

Barbara Helm

Seasonal timing in different environments: comparative studies in Stonechats

Seasonal timing in different environments: comparative studies in Stonechats



Barbara Helm

**Seasonal timing in different environments:
comparative studies in Stonechats**

**Dissertation der Fakultät für Biologie an der
Ludwig-Maximilians-Universität München**

vorgelegt von Barbara Helm

am 29. November 2002

Gutachter

Prof. Dr. E. Gwinner
Prof. Dr. G. Neuweiler
Prof. Dr. G. Heubl
Prof. Dr. E. Weiß

Tag der mündlichen Prüfung

11. April 2003

Table of Contents

<u>Summary</u>	<u>1</u>
<u>Deutsche Zusammenfassung</u>	<u>4</u>
<u>Introduction</u>	<u>9</u>
Four subspecies of Stonechats	11
Approaches used in the studies	16
Organization and scope of the dissertation	17
Prior publications of dissertation material	19
<u>General methods</u>	<u>21</u>
Birds and holding conditions	21
Photoperiodic conditions	21
Monitoring molt, derivation and analysis of variates	22
Quantitative genetic analyses	23
Monitoring migratory activity and derivation of data	24
Measuring growth and fluctuating asymmetry	24
Assessing the size of reproductive organs	25
Ringing recovery data	25
<u>Studies of major life cycle events</u>	<u>27</u>
Chapter 1: Growth and developmental precision in young Stonechats: differences between subspecies and effects of short day length	29
Summary	29
Introduction	29
Material and methods	31
Nestling growth	31
Final size and developmental precision	32
Results	35
Growth of Siberian Stonechats	35
Final size and symmetry of Stonechats from four populations	35
Presence of FA in tarsus and P8	38
Influence of subspecies, sex and photoperiod on FA	39
Discussion	40
Growth of Siberian Stonechats	40
Size and FA of wing length	41

Final size of tarsus and the 8 th primary	41
FA of tarsus and the 8 th primary	43
Chapter 2: Postjuvenile molt under a tight seasonal schedule in Siberian	
Stonechats	45
Summary	45
Introduction	45
Birds and methods	46
Results	48
Variations in molt timing	48
Effects of photoperiod	49
Family effects on the timing of molt	51
Comparison of molt timing among three Stonechat subspecies	53
Discussion	53
Chapter 3: Genetic control of molt timing: selection experiments with European	
Stonechats (<i>S.t. rubicola</i>)	59
Summary	59
Introduction	59
Birds and methods	60
Selection regime	60
Statistical treatment	62
Results	64
Heritability estimates	64
Effects of hatching date	65
Discussion	66
Chapter 4: A new type of migrant? Migratory restlessness and postjuvenile molt in	
Stonechats from the British Isles (<i>S.t. hibernans</i>)	73
Summary	73
Introduction	73
Materials and methods	75
Birds and methods	75
Analysis of nocturnal restlessness	76
Results	78
Postjuvenile molt	78
Nocturnal restlessness in Irish Stonechats	80
Temporal correlations between molt and migratory restlessness	86
Comparison with migratory restlessness of European Stonechats	86

Discussion	88
Timing of postjuvenile molt and migratory restlessness	88
Incidence of Zugunruhe	89
Timing of core migratory restlessness	92
Postbreeding nocturnal restlessness	94
Chapter 5: Movements of Stonechats from central Europe and the British Isles	
(<i>S.t. rubicola</i> and <i>hibernans</i>): results from ringing recoveries	97
Summary	97
Introduction	97
Material and methods	100
Results	102
General patterns	102
Comparison of the three focal populations	105
Discussion	116
Chapter 6: Reproductive timing in European and Siberian Stonechats (<i>S.t. rubicola</i>	
and <i>maura</i>) and its implications for hybridization of the two subspecies	119
Summary	119
Introduction	119
Material and methods	121
Results	122
Discussion	126
Outlook: Implications for timing under changing seasonal conditions	131
<u>Conclusions</u>	137
<u>Acknowledgements</u>	143
<u>References</u>	145
<u>List of publications in biology</u>	161
<u>Curriculum Vitae</u>	163

Summary

Birds must time their seasonal activities precisely to best match the specific conditions of their temporal environments. Local populations often differ in seasonal timing. To understand adjustments to temporal environments, I compared major events in annual cycles among four populations of a model species, the Stonechat (*Saxicola torquata*). The studies were carried out on captive Stonechats from African, Central European, Irish and Siberian populations. Among these populations, time-pressure is presumably highest in long-distance migrant Siberian Stonechats that stay on the breeding grounds for the shortest time. Central European and Irish Stonechats migrate short distances and hence have a longer breeding season. In addition, Irish Stonechats are partial migrants so that for parts of the population migration is not a necessary component of their seasonal organization. African Stonechats are year-round residents. By comparing the populations' temporal organization I aimed to contribute to an understanding of how seasonal timing can be modified and how modifications of one life cycle stage affect others.

The dissertation consists of six studies exploring the first annual cycle of Stonechats, from hatching until reproduction. The first section is dedicated to growth and developmental precision in the young. I compared growth of time-constrained Siberian Stonechats to that of other subspecies to assess if seasonal pressure accelerates development. Wing growth was faster than in the other subspecies and hence differed in the predicted direction. However, body mass grew just as fast in African nestlings which presumably were subject to the lowest seasonal pressure. Therefore, seasonal pressure may accelerate growth, but other selection pressures may have similar effects. A possible cost of fast growth could be reductions of size or developmental precision. I compared fluctuating asymmetry (FA) and final size of tarsus and wing among the four populations. In addition, birds were kept under two photoperiods indicating different seasonal pressure. A significant amount of FA was present, but FA differed neither among populations nor in response to day length. In contrast, wing size but not tarsus size of European and Siberian Stonechats was significantly reduced under time pressure. These results suggest that nestlings from late clutches incur the price of a reduced wing span to compensate for some of their delay.

The next major developmental stage is postjuvenile molt. The great plasticity in the Stonechats' body molt timing in response to photoperiodic cues can be described by reaction norms. One study in my dissertation investigates molt under a tight seasonal schedule in Siberian Stonechats. Siberian Stonechats molted faster and at earlier ages than their conspecifics. Under short day length molt was not advanced but its duration was

greatly reduced. Siberian Stonechats differed from other subspecies in their reaction norms to photoperiod in a way that may be related to requirements of their temporal environments. For Siberian Stonechats, duration but not the timing of molt was highly heritable. In a second study, I tested the heritability (h^2) of molt timing in European Stonechats in selective breeding experiments. Initial results of the long-term experiments confirmed high h^2 and suggested a correlated selection response of photoperiodic reaction norms. Micro-evolutionary mechanisms of timing adjustments in Stonechats may hence proceed through adjustments of photoperiodic reaction norms.

After molt, migratory Stonechats set out on their journey to wintering grounds. In a case study of Irish Stonechats I related migratory restlessness to the timing of postjuvenile molt. Because of their partially migrant behavior, I expected individual differences among birds in Zugunruhe and in molt timing. Unexpectedly, all Irish Stonechats showed pronounced migratory restlessness. Timing of molt and migratory urge were closely correlated. The birds initiated Zugunruhe soon after the peak of molt but before its completion. In addition, many birds showed low levels of restlessness coinciding with the time of juvenile dispersal. The consistently migratory behavior of Irish Stonechats contrasts with observations from other partially migrant passerines but needs to be tested more rigorously. A consolidation of results would imply a more differentiated approach to the regulation of partial migration. In this study I introduced new techniques for the analysis of nocturnal activity patterns that are based on time-series analyses and depend less on the judgment of individual observers than conventional methods.

A common caveat of studies on captive birds is that their behavior may deviate from that of freelifving conspecifics. This concern was addressed by an analysis of all currently available ringing recoveries. The analysis focused on spatial and temporal patterns of three focal populations, from the British Isles, Belgium and the Netherlands, and from Germany. Ringing data of British Stonechats are in close accordance with migratory Zugunruhe of captive Irish Stonechats, except for the proportion of migrants. From ringing records, almost half (42%) of British Stonechats overwintered far from the breeding grounds. Benelux and German Stonechats behaved entirely migratory. Time trends in migratory behavior as reported for other species were not found in Stonechats, nor was there heterogeneity in migratory behavior between sexes and age groups.

Related to differences in migratory behavior, breeding cycles between freelifving Siberian and European Stonechats differ greatly. The two populations have expanded their breeding range and their first hybridization has been observed. I explored the flexibility of their breeding cycles and possible consequences for hybridization. Breeding cycles of birds kept individually under identical conditions largely reflected the subspecies differences. Crossbreeding experiments probed to which extent these programs could be moved by exposure to a mate with a different reproductive schedule. Both female and male Siberian

Stonechats were unable to synchronize with their European mates, leading to a detrimental reduction of reproductive success in crossbreeding pairs. Stonechats differed from some other species by lacking flexibility of reproductive timing. Rigid differences in endogenous programs may contribute to detrimental effects of range expansion and hybridization which many other organisms currently undergo.

An overall conclusion of my dissertation is that the Stonechats' precise endogenous timing programs allow for a differentiated host of responses to timing challenges. Phenotypic plasticity of molt serves as a buffer in the annual cycle and helps the birds stay in time. Molt timing responds to day length via reaction norms tailored to native temporal conditions. Several lines of evidence indicate evolvability of these reaction norms. The close correlation between molt and migration suggests that micro-evolutionary adjustments of molt timing additionally affect the timing of migration.

However, Stonechats also incur costs of rigid timing programs, as illustrated by the lack of social synchronization among breeding partners and the shortened wing-length under time pressure. Disadvantages of a programmed seasonal organization may be exacerbated if selective pressures change rapidly. Thus, fast environmental change as currently observable in climatic conditions could render formerly successful time strategies maladaptive. Since evolutionary adjustments act on a slower time scale than phenotypic plasticity, rigid time programs may hamper the Stonechat's ability to come to terms with anthropogenic environmental changes.

Deutsche Zusammenfassung

Jahreszeitliche Organisation in verschiedenen Lebensräumen: vergleichende Studien an Schwarzkehlchen

Vögel müssen ihre jahreszeitlichen Aktivitäten präzise zeitlich einrichten, um sie möglichst gut auf die saisonalen Lebensräume abzustimmen, in denen sie leben. Populationen unterscheiden sich häufig lokal in ihrer jahreszeitlichen Organisation. Um zu einem besseren Verständnis über Anpassungen an Zeit-Umwelten zu gelangen, habe ich die zentralen Ereignisse im Jahreszyklus von vier Populationen einer Modellart, des Schwarzkehlchens (*Saxicola torquata*), verglichen. Die Studien befaßten sich mit Schwarzkehlchen aus afrikanischen, zentraleuropäischen, irischen und sibirischen Populationen, die an der Forschungsstelle für Ornithologie in Andechs und Seewiesen gehalten wurden. Von diesen Populationen sind die langstreckenziehenden sibirischen Schwarzkehlchen wohl dem größten Zeitdruck ausgesetzt, denn sie halten sich am kürzesten im Brutgebiet auf. Zentraleuropäische und irische Schwarzkehlchen ziehen über kurze Strecken und haben daher längere Brutzeiträume. Irische Schwarzkehlchen sind darüberhinaus Teilzieher, so daß Zugverhalten nur für einen Teil der Population zur jahreszeitlichen Organisation gehört. Afrikanische Schwarzkehlchen verbleiben ganzjährig in Paarterritorien. Der Vergleich der zeitlichen Organisation der Populationen zielt ab auf ein besseres Verständnis der Modifizierbarkeit von jahreszeitlichem Verhalten und der wechselseitigen Abhängigkeit saisonaler Aktivitäten.

Meine Dissertation besteht aus sechs Einzelstudien, die dem Verlauf des ersten Lebensjahres von Schwarzkehlchen vom Schlüpfen bis zur Brut folgen. Sie beginnt mit einer Untersuchung von Wachstum und Präzision der Jugendentwicklung. Das Wachstum der zeitlimitierten sibirischen Schwarzkehlchen habe ich mit dem der anderen Populationen verglichen um festzustellen, ob jahreszeitlicher Druck die Entwicklung beschleunigt. Das Flügelwachstum erfolgte schneller als in den anderen Populationen und unterschied sich damit in der vorhergesagten Richtung. Die Körpermasse von sibirischen Schwarzkehlchen jedoch wuchs ebenso schnell wie bei afrikanischen Jungen, die ja dem mutmaßlich geringsten saisonalen Zeitdruck ausgesetzt waren. Saisonaler Zeitdruck kann somit Wachstum beschleunigen, aber andere Faktoren haben offensichtlich ähnliche Wirkung.

Zu möglichen Kosten von schnellem Wachstum gehören Verringerungen in der Größe oder in der Präzision von wachsenden Strukturen. Um mögliche Kosten abzuschätzen, habe ich daher fluktuierende Asymmetrie (FA) und Endgröße von Tarsus und Flügel der Populationen vergleichend untersucht. Zusätzlich wurden Vögel unter zwei Lichtbedingungen gehalten, die unterschiedlichen saisonalen Zeitdruck simulierten. FA war

in signifikantem Ausmaß nachweisbar, unterschied sich jedoch nicht zwischen den Populationen und photoperiodischen Gruppen. Im Gegensatz dazu verringerte sich unter Zeitdruck die Länge des Flügels von europäischen und irischen Schwarzkehlchen, nicht aber die des Tarsus. Diese Ergebnisse deuten an, daß Nestlinge aus späten Brutzeiten für ihr spätes Schlüpfen die Kosten einer verkürzten Flügelspannweite zu tragen haben.

Die nächste Entwicklungsphase ist die Jugendmauser. Schwarzkehlchen wiesen große Plastizität in der zeitlichen Organisation der Jugendmauser des Kleingefieders auf. Diese zeitliche Plastizität steht in Bezug auf die Tageslänge und kann durch Reaktionsnormen beschrieben werden. Eine Einzelstudie meiner Dissertation untersucht das Mauserverhalten von sibirischen Schwarzkehlchen. Sibirische Schwarzkehlchen mauserten schneller und in jüngerem Alter als ihre Artgenossen. Unter Zeitdruck wurde die Mauser nicht vorverlegt, aber ihre Dauer wurde stark reduziert. Sibirische Schwarzkehlchen unterschieden sich von den anderen Populationen in ihren Reaktionsnormen auf Tageslänge in einer Weise, die vermutlich in Zusammenhang steht mit den Anforderungen ihrer Zeit-Umwelt. Bei sibirischen Schwarzkehlchen war die Dauer, nicht aber der Zeitpunkt der Jugendmauser in hohem Maße erblich. In einer zweiten Studie untersuchte ich die Erbllichkeit der Mauser durch gezielte Zuchtexperimente an europäischen Schwarzkehlchen. Vorläufige Ergebnisse dieser langfristigen Experimente bestätigen eine hohe Erbllichkeit des Mauserzeitpunkts und legen eine korrelierte Selektionsantwort von Reaktionsnormen auf die Tageslänge nahe. Mikroevolutionäre Zeitanpassungen bei Schwarzkehlchen schreiten daher möglicherweise durch Anpassungen photoperiodischer Reaktionsnormen voran.

Nach der Mauser verlassen ziehende Schwarzkehlchen ihre Brutgebiete. In einer Fallstudie an irischen Schwarzkehlchen untersuchte ich den Zusammenhang zwischen Zugunruhe und dem Zeitablauf der Jugendmauser. Wegen ihres Teilziehverhaltens erwartete ich Unterschiede zwischen den Vögeln im Auftreten von Zugunruhe und im Zeitablauf der Mauser. Überraschenderweise zeigten jedoch alle irischen Schwarzkehlchen eindeutige Zugunruhe. Die Zeitabläufe von Mauser und Zugtrieb waren eng korreliert. Die Vögel begannen mit Zugunruhe kurz nach Überschreitung des Mauserhöhepunktes und vor Ende des Gefiederwechsels. Zudem waren viele Vögel schon früh, zum Zeitpunkt der Jugenddispersion, geringfügig zugaktiv. Das durchgängige Zugverhalten irischer Schwarzkehlchen unterscheidet sich von Befunden an anderen teilziehenden Passeriformen, muß aber noch eindeutiger getestet werden. Wenn sich die Befunde erhärten sprechen sie für eine differenziertere Betrachtung der Regulation von Teilzugverhalten. In meiner Studie führe ich neue Techniken zur Analyse von nächtlichen Aktivitätsmustern ein, die auf Zeitreihenanalysen basieren und die Abhängigkeit der Ergebnisse von der Einschätzung der Untersuchenden reduzieren können.

Studien an Vögeln in Käfighaltung laufen Gefahr, Beobachtungen zu registrieren, die abweichen könnten vom Verhalten freilebender Artgenossen. Diesem Vorbehalt

begegnete ich durch die Auswertung aller aktuell verfügbaren Ringwiederfunde von Schwarzkehlchen, die auch einer Neueinschätzung ihres Zugverhaltens diene. Die Auswertung konzentrierte sich auf drei Populationen, und zwar aus Großbritannien, den Beneluxländern und Deutschland. Beringungsergebnisse von britischen Schwarzkehlchen bestätigen die Ergebnisse der Zugunruheuntersuchungen an irischen Käfigvögeln, mit Ausnahme des Anteils der Zieher. Ringwiederfunden zufolge verläßt weniger als die Hälfte (ca. 42%) der britischen Schwarzkehlchen im Winter das Brutgebiet. Schwarzkehlchen aus Deutschland und den Beneluxländern waren durchgängig Zugvögel. Zeitliche Veränderungen des Zugverhaltens, wie sie an anderen Arten beobachtet wurden, ließen sich an Schwarzkehlchen nicht zeigen. Es gab ebenso keine Hinweise auf Heterogenität im Zugverhalten zwischen den Geschlechtern und zwischen jungen und älteren Schwarzkehlchen.

Im Zusammenhang mit ihrem Zugverhalten unterscheiden sich die Brutzeiten von sibirischen und europäischen Schwarzkehlchen im Freiland markant. Die beiden Populationen haben ihr Brutgebiet ausgedehnt, und vor Kurzem wurde die erste Mischbrut beobachtet. An sibirischen und europäischen Schwarzkehlchen habe die Flexibilität von Brutzyklen und mögliche Konsequenzen für die Hybridisierung der Populationen untersucht. Die Brutzeiten von Vögeln, die in Einzelkäfigen unter gleichen Bedingungen gehalten wurden, spiegelten im Wesentlichen die Unterschiede zwischen den Populationen wider. Kreuzungsexperimente sollten ermitteln, in welchem Ausmaß sich die programmierten Brutzeiten durch Verpaarung mit Brutpartnern mit unterschiedlicher Brutzeit beeinflussen lassen. Weder weibliche noch männliche sibirische Schwarzkehlchen konnten sich mit ihren europäischen Brutpartnern synchronisieren. Dies führte zu einer schwerwiegenden Verringerung des Bruterfolgs von Mischpaaren. Schwarzkehlchen unterscheiden sich von einigen anderen Vogelarten in der Unbeweglichkeit ihrer Brutzeiträume. Rigide Unterschiede zwischen endogenen Programmen können zu den schädlichen Wirkungen von Arealausdehnung und Hybridisierung beitragen, die an vielen Organismen in jüngster Zeit beobachtet werden.

Aus den Teilstudien meiner Dissertation läßt sich der Schluß ziehen, daß endogene Zeitprogramme ein differenziertes Reaktionsspektrum auf zeitliche Anforderungen ermöglichen können. Phänotypische Plastizität der Mauser fungiert als ein Puffer im Jahreszyklus, der den Schwarzkehlchen hilft, im richtigen Zeittakt zu bleiben. Der Zeitablauf der Mauser reagiert auf Tageslänge mittels Reaktionsnormen, die auf die zeitliche Umwelt der Populationen zugeschnitten sind. Mehrere Argumentationslinien sprechen für eine Evoluierbarkeit dieser Reaktionsnormen. Die enge Korrelation zwischen Mauser und Zugunruhe deutet darauf hin, daß mikroevolutionäre Veränderungen des Mauserzeitpunkts auch den Zeitablauf des Zugverhaltens beeinflussen könnten.

Schwarzkehlchen tragen aber auch Kosten für ihre strengen Zeitprogramme, wie dargestellt an der fehlenden sozialen Synchronisation zwischen Brutpartnern und an der verkürzten Flügellänge unter kurzer Tageslänge. Die Nachteile einer programmierten saisonalen Organisation können sich verschärfen, wenn Selektionsdrucke sich rapide verändern und vormals erfolgreiche Zeitstrategien maladaptiv werden lassen. Detaillierte Untersuchungen von zeitlichem Verhalten erlauben spezifische Vorhersagen über mögliche Modifikationen des saisonalen Verhaltens von Schwarzkehlchen. Da evolutionäre Anpassungen auf einer langsameren Zeitskala stattfinden als phänotypische Plastizität könnten rigide Zeitprogramme die Reaktionsmöglichkeiten von Schwarzkehlchen auf anthropogene Klimaveränderungen behindern.

Introduction

Organisms face a multitude of challenges when trying to succeed in their respective environments. In animal ecology, an individual's chance to survive and reproduce has mainly been related to predator-prey systems, to population dynamics, and to food and resource acquisition. From the perspective of conservation-related biology, environmental factors like habitat quality and climatic change affect the success of individuals. These different factors have in common that there is an important time-dependent component to them. Therefore, to be successful depends in part on an organism's ability to be "in time". This is a daunting task. For instance, many factors that determine an individual's success fluctuate both within years (e.g., seasonally) and from year to year (e.g., long-term oscillations and trends; random variation). Therefore, while some temporal fluctuations are predictable others are not (Colwell 1974; Wingfield et al. 1992). Organisms cope with this complex situation by a mixed timing strategy: they accommodate their activities by hardwired responses to those temporal fluctuations that can be predicted (e.g., circannual rhythms; Gwinner 1986; reaction norms to environmental factors; Schlichting and Pigliucci 1998). Simultaneously, they retain some flexibility that allows them to respond to unpredictable situations. The delicate balance between rigid and flexible elements in annual timing reportedly differed between species and populations (Gwinner 1999; Jacobs and Wingfield 2000), depending on the time-environment in which they live. Because an intimate relationship between an organism's environment and its timing strategies is decisive for its success, micro-evolutionary processes probably occur constantly and fine-tune time programs.

Recently, anthropogenic changes affecting seasonality have posed a serious challenge to organisms (Penuelas and Filella 2001; Gitay et al. 2002; McLaughlin et al. 2002; Walther et al. 2002). Their ability to properly respond to such changes largely determines their survival chances. There are several mutually non-exclusive ways in which organisms can adjust to altered situations: if changes in time-environments do not exceed naturally occurring fluctuations, organisms may respond properly by phenotypic plasticity (e.g., Przybylo et al. 2000). Changes in phenology that have been observed over the last years may in part be based on this mechanism (Crick et al. 1997; Menzel and Fabian 1999; Penuelas and Filella 2001; Walther et al. 2002). However, the plasticity of timing responses may be limited. For instance, the timing of reproduction is thought to be timed to precisely match maximal food supplies. In parallel with earlier springs several bird species have successively advanced their lay dates but in other species of birds and insects there is evidence for mismatched timing of reproduction (e.g., Mason 1995; Crick et al. 1997; Visser et al. 1998; Visser and Holleman 2001). For some migrant birds, an advancement of clutch

initiation may be limited by their arrival date from wintering grounds and by the migratory distance they have to cover (Both and Visser 2001). Thus, constraints on temporal flexibility may be based on rigid timing programs that may have evolved as optimal solutions of trade-offs between competitive demands (Houston and McNamara 1999; Jacobs and Wingfield 2000). Similarly, a mismatch of reproductive timing of Great and Blue Tits with peaking caterpillar densities may be a consequence of photoperiodic control of their lay date (Lambrechts et al. 1996, 1997; Visser et al. 1998). In contrast to spring temperature, photoperiod has remained constant and therefore the phase relationship between photoperiodic timing cues and the growing season has changed.

