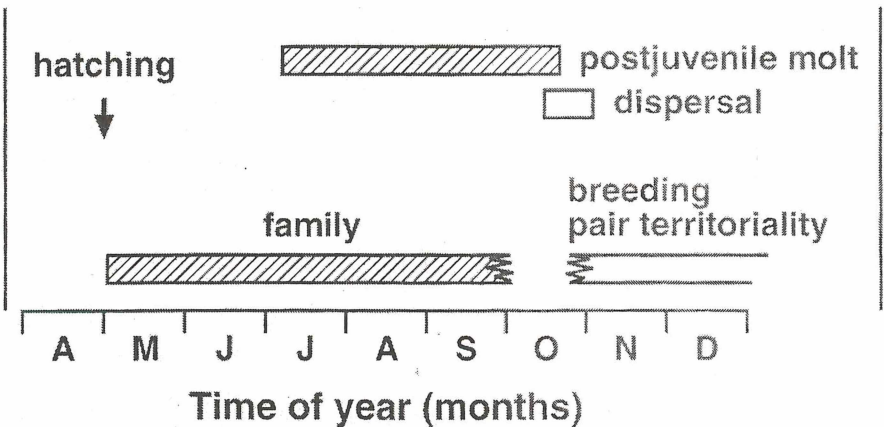


Fig. 1. Schematic representation of seasonal events in first-year Stonechats from Europe (upper diagram) and East Africa (lower diagram). Data are given for birds hatched in early May. For further explanations see text. Based on data in GLUTZ VON BLOTZHEIM & BAUER (1988), DITTAMI & GWINNER (1985), GWINNER (1991). Open bars indicate flexible end or starting points.

Abb. 1. Schematische Repräsentation der saisonalen Ereignisse erstjähriger Schwarzkehlchen aus Europa (oberes Diagramm) und Ostafrika (unteres Diagramm). Die Daten beziehen sich auf Vögel, die Anfang Mai geschlüpft sind. Weitere Informationen s. Text. Daten aus GLUTZ VON BLOTZHEIM & BAUER (1988), DITTAMI & GWINNER (1985), GWINNER (1991). Offene Balken deuten flexible Start- und Endpunkte an.

(GWINNER et al. 1994, RÖDL 1994). Although this pairwise territorial defense resembles that observed in pairs on the breeding grounds, it differs in that the winter territoriality is only very rarely accompanied by song (GWINNER et al. 1994, RÖDL 1994). Moreover, in contrast to reproductive territoriality, winter territoriality does not depend on testosterone or estradiol (CANOINE & GWINNER 2002). Gonads remain small and inactive until shortly before spring departure (GWINNER, unpubl. data; GWINNER & SCHEUERLEIN 1999). Upon departure, pairs split up, and new pairs are formed on the breeding grounds.

East-African Stonechats from Kenya, like their European conspecifics, carry out a postjuvenile moult, but in contrast to the situation in European Stonechats, moult is not followed by a directed migration. Instead the birds disperse into different directions (DITTAMI & GWINNER 1985, SCHEUERLEIN 2000). Subsequently, at an age of about five months, pairs are formed and territories defended against conspecific intruders, and songs are frequently heard during that time. Moreover, gonadal development sets in while territories are being established and plasma testosterone levels begin to rise. The birds are usually ready for reproduction at an age of about 10 months (DITTAMI & GWINNER 1985). Hence, the territorial behaviour that begins to develop in the two subspecies at an age of five to six months, although formally similar, occurs in different contexts, is preceded by different activities, and is almost certainly regulated by different mechanisms.