If phenotypic plasticity does not suffice to meet the challenges of changed seasonality, organisms may respond with spatial relocations to regions that better meet their requirements. Spatial relocations have recently been reported to occur rapidly (Parmesan 1996; Parmesan et al. 1999; Dukes and Mooney 1999). But for many individuals of a population, relocation is not feasible and mismatched timing programs may have severe fitness consequences (e.g., Visser et al. 1998; Sillett et al. 2000; Thomas et al. 2001). Therefore, micro-evolutionary changes of timing programs can be expected to happen quickly. Over the last decades, some micro-evolutionary adjustments to environmental change have reportedly occurred on an observable time scale (Berthold et al. 1992; Grant and Grant 1993; Brown and Brown 2000). Such fast adjustments were related to severe weather (Grant and Grant 1993; Brown and Brown 2000) and are probably exacerbated by climatic change. Micro-evolutionary changes of timing programs may occur via adjustments of responses to photoperiodic timing cues. Recently, pitcher-plant mosquitos (*Wyeomyia smithii*) have adjusted the response of eclosion timing to photoperiod, presumably to better match the milder springs (Bradshaw and Holzapfel 2001). The modified response now allows the mosquitos to eclose under shorter day length, i.e., earlier in the year. These examples indicate that there are ways in which some organisms can accommodate their schedules to altered seasonal conditions. However, timing strategies are complex because of the interdependence of seasonal activities. If we are to predict the ability of organisms to properly respond to climate change we urgently need to study seasonal timing over the entire annual cycles.

Birds are among the prime candidates for such studies. Being among the most mobile organisms they partly compensate for temporal fluctuations in their habitats by spatial relocations and large-scale movements. This ability has enabled them to inhabit a wide variety of habitats from the poles to the equator. But their ability to circumvent temporal constraints, in effect, is a double-edged sword. Flight itself implies costs that affect annual timing. The light-weight build of birds requires time-consuming regenerative processes. Feathers are exposed to abrasion and hence have to be regrown at least once per year in most species. Molt takes up a considerable fraction of the annual cycle and birds

avoid major overlaps with other seasonal activities (Jenni and Winkler 1994). Birds adjust their phenotypes seasonally to cope with changing demands and environmental conditions (e.g., Murton and Westwood 1977; Piersma 2002). Outside the reproductive season, avian gonads regress to a small fraction of their active size. Gonadal regrowth takes time and has to be initiated well ahead of reproduction. Migrations and concomitant physiological and morphological changes require time and necessitate precise temporal control in order to match the seasonality of the respective breeding and wintering sites. Coordination of avian annual activities therefore requires precise timing skills and an ability to anticipate future events in spatially separated areas. Because birds need to keep a calendar they are of special interest for research on timing strategies in organisms.

Comparative studies of birds inhabiting different temporal environments promise insights into the flexibility and evolution of timing. The relationship between timing strategies and environment can best be studied in bird species that inhabit a wide spectrum of time-environments. Among passerine birds, Stonechats *Saxicola torquata* have "the widest north-south breeding range " and hence are exposed to the widest range of photoperiodic conditions (Underhill 1999; see also Moreau 1972; Cramp 1988). This exclusively paleotropical species breeds from the Southern tip of South Africa (35° S) to Siberia (70°N); the habitats that Stonechats encounter on their breeding grounds range from highly seasonal permafrost regions to mild temperate zones and the tropics. Correspondingly, Stonechats have developed a suite of traits that allow them to master the temporality of their respective breeding grounds. Their migratory repertoire includes various strategies, from resident to long-distant migrant, and from obligatory to partial migrant. The Stonechat has served as a model species for comparing life histories and timing responses in different environments. Stonechats from a sedentary population in East Africa and from a short distance-migrating European population differed in several life-history traits (e.g., Gwinner et al. 1983, 1995, König and Gwinner 1995, Starck et al. 1995, Helm and Gwinner 1999). These studies provide an ideal background for a comparison of timing mechanisms. In this dissertation, I want to contribute to our understanding of timing strategies by comparing their relative flexibility in relation to environmental conditions, and by studying the interaction between different parts of the annual cycle in Stonechats.

Four subspecies of Stonechats

The Stonechats in this study belong to four populations representative of the different timing schemes of the species (Fig. 1; for details see General method section). The Stonechat has traditionally been considered a species comprising several subspecies (Cramp et al. 1988; Glutz and Bauer 1988) but recently this view has been questioned by data from molecular systematics (Wittmann et al. 1995; Urquhart 2002; Wink et al. 2002; cf. Fig. 2).

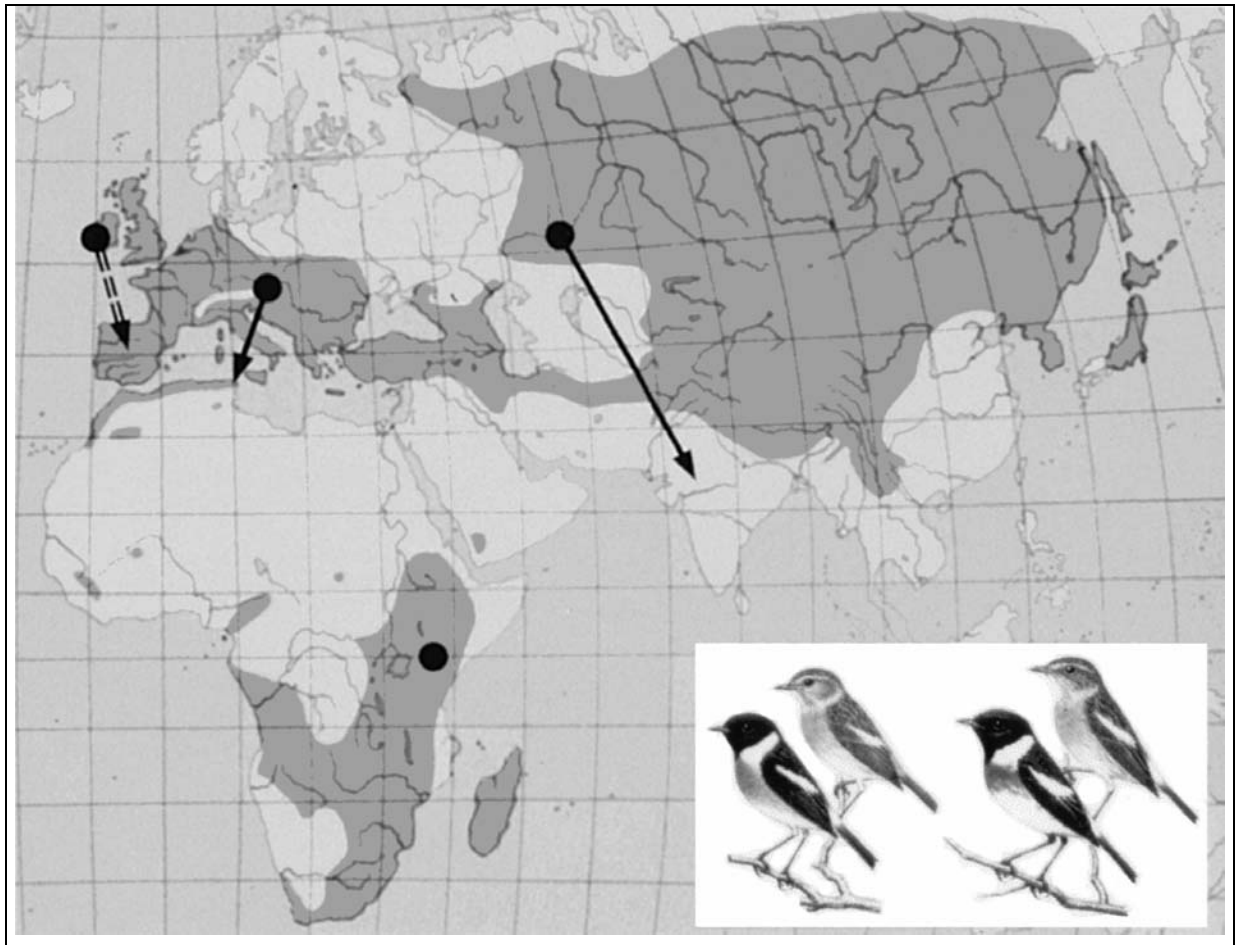


Figure 1

Map showing the distribution of Stonechats and the origin of the four populations studied here. Dots indicate populations, arrows their migratory behavior. Solid arrows indicate obligatory migrants whereas dashed arrows indicate partial migrants. Inlay: Male (black cap) and female (gray cap) of European (left) and African (right) Stonechat, respectively.

Based on results by Wink et al. (2002) the European subspecies *S. t. rubicola* and *S. t. hibernans* may be closely related. Despite behavioral (cf. Chapter 4) and morphological differentiation (Chapter 1) Wink et al. (2002) found no consistent molecular differences between them. However, the molecular distances between some other populations are rather large (Fig. 2). In particular, African Stonechats *S. t. axillaris* and Eastern Stonechats *S. t. maura* appear to form relatively homogenous separate groups. Wink et al. (2002) and Urquhart (2002) therefore suggest that the Stonechat should be considered a superspecies comprising several different species. Until these issues will be resolved I refer to local groups as either subspecies or populations.

Central European Stonechats (S. t. rubicola)

Table 1 summarizes important life-history differences between the four populations. Central European Stonechats are short-distance migrants that winter in the Mediterranean region including North Africa (Cramp 1988; Glutz and Bauer 1988; Urquhart 2002; see Chapter 5). They return early from their wintering areas and breed over a long season. They are multi-clutched and produce two or three broods of about five eggs each season. All Stonechats initiate incubation after laying the last egg so that the young hatch synchronously. Like many ground-nesting passerine species they leave the nest after c. two weeks and are fed by the parents for a short time. Often parents "telescope" subsequent broods in that the female starts a new clutch while its mate continues feeding the fledged young of the preceding brood. When the new young hatch, siblings from previous clutches are driven out of the territory. Immatures can form small aggregations while undergoing postjuvenile molt (Flinks 1999). Young of late clutches often depart with the parents and must prepare for migration much faster than their older siblings. The so-called "calendar effect" (also "calendar reaction") relates an earlier and quicker development and molt to a later hatching date (Jenni and Winkler 1994; Berthold 2002). Young of late clutches may reduce the extent of their flight feather molt and sometimes start migration while still molting (Flinks 1999). For late hatched young and late breeding adults, time pressure to complete molt is high, as indicated by their sensitive response to short day length (Gwinner et al. 1983). European Stonechats leave Central Europe around October (cf. Chapter 5) and form pair territories immediately after arriving at their wintering grounds (Gwinner et al. 1994; Rödl 1994).

East African Stonechats (S.t. axillaris)

African Stonechats studied here originate from equatorial Kenya where they are exposed to almost constant photoperiods. The climate undergoes seasonal changes between a dry season and two rainy seasons (Brown and Britton 1980). Birds maintain pair territories all year round (Dittami and Gwinner 1985). With the beginning of the first rainy season, the Stonechats quickly initiate breeding (Scheuerlein 2000). The birds anticipate the approximate timing of the rainfall to prepare their reproductive systems, relying on an endogenous circannual rhythm (Gwinner and Dittami 1990). They usually produce only one clutch of three eggs per year, but some east African populations have been shown to be double-brooded if conditions are suitable (Scheuerlein 2000). The young stay within parental territories for several months before dispersing and presumably undergo postjuvenile molt without time pressure. However, African Stonechats are able to modify molt timing in response to seasonal pressure as conveyed by day length (Gwinner et al. 1983; Gwinner and Dittami 1985; Helm and Gwinner 1999).

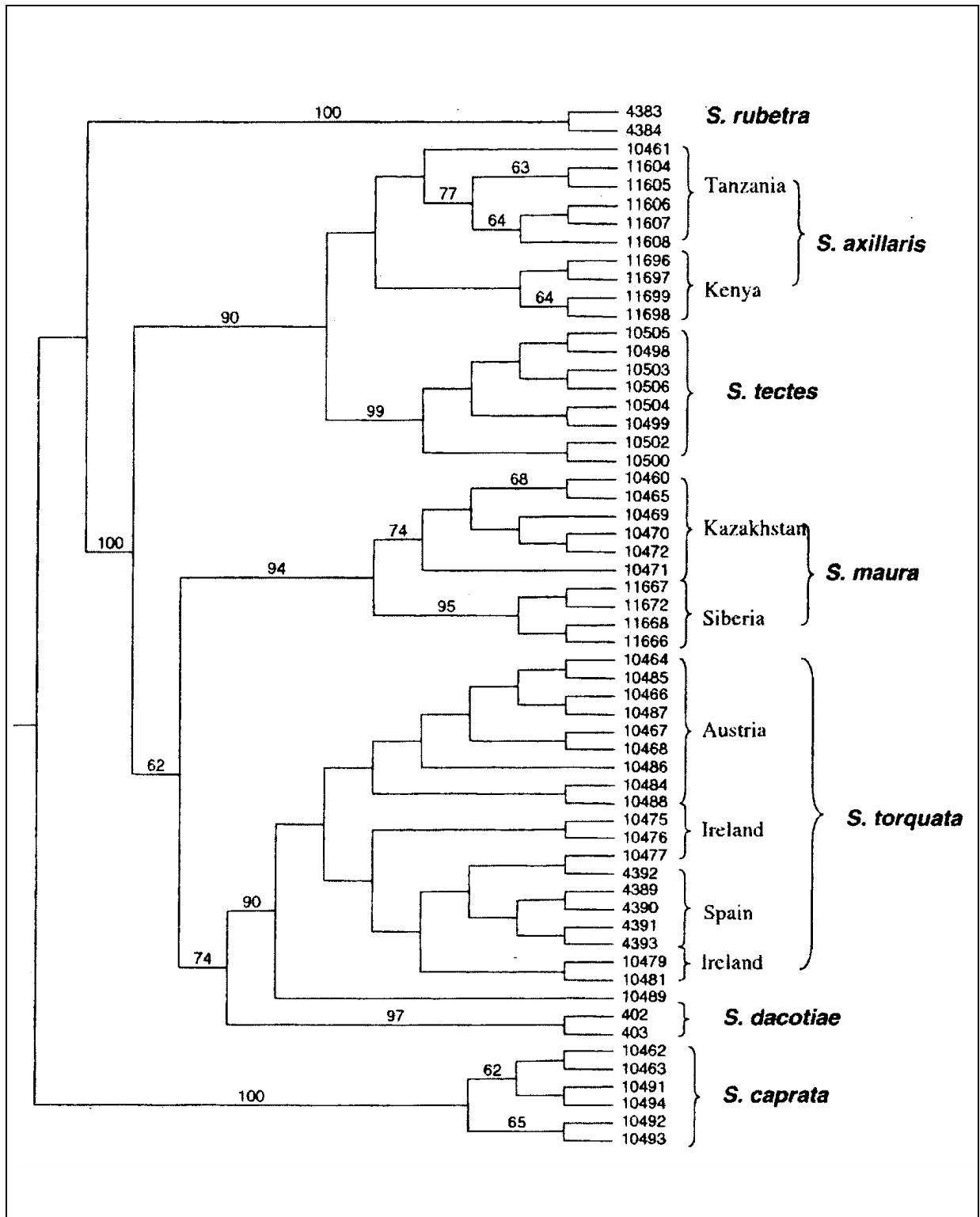


Figure 2

Cladogram of Stonechat populations and related turdids based on genomic fingerprinting data (cluster analysis of ISSR profiles; bootstrap values at bifurcations are those above 60%; other numbers are internal codes). Adapted from Wink et al. 2002. A similar phylogeny was attained by analysis of cytochrome b sequences (Wink et al. 2002).

Table 1

Life-history information on the four Stonechat populations (after Johansen 1954; Dementiev and Gladkov 1968; Kuz'mina 1970; Glutz and Bauer 1988; Cramp et al. 1988; Keith et al. 1992; Cummins 2002; Urquhart 2002).

	Kazakhstan (<i>S. t. maura</i>)	Central Europe (<i>S. t. rubicola</i>)	British Isles (<i>S. t. hibernans</i>)	East Africa (<i>S. t. axillaris</i>)
Geographical range	40 – 70° N	c. 25 – 60° N	c. 40 – 60° N	equatorial
Migratory status	long-distance	short-distance	partially short-distance; winter movements	sedentary
Present on breeding grounds	early May to August or early September	March to late September or mid October	seasonal density changes; migrants absent from Oct. until February	throughout the year
Number of clutches	1 clutch, occasionally relaying after nest loss	2 – 3	3, occasionally 4	1 (–2)
Clutch size	6	5	5	3
Time of hatching	late May, June	mid April to August	early April to August	(related to rainy season)

Siberian Stonechats (S.t. maura)

The Siberian Stonechat population in this study is native to Kazakhstan. The birds have an extremely seasonal life cycle and a very short reproductive period. Although they live at a similar latitude as Central European Stonechats, the continental climate sets strict temporal limits to reproduction and development of the young (Dementiev and Gladkov 1968; Kuz'mina 1970; Johansen 1943). Siberian Stonechats are long-distance migrants that fly to India, southern continental China, and north east Africa (Glutz and Bauer 1988, Cramp et al. 1988). They arrive late on their breeding grounds, shortly after the May thaw, and usually raise only one brood of six eggs. Re-laying after nest loss has been reported (M. Raess, pers. comm.). The more southern populations appear to start breeding earlier and may lay second clutches (Kuz'mina 1970). Immediately after breeding the birds start movements that may initially be nomadic. Siberian Stonechats initiate outward migration in August and early September. Hence, Stonechats from Kazakhstan spend only about half as much time on their breeding grounds as the short-distance migrants of Central Europe.

British and West European Stonechats (S. t. hibernans)

Stonechats of the subspecies *S. t. hibernans* breed in western Europe, mostly along the Atlantic coast and on the British Isles (with a possibly separate subspecies *S. t. therease* breeding in north-west Scotland and on some Scottish isles). They are generally considered partial migrants (cf. Chapter 5) but there may be local variation in migratory propensity within their range. A gradient of migratory behavior has been reported on the British Isles, with higher winter densities along the coast (Lack 1986; Gibbons et al. 1993). Because of local differences, the life history information below refers to a well-studied Irish population that lives close to the place of origin of the Irish Stonechats used in this study.

Irish Stonechats from this population have been investigated in a 3-year field study by Cummins (2001). She reported lay dates between March 18 and July 13, indicating a long breeding season that may start before that of Central European Stonechats. Literature data (Parrinder and Parrinder 1945) suggest that the resident part of the population may start laying very early before the migrants arrive. Because of the extended breeding season, most pairs lay three and occasionally four clutches. Cummins observed a mode of clutch size of five eggs (mean 5.2 eggs). Second clutches were significantly larger than first and third clutches. However, because of higher nest survival and a higher growth rate, broods laid early in the season had the greatest fledging success. In the winter, local densities of the birds dropped from 1.45 adults per km² in summer to 1.21/km². Cummins (2002) also reported a redistribution from heath and upland habitats in summer to the coast in winter.

Approaches used in the studies

Because of the complex interaction of annual timing with environmental cues and various seasonal demands, the study of timing strategies requires an integrative approach. In this dissertation, I explore timing in Stonechats around the year but an exhaustive coverage of their annual cycles would not be feasible. Instead, I address the complex subject by selected case studies during the major life cycle stages. I focus on the first year of a Stonechat's life to exclude confounding effects of differing individual histories (e.g., between breeders and individually caged birds). Annual activities have been described for many bird species in detail (e.g., Lack 1946). Here I focus on the following major life cycle events: growth and development of the young (Chapter 1), postjuvenile molt (Chapters 2 and 3), first fall and spring migration (Chapters 4 and 5) and reproduction (Chapter 6). These life cycle stages are tightly interlocked, and the timing of each is consequential to others. Current benefits of timing decisions may impose future costs and therefore timing strategies may result from trade-offs.

Such trade-offs may depend on the particular temporal environments that the birds inhabit. As pointed out by Garland and Adolph (1994), for logical and statistical reasons it is advisable to compare more than two different groups. Bradshaw (1987) has convincingly advocated comparisons of subspecies rather than of species: "The great value of comparisons based on different populations of a species is that any differences are far more readily related to the environments in which the populations occur, and are much less confounded by changes in characteristics acquired at some time past and of little relation to the present environment in which the species occur." Therefore, to address the relationship between timing strategy and environment I compare annual cycle elements of the populations and relate them to the length of their breeding season and to their migratory behavior.

In particular, differences in flexible and fixed elements of their schedules may provide insights into the evolutionary adjustment of timing. To tease apart flexible and tightly controlled timing patterns, I compare their responses to experimental manipulations of factors that may affect timing (cf. Visser and Lambrechts 1999). Experimental conditions designed to test timing responses include simulations of seasonal time pressure by short day length (Chapters 1 and 2) and breeding experiments in aviaries (Chapters 3 and 6). Wherever possible, field data are discussed to relate the data from captive birds to those of freelifving conspecifics. In addition, an entire chapter is dedicated to extracting and analyzing temporal and spatial patterns of freelifving Stonechats from ringing recoveries (Chapter 5).

Comparisons between population means are insufficient to understand the evolutionary processes that shape timing strategies. Some knowledge of individual variation is mandatory because selection acts on differences between individuals. Studies that included quantitative genetical analysis have revealed surprisingly high heritabilities of the timing of migration, molt, and reproduction (Van Noordwijk et al. 1981; Dingle 1994, 1996; Merilä and Sheldon 2001; Roff and Fairbairn 2001; Pulido 2002). As suggested by Gwinner and Helm (2002), quantitative genetic analyses may provide a bridge between the study of existing timing mechanisms and an evolutionary perspective that investigates how organisms adjust to their time-environments. Therefore I study the basis of individual differences among birds, employing selective breeding (Chapter 3) and analytic methodology derived from quantitative genetics (Chapters 2 and 5).

Organization and scope of the dissertation

The dissertation starts with a general method section that provides the common methodological background of the study. The detailed methods of individual case studies are included in the chapters. The study of Stonechat timing is organized into six chapters that explore important aspects of their annual cycles, from hatching until reproduction.

The chapters differ in perspective, emphasizing one or several of the approaches outlined above.

Chapter 1 investigates the timing of growth and searches for possible effects of time-constraints. I compare growth of highly time-constrained Siberian Stonechats to that of the other populations to find out if their growth parameters differ to accommodate seasonal pressure. Developmental precision and final sizes of tarsus and wing are assessed under different day lengths in all populations. Time pressure during development may reduce the size and quality of growing structures, and the populations could differ in their respective susceptibility to time-related quality costs.

Chapter 2 takes a close look at the next stage of development, the timing of postjuvenile molt. The study of molt serves as an in-depth analysis of timing responses to environmental cues, i.e., photoperiod. Simultaneously, I employ quantitative genetical methods to investigate the importance of heritable components to timing. I compare molt timing mechanisms of Siberian Stonechats under a tight seasonal schedule to published material on European and African Stonechats.

Chapter 3 puts the high heritability estimates in European Stonechats to a critical test. By selectively breeding for molt timing differences I explore in greater detail the possible micro-evolutionary mechanisms that adjust molt schedules. I report initial results of long-term breeding experiments with European Stonechats that are currently being continued.

Chapter 4 focuses on the next life cycle stage, migration, and relate it to the timing to molt. By investigating migratory restlessness in partially migrant Irish Stonechats I explore endogenous correlates of migratory disposition. In particular, I expected differences among birds in migratory propensity and related differences in the timing of molt and nocturnal activity. To improve the assessment of migratory propensity and timing, part of the chapter is dedicated to developing new techniques for analyzing Zugunruhe.

Chapter 5 provides a field-based background for the studies on captive birds. In an analysis of all currently known ringing recoveries, I review the current state of knowledge about migration of British and Central European Stonechats. The ringing recovery data are related to the migratory restlessness data from captive Irish Stonechats in the preceding chapter to explore the relationship between field (ringing) data and Zugunruhe in captive Stonechats.