An important question arising from this situation concerns the mechanistic basis of these different patterns of territorial aggression and the states preceding and accompanying it. Previous work on Stonechats has revealed that basic processes like moult, migration and gonadal activity depend on an endogenous circannual rhythmicity which, when synchronized with photoperiod, provides for an accurate seasonal timing of these activities (GWINNER & DITTAMI 1990, GWINNER 1991). Subspecies differences in seasonal patterning (e.g. of postjuvenile moult) were found to be the result of genetically determined differences in circannual programs and their reaction norms to environmental stimuli (KÖNIG & GWINNER 1995, HELM & GWINNER 1999). It appeared likely, therefore, that territorial behaviour and the associated endocrine changes are also controlled by circannual factors and their interaction with photoperiod. If this were true, seasonal changes of aggressive behaviour and of the preceding and ensuing activities should be expressed with their characteristic and subspecies-specific patterns even if environmental factors other than photoperiod are kept constant. The alternative hypothesis is that aggression patterns emerge as a result of seasonal changes in the non-photic environment. Winter territoriality could, for instance, be the exclusive result of food shortage or high pressure by predators or competitors in their winter quarters; likewise, breeding territoriality might be induced by the availability of a habitat suitable for reproduction. If aggressiveness were to depend largely on changing non-photic environmental factors, it should not change in captive birds. - To distinguish between these two possible hypotheses, we studied aggressive behaviour and changes in testosterone levels in three groups of European and six groups of African Stonechats during the first seven months of their life under semi-natural aviary conditions. Simultaneously we collected data on moult, body mass and migratory activity as time references.

Methods

Origin and maintenance of birds

Birds were taken from the respective field sites as nestlings (European Stonechats (E): Eastern Austria (48° 13' N, 16° 22' E); African Stonechats (A): Lake Nakuru region, Kenya (0° 14' S, 36° 0' E). In total, seven European broods (mean hatching date: May, 25th) and 14 African broods (mean hatching date: April, 15th) were hand raised (GWINNER ET AL. 1987). Raising groups stayed together in cages until the start of the experiment. All birds were individually colour banded.

Young of both subspecies experienced their respective natural photoperiodic conditions (E: natural changes of light/dark cycle at Andechs 48° N, 11° E, outdoor aviaries; A: constant equatorial day of 12.25 h, indoor aviaries). Indoor aviaries were provided with a dim night light (0.095 - 0.101 lux).

Aviaries had a size of 320x210x260 cm for large groups (7-8 birds) and 200x88x200 cm for small groups (four birds). Adjacent aviaries were visually separated from each other. All aviaries were richly structured with branches, bushes and diverse floor coverings providing several potential shelters. In late autumn heaters prevented the ambient temperature from falling below 10°C.

Birds were fed a basic food mixture ad lib. (GWINNER ET AL. 1987), plus 10 mealworms per bird and day. Food and water were renewed daily.

Experimental groups

From the 7th week of life birds were transferred to aviaries. Within the newly established experimental groups all birds were unfamiliar with each other. Group size was adjusted to the field situation of young before migration or juvenile dispersal; for European Stonechats a group size of 7-8 young resembled the average flock size of independent young (H. FLINKS, pers. comm., CRAMP ET AL. 1988, GLUTZ VON BLOTZHEIM & BAUER 1988); for African Stonechats, a group size of four approximated the family size (DITTAMI & GWINNER 1985, KEITH ET AL. 1992, SCHEUERLEIN 2000). In total, 23 European and 24 African Stonechats formed three and six groups, respectively (E₁ - E₃ and A₁ - A₆). Sex ratio was balanced in all African and in one European Group (E₃) and unbalanced in the two other groups (E₁: 3♂:4♀; E₂: 3♂:5♀).

One bird died in each of the groups A₁, A₃, A₅, A₆ within the first weeks of the experiment. These birds were replaced by other juveniles of about the same age. Data were analyzed in the final group composition. One European and one African Stonechat (E₁, A₅) died in October. These birds were not replaced in order to prevent any further social turnover at this advanced experimental stage. Within each group, the experiment ended when escalating aggression made removals of birds necessary.

Data collection

Aggression. Observations took place within the 3rd to 6th hour after daybreak, defined as the onset of civil dawn for outdoor aviaries and onset of light for indoor aviaries. Behaviour was recorded in biweekly or weekly intervals. During one observational session all group members were individually monitored in succession, each for 10 to 20 min, through a one way mirror. All successful aggressive interactions initiated by the focal bird and - if possible - the identity of the opponent were recorded. Success was defined by an escape reaction of the rival. Aggressive acts were mainly supplantings without body contact between the competitors and - more rarely - attacks with body contact (e.g. pecking, occasionally escalating into injurious fights).

Migratory activity was measured as nocturnal activity in one European group (E_1) by means of two ultrasonic sensors (40 kHz, AEI U 81 D, Conrad Electronics) placed at the level of the main perches. Activity signals were registered by an Esterline-Angus event recorder. For the analysis we counted all 15-minute units in which nocturnal activity occurred.

Juvenile body moult and body mass were recorded weekly at approximately the same hour of day. We classified each of 19 plumage regions as either moulting or non-moulting, resulting in a moult score ranging from 0 (none of the 19 regions moulting) to 19 (all regions moulting; modified from BERTHOLD ET AL. 1970). Body mass was measured on a digital balance with an accuracy of 0.1 g.

Blood sampling and testosterone assay. Blood was collected every other week following observations and in selected groups only (E_1 , E_3 and A_3 - A_6). At the end of the experiment we took blood samples in all groups. We collected up to 200 µl blood from the big wing vein using heparinized capillaries. Plasma was deep-frozen at -70° C until analysis. For analysis samples of both subspecies and all periods were evenly split up into six radioimmunoassays (RIAS), all being assayed within 16 days.

In the RIA we largely followed the modified procedure of WINGFIELD & FARNER (1975) described in Hall et al. (1987). The following adaptations to low juvenile plasma hormone levels were worked out. Chromatography was omitted as we used a highly specific antibody with a maximal cross reaction of 9.6 % with DHT (with other steroids: max. 0.1%; Zeman et al. 1986), provided by M. Zeman. Measured steroid concentrations were 90 % derived from testosterone and 10 % from DHT; for simplicity we will use the term testosterone (T) for these results. For the low plasma T levels of the juvenile birds, we increased concentrations by using less buffer for dissolving the extracted samples (recovery volume reduced to 50 µl (longer counting time), assay volume unchanged 2 x 200 µl). Finally we used a short incubation of the assay (1 h at 37° C followed by 2 h at 4° C).

Two to three Stonechat low-T pool plasma samples (assay variation) and two samples of stripped plasma (assay blanks) were run with each assay as quality controls. The following quality control parameters were calculated according to CHARD (1987): Recoveries: 90.8% ($\pm$ 5.3%). Background radioactivity of extraction media: 5.6% ($\pm$ 0.6%). Specific binding: 35.8% ($\pm$ 1.4%). Nonspecific binding 1.4% ($\pm$ 0.2%). Assay blanks: negative in all assays,

showing almost 100% binding. Lower limit of detection: 2.99 pg/tube (± 1.1 pg/tube) or 72 pg/ml (± 26 pg/ml). Interassay variance: 10.6%. Intra-assay variance: 7.8 ($\pm 6.5\%$).

Gonadal size: In African Stonechats we measured follicular and testicular width to the nearest 0.1 mm by means of laparotomy (GWINNER 1975) one week after the end of the experiment (1st week of December). We did not submit European Stonechats to this procedure since several other studies have shown that gonadal growth never occurs before late February (GWINNER, unpubl. data; GWINNER & SCHEUERLEIN 1999, GWINNER 1990).

Data treatment and statistical analyses

Statistical analyses were carried out on the data from the first week of August until the end of the experiments. Because of their earlier hatching, additional data for African Stonechats were available from late June and July. They are shown in the figures and are discussed in the text.

The distribution of individual aggression rates was rather heterogeneous, with some Stonechats showing high aggression whereas others showed little or none. It seemed likely that aggression of some birds may have restricted aggressive tendencies in other group members. We therefore analyzed the totals of aggressive encounters of each group. Seasonal changes of aggression totals were examined in three steps:

Firstly, we applied time-series techniques to examine whether aggression rose predictably. Time series analyses estimate the correlations of current values such as aggression rate with those of the preceding measurement days (autocorrelations, DIGGLE 1990). If data can be predicted by their preceding values, the coefficient of autocorrelation r assumes positive values. Values of r close to zero indicate that current values cannot be predicted from preceding values. This would imply that aggression either remained constant but displayed some white noise or that changes occurred suddenly. Significance testing of r used Box-Ljung statistics. Time series analyses assume equally spaced data. Since aggression scores were gathered in part on a biweekly basis, we examined biweekly observations only. This necessitated interpolation of individual missing data in European birds: instead of the measurements from calendar weeks 39, 41, 43, and 45, we used their intermediate values as interpolated data for the weeks 40, 42, and 44. For all other analyses, we used the original data sets.

In a second step of analysis we assessed whether rises in aggression at the end of the season were significant in order to distinguish between white noise and real change. For that purpose, we tested whether the highest aggression totals of each group qualified as outliers in relation to all preceding values (applying Dixon's Test, SOKAL AND ROHLF 1995, A, B).