Chapter 6 investigates the flexibility of reproductive timing in adult Siberian and European Stonechats. Freelifving Siberian Stonechats have a much shorter breeding season than European Stonechats. In a first experiment, reproductive timing programs are studied in individually caged birds. In a second experiment I probe for possible timing flexibility and for consequences of rigid reproductive cycles by breeding and crossbreeding the two populations under identical aviary conditions. The study addresses conservation concerns

related to range expansion and hybridization that both populations, like many other organisms, currently undergo.

The overall purpose of this dissertation is to study seasonal timing in a model species and contribute to our understanding about the ways in which organisms could come to terms with anthropogenic climatic alterations. Therefore, in the final concluding section I summarize relevant results from the individual chapters, and, in parallel, relate them to predicted changes of seasonality that may affect Stonechats, along with many other organisms.

Prior publications of dissertation material

Parts of this dissertation have already been published. The material of Chapter 2 and the section on growth in Chapter 1 were published as Helm, B., and E. Gwinner. 2001. Nestling growth and post-juvenile molt under a tight seasonal schedule in stonechats *Saxicola torquata maura* from Kazakhstan. *Avian Science* 1(1): 31–42. In addition, Chapter 2 and a short section of Chapter 1 make comparative use of material published by Helm and Gwinner (1999).

Some of the conceptual considerations are published in Gwinner, E., and B. Helm. 2002. Circannual and circadian contributions to the timing of avian migration. In: P. Berthold, E. Gwinner and E. Sonnenschein: *Avian Migration*. Heidelberg: Springer; and in Helm, B., and E. Gwinner. 2003. Molt timing as a buffer in the avian annual cycle. In: Schodde, R. (ed.) *Proceedings of the 23. International Ornithological Congress Beijing 2002*; *Acta Orn. Sinica*.

General methods

Birds and holding conditions

Most of the Stonechats in this study were collected as nestlings between 1997 and 2000 in one of four locations or are offspring from those populations: African Stonechats (*Saxicola torquata axillaris* SHELLEY 1884) originate from the Lake Nakuru region in Kenya (0°14'S, 36°0'E). Central European Stonechats (*S. t. rubicola* L. 1776) were collected in Lower Austria (48°14'N, 16°22'E), and Stonechats of the subspecies *S. t. maura* (PALLAS 1773) were picked up in May and June of 1997 and 1998 in the vicinity of Naursum National Park (c. 51.5°N, 63°E), south of Kustanaj, Kazakhstan, at an altitude of c. 200 m a.s.l. Irish Stonechats of the subspecies *S. t. hibernans* (HARTERT 1910) were collected in 1999 on the Iveragh Peninsula near Killarney, in the County of Kerry (c. 52°N, 10°W). All nestlings were transported to Andechs, Germany, and hand-reared as described by Gwinner et al. (1987).

The remaining Stonechats hatched in captivity between 1997 and 2001 and were offspring of birds collected at the four localities mentioned above. Three African birds provided an exception because they were offspring from a Tanzanian population from Arusha National Park (Scheuerlein 2000; c. 3°5'S, 36°5'E). Birds of all populations successfully bred in large aviaries. Most were located outdoors on the grounds of the institute in Seewiesen, Germany. A few aviaries were located inside institute buildings in Andechs and Seewiesen. The aviaries had a wood-chip flooring and were equipped with vegetation, branches, and nest boxes for nesting opportunities and shelter. Breeding pairs were placed in the outdoor aviaries in spring. During the breeding season, controls were carried out at least twice a week so that laying dates could be precisely determined. Young were taken from their nests at an age of five days and treated like the birds collected in the field.

After fledging, birds were housed individually in cages inside the institute buildings until the next spring. Their body masses and molt scores were checked twice per week, and for most birds, locomotor activity was recorded day and night. After their first winter, birds either remained in cages or were kept pairwise in aviaries. All birds were fed a basic food mixture ad lib. (Gwinner et al. 1987), plus ten mealworms per bird and day. Food and water were renewed daily.

Photoperiodic conditions

In all experiments, the light intensity was about 400 lx during daytime, and 0.01 lx at night. The birds were assigned to photoperiodic (PP) groups, experiencing one or more of the following three types of light-dark regimes:

1. Constant equatorial PPs: Short day length (SD) represented the native condition for African Stonechats. For high latitude populations it was a simulation of late fall conditions and thus indicated severe time pressure. To approximate the day length equatorial birds perceive in the field, measured as the time between a 10 lx threshold in the morning and evening (Gwinner and Dittami 1990), a light-dark cycle was set to 12.25:11.75 h (Dittami and Gwinner 1985).

2. Naturally fluctuating European PPs: ND was the control condition for Kazakh, British and Central European Stonechats. Birds exposed to this photoperiodic cycle lived either outdoors in the light conditions of Andechs (48° N, 11° E) or under a simulation of the light conditions at 47.5°N 45°E (Fig. 1). Day length was changed at weekly intervals, and in October and February, it was adjusted to simulate migration to and back from a latitude of 40°N (Gwinner et al. 1983).

3. Long PP (LD): Initially, nestlings were kept in ND to approximate their native daylight conditions. On the day of the summer solstice, day length was arrested to simulate persistent midsummer (light-dark cycle was set to 17.33:6.66 h).

Since photoperiods in LD and SD were constant, these birds received no further photoperiodic time cues. Exposure of birds to either natural photoperiods or their simulation in the laboratory had no observable effects (Helm 1997). Sibling groups were usually divided into groups subjected to different light conditions in a split-plot design.

Monitoring molt, derivation and analysis of variates

Postjuvenile molt corresponds to "postjuvinal molt" and to the first prebasic molt in the terminology of Humphrey and Parkes (1959). Wing molt is incomplete in Stonechats because they renew at most some of their tertiaries and secondaries during postjuvenile molt (Gwinner et al. 1983). Therefore, I restrict myself to the analysis of body molt only. After fledging, immature Stonechats were inspected for body molt in 19 plumage areas (modified from Berthold et al. 1970). Initially, birds were examined every second day, and later two to three times per week. The number of simultaneously molting plumage areas provided a molt score (ranging from 1 to 19). A molt score of 19 indicated maximal molt intensity when all plumage areas were affected by molt. Molt scores were plotted against the age at checking, resulting in roughly bell-shaped individual molt curves for each bird. For statistical analysis, I derived four molt timing parameters as follows: onset (age when first molting at least five body parts), peak (mean age between the first and last recorded molt in 17 or more body parts), completion (age when last molting at least five body parts), and duration (interval between onset and completion of postjuvenile molt). By defining a threshold of five simultaneously molting body parts, my study focuses on the timing of the main portion of postjuvenile body molt, rather than on its absolute onset, completion, and duration (for details, see Helm 1997; Helm and Gwinner 1999). Day length on the date of

each molt parameter was extracted for each bird from the original light protocols. No unique day length could be assigned to molt duration. Therefore, no mathematical relationships between day length and molt duration were calculated.

The statistical analysis of molt data faced two major difficulties. One was heteroscedasticity, which occurred because under SD birds started molt extremely early, leading to severe skewness of the data and small variance. Under more relaxed conditions, variances were higher and more evenly distributed. Transforming to natural logarithms reduced the heteroscedasticity but did not completely remove it. I used significance of Bartlett's test for homoscedasticity as the criterion because it is also highly sensitive to departures from normality (Sokal and Rohlf 1995). When heteroscedasticity remained significant I employed non-parametric statistical methods. The second problem I faced were imbalanced data sets, which I addressed by applying Residual Maximum Likelihood Estimation (REML). This method was introduced specifically to recover inter-block information which is otherwise lost in unbalanced data sets (Patterson and Thompson 1972). REML estimates effect sizes and calculates Wald statistics as the change in model fit for each factor entered into the model. Wald statistics are asymptotically distributed as χ^2 and were used for significance testing. Robinson (1987) showed that REML yields the same results as conventional ANOVA in balanced designs, but avoids the bias created by conventional methods in unbalanced designs. The method is becoming increasingly popular, especially in quantitative genetics (Arnold 1994, Boake 1994, Falconer and Mackay 1996, Roff 1997), and has been previously employed for analyses of compiled Stonechat data (Gwinner et al. 1995; Helm and Gwinner 1999). In general, I started by analyzing full models that included all factors (year, photoperiod, their interaction, and sex) and later eliminated non-significant factors from the analyses.

In contrast to postjuvenile molt, postnuptial molt in Stonechats is a complete molt. Therefore, flight-feather molt can be used to measure molt timing in adult Stonechats. Chapter 6 includes a small set of flight-feather molt data collected on a single measuring day. The data are primary and secondary molt scores that have been collected as described in Gwinner and Biebach (1977). The flight feather scores are analyzed as raw data.

Quantitative genetic analyses

In the subsequent analyses, I faced the problems common to most quantitative genetic studies of animal behavior concerning the applicability of laboratory-derived methodology (Hailman 1986; Boag and van Noordwijk 1987; Stearns 1992; Arnold 1994; Boake 1994; Dingle 1994; Merilä and Sheldon 2001). Most importantly, sample sizes were small and estimates are therefore tentative. Their publication is justified by the relative novelty of genetic parameters for avian timing studies.

In the analyses of molt timing (Chapters 2 and 3), I estimated (narrow sense) heritability h^2 through full-sib analysis (Boag and van Noordwijk 1987, Roff 1997) as twice the family resemblance, t , given by the ratio of the among-sibship variance component to the sum of the variance components among and within sibships. If most variance is among sibships, t assumes values close to unity. t -values may be inflated by non-genetic factors that siblings have in common, and also by nonadditive genetic effects (Falconer and Mackay 1995). I assessed the significance of h^2 estimates based on the probabilities for intra-class-correlation coefficients in full-sib analysis (Sokal and Rohlf 1969, 1995; Boag and van Noordwijk 1987; Roff 1997). In a split-brood experiment, siblings were divided into groups exposed to different photoperiods. For these birds I plotted family reaction norms for visual inspection (Groeters and Dingle 1987, Dingle 1990, Stearns 1992). The quantitative genetic approach used to analyze the selective breeding experiments (Chapter 3) is detailed in the corresponding section.

Monitoring migratory activity and derivation of data

To assess migratory activity (or Zugunruhe), activity of most birds was measured in registration cages equipped with passive infrared detectors. The motion sensor was Intellisense XJ-413T, by CK Systems (12m/40°range). In contrast to microswitches that are often used to record activity, infrared detectors record not only perch hopping but all kinds of spatio-temporal changes of (body) temperature. As data, the number of movements per two-minute interval are recorded. The data of five consecutive two-minute intervals were pooled. Because infrared detectors are highly sensitive a threshold was applied. Screening of the data showed that white noise patterns were lowest if values below 20 activity counts per ten minutes were omitted (I. Schwabl-Benzinger, pers. comm.). Therefore, a ten-minute interval was scored as "activity" if a total of 20 or more activity counts were registered in the five two-minute intervals. From these data, the total number of ten-minute intervals with activity during the dark fraction of the LD cycle was extracted. One transitional ten-minute interval in the morning and in the evening, respectively ("dawn and dusk"), were discounted. The remaining nocturnal restlessness was interpreted as reflecting migratory activity. The data for Zugunruhe used in this thesis are thus based on the number of ten-minute intervals with migratory activity per night.

Measuring growth and fluctuating asymmetry

For the comparison of nestling growth, offspring from two breeding pairs of birds collected in Kazakhstan were measured daily to assess their growth of wing length and body mass. To estimate FA in the four populations of Stonechats, the length of the 8th primary (P8) and of tarsus were monitored in 173 handraised Stonechats hatched in 1999

and 2000 by a single observer. In addition, wing length was measured in 116 of these birds by two different investigators. The assessment of tarsus length and of maximum chord wing length followed the protocol outlined by Svensson (1992). The length of P8 was measured by inserting a ruler between the 9th and 8th primary, as suggested by Berthold and Friedrich (1979).

Each measure was repeated three times for each side, alternatingly. All birds were measured in one session on one day. From the three repeat measurements, I calculated the mean size of P8, tarsus, and wing for an analysis of final size. I also computed various FA measures, such as absolute and signed asymmetry values (right side minus left side) for each bird (Palmer 1994).

The measurements of wing length were fraught with a series of difficulties. Wing length of live birds is hard to measure because great care must be taken to avoid injury to the fragile avian wing. Therefore, the measuring techniques are complicated (Berthold and Friedrich 1979; Jenni and Winkler 1989; Svensson 1992). Subsequent analyses in a factorial ANOVA (Palmer and Strobeck 1986) revealed significant FA for all three traits. For wing length only, there was additional significant directional asymmetry. However, in an additional series of measurements taken on Stonechats, Helm and Albrecht (2000) showed that this directional component was owing to the handedness of the observer.

Assessing the size of reproductive organs

In African Stonechats follicular and testicular width was measured by means of laparotomy. The diameter of the largest ovarian follicle in females and testicular width in males was determined to the nearest 0.1 mm (Gwinner et al. 1995) at approximately monthly intervals. Onset and end of the testicular and follicular cycle were defined as the first and last dates on which females had a follicular diameter of more than 0.8 mm and males a testicular width of more than 1.5 mm.

Ringling recovery data

Ringling recovery data were obtained from the British Trust for Ornithology (BTO), Thetford, UK, and from the EURING database in Heteren, NL. Maps were produced at the Vogelwarte Radolfzell, Germany, using GIS Arcview 3.0, with the kind support of W. Fiedler. Details of the data extractions and the criteria applied are given in Chapter 5.

Studies of major life cycle events

Chapter 1

Growth and developmental precision in young Stonechats: differences between subspecies and effects of short day length

Summary

Growth and development of young are time-dependent processes that are an important part of the annual routine of birds. The rate of growth in bird populations has been related to their migratory behavior and length of their breeding season. I studied growth of the long-distance migrating Siberian Stonechats *S. t. maura* in comparison with data from resident conspecifics from Africa and short-distance migrants of Central Europe. Siberian Stonechats had a faster wing growth than the other subspecies, in accordance with predictions for a long-distance migrating species with a short breeding season. Nestling growth of body mass was intermediate, faster than in European but similar to that in African Stonechats which presumably were under the lowest seasonal pressure. Taken together, these results suggest that although seasonal pressure may promote rapid development, other factors, in African Stonechats possibly predation, may have similar effects on growth.

Rapid development under time pressure may impose costs on birds. To assess if accelerated growth was associated with less precise development I compared fluctuating asymmetry (FA) of tarsus and the 8th primary (P8) among the populations. In addition, to directly estimate effects of time-stress I exposed Stonechats of all subspecies to a short day and a natural day photoperiod. I found significant FA in both traits, but its magnitudes was unrelated to population and to photoperiodic time-pressure. However, final size of the wing but not the tarsus was significantly reduced under time pressure in European and Siberian Stonechats. Nestlings that hatch late may save time by growing shorter wings, but may incur costs of a reduced wing span. The relative length of the 8th primary is an efficient measure for time stress within a population.

Introduction

Temporal environments differ greatly in the length of the breeding season. These differences presumably influence avian development. In general, pressure on a bird to finish growth early is thought to increase with a shorter breeding season and a longer migratory route. In some studies, nestling growth rate has been found to increase with both the migratory tendency of a population and the latitude of its breeding area, which in turn has effects on the length of the breeding season (e.g., Ricklefs 1976; Berthold 1988a, 2002; Klaassen 1994; Dingle 1996). Growth of sedentary African Stonechats, short distance-migrating European Stonechats, and their hybrids has been studied in detail

(Starck et al. 1995). Among nestlings of the two subspecies raised in captivity, body mass of African Stonechats unexpectedly increased faster than that of their European conspecifics. Wing length growth rate was identical for the two subspecies. From these results, nestling growth was not related to migratory behavior and the length of the breeding season in Stonechats. Here I put these results to a test by comparing them to the growth of Stonechats from Kazakhstan (*S. t. maura*). Their extremely seasonal life cycle and very short reproductive period should lead to hastened development if there is indeed a relationship between growth rate and tight seasonal schedule.

A possible consequence of hastened growth may be a reduction in quality of growing structures. Faster growth may thus have a prize for birds. Studies of feather growth have shown that fast molt can impair the quality and size of wings (Serra 1999, 2000; Dawson et al. 2000; Helm and Gwinner 2003). A quality measure that has recently received much attention is the magnitude of deviations from bilateral symmetry (fluctuating asymmetry, FA; Palmer 1994). Although the qualities of FA as a stress measure are still debated previous research has shown that FA can increase under developmental and environmental stress (e.g., Leary and Allendorf 1989; Clarke 1995; Lens et al. 1999, Lens et al. 2002). Faster development has been suggested to increase FA (e.g., Björklund 1996; Teather 1996; Hovorka and Robertson 2000). There is evidence that molting under stress may reduce wing symmetry in birds (Swaddle and Witter 1994; Dawson et al. 2000). Nestlings that grew up under stressful conditions were found to be more asymmetrical in some studies (e.g., Swaddle and Witter 1994; Möller 1995, Björklund 1996) but not in others (Hovorka and Robertson 2000). To my knowledge, a significant relationship between nestling growth rate and asymmetry has not yet been found in birds (Björklund 1996; Teather 1996; Hovorka and Robertson 2000). Therefore, I examine possible costs of time stress during development by comparing FA among Stonechats of different subspecies. If fast growth came at a cost of developmental precision, populations with the fastest growth should deviate more markedly from perfect symmetry than those that have more time to grow.

In addition, I test for effects of time-stress in each subspecies separately by comparing young that were raised under different experimental conditions. To simulate time pressure, young of all subspecies were held under two different photoperiods, short day length and European natural day length. Short day length indicates time-pressure for the three subspecies from northern latitudes whereas for African Stonechats it is the natural photoperiodic condition. Among high-latitude populations, time-stressed birds should be less symmetrical than those that grow up under natural day length conditions.

The size of structures can also be reduced under time stress. Studies on freelifving and captive passerines (Dhondt 1981; Hall and Fransson 2000; Dawson et al. 2000) reported shorter wing length of birds that molted under time pressure. For growing nestlings, some

studies reported size reductions over the breeding season but related them to deteriorating growth conditions such as a shortened feeding time (e.g., Järvinen and Ylimaunu 1986). To my knowledge, no study has shown size reductions of nestlings solely in response to timing cues. Therefore, I investigated if final sizes were affected by simulated different time-pressure while feeding was unchanged. This comparison was carried out only within populations of Stonechats. Final sizes differ between populations (Urquhart 2002) and cannot be directly related to the length of the breeding season.

Different traits may vary in their susceptibility to stress-induced quality costs. Selection is thought to lead to higher stability (canalization) of development in those traits that are functionally important (e.g., Palmer and Strobeck 1986; Clarke 1998b). In general in birds, dimensions of the wing are assumed to bear on flight performance, and therefore its development should be especially precise (Balmford et al. 1993; Thomas 1993). Therefore, length of wing and the 8th primary (P8) were monitored and compared to that of tarsus as a reference structure that is unrelated to flight. Fitness costs of wing quality reductions may also depend on the migratory behavior of birds in that selection may favor higher developmental precision of wings in long-distance migrants. Precision of tarsi development should not be related to migratory distance.

Taken together, I make the following predictions: 1. Siberian Stonechats should grow faster than the other populations. 2. If so, their tarsi but not their wings should be less symmetrical than those of the other subspecies. 3. Within the Northern latitude populations, time-constrained birds should grow smaller and less symmetrical wings and tarsi than those kept in ND. 4. This effect should be less pronounced for wings than for tarsi, and less so for wings of Siberian than of European and Irish Stonechats.

Material and Methods

Nestling growth

Two breeding pairs of birds collected in Kazakhstan were placed in outdoor aviaries where they produced ten young from four clutches (four females and six males). The young were taken from their nests at an age of five days and hand-raised. Wing length and body mass of seven young were measured daily from the first or second day of life. For two birds measured from day 5 only wing growth was analysed. For each bird, I calculated the following individual growth parameters by fitting three-parameter logistic growth curves to their empirical data: growth rate constant K , asymptotic value A , and point of inflection of the curve t_{σ} . Mean growth parameters \pm sd were averaged over individual values. The procedure was identical to that of Starck et al. (1995) in their growth analysis of European and African Stonechats. The data on European and African Stonechats used here for comparison are subsets of their data. I included data from 23 African and 14 European

Stonechats in the comparative analysis of nestling growth, a subset of young that were fed by their natural parents for the first days after hatching and subsequently hand-raised. I excluded birds that were hand-reared from hatching because these birds behaved differently from all others. As a consequence, descriptive growth values for European and African Stonechats differ slightly from those given by Starck et al. (1995), but all birds in my comparison were raised under identical conditions. I tested growth parameters in one-way ANOVAs and employed Tukey's Honestly Significant Difference Test (Tukey's HSD) for post hoc comparisons. If variables were slightly heteroscedastic between subspecies, I used Games-Howell's pairwise comparisons, which do not assume homoscedasticity (Sokal and Rohlf 1995).

Final size and developmental precision

To estimate FA in the four populations of Stonechats, length of the 8th primary (counted from the inside) and tarsus of 173 Stonechats were repeatedly assessed. FA measurements were carried out as described in the General method section. Final size was calculated as the mean of three repeat measures of each side. To simulate time pressure, some Stonechats of all subspecies were kept under short day length (SD) while others were raised under European natural day length (ND). Since the feeding time was the same for all young (12 h per day) possible differences in FA reflect responses to timing cues in development but not nutritional stress. The age at which the young birds first experienced SD was from hatching in African, European and Siberian Stonechats and at a mean age of 14.7 days (from 10 to 19) in Irish Stonechats.

Table 1.1 shows the number of birds of the different subspecies measured in the experiment. For origin and keeping conditions of birds, see the General method section. The three African birds in the ND group originated from Tanzania and hence were potentially different from those of the SD group which all came from Kenya. Overall, the sex ratio was quite balanced but in Irish Stonechats, the proportion of females was much higher than

Table 1.1

Number of birds of different subspecies from which FA measures were taken, listed by sex and by the photoperiodic group under which they were kept (SD: short day length; ND: European natural day length); one unsexed bird (see text) is not listed among sex categories.

	photoperiod		sex		totals
	SD	ND	female	male	
African	34	3	17	20	37=21.4%
European	15	63	36	41	78=45.1%
Siberian	6	13	10	9	19=11.0%
Irish	12	27	26	13	39=22.5%
totals	67	106	89	83	173

that of males. One bird (European, ND) was excluded from ANOVA analyses because it died early and before its sex was known. In addition, because of external damage tarsus length could not be assessed in two birds and P8 length in eight birds. All birds were measured at the time when they first approximated their asymptotic size but before asymmetries due to usage or abrasion could arise (between ages of 35 and 50 days). Young of the four subspecies were measured at similar mean ages (means: African=38.19; European=40.36; Siberian=37.58; Irish=38.38). In addition, wing length was measured repeatedly in 116 Stonechats to assess FA, and routinely once for the right wing when the birds gained independence.

The repeated measurements of the left and right side were tested for a significant component of FA in a two-way factorial ANOVA as suggested by Palmer and Strobeck (1986). Factors in the analysis were side, individual, and their interaction. For all three measures (tarsus, wing, and P8) there was a significant interaction between side and individual (significant FA). Hence, I proceeded with rigorous testing if the distribution of absolute FA was unaffected by biasing properties ("ideal FA", Palmer and Strobeck 2003). I followed instructions of Palmer (1994, Palmer and Strobeck 2003), and made use of a program written by Palmer. As a final step, I calculated the mean absolute asymmetry values (right side minus left side) for each bird from the three repeat measurements (Palmer 1994) as the data used in subsequent analyses. The absolute FA data were analyzed in an extension of Levene's test which in effect amounted to a factorial ANOVA over absolute FA values (Palmer and Strobeck 2003). The initial model was a full three-way factorial ANOVA with sex, subspecies, and photoperiod as fixed factors but since three-way interactions were not significant I dropped them from analyses. For post-hoc comparisons of main effects of subspecies, I employed Tukey's HSD, and for post hoc comparisons of interactions I conducted t-tests for independent samples within the subspecies.