Thirdly, we divided postjuvenile development into two biologically meaningful periods, using the end of postjuvenile moult as a marker date (defined as the earliest day on which on average no more than three simultaneously moulting plumage areas were recorded).

Cut-off dates were the following weeks (in sequence of group numbers): European, all after week 42 (mid-October); African after weeks 44, 41, 40, 41, 39, 41 (late September until late October). We then compared the moulting groups and the post-moulting groups with Kolmogorov-Smirnov (KS) tests to determine whether aggression changed after moult completion.

In contrast to aggression, we used group means of body moult and body mass for data of time-series analyses. Nocturnal activity was measured continuously, and therefore we analyzed weekly means of the number of 15-minute intervals per night. Data on testosterone were too few for group-wise time series analysis. To approximate time-trends, overall medians of both subspecies were used for autocorrelation analyses and for KS-tests between moulting birds and post-moulting birds. Time spacing was consistently biweekly in African Stonechats, whereas in European Stonechats a one-week spacing was followed by a three-week spacing. All analyses were carried out with SPSS 10.07.

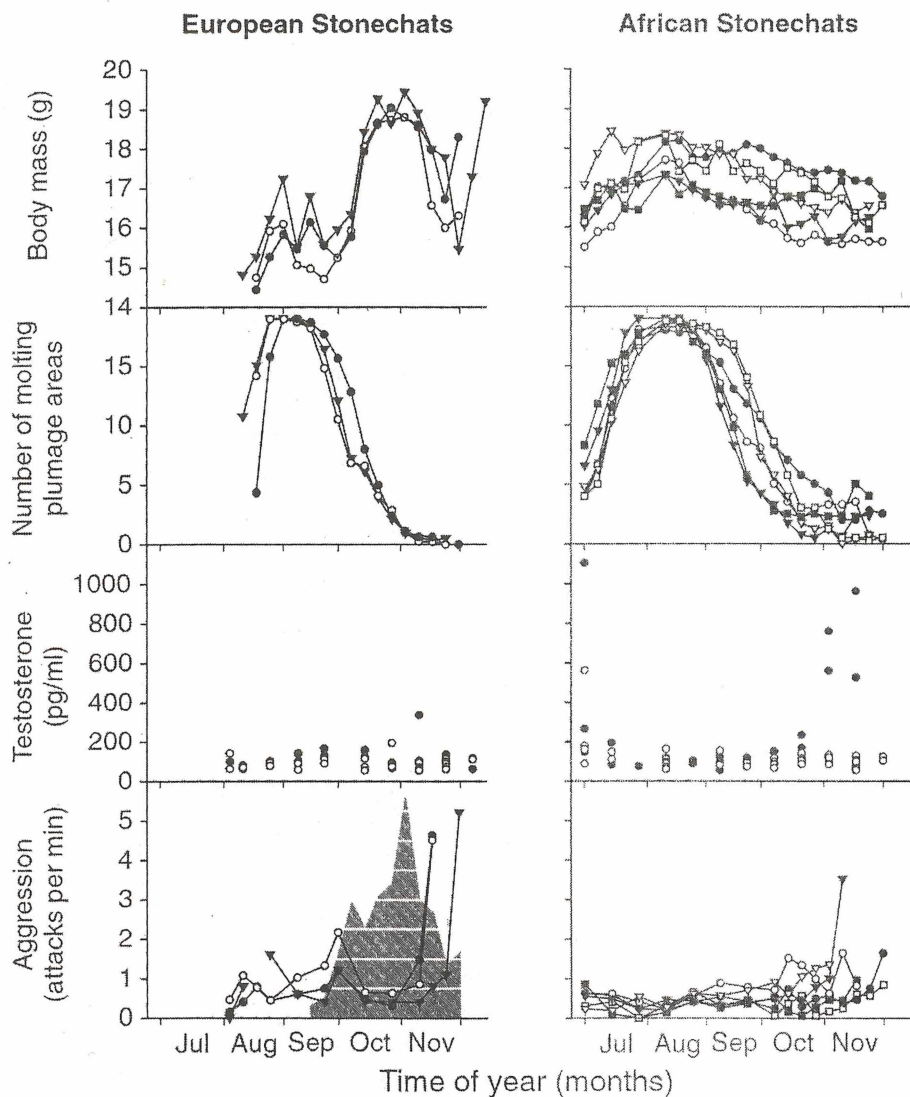
Results

Aggression

Aggressive behaviour was generally low in moulting young of both subspecies during August and September (Fig. 2). In October, during the migratory period of European Stonechats, aggression totals seemed slightly depressed. In November aggressive interactions increased sharply in all European groups. In the non-migratory African Stonechats aggression began to rise as early as October and peaked from late October onwards. In neither subspecies was there significant autocorrelation in any of the groups (mean $r = 0.06$). In all three European groups and three of the six African groups, the last aggression score was significantly higher than all preceding values (Dixon's test, $p < 0.01$). Therefore aggression had risen instantaneously. In both subspecies, aggression was lower during than after moult (European: mean rank moulting 16.1; postmoult 20.4 of 34; African: mean rank moulting 28.8; postmoult 40.9 of 67). KS-tests of differences between moulting and post-moulting aggression were significant in African (KS-Z 1.42; $p = 0.04$; $n = 67$) but not in European Stonechats (KS-Z 0.76; $p = 0.62$; $n = 34$).