Table 1.2

Growth parameters (mean \pm sd) for the three subspecies of Stonechats. The estimates for African and European Stonechats are calculated from a subset of the data analysed by Starck et al. 1995.

Subspecies	Body mass			Wing length		
	Siberian (n=7)	European (n=14)	African (n=7)	Siberian (n=9)	European (n=11)	African (n=7)
Growth rate constant K (day⁻¹)	0.600 ± 0.057	0.454 ± 0.073	0.603 ± 0.037	0.262 ± 0.011	0.235 ± 0.014	0.236 ± 0.016
Age at inflection point t_0	5.18 ± 0.47	6.93 ± 1.10	5.04 ± 0.37	9.95 ± 0.64	11.78 ± 0.51	10.49 ± 0.56
Final asymptotic size A	15.01 ± 0.29	15.72 ± 1.28	18.0 ± 0.89	68.34 ± 1.39	65.56 ± 1.60	71.96 ± 1.45

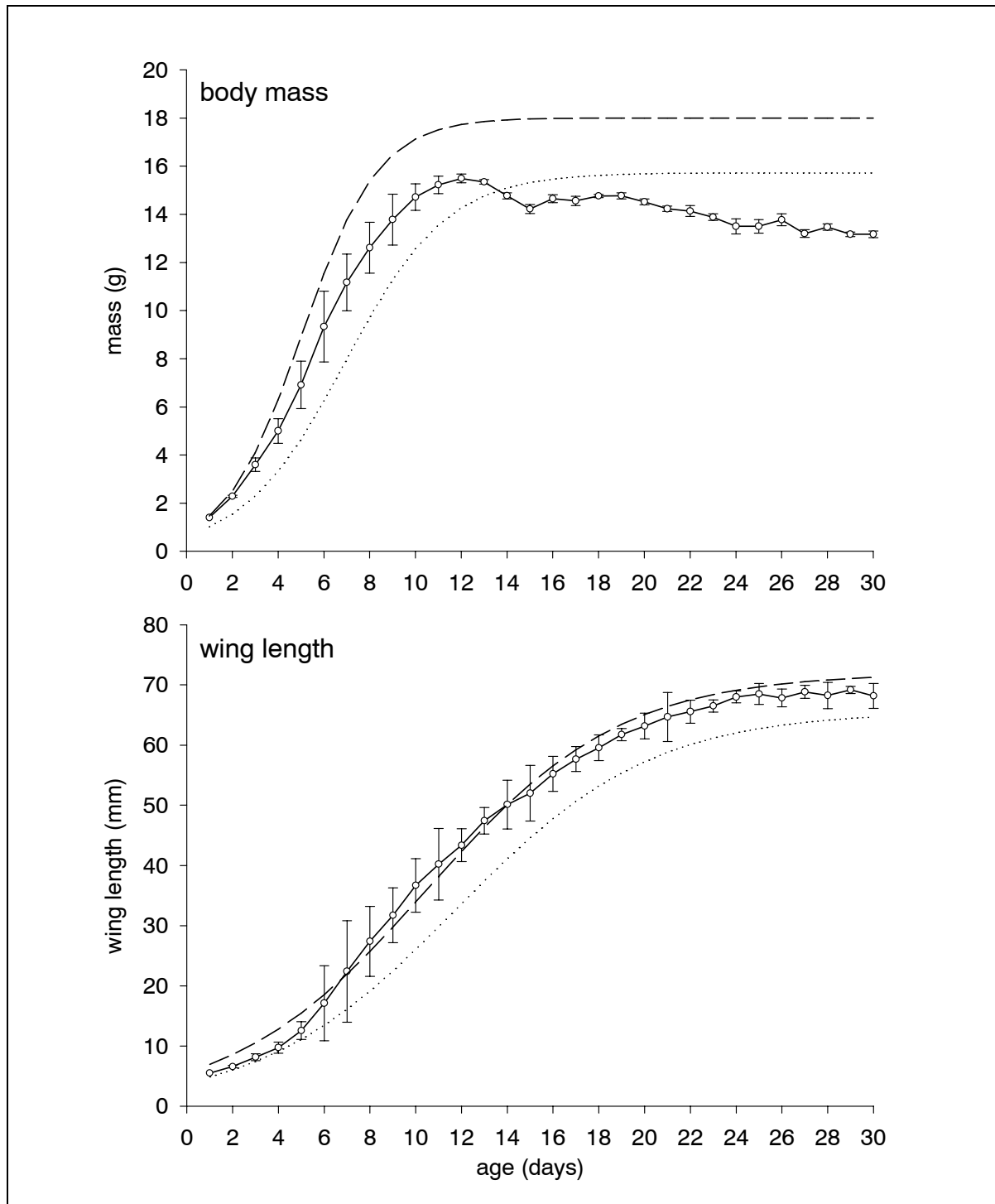


Figure 1.1

Growth curves for body mass (upper diagram) and wing length (lower diagram) of three Stonechat subspecies. Growth curves of Siberian Stonechats (solid lines) show empirical means sizes and standard deviations over the growth period, those of European (dotted lines) and African Stonechats (dashed lines) were generated from growth parameters in Table 1.2.

Results

Growth of Siberian Stonechats

Figure 1.1 shows the mean growth curves for body mass and wing length of Siberian Stonechats, in relation to growth of the other two subspecies. Both body mass and wing length of the Siberian Stonechats reached their asymptotic size before those of the other two subspecies. Males were of slightly larger final sizes than females, but as sample sizes were small, statistical testing was not possible. Table 1.2 specifies mean growth parameters for the populations. In one-way ANOVAs, subspecies was a significant factor for all parameters ($P < 0.001$). Siberian Stonechats had lower final body masses than African (Games-Howell's: $P < 0.001$), but not European birds. The final wing length differed between all three subspecies. Siberian Stonechats had significantly longer wings than European Stonechats (Tukey's HSD: European v. Siberian $P < 0.01$), but shorter wings than African Stonechats (Tukey's HSD: $P < 0.001$). Siberian Stonechats gained body mass at significantly higher rates than European (Tukey's HSD, $P < 0.001$), but not African Stonechats. They reached the age of fastest body mass growth (t_0) significantly earlier than European Stonechats (Tukey's HSD, $P < 0.001$), but slightly later than their African conspecifics. For wing length, Siberian Stonechats had the highest growth rate constant of all three subspecies (Tukey's HSD, $P < 0.01$). The age of fastest growth (t_0) was earlier in Siberian Stonechats than in their European conspecifics (Tukey's HSD, $P < 0.001$), but similar to that of African Stonechats.

Final size and symmetry of Stonechats from four populations

Tarsus size

The final size of tarsus differed significantly among the subspecies (three-way factorial ANOVA; for subspecies $F(3, 157)=17.13$; $p < 0.000$; Fig. 1.2A). Overall, tarsi were longer in African and Irish than in European and Siberian Stonechats (Tukey's HSD; $p < 0.05$). Siberian Stonechats had the smallest tarsi but the difference to European Stonechats was not quite significant (Tukey's HSD; $p = 0.070$; Table 1.3). Photoperiod had no influence on the size of tarsi ($F(1, 157)=0.03$; $p < 0.863$). There was a significant effect of sex on tarsus size ($F(1, 157)=4.15$; $p < 0.043$), with males being overall the sex with the larger tarsi. However, there was a significant interaction between sex and subspecies ($F(3, 157)=3.67$; $p < 0.014$). Post-hoc testing by t-tests within the subspecies showed that tarsi in males were significantly larger in African Stonechats only ($t=-4.03$ on 35 df; $p < 0.000$; $p > 0.25$ for all other subspecies).

Sizes of the wing

Wing length showed highly significant FA (F-ratio 2.45 on 117df; $p < 0.001$). In addition, birds differed significantly from each other in their wing length (F-ratio 237.6 on

162df; $p < 0.001$). I also detected highly significant differences between the left and right side. One side was consistently measured as longer than the other (F-ratio 100.4 on 1df; $p < 0.001$). As wing length was the only trait measured by two different observers, there was an additional risk of observer effects (Palmer and Strobeck 2003). Maximum chord wing length measures were thus complicated and will not be pursued in great detail.

Table 1.3

Final sizes of tarsus and 8th primary (mm) for the two sexes of the four subspecies.

subspecies	sex	tarsus			P8		
		mean	SD	n	mean	SD	n
African	female	22.10	0.96	17	53.70	1.55	16
	male	23.26	0.79	20	55.70	1.44	20
European	female	21.72	0.81	36	48.23	1.14	33
	Male	21.77	0.88	41	49.55	1.81	38
Siberian	female	21.12	0.67	10	49.28	3.08	10
	Male	21.40	0.76	9	53.01	1.83	9
Irish	female	22.97	0.61	25	50.42	0.81	26
	Male	22.89	0.57	12	51.72	0.85	12

However, wing length was highly correlated with that of P8 (correlation between mean length of wing and P8: 0.91; $n=123$; cf. Berthold and Friedrich 1989). Regression of P8 against wing length was described by linear relationships (for all birds: constant 2.65 ± 8.53 ; slope 0.73 ± 0.12 ; $p < 0.001$; $r^2=82.8$). Slopes were lowest for African Stonechats and slightly higher in European and Irish Stonechats. Siberian Stonechats had a significantly steeper slope of P8 on wing length (slope 1.2; probability of equal slopes $p=0.009$). Therefore P8 increased in length more quickly with longer wings in Siberian Stonechats. Because of the problems of wing length measurements and the high correlation with P8, I preferred P8 as a measure of wing length in all subsequent analyses. However, all results for final size of P8 were precisely paralleled by results of corresponding analyses of wing length.

Final size of P8 differed between the subspecies ($F(3, 151)=48.82$; $p < 0.000$; Table 1.3; Fig. 1.2B). It was longest in the African Stonechats, of intermediate size in both the Siberian and Irish Stonechats, and smallest in European Stonechats (Tukey's HSD; $p < 0.05$). There was also a significant effect of sex with males having larger 8th primaries ($F(1, 151)=62.91$; $p < 0.000$). This was consistent among subspecies ($F(3, 151)=2.19$; $p < 0.092$).

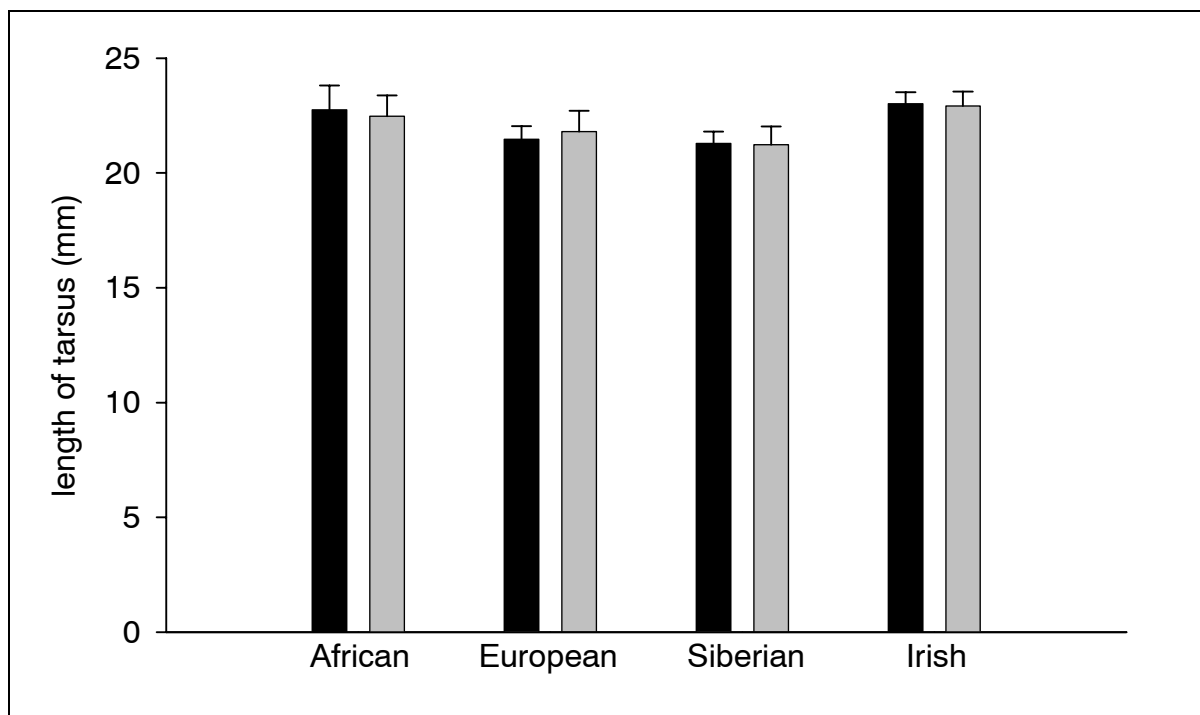


Figure 1.2A

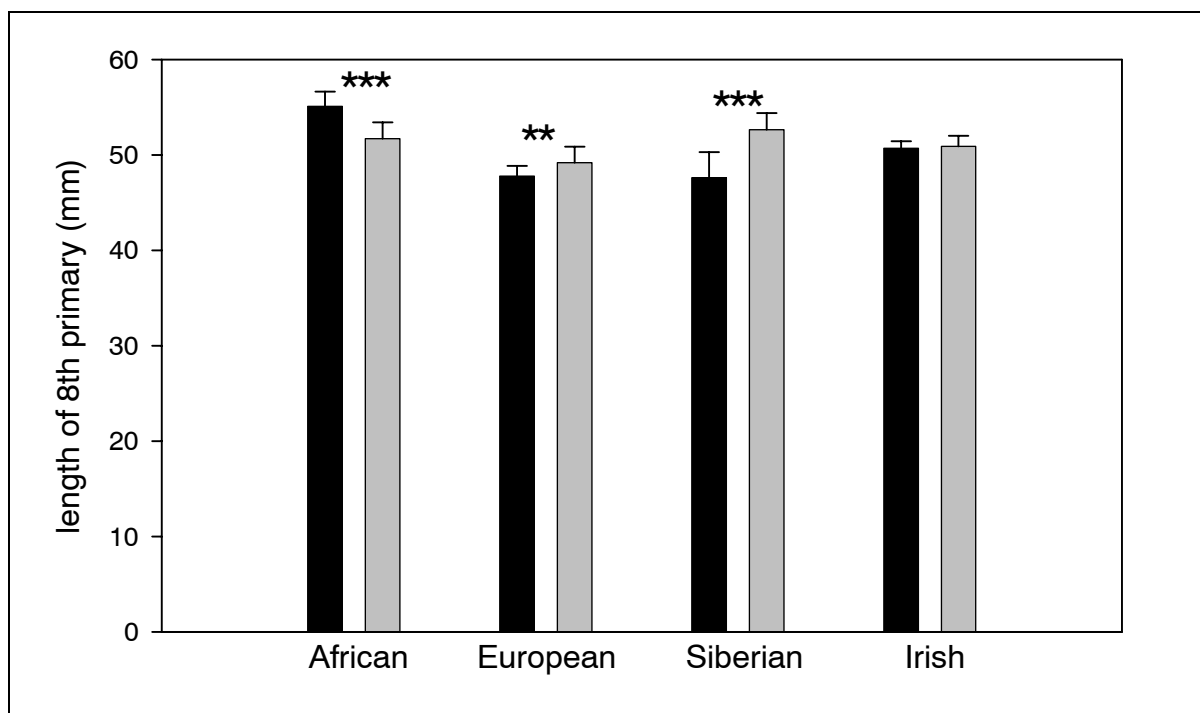


Figure 1.2 B

*Final sizes of tarsus and the 8th primary under different day lengths. Final sizes (means \pm SD) are shown for all four subspecies under short day length (black bars) and European natural day length (gray bars). A. Final size of tarsus; B. Final size of the 8th primary; asterisks indicate significance levels of post-hoc comparisons between photoperiodic effects within the subspecies (** = $p < 0.01$; *** = $p < 0.001$).*

Photoperiod as a main effect had no influence on P8 size, but its interaction with subspecies was highly significant ($F(1, 151)=24.53$; $p<0.000$). Post-hoc testing by t-tests showed that in European and Siberian Stonechats, P8 was significantly shorter under SD than under ND (European: mean SD $47.77\pm 1.06\text{mm}$; ND $49.19 \pm 1.65\text{mm}$; $t=-2.96$ on 70 df; $p<0.004$; Siberian: SD $47.60\pm 2.70\text{mm}$; ND $52.64\pm 1.76\text{mm}$; $t=-4.91$ on 17 df; $p<0.000$). African Stonechats differed from the other subspecies by growing larger wings under their native short day photoperiod. Their mean P8-length was 55.09 ± 1.52 mm under SD compared with 51.72 ± 1.71 under ND ($t=3.65$ on 34 df; $p<0.001$). However, the mean of the ND group was based on only three birds which in addition came from a different African population, and results are very tentative. There was no difference between photoperiodic groups in Irish Stonechats (mean SD $50.68\pm 0.75\text{mm}$; ND $50.90 \pm 1.12\text{mm}$). However, inspection of growth data showed that at the average age of first exposure to SD, 14.7 days, a subsample of Irish Stonechats ($n=25$ of the 39 birds analyzed here) had already completed 69.6% of the growth of P8 (mean length 35.4mm) and 99.2% of that of tarsus (mean length 2.28mm). Photoperiodic treatment may have occurred too late in Irish Stonechats to affect growth.

Presence of FA in tarsus and P8

Tarsus and P8 measurements showed highly significant FA (Table 1.4). Individuals differed significantly from each other. For neither measure were there significant side effects, and hence unlike for wing length, directional asymmetry was absent. Measurement error as a proportion of FA was very similar for both traits. For tarsus, it was 20.14% and for P8 it was 20.42% of the magnitude of FA. Absolute FA (the absolute value of the side difference) for tarsus and P8 was scrutinized for distributional properties (Palmer and Strobeck 2003). Both traits displayed no skewness. Kurtosis (i.e., the "tailedness" of a distribution; cf. Palmer and Strobeck 2003) can cause problems in analyses of FA if tails are drawn out and bimodality is suggested (platykurtosis); this risk was excluded for both traits. Conversely, P8 but not tarsus FA was significant leptokurtic (kurtosis= 1.46 ± 0.37 ; $p<0.001$). However, leptokurtosis does not bias FA and is frequently regarded a result of between-individual differences in subtle deviations from symmetry (Palmer and Strobeck 2003). Therefore, both traits can be assumed to display ideal FA.

Although all birds were measured within a short time interval between 35 and 50 days after hatching, age may have affected FA. Therefore, I tested for effects of age differences by linear regression but found no significant relationship (for P8: $p=0.211$; for tarsus: $p=0.068$). In addition, many birds were re-measured over the 16 days of the measurement interval and none of them showed growth. Size differences among birds did

Table 1.4

Two-way factorial ANOVA of tarsus and P8. The ANOVA tests for significance of DA (given by the main effect of side), of individual differences (given by the main effect of individual), and of FA (given by the interaction between individual and side) in relation to measurement error.

	tarsus				8 th primary			
	df	mean squ.	F	p	df	mean squ.	F	p
individual	164	49.444	345.59	0.000	170	6.307	83.73	0.000
DA	1	0.159	1.11	0.294	1	0.046	0.61	0.437
FA	164	0.143	4.90	0.000	170	0.075	4.97	0.000
residual	660	0.029			684	0.015		

not affect FA (correlations between trait size and FA: tarsus: $r=0.04$; $p=0.635$; $n=171$; P8: $r=0.03$; $p=0.703$; $n=165$).

Estimates of different FA measures for tarsi and P8 are given in Table 1.5. Mean absolute FA of tarsus was 0.17 mm, or 0.76% of tarsus size. For the 8th primary, mean absolute FA was 0.21 mm, which is 0.41% of its length. Therefore, FA was comparatively small (Palmer and Strobeck 1986) but almost twice as high in tarsus compared to P8 (see also the magnitude of FA 10 in Table 1.5). Overall, there was no correlation between absolute FA of the two traits ($r=-0.03$; $p=0.718$; $n=163$).

Influence of subspecies, sex and photoperiod on FA

The comparison between subspecies was carried out among birds that grew up under the native photoperiod of their population; i.e., European, Siberian, and Irish Stonechats kept under ND and African Stonechats raised in SD. Table 1.6 specifies the mean absolute FA values for the populations for both sexes together and separated. ANOVA testing showed that for P8, the effect of sex was significant ($F(3, 122)=6.12$; $p=0.015$).

Table 1.5

FA measures for the tarsi and P8 of all Stonechats in the study; numbering refers to the definitions by Palmer (1994), the standardization to the modification suggested by Palmer and Strobeck (2003).

trait	overall mean size	FA1: mean absolute FA	FA4: var (R-L)		FA10: FA after removal of measurement error	
			regular	standardized	regular	standardized
tarsus	22.167	0.168 mm	0.050	0.178	0.038	0.220
P8	50.897	0.209 mm	0.095	0.246	0.020	0.160

Overall, males had lower FA than females (mean absolute FA: males:0.180±0.213; females:0.234±0.260; Table 1.6). The effect of subspecies remained just below significance ($F(3, 122)=2.56$; $p=0.058$). Asymmetry of the 8th primary was lowest in Irish Stonechats, intermediate in European Stonechats, and of similarly high magnitude in African and Siberian Stonechats. For tarsus, ANOVA revealed no significant effects of sex and subspecies ($p>0.80$ for both factors; Table 1.6). Tarsus asymmetry was lowest in Siberian Stonechats and slightly higher in the three other populations. There was a slight but non significant indication of an interaction effect between sex and subspecies ($F(3, 126)=2.15$; $p=0.098$; Table 1.6). For the assessment of photoperiodic effects on FA, I compared all four subspecies in a separate analysis with photoperiod, subspecies, and sex as fixed factors. FA of both tarsus and P8 was not significantly affected by any of the factors ($p>0.20$ in all cases except for the interaction between sex and photoperiod: $F(1, 155)=2.80$; $p=0.096$). The same was true when the comparison focused on Siberian and European Stonechats where photoperiodic effects were likely to occur.

Table 1.6

Mean absolute FA (FA1) for tarsus and P8 for the four subspecies. The table shows grand mean and means for each sex ± standard deviation.

subspecies	8 th primary mean FA ± SD				tarsus mean FA ± SD			
	n	all	females	males	n	all	females	males
African	33	0.263 ±0.250	0.300 ±0.283	0.232 ±0.222	34	0.173 ±0.145	0.234 ±0.174	0.120 ±0.092
European	58	0.187 ±0.240	0.173 ±0.257	0.197 ±0.230	62	0.172 ±0.176	0.181 ±0.163	0.165 ±0.188
Siberian	13	0.282 ±0.284	0.444 ±0.292	0.143 ±0.203	13	0.138 ±0.122	0.082 ±0.021	0.186 ±0.154
Irish	26	0.131 ±0.156	0.183 ±0.172	0.069 ±0.111	25	0.179 ±0.089	0.161 ±0.092	0.197 ±0.087

Discussion

Growth of Siberian Stonechats

Body mass increased faster in Siberian than in European Stonechats (Fig. 1.1). These results are in line with studies from other taxa that related faster growth to a shorter breeding season and to longer migratory routes (Ricklefs 1976; Klaassen 1994; Dingle 1996). However, in spite of even more pronounced differences in migratory behavior and breeding range, Siberian Stonechats did not differ from African conspecifics in body mass growth. The fast growth of African Stonechats may be related to other selective pressures,

e.g. high nest predation rates (Scheuerlein 2000). Starck and Ricklefs (1998) calculated a body mass growth rate constant of 0.548 day^{-1} from field data of the British Stonechat *S. t. hibernans* (Greig-Smith 1985). This subspecies is partially migratory, and its breeding season is even longer than that of Central European Stonechats (Cramp 1988). Its growth rate constant in the field is close to that of Siberian and African Stonechats bred in captivity. Thus, the relationship between body mass growth, breeding range, and migratory behavior in Stonechats remains ambiguous. Similar results have also been reported in other studies of growth under tight seasonal schedules (e.g., Järvinen and Ylimaunu 1986; Järvinen; 1989).

Data on wing growth are in better accordance with predictions made about the influence of these factors. Wings of *S. t. maura* grew faster than those of European and African Stonechats. However, the fast wing growth of *S. t. maura* from Kazakhstan might also be related to several other factors affecting their juvenile development. Avian growth rates are considered to evolve as a compromise between limitations in food availability on the one hand, and acceleration through time-dependent mortality on the other (Lack 1968; Järvinen and Ylimaunu 1986; Bosque and Bosque 1995; reviews of ongoing discussion in Gebhardt-Henrich and Richner 1998, Ricklefs et al. 1998). Mortality due to sibling competition has been shown to select for fast growth (Werschkul and Jackson 1979), and Greig-Smith (1985) found sibling competition to affect body mass growth in British Stonechats. Given the large clutch size of Siberian Stonechats, this factor may have selected for their fast wing growth.

Size and FA of wing length

Wing length FA has been of particular interest in ornithological research (e.g., Balmford et al. 1993; Thomas 1993; Polak and Trivers 1994) but in living birds it can be strongly affected by handedness of the measuring researcher (Helm and Albrecht 2000). A directional trend in asymmetry measurements of avian wing length has also been reported in other studies (Dufour and Weatherhead 1998; Teather 1996). The measure of maximum length of the „flattened and straightened wing“ (Svensson 1992) is highly influenced by the pressure an observer exerts when holding the wing against the ruler. Therefore, one reason for effects of handedness on wing length may be unintentional differences in pressure between both hands. Some studies have used museum skins for measurements of greater precision, but for wing length, there are drawbacks of this procedure, e.g., shrinkage and error due to differential wing abrasion. Berthold and Friedrich (1979) and Jenni and Winkler (1989) recommended the use of 8th primary as a reproducible and clearly defined measure of wing length. The robustness against handedness bias found here suggests that it may be a good replacement for FA measures of wing length (e.g., Swaddle et al. 1996; Dawson et al. 2002; cf. Helm and Albrecht 2000). In

the context of bird migration P8 might be the more important wing length measure because with longer migratory distance wings become more pointed (Fiedler 1998). In Stonechats, this was documented by the observation that in the long-distance migrating Siberian population P8 increased in length more quickly with longer wings than in the other populations. Therefore, P8 may accentuate the properties of wing length in species that undertake long migratory journeys.

Final size of tarsus and the 8th primary

The final sizes of both tarsus and P8 differed between the sexes and subspecies. The larger size of male Stonechats is in accordance with the literature (Cummins 2002; Urquhart 2002). Overall, African Stonechats are the largest subspecies. The 8th primary of Irish Stonechats was almost as long as that of African Stonechats and as long as that of the long-distance migrating Siberian Stonechats. Tarsi sizes of Irish Stonechats were as large as those of African Stonechats. Tarsi sizes of Irish Stonechats from a nearby locality specified by Cummins (2002) are even higher but may have been measured differently. The similar sizes of Irish and African Stonechats are surprising because phylogenetically Irish Stonechats appear more closely related to European Stonechats (Wink et al. 2002; cf. Introduction). In African Stonechats, sex differences in tarsus size but not in P8 length were more pronounced than in the other populations.

Time-constraint under SD did not affect the final size of tarsus. Although this result was counter to predictions, the consistency of tarsus size is in accordance with other studies. Tarsus size has been shown to be highly genetically determined and developmentally relatively stable (e.g., Merilä 1997; Merilä and Sheldon 2001).

Unlike tarsus size, time-constraints strongly reduced the size of the 8th primary. The two obligatory migrant populations of Stonechats, Siberian and European, clearly grew shorter wings when day length indicated time pressure, i.e., time to depart on outward migration. This is in accordance with studies that reported shorter wings of birds molting under SD (Dhondt 1973, 1981; Hall and Fransson 2000; Dawson et al. 2002). Here I show that SD has the same effect on wing growth in nestling birds. Because under both conditions nestlings were hand-raised with the same amount of food and over the same time, this is a true effect of day length rather than of reduced feeding under SD (Boon 1990; Järvinen and Ylimaunu 1986). Dhondt (1973, 1981) proposed that a size reduction of wing length may be a price that adults pay for raising late broods and thereby compromising their molting time. I like to extend his proposal by suggesting that, in Stonechats, the young, too, pay this price when hatching under shortened photoperiods. The benefit of size reductions may be a shortened growth and molt period and perhaps the advantage of higher relative fuel loads (Hall and Fransson 2000). The relative length of P8

within a population may be an efficient measure for the time stress that both, young and adult birds experienced during feather growth.

The shortened P8 under SD is in apparent contradiction to the results of Starck et al. (1995) who found no differences between photoperiodic groups in final wing length and body mass. However, in their analysis age at photoperiodic shift was not considered, and the photoperiodic change may have occurred too late affect growth. Similarly, the lack of an effect of SD on Irish Stonechats may be explained by a late photoperiodic shift when 69.6% of P8 growth and 99.2% of tarsus growth were completed. The apparent reversal of photoperiodic effects on African Stonechat cannot yet be judged because the sample under ND was too small and the birds were offspring from a different African population that has been shown to be genetically distinct from Kenyan conspecifics (Wink et al. 2002). Nevertheless, as SD is the native day length of African Stonechats it is possible that their larger wings under this photoperiod may be a local adaptation of the feather growth response to day length.

FA of tarsus and the 8th primary

FA of both tarsus and P8 was highly significant and unaffected by bias ("ideal FA"). In proportion to trait size, it was much lower in P8 than in tarsus, in accordance with predictions for the presumably functionally more relevant symmetry of the wing. However, none of the other predictions were met. Symmetry of both traits was statistically indistinguishable between the subspecies. Counter to the predictions, FA of tarsi was not elevated but, in fact, lowest in the time constrained Siberian long-distance migrants. FA of P8 was lowest in the partially migrant Irish and high in the long distant migrant Siberian Stonechats. These results support neither the prediction that wing precision was most rigidly canalized in long-distant migrants nor the prediction that fast growing populations have higher tarsus FA.

Time-constraints also did not affect FA. For tarsus, these results correspond to the lack of photoperiodic effects on final size and corroborate the tenet that tarsus growth is rigidly determined (but see Carbonell and Telleria 1998). In contrast, for P8 photoperiod affected final size and FA differentially. While feather length was reduced its symmetry remained undiminished. Other studies reported similar results. Blue tits chicks (*Parus caeruleus*; Björklund 1996) that grew up without paternal feeding grew shorter wings but wing FA remained unchanged. Dawson et al. (2000) compared feathers of fast molting and slowly molting starlings *Sturnus vulgaris*. They found differences in primary length but initially none in FA. However, due to quality differences, feathers of fast molting starlings broke off more frequently and hence, FA increased over time. Differences in FA were thus not due to differential growth but to differences in quality. The consistency between

studies suggests that while overall wing growth in birds is affected by environmental stress, the wings still tend to grow symmetrically.

The discrepancy between the effects of time-stress on size and FA may indicate that time pressure is an insufficient stressor for an increase in FA. In my study, time pressure was conveyed by short day length only and not correlated with changes in feeding. Although short day length has been shown to accelerate growth (Boon 1999), faster growth itself has so far not resulted in higher FA in birds (Björklund 1996; Teather 1996; Hovorka and Robertson 2000). Nutritional stress has also not increased FA in nestlings (Björklund 1996; Hovorka and Robertson 2000). The only stress during growth that has elevated FA was related to suboptimal habitats (Swaddle and Witter 1994; Møller 1995; Lens and van Dongen 1999; Lens et al. 1999). Some of the studies were carried out on adults and it therefore is not clear if FA resulted from differential growth or from differences in quality that secondarily led to asymmetry.

Taken together, symmetry of the wing may be under rigid control. Deviations from symmetry in wing length may be more costly than size reductions. Studies on starlings *Sturnus vulgaris* (Swaddle et al. 1996; Swaddle and Witter 1997) have shown that FA caused by molt impaired bird flight. Lind (2001) found that experimentally increased side differences between wings strongly affected flight in tree sparrows (*Passer montanus*), in contrast to the low FA levels during its slow natural molt. Similarly, Thomas (1993) calculated that asymmetry under 2% of the wingspan did not result in large costs, but that more pronounced side differences had highly negative effects on flight. He concluded that selection for symmetry was probably very high. The low magnitude of FA in my study may hence result from selection against asymmetry.

Chapter 2

Postjuvenile molt under a tight seasonal schedule in Siberian Stonechats

Summary

The time taken for molt varies greatly among birds, and its precise timing is important especially in migrants. Earlier studies in European and African Stonechats showed plasticity of molt timing in response to photoperiodic cues, but differences between the subspecies in molt schedules. As predicted for migrants, European Stonechats molted earlier and faster, and their photoperiodic response, as described by reaction norms, was more pronounced than in African Stonechats. Here I tested the pertinence of the relationship between migratory distance and molt timing in long-distance migrating Siberian Stonechats. Postjuvenile molt was monitored to assess their reaction norms to different photoperiods (European natural day; long-day hold; short day). Under natural changes in day length, *S. t. maura* molted earlier and faster than its European and African conspecifics, as expected from its migratory behavior. Constant long day length did not change molt timing in *S. t. maura*. Under short day length, molt started only slightly earlier than in the natural day length, but was completed rapidly. In contrast, European and African Stonechats advanced molt markedly under short photoperiods, but its duration was unchanged. Heritability estimates from full-sib analyses in *S. t. maura* were low for molt onset, but high for molt duration. The opposite pattern was observed in the other subspecies. The data suggest that the Stonechat subspecies differed in the reaction norms of molt timing to photoperiodic conditions. These differences may be related to the temporal environments of the subspecies. They were paralleled by differences in additive genetic variance over the course of molt.

Introduction

Soon after fledging, young Stonechats face the challenge of having to renew their plumage and grow a more sturdy, adult-coloured set of feathers (Jenni and Winkler 1994). In temperate zone and high latitude populations, the deterioration of climatic conditions towards the end of breeding exerts high pressure to accelerate molt, which may be opposed by energetic limitations. Molt is an expensive physiological process, both in terms of direct costs of changing the plumage, and of indirect costs such as increased mortality (Jenni and Winkler 1994; Helm and Gwinner 2003). African and European Stonechats have been shown to increase their resting metabolic rate (RMR) during postnuptial molt by over 30% (Klaassen 1995) compared to non-molting times. Birds tend to avoid overlaps of molt with other costly activities such as reproduction and migration (cf. Chapter 4). Following this rationale, the timing of postjuvenile molt in bird populations seems related to

migratory distance and length of their breeding season (e.g., Noskov and Rymkevich 1985, Jenni and Winkler 1994, Berthold 1996, Voelker and Rohwer 1998, Noskov et al. 1999). With shorter reproductive seasons and longer migratory journeys birds are under increasing pressure to finish postjuvenile molt early. The general relationship between the length of the breeding season and postjuvenile molt has been shown by Jenni and Winkler (1994). It is therefore likely that migratory populations of Stonechats are under time constraints to finish molt in time for departure for their outward migration.

Differences in the timing of postjuvenile molt might be due to different environmental conditions, to different reaction norms (defined as the set of all phenotypes that a given genotype produces, depending on the environmental conditions; Van Noordwijk 1990), or to a combination of the two. The sources of variation can be distinguished if distinct populations are compared under a variety of experimental conditions. Photoperiodic manipulations have been widely used as a tool for studying seasonal behavior in organisms (e.g., Gwinner 1986, Dingle 1996). For birds at high latitudes, decreasing day lengths indicate the approaching end of the breeding season. In a previous study (Helm and Gwinner 1999) postjuvenile molt timing has been compared between African and European Stonechats and their hybrids. The subspecies differed genetically in the timing and duration of their postjuvenile molt, with European Stonechats molting earlier than African conspecifics (Gwinner et al. 1983). Both subspecies advanced molt in response to short day lengths, but the molt advance was much more pronounced in European than in African Stonechats. We estimated high heritabilities (h^2) in both subspecies for the timing of molt onset and peak, indicating a great potential for evolutionary adjustment to local conditions (Helm and Gwinner 1999). From these results, molt timing was clearly related to migratory behavior and the length of the breeding season in Stonechats. In the present chapter, I test the pertinence of these earlier results by studying Stonechats from Kazakhstan (*S. t. maura*) with their extremely seasonal life cycle and a very short reproductive period. Thus, I expected their postjuvenile molt to give insights into timing mechanisms under a tight seasonal schedule. I studied the timing of postjuvenile molt in Siberian Stonechats under three different photoperiodic conditions and compared it to that of the other two Stonechat populations. The timing of postjuvenile molt of Irish Stonechats will be covered in Chapter 4 in the context of migratory timing.

Birds and methods

The data in this chapter were obtained between 1997 and 1999 from 78 Siberian Stonechats (median hatching date: June, 5th; range: 30 days). In May and June of 1997 (cohort 1) and 1998 (cohort 2) 68 birds were collected as nestlings in Kazakhstan, transferred to Andechs and subsequently hand-raised. Ten additional young from four clutches were offspring from two breeding pairs in 1999 (cohort 3, four females and six

males). Initially, all nestlings were kept in the natural photoperiod of 47.5°N (ND) to approximate their native daylight conditions. Sibling groups of cohorts 1 and 2 were later divided into groups subjected to different light conditions (Table 2.1) in a split-plot design. Short day length (SD) represented the native condition for African Stonechats and indicated severe time pressure for high latitude populations. ND was the control condition for Siberian and European Stonechats. Long day length (LD, only cohort 2 of 1998) simulated persistent midsummer.

The data on European and African Stonechats, *S. t. rubicola* and *S. t. axillaris* used here for comparison are taken from Helm and Gwinner (1999). The Stonechats were collected between 1982 and 1990 in Austria (median hatching date 27 May) and Kenya (median hatching date 24 April). Most were taken as nestlings and hand-reared in Andechs. About one quarter of the Stonechats had hatched in captivity. The light conditions for European Stonechats were the same as those for the Siberian subspecies. African Stonechats were treated in an analogous way (Table 2.1). I included data from 103 African and 80 European Stonechats in the statistical comparisons of postjuvenile molt. For the calculation of reaction norms, I included additional data from Helm and Gwinner (1999).

Table 2.1

Experimental groups and day length conditions under which the three Stonechat subspecies molted.

	short day (SD)	natural day (ND)	long day hold (LD)
<i>S.t. maura</i>	16 birds in ND until day 14-25; then constant equatorial day length (LD 12.25:11:75 h)	56 birds kept in European natural day length of 47.5° N	6 birds in ND until maximal day length (age 16 – 21 days); then constant maximal day length (LD 17.33:6.66 h)
<i>S.t. rubicola</i>	23 birds, treatment like <i>S.t. maura</i>	57 birds, treatment like <i>S.t. maura</i>	
<i>S.t. axillaris</i>	88 birds kept in SD from hatching	15 birds hatched in SD; ND from ages 1 – 9 days	

Postjuvenile molt was assessed as described in the General method section. Ln-transformed data were analyzed using REML. Year, photoperiod, their interaction, and sex were tested as fixed factors by assessing the difference in model fit for each factor. The factors sex and interaction between year and photoperiod were non-significant and dropped from the main model. Post hoc testing was carried out on the original data, using Mann-Whitney and Kolmogorov-Smirnov tests which differ in their assumptions. The more conservative results are included. In 1998, when birds were assigned to three groups,

photoperiodic effects were tested in a Kruskal-Wallis analysis. In addition, I used linear regressions to test for effects of hatching date and effects of age differences during photoperiodic manipulation in the SD group (Table 2.1).

Heteroscedasticity among some groups complicated my analysis. For molt onset, the LD group had to be dropped from the main model. Variances were also very heterogeneous between subspecies. Therefore, I compared them in non-parametric Kruskal-Wallis analyses separately for the photoperiodic groups of SD and ND. I quantified and compared the photoperiodic responses of the subspecies in median regressions (median of age at molt against median of day length for each cohort and photoperiodic group).

Family effects were tested over the residuals of the main analysis. I kept sample sizes relatively large but avoided inflating family effects by photoperiod and cohort differences. I excluded a few values gathered by a different investigator to avoid potential observer effects. The remaining data (16 families; number of birds: onset $n = 72$; peak $n = 77$; completion and duration $n = 70$) were analysed for significant family effects, and variance components were estimated. I calculated upper limits of heritability (h^2) as twice the sibling correlation t given by the ratio of the between-nest variance component over the sum of between-nest and within-nest variance components (Helm and Gwinner 1999). For comparison, I conducted a one-way ANOVA over families and calculated h^2 as described by Roff (1997) for unequal family sizes. Since h^2 estimates differed at most by 0.002, I publish only REML results. Standard errors were calculated as described by Roff (1997). In addition, I estimated h^2 separately for the photoperiodically unmanipulated birds kept under ND. From the split-brood design, we approximated "family reaction norms" by calculating the medians of each sibling group under SD and ND. Family medians under both light conditions were plotted and connected by thin lines as bundles of "family reaction norms" to visualize family patterns (e.g., Dingle 1990). Unfortunately, some sibling groups were represented by a single bird in one photoperiodic group, so that "family reaction norms" were only approximated, and plasticity could not be quantified from intersecting lines.

Results

Variation in molt timing

Siberian Stonechats started molt early and finished it quickly. Their first molt was recorded at an age of 21 days, before growth of wing feathers was completed. Variation in molt timing increased during the course of molt (age ranges: onset 19, peak 37.5, completion 51, duration 43 days). The factors that were associated with differences in molt timing changed over the course of molt. At molt onset, the highest proportion of the variance between Stonechats was associated with individual differences (variance

component of 63.6%). The variance components associated with cohort and photoperiodic group were smaller and similar in magnitude (17.4% and 19.0%, respectively). During the course of molt, the proportion of variance associated with photoperiod increased to 73.9% (peak), 82.5% (completion), and 87.6% (duration). Thus, by the time of molt completion differences between birds were mostly related to photoperiodic treatment. Variance components for cohort and individual decreased to 11.5% and 2.4% respectively (peak), 9.1% and 8.4% (completion), and 3.8% and 8.6% (duration). The three cohorts differed significantly ($n = 78$; Wald statistics on $df = 2$: for onset = 13.6; $P < 0.01$; for peak = 24.4; $P < 0.001$; for end = 35.5; $P < 0.001$; for duration = 16.7; $P < 0.001$). Nestlings collected in Kazakhstan in 1998 started molt earliest, those from 1997 at intermediate ages, and Stonechats raised in captivity in 1999 last. However, the cohorts responded in precisely the same manner to the photoperiodic manipulations.

Effects of photoperiod

Molt timing differed markedly between the photoperiodic groups (Fig. 2.1A; $n = 78$; Wald statistics on $df = 2$: peak = 227.4; $P < 0.001$; end = 372.0; $P < 0.001$; duration = 378.8; $P < 0.001$; onset without LD group: $n = 72$; Wald statistics on $df = 1$: 11.8; $P < 0.001$). Siberian Stonechats initiated molt slightly earlier under SD than under ND and LD (Table 2.2) and progressively accelerated molt in SD so that the differences between the photoperiodic groups increased with time. Effects of all three photoperiodic treatments were compared within the cohort of 1998. Day length affected all molt parameters except for onset (Kruskal-Wallis, onset: $\chi^2(2df) = 4.3$; *n.s.*; peak: $\chi^2(2df) = 18.0$, $P < 0.001$; completion: $\chi^2(2df) = 18.1$, $P < 0.001$; duration: $\chi^2(2df) = 17.9$, $P < 0.001$). Post-hoc analyses revealed that molt timing of birds kept in SD differed from that of the other groups, whereas Stonechats kept in LD molted at the same ages as those kept in ND (LD: Median \pm interquartile range (IR): onset 31 ± 1 ; peak 51.5 ± 4 ; completion 72 ± 16 ; duration 40 ± 18 ; $n = 25$; Mann-Whitney *n.s.*). Unexpectedly, I found no effect of hatching date on molt timing among Siberian Stonechats under ND. In the SD group, the age at the photoperiodic switch exerted a significant influence on all molt timing measures, except for molt duration (linear regression with cohorts as groups: onset slope 0.9 ± 0.11 ; constant 12.3; $r^2 = 81.9$; peak: slope 0.8 ± 0.13 ; constant 23.4; $r^2 = 79.2$; completion: slope 0.8 ± 0.24 ; constant 38.4; $r^2 = 64.2$; for all molt measures, $n = 16$; $P < 0.001$). The earlier a bird was placed under SD, the earlier it molted. Effects of the age at first exposure to SD were identical in slope for the cohorts of 1997 and 1998.

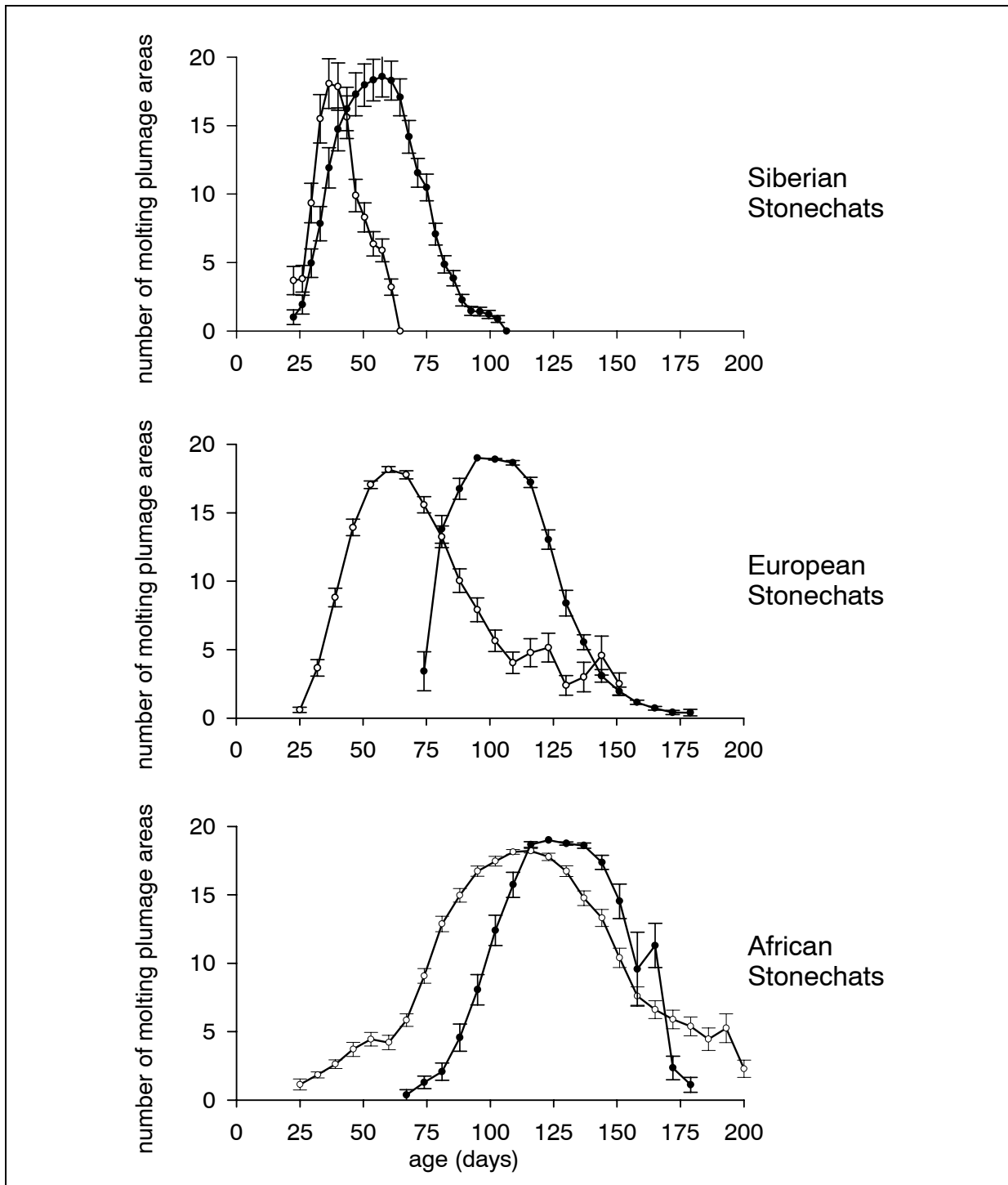


Figure 2.1

Molt curves of juvenile Siberian, European, and African Stonechats kept under short day length (open circles) and natural day length (filled circles); the LD group overlapped with ND and was left out for clarity. Curves show the mean number (\pm SE) out of a total of 19 plumage areas that were molting at any given age. A: bi-weekly means of Siberian Stonechats. B + C: weekly means of European and African Stonechats. Standard errors are smaller than those given in Helm and Gwinner (1999) owing to a computational error detected in the original values.