Fig. 2 (next page). Seasonal course of body mass, juvenile body moult, plasma testosterone and aggression in first-year European (left panel) and African (right panel) Stonechats. Body mass and moult are plotted as group means, testosterone concentrations are given for individual birds (filled symbols: males; open symbols: females), aggressive encounters as group totals. Nocturnal activity in group E_1 is shown in the background of the graph for aggression in European groups; the maximal value of migratory restlessness in week 44 corresponds to 37.5 intervals of 15-minutes during which nocturnal activity occurred. In each panel identical symbols in graphs identify the groups (European, left: E_1 - E_3 , African, right: A_1 - A_6).

Abb. 2 (nächste Seite). Saisonaler Verlauf von Körpermasse, Jugendmauser des Körpergefieders, Plasmakonzentration von Testosteron, und dem Auftreten von Aggression von erstjährigen europäischen (linke Teilabbildung) und afrikanischen (rechte Teilabbildung) Schwarzkehlchen. Körpermasse



und Mauser sind als Gruppenmittel aufgetragen, Testosteronkonzentrationen sind Werte einzelner Vögel (gefüllte Kreise: Männchen; offene Kreise: Weibchen); Aggression bezieht sich auf die Gesamtzahl aggressiver Interaktionen pro Minute innerhalb einer Voliere. Nächtliche Zugunruhe der Gruppe E_1 wird im Hintergrund der Abbildung der Aggression europäischer Schwarzkehlchen gezeigt; der Maximalwert der Zugunruhe in der Woche 44 belief sich auf 37.5 zugaktive 15-Minuten-Intervalle innerhalb einer Nacht. Identische Symbole innerhalb einer Teilabbildung bezeichnen identische Gruppen (europäisch, links: E_1 - E_3 , afrikanisch, rechts: A_1 - A_6).

Testosterone

The early measurements from African Stonechats indicated elevated testosterone levels in two of the young birds (Fig. 2). From August onwards testosterone concentration fluctuated around 100 pg/ml in both subspecies and increased toward the end of the experiments in some of the male African Stonechats. In both subspecies, there was no significant autocorrelation (European: $r = -0.06$, $p = 0.84$; African: $r = 0.26$, $p = 0.31$). The KS-tests showed that in African Stonechats, post-moulting birds had significantly higher testosterone values than moulting birds (KS-Z 1.49; $p = 0.02$; $n = 9$), whereas in European Stonechats the groups did not differ (KS-Z 0.76; $p = 0.59$; $n = 10$).

Gonads

At the end of the experiment in early December testicular width in African Stonechats ranged from not measurable ($< 1.0\text{mm}$) to fully developed (4.8mm). It was not measurable in four out of 12 males, about 1.0 mm in two, and well above 1.0 mm in six males (overall median = 1.1mm). Female gonadal development was not advanced. Only three out of 11 birds had follicles at the limit of measurement (0.8 mm), eight were below the limit.