Family effects on the timing of molt

There were significant family effects for all molt parameters except for onset (after accounting for effects of photoperiod and year; onset: Wald statistics = 22.7; n.s.; peak = 35.1; $P < 0.01$; end = 28.6; $P < 0.05$; duration = 81.9; $P < 0.001$; analyses based on 16 families; number of birds: onset $n = 72$; peak $n = 77$; completion and duration $n = 72$). I calculated the following h^2 values: onset $h^2 = 0.22 \pm 0.23$; peak $h^2 = 0.44 \pm 0.24$; completion $h^2 = 0.36 \pm 0.25$; duration $h^2 = 1.00 \pm 0.25$. Separate h^2 estimates for the birds kept in ND only were slightly elevated (n families = 15, n birds = 50 to 56): onset $h^2 = 0.25 \pm 0.28$; peak $h^2 = 0.64 \pm 0.30$; completion $h^2 = 0.55 \pm 0.32$; duration $h^2 = 1.09 \pm 0.28$. Fig. 2.2 shows family patterns under SD and ND. For molt onset, there was a considerable number of intersections between "family reaction norms". Family members under different photoperiods began their molt at different ages, statistically expressed by the lack of significance of family effects. Later during molt, family effects became more conspicuous. Birds with siblings molting early under one photoperiod were more likely to do so under the other as well.

Table 2.2

Timing of molt under natural and short daylight for the three subspecies of Stonechats. The table shows sample size, median (med.), interquartile range (IR), and results from a Kruskal-Wallis analysis of the four molt parameters. Comparative data on European and African Stonechats were taken from Helm and Gwinner 1999.

	Siberian			European			African			Kruskal-Wallis	
	n	med.	IR	n	med.	IR	n	med.	IR	χ^2 (2df)	$P \leq$
European natural day length											
Onset	56	31	6	9	84	4	15	94	11	50.94	0.001
Peak	56	54	8.25	23	101.5	33	15	129	7.3	71.66	0.001
Completion	56	76.5	9.5	22	134	11	15	161	8.2	70.38	0.001
Duration	56	44	7.5	9	48	2.75	15	64	6.5	39.73	0.001
Short day length											
Onset	16	29.5	5	53	38	8	73	72	16	103.56	0.001
Peak	16	39.5	4.5	57	63.5	13.5	88	111.5	24	126.43	0.001
Completion	16	49.5	7	57	91	20	86	159	24	121.97	0.001
Duration	16	20.5	5	53	55	21.25	71	91	27.25	87.90	0.001

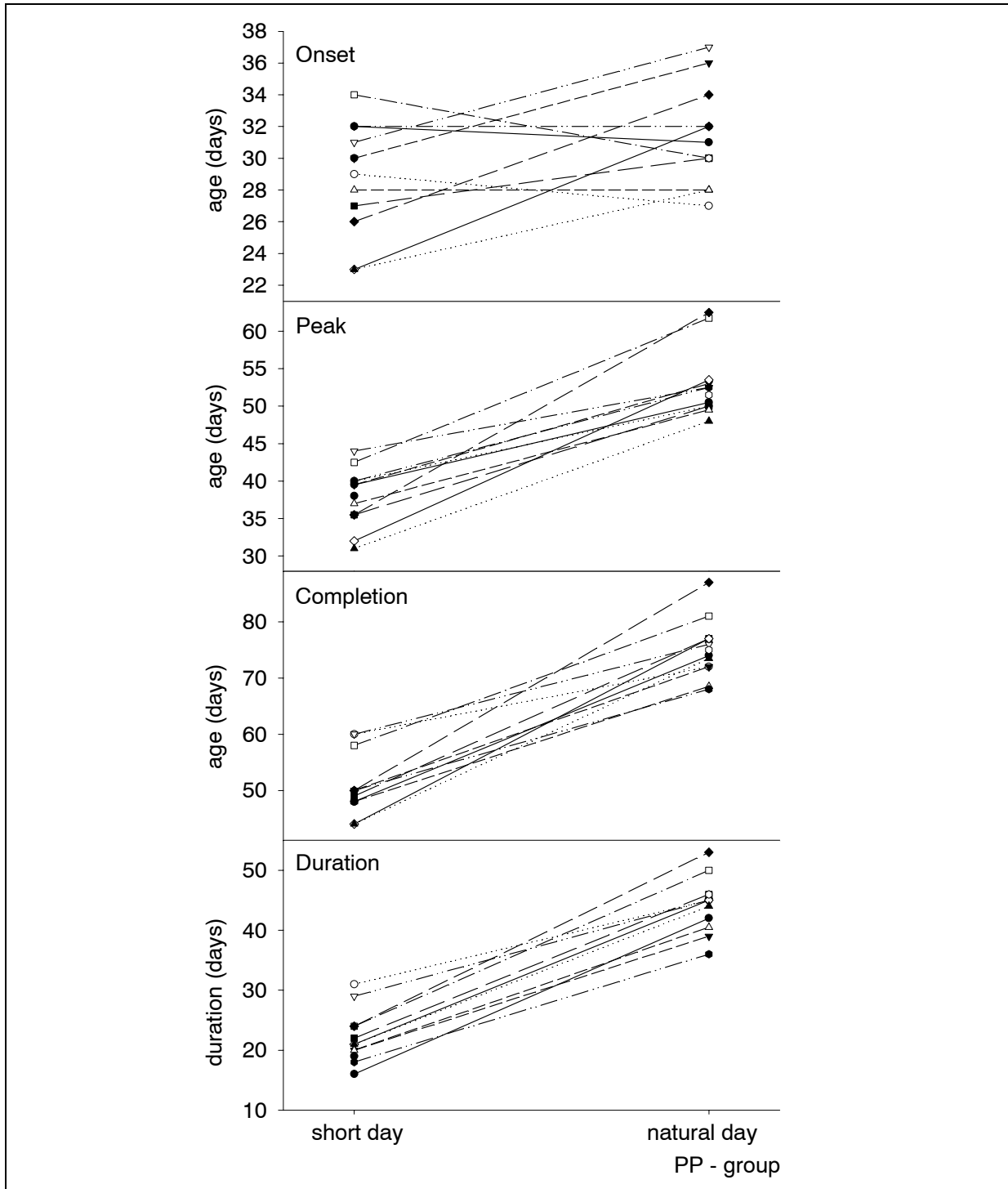


Figure 2.2

"Family reaction norms" of molt timing in split broods. The graph plots the mean molting ages of Siberian Stonechat families under two photoperiodic conditions, connected by lines. The photoperiod for the short day group remained constant at LD 12.25:11.75 h, the one for the natural day group changed according to the photoperiodic conditions of 47.5°N. The four panels show bundles of reaction norms for molt onset, peak, completion, and duration.

Comparison of molt timing among three Stonechat subspecies

Siberian Stonechats initiated molt at earlier ages than the other subspecies. In ND, the three Stonechat subspecies differed significantly in the timing and duration of their molt (Table 2.2, Fig. 2.1). Siberian Stonechats started molt much earlier than European Stonechats and were quicker to finish it (Kolmogorov-Smirnov Test: onset $Z = 2.79$; $P < 0.001$; peak $Z = 4.04$; $P < 0.001$; completion $Z = 3.97$; $P < 0.001$; duration $Z = 1.73$; $P < 0.005$). European Stonechats, in turn, molted earlier and for a shorter time than African Stonechats. The differences between the three Stonechat subspecies in molt timing and duration were even more pronounced under SD. Siberian Stonechats molted earlier and faster than European Stonechats (Kolmogorov-Smirnov Test: onset $Z = 2.45$, $P < 0.001$; peak $Z = 3.47$, $P < 0.001$; completion $Z = 3.54$, $P < 0.001$; duration $Z = 3.51$, $P < 0.001$), which, in turn, molted earlier and more quickly than African Stonechats.

In all subspecies, molt timing was systematically related to day length by linear regression (Fig. 2.3). The shorter the day length, the earlier the molt occurred. I present the subspecies responses to day length for peak molt as an example but attained similar results for molt onset and completion. The median regression with subspecies as groups was highly significant ($n=18$, $r^2=96.7$; $P<0.001$). Stonechats from Kazakhstan responded to short day length with the smallest advance of their molt peak. Their response differed significantly in slope from that of their European conspecifics (slope of Siberian + additional slope of European Stonechats: $3.5+21.0$; $P<0.001$), but not from that of African Stonechats ($3.5+4.3$; n.s.).

Discussion

Postjuvenile body molt in *S. t. maura* started and ended at very young ages. Our results from captivity are comparable to the only field record from Kazakhstan that has come to my attention. Dementiev and Gladkov (1968) observed young Stonechats that had almost finished molt in early August. In view of the fairly constant hatching time in early June (Johansen 1954, Dementiev and Gladkov 1968), the Stonechats were presumably about two months old, in good accordance with the median age of 76.5 days at molt completion calculated here.

In my study, the differences between subspecies in the timing and duration of postjuvenile molt were pronounced. *S. t. maura*, under all photoperiodic conditions, molted earlier and more quickly than European Stonechats, which in turn molted before African Stonechats (Fig. 2.1). This sequence of molt timing is precisely as expected on the basis of migratory behavior of the subspecies and length of their breeding seasons (Jenni and Winkler 1994, Noskov et al. 1999). All subspecies displayed plasticity of molt timing by advancing their molt under SD. However, they differed in the slopes of their estimated

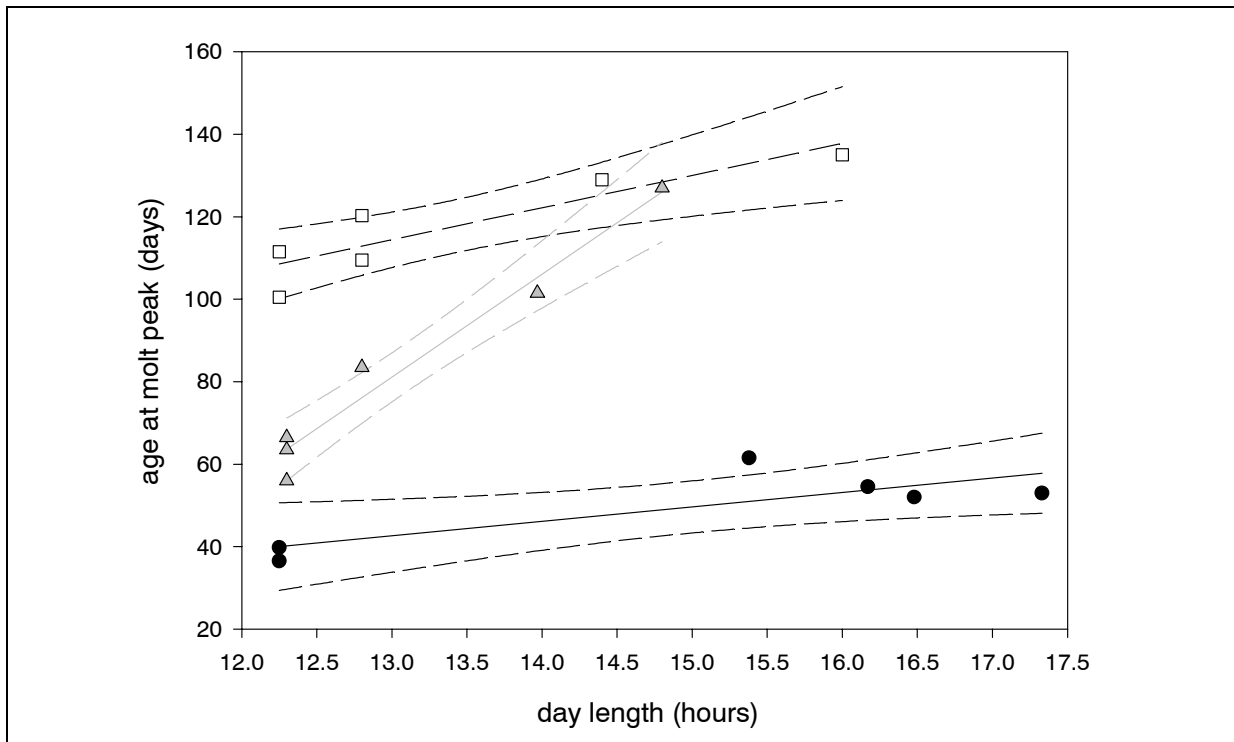


Figure 2.3

Mean population reaction norms of molt peak in relation to photoperiod. The graph relates molt timing to day length (linear regression slopes with confidence intervals); data are median ages at molt peak of several experimental groups in relation to the median day length on the respective date; different symbols indicate Siberian (black solid line and black filled circles), European (gray solid line and gray triangles), and African Stonechats (black dashed line and open squares).

"mean reaction norms" (Fig. 2.3; Van Noordwijk 1990, Helm and Gwinner 1999). *S. t. maura* showed the smallest advance of molt under SD relative to ND. The regression slope was similar to that of African Stonechats but much smaller than in European Stonechats. One could argue that transfer to SD occurred too late to fully affect molt onset (Lindström et al. 1994). However, unpublished data from six Stonechats that hatched under SD in 2000 make this interpretation unlikely. These birds molted at a median age of 31 days, and hence no earlier than the SD group in the present study (Helm and Gwinner, unpubl. data). Theoretically, physiological constraints may keep Stonechats from advancing their molt below the age of about 30 days in *S. t. maura*. However, literature data from other passerine species indicate that postjuvenile molt can start at earlier ages. Widmer (1999) found a mean molt onset of 16 days (minimum: 14 days) for an Alpine population of *Sylvia borin*. Out of 13 Russian passerine species studied by Noskov et al. (1999) Ten species started postjuvenile molt at younger ages than *S. t. maura*, with 19 days for *Sylvia borin* as

the lowest value. In view of such early molting ages, the small SD-induced advance of molt onset in *S. t. maura* does not appear to be due to physiological limitations.

While molt onset in Siberian Stonechats was only slightly affected by SD, later stages of molt were increasingly more advanced. As a consequence, molt duration was drastically reduced. Such a time-dependent increase of the photoperiodic response in *S. t. maura* was also indicated by the growing variance components associated with photoperiod. Apparently, Stonechats from Kazakhstan achieve the timely completion of their molt by starting at a fairly inflexible early age, and by subsequently adjusting molt rate according to photoperiodic cues. Conversely, the other two subspecies responded most strongly to SD by advancing molt onset, whereas molt duration was hardly affected (Helm and Gwinner 1999). The Stonechat subspecies thus differed in the plasticity patterns of postjuvenile molt timing. A possible interpretation of these differences in view of their native photoperiods is given in Gwinner and Helm (2002). The overall effect – an earlier completion of postjuvenile molt in SD compared to ND – was negligible in resident equatorial Stonechats. In contrast, the two migrant populations advanced molt completion considerably. Despite their different plasticity patterns of molt timing, Stonechats from Europe and Kazakhstan achieved very similar advances of molt completion under SD compared to ND (Europe: 67.9%; Kazakhstan: 64.7% of ND under SD). It is not clear if the shortening of molt duration was to some extent achieved by an incomplete molt. Whereas other species, for instance members of the *Sylviidae* are known to arrest molt under time pressure, Snow (1969) stated that among turdid passerines, none have moved their molt to winter. Siberian Stonechats may differ from that general rule because a limited winter molt has been observed in first year birds (E. Gwinner, pers. comm.).

The low photoperiodic responsiveness of molt onset in *S. t. maura* confirms previous studies of bird populations with short breeding seasons (Jenni and Winkler 1994, Lindström et al. 1994). In the two Northern hemisphere Stonechats, the different plasticity patterns of molt timing may reflect characteristic selection pressures. Given the short reproductive period of Stonechats from Kazakhstan around midsummer, photoperiod may not be a useful cue for the timing of molt onset because nestlings are not exposed to day lengths that differ markedly from the maximal midsummer photoperiod. Unpredictable seasonal conditions such as a rapid deterioration of environmental conditions in some years may select for an early start of postjuvenile molt (M. Raess, pers. obs.) as a low-risk strategy to avoid changing plumage under unfavourable conditions. In contrast, young of the multi-clutched European Stonechats experience a wide range of photoperiods from hatching and differ distinctly in the age at which they initiate postjuvenile molt (Flinks 1999). Photoperiod becomes more useful as a time cue for *S.t. maura* later during molt because decreases in day length become accelerated in late summer (cf. Gwinner and Helm 2002). Hence, the range of day lengths experienced by birds from early versus late clutches at a

given age widens as the season progresses. Small differences in hatching date can lead to large day length differences at late molt stages. In response to short day length, immatures reduce molt duration by increasing molt rate, presumably incurring high costs. An increased speed of molt can raise energetic and life history expenses and reduce the quality of the replaced plumage (Hahn et al. 1992; Serra 1999; Dawson et al. 2000; Hall and Fransson 2000; Lind 2001). In addition, passerine feathers that were grown more quickly have been shown to be shorter, lighter, and less resistant (cf. Chapter 1; Dawson et al. 2000; Hall and Fransson 2000; Dawson et al. 2000).

Estimates for h^2 also indicate low flexibility of molt onset in *S. t. maura*. Family effects were not significant at the beginning of molt, and additive genetic variance was low. Later during molt, family patterns were more clearly expressed, and the h^2 estimate for molt duration was high. The "family reaction norms" for different photoperiods illustrate this point. In *S.t. maura*, the bundle of curves had most intersections during molt onset, implying low family influence across photoperiods (Fig. 2.2). As molt went on, the lines became increasingly more parallel. Family effects persisted more clearly across photoperiodic groups towards the end of molt. In contrast to the results for *S. t. maura*, h^2 estimates from European and African Stonechats were consistently high for molt onset and declined later. "Family reaction norms" in African Stonechats were most parallel for molt onset, and intersected increasingly for peak and completion (Helm and Gwinner 1999). Heritability estimates from full-sib analyses represent upper limits of additive genetic variance since they are inflated by nest effects and dominance deviation (Roff 1997). However, the first results from breeding experiments with European Stonechats (Chapter 3) indicate that heritabilities estimated from sibling correlations are matched by realized heritabilities, i.e., that parental molt timing markedly affect that of their offspring. Comparative data on the genetics of molt timing are scarce. Larsson (1996) published h^2 values for the onset of wing molt in wild adult Barnacle geese *Branta bernicla*. Estimates for h^2 from parent-offspring regressions ranged between 0.2 and 0.4, and estimates from full-sib analysis were similar except for one outlier. Widmer (1999) found altitudinal differences in molt timing between Alpine and lowland populations of *Sylvia borin*. Values of h^2 for onset, median, and end of postjuvenile molt ranged between 0.41 and 0.64 in both populations. High-altitude birds with a short breeding season showed a slight increase of h^2 values over the course of molt, whereas in lowland birds, h^2 remained constant. In contrast to lowland birds, molt of mountain birds was not responsive to short day length and different hatching dates (M. Widmer, pers. comm.). The similarity of the results obtained by Widmer in his altitudinal study and my findings obtained from comparing different breeding season lengths supports the tenet that under high seasonal pressure, bird populations initiate their molt early and that family differences and responses to timing cues become evident later during molt.

It is interesting to note that in all subspecies the changes in additive genetic variance over the course of molt paralleled those of photoperiodic responsiveness. While in *S. t. maura* both h^2 and the plasticity of the photoperiodic response were initially low but increased over the course of molt, the opposite was true in European and African Stonechats. Based on h^2 estimates, and thus on the genetic potential to respond to changing selection pressures, I would expect the three subspecies to evolve differently when exposed to new seasonal pressures. Siberian Stonechats should respond with successive timing adjustments over the course of molt, and specifically change molt duration. The other two subspecies should advance or delay onset and peak of molt but keep its duration approximately constant. This is exactly in line with the respective responses of the subspecies to different photoperiods.

Chapter 3

Genetic control of molt timing: selection experiments with European Stonechats (*S.t. rubicola*)

Summary

Previous studies have suggested high heritability (h^2) of molt timing in Stonechats. Estimates of h^2 were mostly derived from sibling correlations which are generally known to be inflated, e.g., by effects of common environment. Therefore, I critically tested the genetic control of molt timing in selective breeding experiments on European Stonechats. The Stonechats were classified into three groups, those that molt early in life, those that molt late, and controls. The long-term breeding experiments are still being continued but first results are promising. Among offspring of the F1 generation, young of the three groups molted at distinct ages and differed from each other in the direction predicted from the selection protocol. Among controls, h^2 as estimated after taking account of different hatching dates was high and hence in accordance with earlier studies. In addition, there is some indication for a correlated response to selection. Offspring from early-molting parents differed from other young in their response (mean "reaction norm") to hatching date. The timing of molt onset was advanced to a lesser degree by the changing photoperiod than in the other groups. Therefore, the observed differences in molting ages could be a consequence of different reaction norms to photoperiod. Micro-evolutionary adjustments of molt timing function possibly through modifications of photoperiodic reaction norms.

Introduction

Molt timing is a relatively flexible element of the Stonechats' annual cycle. It is highly sensitive to seasonal information as conveyed by photoperiod (Chapter 2). Freelifving birds that hatch late compensate at least in part for their later birth by molting at younger ages (Gwinner 1968). This timing mechanism, the "calendar effect", can be described by a reaction norm of molting age to day length. Postnuptial molt appears to be responsive to social factors (Chapter 6). In addition to its phenotypic plasticity in response to seasonal cues, molt timing can presumably be readily fine-tuned by micro-evolutionary processes (Helm and Gwinner 1999; Chapter 2). Heritabilities (h^2) of postjuvenile molt timing in Stonechats were found to be high after accounting for seasonal trends. Comparative data from other bird species have been scarce but tended to confirm a high degree of genetic control over molt timing (Larsson 1996; Widmer 1999). However, the high estimates for h^2 of molt timing, especially those derived from full-sib correlations, may have been inflated by other factors such as common environment effects. Estimates of h^2 provide upper limits

of the heritability of a trait (Boag and van Noordwijk 1987; Roff 1996; Merilä and Sheldon 2001). One rigorous but rarely used approach to testing the reliability of h^2 estimates is by selective breeding (Pulido 1999; Merilä and Sheldon 2001). Selective breeding uses the birds' response to selection to estimate realized h^2 (narrow sense heritability). It thus helps calculate the component of genetic variance that is truly additive (V_A). In this chapter I investigate the inheritance of postjuvenile molt timing by selectively breeding European Stonechats according to their age at postjuvenile molt.

The very fact that molt timing shows both, phenotypic plasticity in response to environmental conditions and strong genetic control, makes it an interesting subject of study. If molt timing responds to timing cues and is adjusted by micro-evolutionary processes, there is reason to assume that the photoperiodic timing mechanism itself is being fine-tuned by selection. Studies on African and Siberian Stonechats suggested that bird families differ in their mean response to photoperiod (Helm and Gwinner 1999; Chapter 2). Such interfamily differences are a necessary condition for evolutionary adjustments of photoperiodic reactions. Therefore, in the selective breeding experiments I pursue two questions: one is to assess the overall effect of selection on molt timing. The second question is whether selective breeding affects the photoperiodic response of birds over a range of day lengths. To answer these questions I estimate h^2 of molt timing after accounting for differences in day length (analysis of residuals). Secondly, I compare the relationship between molt timing and day length in offspring of the selection groups (analysis of raw data).

Selective breeding experiments in birds are time-consuming because of the long generation time, which makes accumulating sample sizes sufficient for sophisticated quantitative genetic analyses a long-term project. Due to the still limited sample sizes I summarize preliminary results in the present chapter.

Birds and methods

Selection regime

Beginning in 1999, I have paired European Stonechats into three parent groups depending on the age at which they had reached peak postjuvenile molt. These parent groups were allowed to breed in outdoor aviaries and molt timing of their offspring was monitored (see General method section). One parent group was selected for reaching the peak of postjuvenile molt at a particularly young age and a second one for reaching it late. The third and largest parent group consisted of controls intended to assess genetic drift and to independently estimate general effects of season and year. Controls were derived in one of two ways: in some of the birds molting ages were known; pairs were matched so that parental molting ages were uncorrelated. The control mean approximated the overall population mean. Control breeders did not differ from the remaining breeding stock (U-

test; $U=614.0$; $Z=0.523$; $P=0.639$; $df=119$). In addition, I measured a second group of "blind" controls by breeding birds of unknown molting age and by measuring molt timing of their offspring. Breeding pairs of control groups were chosen from the total breeding stock of 128 Stonechats in order to maximize genetic diversity. In total, birds belonged to six cohorts. At the beginning of a new season the breeding stock was supplemented by offspring from all groups from the preceding year and once by additional nestlings collected in Austria (year 2000).

In contrast to controls, breeding pairs of the early and late molting groups were all chosen among birds of known molt records. With one exception, birds from the F1 generation of early and late molting groups were not eligible as selective breeders (one brood in the late molting groups was a F2 generation). Breeders were selected out of 96 European Stonechats that had hatched between 1997 and 2000 and for which postjuvenile molt had been recorded (see General methods). Of the four molt parameters analyzed in Stonechats (molt onset, peak, completion, and duration), peak of molt had been scored for the most birds ($n = 85$). Therefore and because peak of molt has proved the most robust measure of molt timing (Helm 1997), I used it as the criterion for selection of breeding pairs. Birds qualified as breeders in the experimental groups if they belonged to the 20% of the youngest or oldest birds to reach peak molt, respectively.

For the selection of early and late molting breeders, ages at peak molt were corrected for differences between years and for effects of hatching date on molt timing (see below). The use of residuals was necessitated because birds had to be as comparable to each other as possible for proper selection. Photoperiodic effects on molt timing would confound phenotypic plasticity with family differences. However, since photoperiod-induced responses to hatching date may differ between birds that molt early and those that molt late, correcting for hatching date may have created some artefacts (see below). For this reason and because not all birds were successful breeders, the selection criterium was not met in all individual cases. By median value, parents of the early molting group reached molt peak at a younger age than 17.6% of the population. Parents of the late molting group were older than the 15.2% oldest birds in the total population.

Until fall of 2001, the three parent groups had produced 69 offspring belonging to the following groups: Parents of the early molting group laid four broods in three families, totalling 13 offspring. For molt onset only, data from one brood of a family are missing. Five families of the late group laid six clutches, amounting to 14 offspring. The two types of control totalled 13 broods of nine families (total number of offspring 42; molt peak data for 35). Of these, 13 young hatched from five broods of three families belonging to blind controls; 29 young originated from eight broods of six families with known molt data.

Statistical treatment

Since molt ages of all birds had to be comparable for optimal selection of breeders, it was necessary to account for differences that were likely to be based on phenotypic plasticity in response to environmental cues. One important factor affecting molt timing is the changes of photoperiod over the season. To account for these effects of calendar, I calculated regressions of molt timing against hatching date for all birds. To solidify the estimate of the calendar effect through a larger sample size, I included molt data from additional European Stonechats from previous experiments (Helm and Gwinner 1999). In addition to the effects of hatching date, avian timing of seasonal activities frequently differs between years even in captivity (e.g., Pulido 2000; Chapter 2). Therefore, year was entered into the regression model as a grouping factor. Figure 3.1 shows the calendar effect on molt peak for all European Stonechats under European day length in relation to hatching date. Years are separated by different symbols. From the figure, it is clear that hatching date significantly influences molt timing, but year-to-year differences are also discernible and were significant ($p < 0.001$). I retained a common slope to get as general as possible an estimate of the calendar effect ($r = -0.45$; $df = 134$; $p < 0.001$; $r^2 = 76.7$). Inclusion of differences in slopes between years would have added little information ($r^2 = 78.0$) and risked biasing the selection due to the photoperiodic response that prevailed among the birds of each year. Hence, I calculated residuals by regressing age at molt peak against hatching date and correcting for main effects of year. The ranked residuals were used for the selection of breeders (see above). A negative side effect of the use of residuals was that it reduced the correlations between molt timing measures. For representative examples, in the F1 generation the correlation between molt onset and peak dropped from 0.90 in the raw data to 0.76 in the residuals. The correlation between molt onset and completion fell from 0.83 in the raw data down to 0.33 in the residuals. The reduced correlation was most likely a consequence of the fact that differences between years were corrected by an average factor for the whole population. Apparently, this has masked differences between individuals.

The first goal of this chapter was to derive estimates of heritability through selective breeding. I derived two different estimates for h^2 from residual analyses. For the randomly mated control group, I estimated h^2 from full-sib correlations (see General methods). For the assortatively mated early and late molting groups, I derived h^2 estimates from their response (R) to selective breeding. The response R of the F1 generation is defined by the mean (here because of small sample sizes: median) deviation of the selectively bred groups from the controls. The offspring response R is then compared to the difference of the parent generation from the population mean (selection differential S). Division of the offspring response R by the parental selection differential S indicates which proportion of

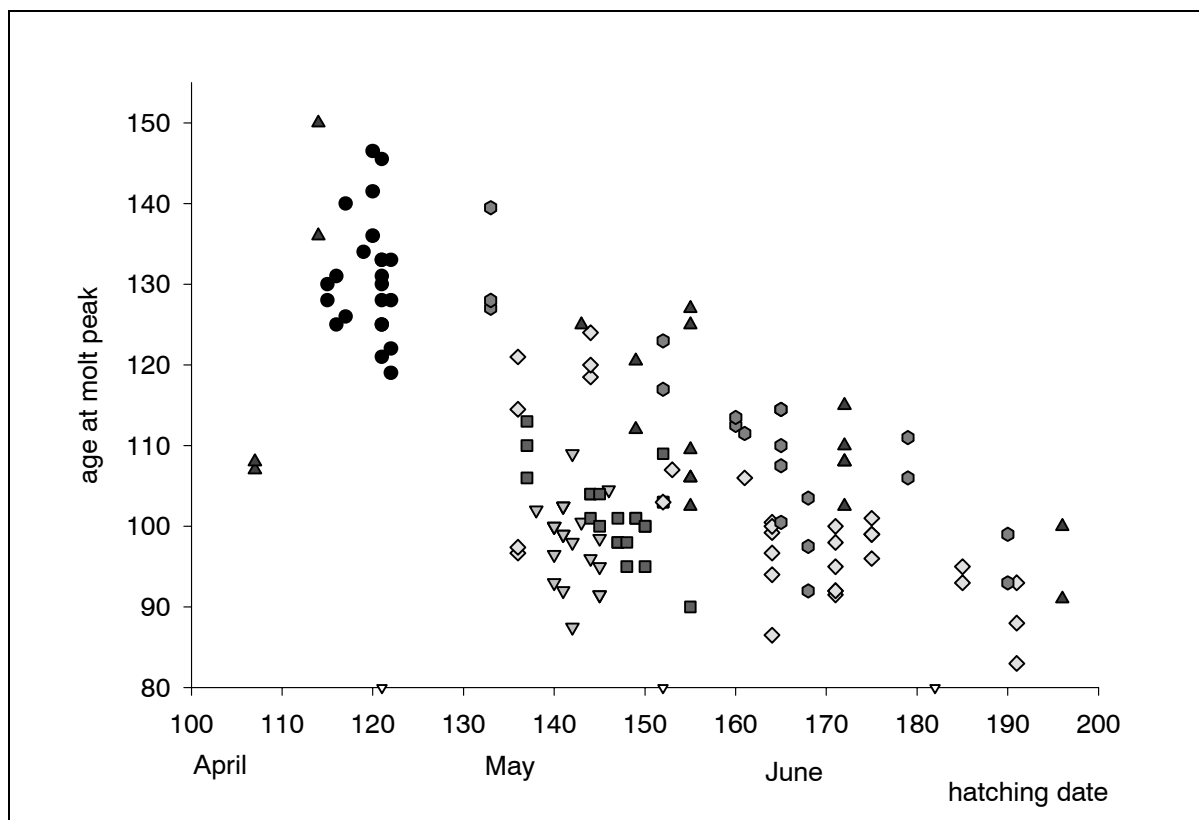


Figure 3.1

Peak molt in relation to hatching date (calendar effect). The graph shows data from 146 Stonechats kept under natural European day length; different symbols represent different years. The abscissa shows time of the year as Julian date and month in the year (triangles mark the beginning of a month); the ordinate shows the age of a bird at the time of peak postjuvenile molt.

parental differences is passed on to the offspring, and hence estimates realized heritability: $h^2 = R/S$ (Falconer and Mackay 1996). However, since h^2 is estimated from a ratio, small deviations from the group mean can lead to high estimates of h^2 . In view of the low sample sizes that are currently available, such small deviations are expected to arise by chance. To safeguard against spurious effects, I first tested via Kruskal-Wallis Analysis of Variance for significant differences between the parental groups. I calculated realized h^2 only for molt metrics with significant selection differentials.

The second goal of this chapter was to explore if there is indication for group differences in the calendar effect. To this purpose, I employed regressions of all molt measures against hatching date, using the raw data. To avoid pseudoreplication I used as data brood medians for the F1 generation and parental medians for the breeders. If selective breeding caused consistent differences in mean molting age over the range of hatching dates, breeding group should only affect the regression constant. However, if there is a correlated response on the calendar reaction, breeding groups should also differ in slopes (i.e. the interaction term between hatching date and breeding group).

Results

Heritability estimates

Heritabilities of the control group were estimated from full-sib correlations of the residual data. They ranged between 0.77 for onset, 1.0 for molt peak, 0.33 for molt completion, and -0.04 for molt duration. Since these values are based on small sample sizes (data derived from 35 birds from nine families) and have to be considered preliminary, specification of significance levels and standard errors would be premature. The negative h^2 estimate is biologically speaking nonsense. However, I give the precise estimate because the habit of setting negative variance components to zero may contribute to inflated average h^2 estimates in meta-analyses (Palmer 2000).

Analyses of the early and late-molting groups revealed that the parent generation had differed significantly from the breeding stock. The assortatively mated parents differed from the population in their residual age at molt onset, peak, and completion (Kruskal-Wallis for onset: $H=8.72$; $df=2$; $p=0.013$; peak: $H=13.99$; $df=2$; $p=0.001$; completion: $H=11.79$; $df=2$; $p=0.003$) but not in molt duration ($H=1.33$; $df=2$; $p=0.515$). Among the F1 generation a similar trend was observed. Offspring from the breeding groups differed from controls most markedly in the age at peak molt, the selection criterion for their parents. For molt onset and molt completion group differences were too small to attain significance (onset: $H=5.05$; $df=2$; $p=0.080$; peak: $H=7.08$; $df=2$; $p=0.029$; completion: $H=4.63$; $df=2$; $p=0.099$). For molt duration, there was no indication of a correlated response ($H=1.32$; $df=2$; $p=0.518$).

Table 3.1

Molt timing of parents and offspring of selective breeding groups and controls. For parents, timing of the entire breeding stock is given as super-control; for offspring, results are from pooled controls. Data are medians and sample sizes for residuals from the regression of molt timing against hatching date, grouped by year.

breeding group	onset (n)	peak (n)	completion (n)	duration (n)
parent generation				
early molting	-0.58 (6)	-0.83 (6)	-1.40 (6)	-0.40 (6)
late molting	0.68 (10)	0.86 (10)	0.67 (10)	0.23 (10)
controls	-0.06 (13)	0.15 (13)	-0.26 (13)	-0.19 (13)
breeding stock	0.04 (95)	0.00 (106)	-0.05 (104)	-0.01 (83)
offspring generation				
early molting	-0.46 (7)	-0.57 (13)	-0.49 (13)	0.17 (7)
late molting	0.09 (14)	0.36 (14)	0.26 (14)	0.05 (14)
controls	0.09 (42)	0.01 (35)	0.02 (32)	-0.09 (32)

Table 3.1 shows mean molt timing of the experimental groups for the parental and F1 generation. The values are residuals of the calendar effect and cohort regression. They indicate the mean (median) deviation of the breeding group from controls after accounting for differences between years and different hatching dates. The early and late molting parent groups were rather symmetrically distributed around the breeding stock median which, in turn, was close to zero. The differences between groups increased over molt but were low for molt duration. Among the F1-generation, young from early-molting parents deviated more strongly from controls than those of late-molting parents.

From the median values given in Table 3.1, I calculated realized h^2 separately for the early and late molting groups (Table 3.2). Values are given for all molt measures that showed significant differences between the parental breeding groups, indicating a selection differential that was significantly different from zero. Realized h^2 was not calculated for molt duration because there was no indication of a significant selection differential.

Table 3.2

Molt timing response of the F1 generation to selective breeding, selection differential of the parent generation, and estimated realized heritabilities in the assortatively mated early and late molting groups. Values are derived from Table 3.1.

	onset		peak		completion	
	early	late	early	late	early	late
response R of F1	-0.55	0	-0.58	0.35	-0.51	0.24
selection differential S	-0.62	0.64	-0.83	-0.86	-1.35	0.72
of parent generation						
realized heritability	0.89	0	0.70	0.41	0.38	0.33

Effects of hatching date

Hatching dates were evenly distributed among the breeding groups in the parent and F1 generation (Kruskal-Wallis Anova, n.s.). Therefore, there was no seasonal bias due to hatching dates. To test for group differences in photoperiodic response, I regressed molt timing against hatching date for parents and offspring of the three breeding groups. The family medians which I used as variates in the regression were raw data and therefore not corrected for differences between cohorts. Yet, year-to-year differences had probably little bearing on the offspring data because the three F1 cohorts (1999-2001) did not differ significantly in molt timing. In contrast, differences between the parental cohorts were marked (see above and Fig. 3.1) and may have caused artefacts in the parental regressions.

Figures 3.2 to 3.5 show the grouped regression of molt for the offspring and the parental generations. Among the offspring generation median calendar regressions were significant for the three metrics of the timing of molt ($p < 0.001$) but not for its duration ($p = 0.96$). For molt timing, inclusion of selection group into the model increased the percentage of explained variance (r^2 for onset: from 82.5 to 87%; peak: from 72.4 to 78.5%; completion: 80.1 to 82%). At the beginning of molt, young of the fast molting group were distinguished from the controls both by an overall earlier molt (constant; $p = 0.029$) and by their less pronounced response to day length (slope; $p = 0.040$). The differences did not persist for molt peak and molt completion. Young from the late molting group did not differ from controls (constant; $p = 0.866$; slope; $p = 0.939$). Among the parent generation, there was greater spread among the data and hence none of the regressions were significant. The greater spread was at least in part related to the large differences between cohorts mentioned above (cf. Fig. 3.1).

Discussion

The first results from selection experiments confirm high heritabilities of molt timing as calculated from family comparisons (Chapter 2). In controls h^2 corresponded closely to earlier estimates for European Stonechats kept under natural day length. Helm and Gwinner (1999) calculated values for h^2 of 1.16 for molt peak and of 0.24 for molt completion. Values estimated in the present chapter were well within the range given by standard errors. The reproducibility of results fulfills one of the criteria for reliable estimation of h^2 suggested by Van Noordwijk (1990). For molt duration h^2 was close to zero. No comparative values have been estimated for European Stonechats but a lack of genetic control of molt duration under natural day length was shown for African Stonechats (Helm and Gwinner 1999) and tentatively for Irish Stonechats (Chapter 4). In contrast, for Siberian Stonechats family effects were strongest for molt duration (Chapter 2).

Young of parents selected for early and late molting changed their plumage at distinct ages and differed from each other in the direction predicted by the selection protocol. The timing of peak molt of the F1 generation differed significantly from controls. For the other measures of molt timing, group differences from controls were in the expected direction but not significantly so. The fact that the response to selective breeding was most pronounced for the peak of molt accords to the use of molt peak as the selection criterion. In view of the still small sample sizes and the resulting low power of statistical testing, these results are encouraging.

However, the magnitude of estimates for realized h^2 can only be considered preliminary (Table 3.2). In both, the early and late molting groups, h^2 was relatively high for peak molt but clearly lower than that estimated from full-sib correlations. The realized h^2 of molt completion corresponded more closely to full-sib estimates of controls and in the

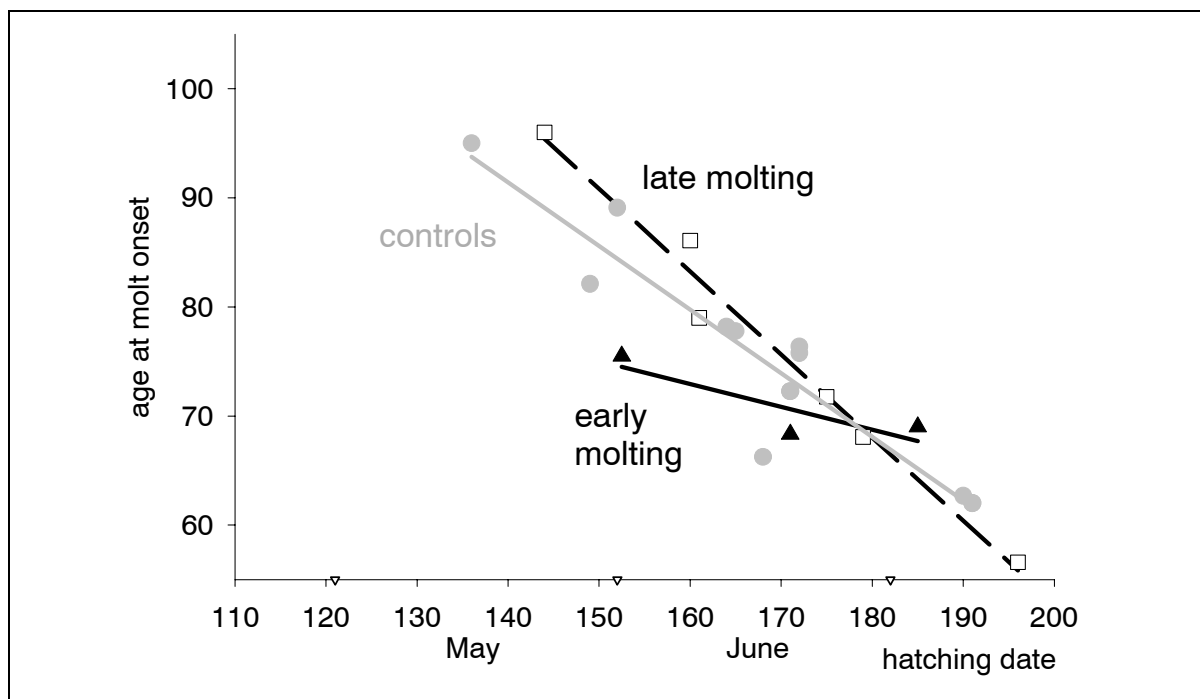


Figure 3.2A

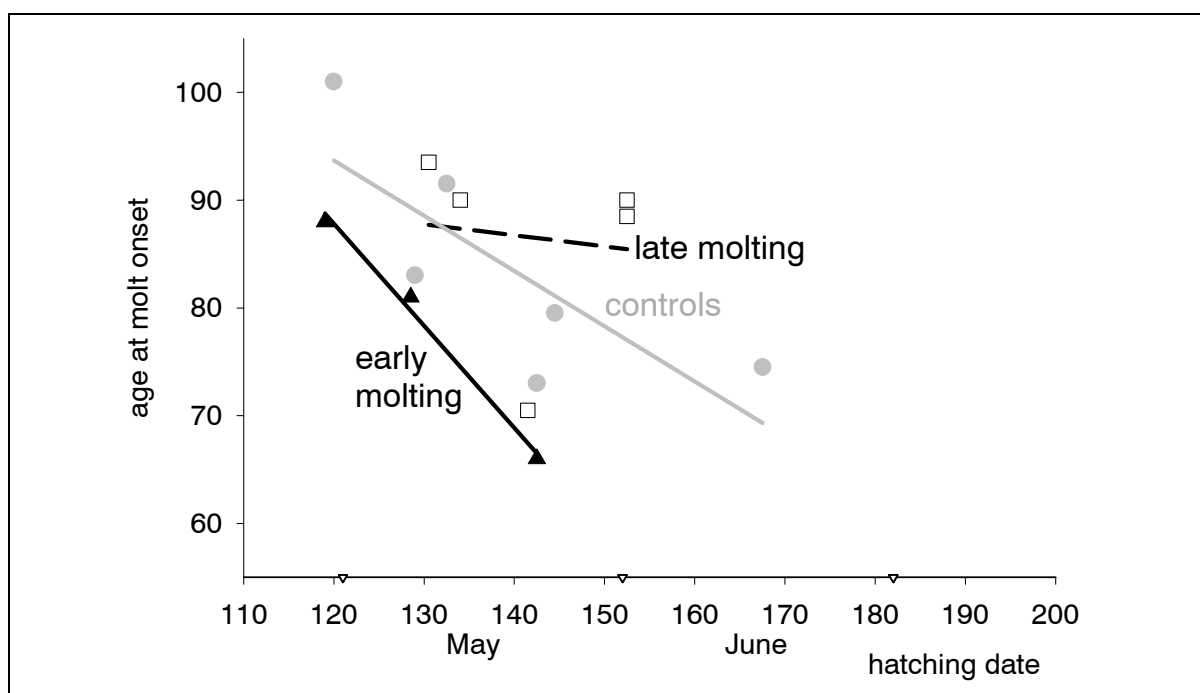


Figure 3.2B

Molt onset. Relationship between age at onset and hatching date in the breeding groups, plotted as in Fig. 1; different symbols indicate controls: gray solid lines and gray filled circles; early molting group: black solid lines and black filled triangles; late molting group: black dashed line and open squares. Regression lines indicate the best fit but no significance of the regression (see text). A. Offspring generation; controls are young from both kinds of control groups. B. Parent generation; controls are the entire remaining breeding stock.