Body moult

Unlike aggression and testosterone, moult proceeded in a steady manner and was the most highly autocorrelated parameter in both subspecies (Fig.2: European Stonechats: mean $r = 0.67$, $p < 0.05$ in all three groups; African Stonechats: mean $r = 0.76$; $p < 0.05$ in all six groups). All groups had finished moult before aggression peaked.

Body mass

Seasonal variation of body mass was observed in both subspecies. Autocorrelations were significant in one out of three European groups (mean $r = 0.46$) and in four out of six African groups (mean $r = 0.45$). The time course of body mass changes differed conspicuously between the subspecies. In the European birds a first small peak coincided with peak moult; the second much more pronounced peak in October coincided with intensive migratory restlessness. In the non-migratory African subspecies there was only one peak, which coincided with moult (Fig. 2).

Migratory restlessness

Nocturnal activity in the one European group rose by the end of September, and increased in October with a sharp peak in the two last weeks of the month. The first week of November revealed variable but decreasing values. Thereafter, nocturnal activity remained low. Migratory restlessness was most intense right after completion of moult and had declined to very low levels at the time at which aggression peaked (Fig. 2). Time series analysis of the 12 weekly observations revealed a significant autocorrelation ($r = 0.50$; $p = 0.05$).

Discussion

In our study we focussed on the temporal control of territorial aggression in young European and African Stonechats: the role of internal programs versus environmental factors. Under stable aviary conditions aggressive behaviour rose significantly in the fall. The rise was sharp and instantaneous as opposed to a steady and predictable increase as in body moult. In the field, external stimuli such as food supply and intruder density may influence social tolerance (e.g. DAVIES 1976, MYERS et al. 1979, ZAHAVI 1971). Stimuli emanating from territories, partners, rivals or experience can modulate the individual's readiness to attack (e.g. KELSEY 1989, RAPPOLE 1986). Our results obtained under stable aviary conditions in the absence of external stimuli associated with actual migration, dispersal and settlement in a breeding or wintering site strongly suggest a time program for territorial aggression in young Stonechats that is independent of these environmental factors.

Although the timing of territorial aggression is endogenously programmed in both subspecies, aggression occurs in different functional contexts and proximate control mechanisms seem to differ. Differences of this kind are suggested by our results on plasma testosterone concentrations. Aggression in the *context of nonbreeding territoriality* in European Stonechats was accompanied by persistently low plasma testosterone levels in both sexes. These findings are consistent with field data on wintering European Stonechats (GWINNER et al. 1994, CANOINE & GWINNER 2002) and with those from several studies on non-reproductive territoriality in other species (e.g. SCHWAB & KRINER 1991, SOMA & WINGFIELD 1999, SCHLINGER et al. 2001 for review). In African Stonechats, in contrast, territorial aggression in the wider *context of breeding* was accompanied by significantly elevated post-moulting testosterone concentrations. As shown in Fig. 2, an increase in testosterone was only found in males at the end of the experiment when testes had started to develop. The fact that only some of the males had elevated testosterone concentrations resembles the situation in other species (e.g. Willow Tits, *Parus montanus*, SILVERIN 2002) and possibly indicates that dominance relationships may play a role. An association of male territorial aggression with high levels of testosterone during the reproductive season is common among passerines (e.g. WINGFIELD & RAMENOFKY 1985, WINGFIELD et al. 1987, Wingfield

et al. 1990, SCHWABL & KRINER 1991, CANOINE & Gwinner 2002). Our data are consistent with the idea that testosterone is also involved in the control of territorial aggression in young male African Stonechats.

In female African Stonechats, however, which also became markedly aggressive, circulating testosterone levels remained baseline (Fig. 2). These findings are in accordance with the few studies on the endocrine control of female aggression, which indicate the independence of aggression from testosterone in all seasons. Even in sex-role reversed species in which the female shows more territorial aggression than the male, testosterone does not appear to play a major role (FIVIZZANI et al. 1990, KRINER & SCHWABL 1991, ELEKONICH & WINGFIELD 2000).

Two African juveniles (and two of the birds that died during the first experimental weeks; data not shown) had elevated testosterone levels at the beginning of the experiment (one male and one female, Fig. 2). Social instability during group establishment is often accompanied by temporal rises in testosterone (e.g. SILVERIN et al. 1986, HIEGNER & WINGFIELD 1987, SCHWABL et al. 1988, BELTHOFF & DUFTY 1994). It is likely that this phenomenon applies to our Stonechat data. The measurements were taken five days after group formation, and aggression levels observed on the day of blood sampling were still higher than in the following weeks. Other factors than social instability might have also influenced the hormone levels since they were unusually high for young birds (>500 pg/ml). Similarly high testosterone levels with as yet unclear function are known from juvenile Willow Tits (SILVERIN et al. 1986, SILVERIN 2002).

In birds of both subspecies aggression within the captive groups rose at approximately the time at which it rises in free-living conspecifics (external time reference). The majority of European Stonechats (*S. t. rubicola*) arrives in the wintering quarters in the Mediterranean from mid-October to mid-November (GWINNER ET AL. 1994, RÖDL 1994, GLUTZ VON BLOTZHEIM & BAUER 1988). In the Negev, Israel, territorial defense is documented for late October and November onwards (GWINNER ET AL. 1994, RÖDL 1994) - concurrent with peak aggression in our captive groups. In the Kenyan population *S. t. axillaris* dispersing and newly settled juveniles are found as early as October (DITTAMI & GWINNER 1985), when social tolerance in our captive groups declined.

Aggression rates appeared to be coupled to different annual cycle events in both subspecies of Stonechats (Fig. 2). Aggressive interactions were reduced during postjuvenile body moult. Moult end was a good internal time reference for increasing aggression in African Stonechats: the rise in aggression was tightly coupled with moult end. The lack of a similar relationship in European Stonechats is due to the low values in October. This might indicate that aggression is suppressed during the migratory season. Possibly, in the European subspecies the end of migratory disposition is more relevant for the onset of aggression. There is some evidence for social tendencies in migrating Stonechats (FLINKS 1999, URQUART 2002) which may be facilitated by reduced aggression. Figure 2 shows values of within-group aggression close to zero during the first post-moulting weeks in October, coincident with the main migratory period in the field (GLUTZ VON BLOTZHEIM & BAUER 1988). Concurrent

with this depression was a conspicuous peak of body mass (and fat score, unpublished data) in all groups and nocturnal restlessness in the one group examined for this parameter, which indicates migratory disposition.

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Abstract

At an age of about five to six months temperate-zone and tropical Stonechats establish their first territories: winter territories in the European and year-round territories in the African subspecies. Thus, following the juvenile social periods, birds are abruptly confronted with intense intraspecific competition. We studied territorial aggression in captive Stonechats to assess the role of internal programs versus environmental factors in its regulation. If mainly controlled by endogenous factors and their interaction with photoperiod, aggressive behaviour would be expected to peak, even in the absence of other normally experienced changes in the ecological and social conditions, at about the time when territories are established in the field; in contrast, if mainly dependent on environmental changes other than photoperiod, aggression rates should remain constant under conditions in which the only changing environmental factor is photoperiod.

To distinguish between these two hypotheses, 23 first-year European and 24 African Stonechats were kept in captivity in naturally-sized groups (3 European groups, 6 African groups), with an unchanging social and local environment and stable food supply. Birds were exposed to their respective natural photoperiodic conditions, i.e. European birds to a seasonally changing, African birds to a constant equatorial photoperiod. Behavioural data as well as data on body mass, postjuvenile moult, testosterone and migratory restlessness were recorded during summer and the time of territorial establishment in the field as long as social tolerance within groups lasted. Time-series analyses tested whether group totals of aggression changed predictably, and whether changes occurred specifically at the end of the experiment. In addition we compared aggression scores during and after moult.

In all groups totals of aggressive interactions rose suddenly. In all 3 groups of European Stonechats the last recorded aggression score was significantly higher than all preceding values. In the African groups aggression also increased, but significantly in only three out

of six groups. For this subspecies moult end was closely related to aggression rise: in all groups post-moulting aggression totals were significantly higher than moulting aggression totals. Differences in plasma testosterone concentrations corresponded to the function of territorial aggression. In European Stonechats testosterone values remained baseline, as expected of birds defending winter territories. In contrast, in African males defending prospective breeding territories elevated plasma testosterone concentrations were found. Our study shows that the rise of aggression was correctly timed with respect to both the birds' annual cycle and the calendar year. The correct timing under constant social and environmental conditions strongly suggests that a program based on the interaction of endogenous factors with photoperiod is mainly responsible for the development of territorial behaviour in first-year stonechats.

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