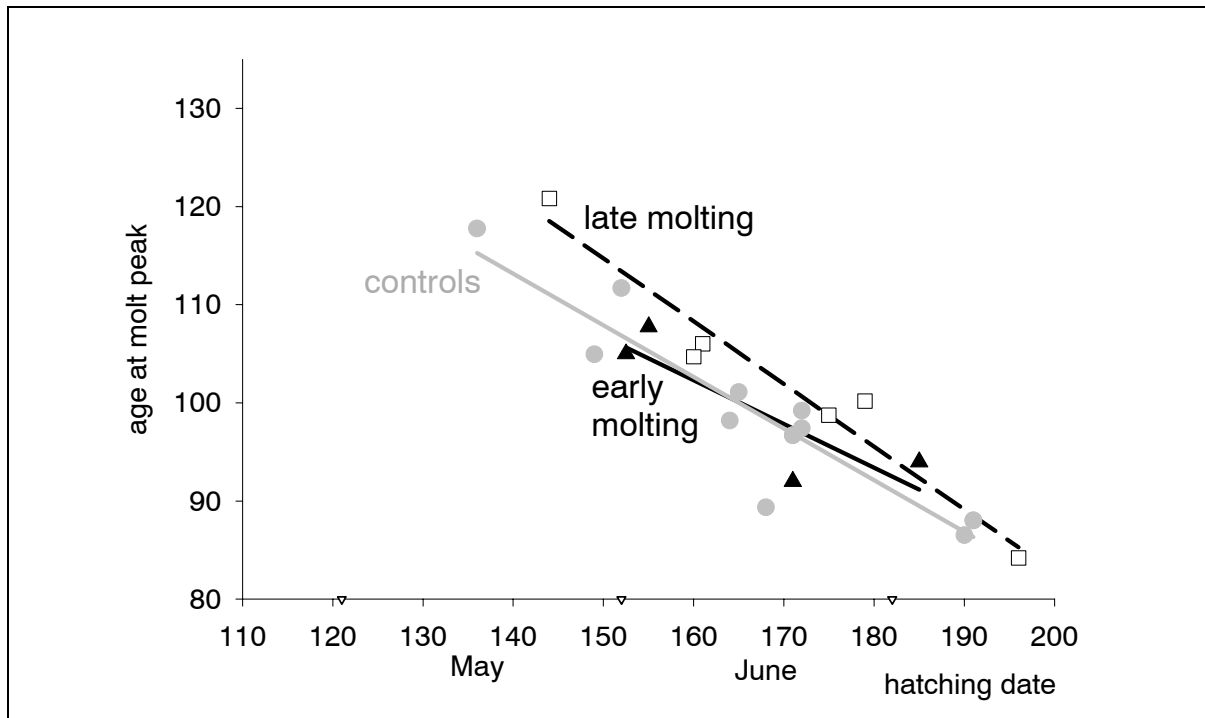


Figure 3.3A

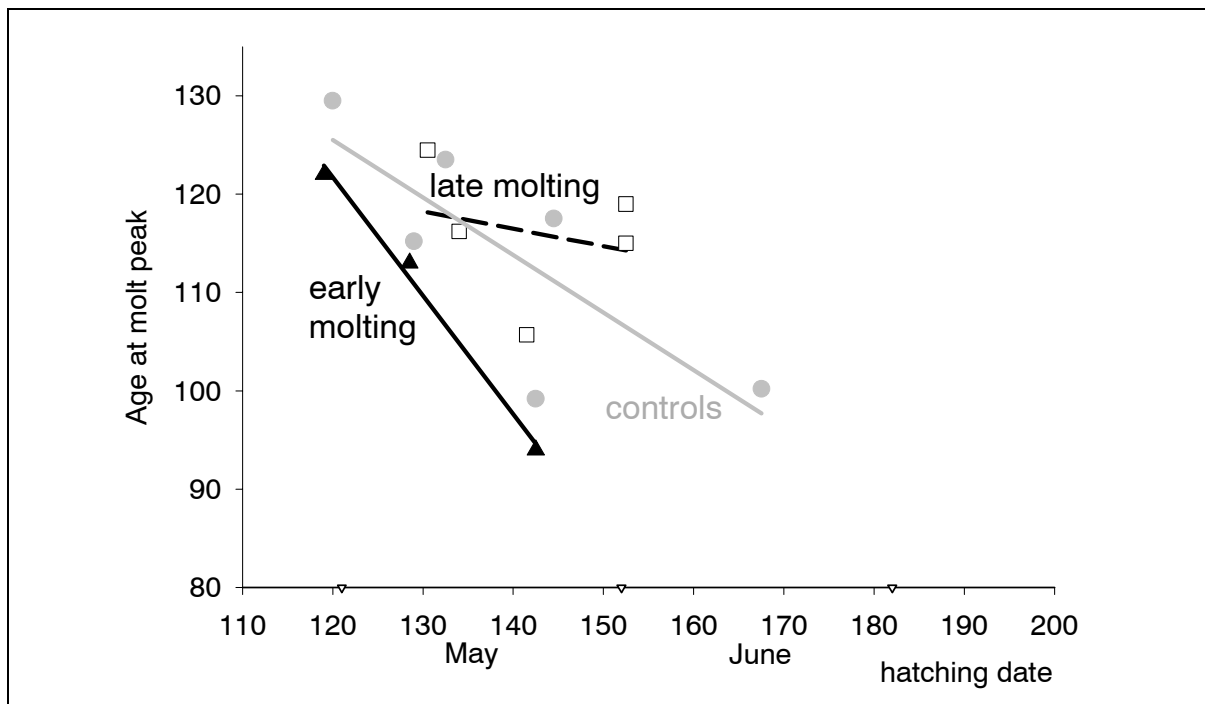


Figure 3.3B

Selection experiments: peak molt. Relationship between age at molt peak and hatching date in the breeding groups (see Fig. 2 for details); different symbols indicate controls: gray solid lines and gray filled circles; early molting group: black solid lines and black filled triangles; late molting group: black dashed line and open squares. A. Offspring generation. B. Parent generation.

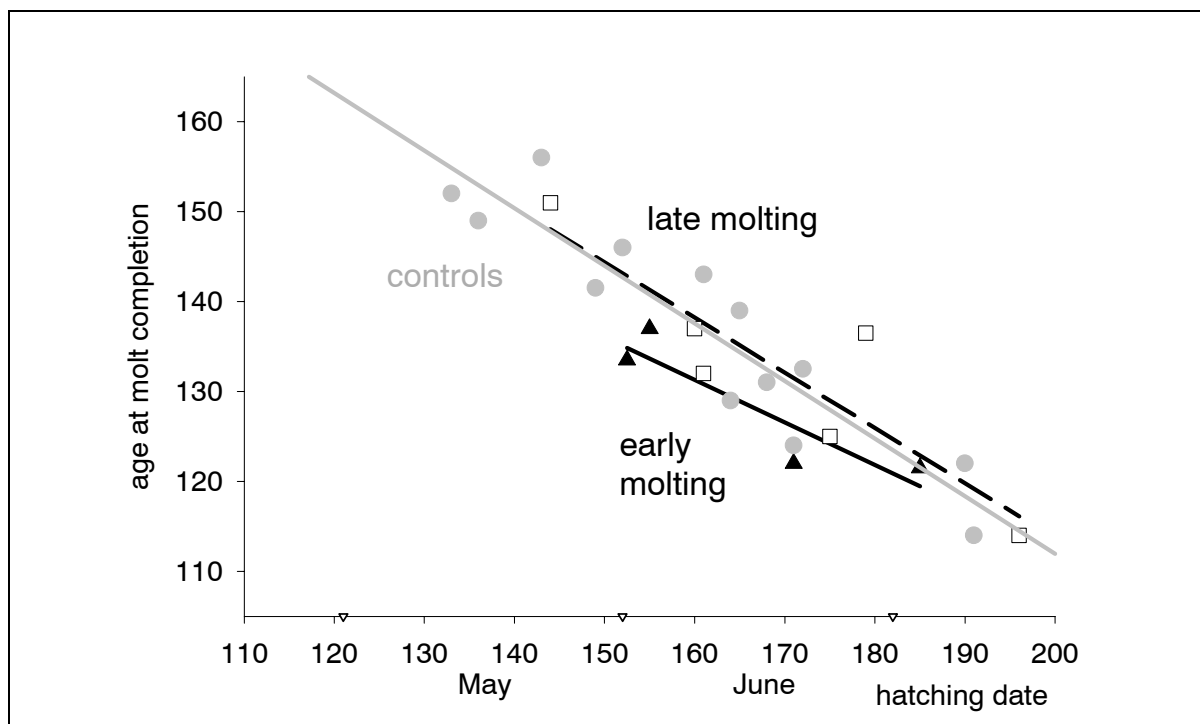


Figure 3.4A

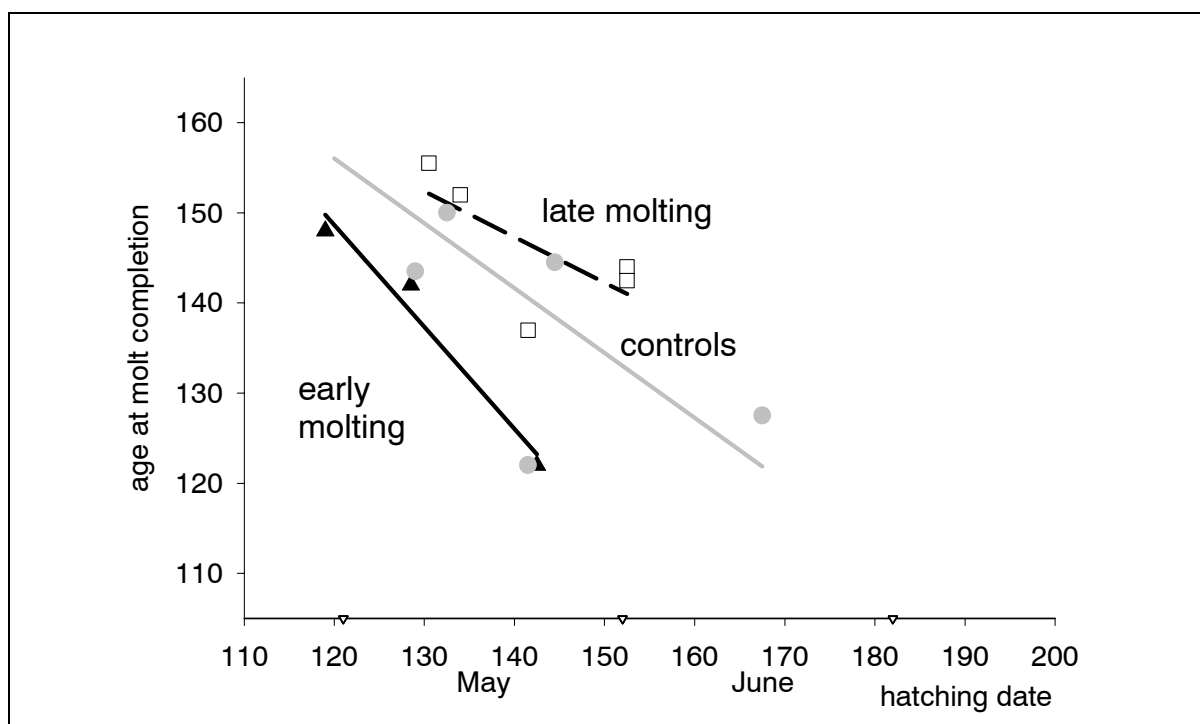


Figure 3.4B

Selection experiments: molt completion. Relationship between age at molt completion and hatching date in the breeding groups (see Fig. 2 for details); different symbols indicate controls: gray solid lines and gray filled circles; early molting group: black solid lines and black filled triangles; late molting group: black dashed line and open squares A. Offspring generation. B. Parent generation.

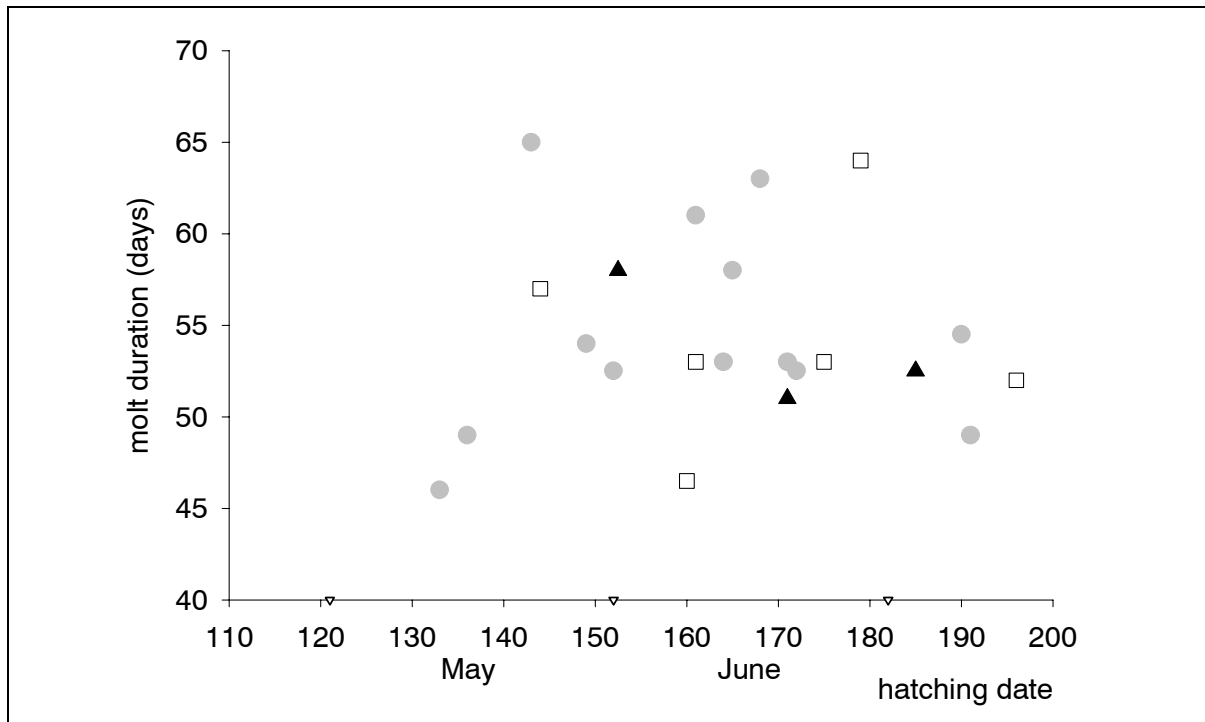


Figure 3.5A

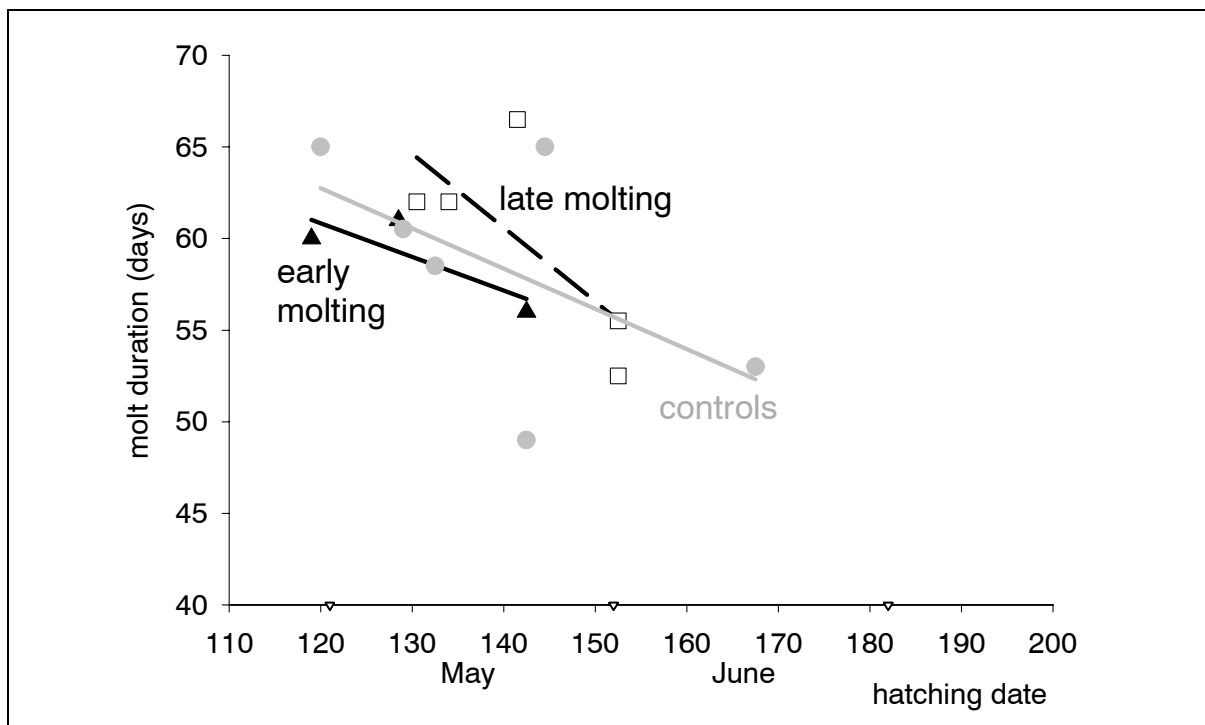


Figure 3.5B

Selection experiments: molt duration. Relationship between molt duration and hatching date in the three breeding groups (see Fig. 2 for details); different symbols indicate controls: gray solid lines and gray filled circles; early molting group: black solid lines and black filled triangles; late molting group: black dashed line and open squares. A. Offspring generation. B. Parent generation.

earlier study (Helm and Gwinner 1999). The consistent drop of h^2 after molt peak in both studies suggests that in European Stonechats, differences between families decrease over molt, possibly due to synchronization by the shortening photoperiod. This interpretation is suggested by the fact that under constant short day conditions, h^2 of molt timing remained high (Helm and Gwinner 1999).

For molt onset estimates of realized h^2 were equivocal: whereas the F1 generation of the early molting group appeared to respond strongly to selection, no response was detected in young of the late molting group. These differences may be spurious in view of small sample sizes, especially for the early molting group (data from three broods of two families only). Alternatively, the response to selecting for early and late molt may be asymmetrical (Roff 1997), as for instance in the selection experiments for migratory behavior in Blackcaps (Berthold 1998). The differential response to selection was related to differences in photoperiodic response of the breeding groups: for molt onset, young of early molting parents showed a significantly weaker calendar effect than those of control and late molting parents (Fig. 3.2A).

The difference in calendar effect indicates a possible mechanism of selective changes in molt timing. Figure 3.6 relates the calendar effect to changes in day length during the corresponding time of year. Early in the season daily changes in day length are most pronounced (Fig. 3.6B). The magnitude of group differences in the timing of molt onset (Fig. 3.6A) roughly corresponds with that of day length changes during the corresponding time of year (Fig. 3.6B). Group differences in photoperiodic responses were most marked in young birds that hatched early in the season when day length changes were pronounced. Offspring that hatched when day length levelled off around midsummer initiated molt at similar ages in all groups. Young European Stonechats may therefore differ in the magnitude of their response of molt initiation to changing day length, and it may be the magnitude of the response that is heritable. By selection for molt timing, birds hence may have been bred for the reaction norm of molt initiation to day length differences, i.e., their family-specific "calendar effect".

Objections against this interpretation may be based on the lack of group differences in reaction norms for timing of molt peak and completion. However, there is ample indication that in European Stonechats, molt timing is most sensitive to photoperiod during molt onset (Helm and Gwinner 1999). The variance components of molt timing were highest for photoperiod during molt initiation (explaining 60.2% of the variance; variance components dropped to 43.5% for molt peak, and to 36.2 for molt completion; Helm 1997). Molt in European Stonechats may be timed by early photoperiodic sensitivity shortly after hatching. Calendar effects persisted in young European Stonechats under constant conditions if they had experienced natural day length early in life (Helm 1997). Comparisons with molt timing in other Stonechat subspecies have also highlighted the

particular photoperiodic sensitivity of molt onset in European Stonechats and related it to their hatching times over a long breeding season (Chapter 2; Gwinner and Helm 2002). Because changes in day length are most pronounced early in the season (Fig. 3.6B) photoperiodic cues may be most informative for European Stonechats soon after hatching and exert their strongest influence on a timely initiation of molt.

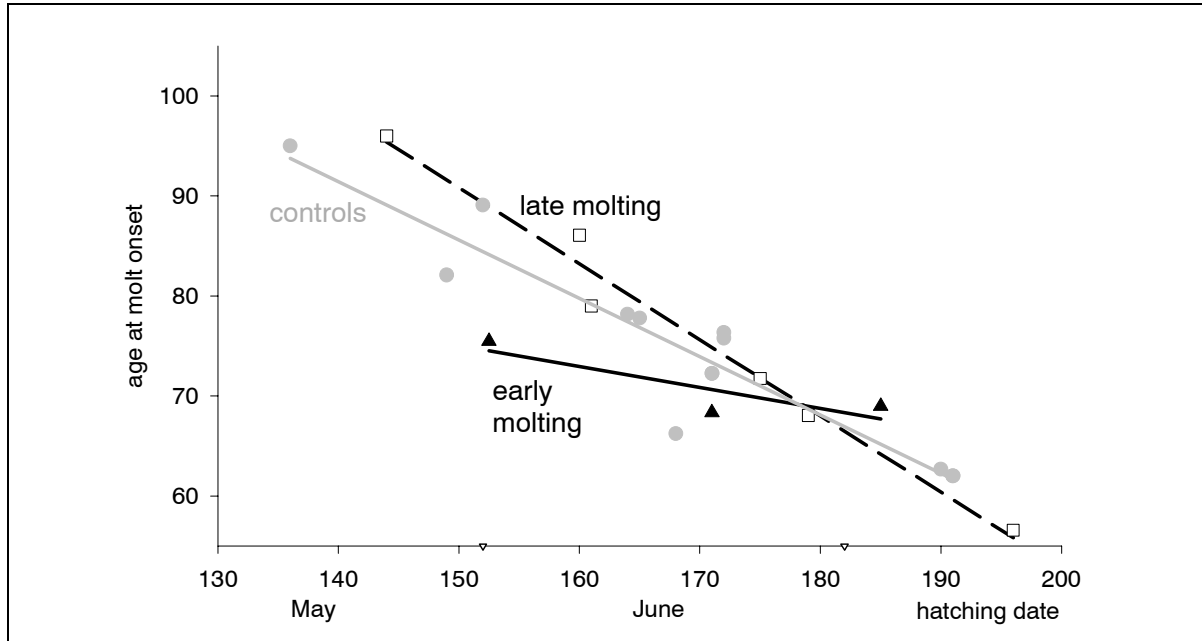


Figure 3.6A

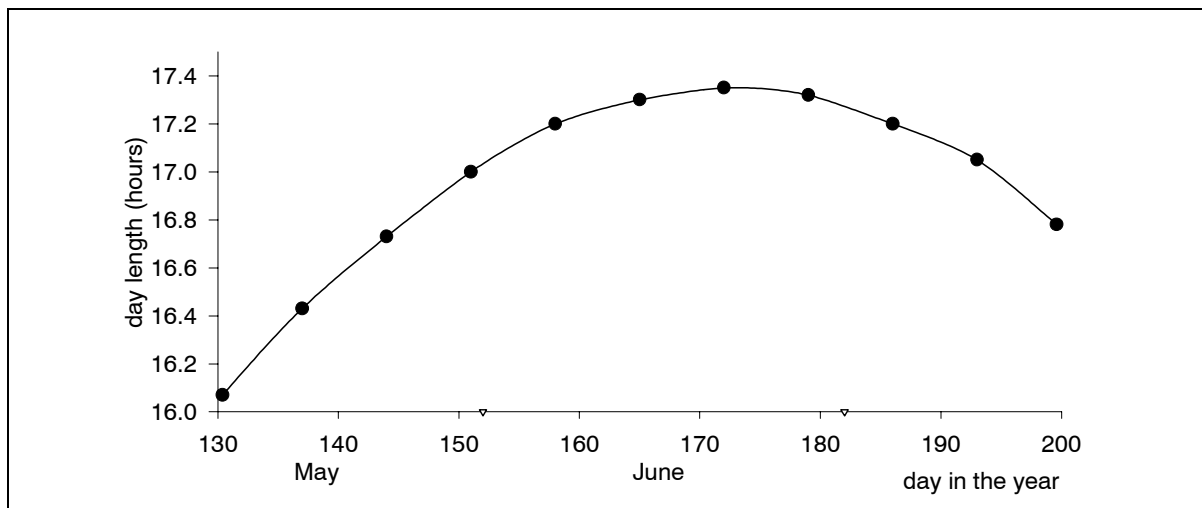


Figure 3.6B

Offspring generation: molt onset in relation to hatching date and seasonal changes in day length. A. Timing of molt onset as in Fig. 2.A; different symbols indicate controls: gray solid lines and gray filled circles; early molting group: black solid lines and black filled triangles; late molting group: black dashed line and open squares. B. Changes in day length (hours and decimal minutes) over the corresponding time period (see General methods).

Chapter 4

A new type of migrant? Migratory restlessness and postjuvenile molt in Stonechats from the British Isles (*S.t. hibernans*)

Summary

Migration and molt are taken to impose competing demands on birds, and overlaps between both activities are frequently avoided. Here, I investigated migratory restlessness and related its timing to that of postjuvenile molt. The study was carried out on Irish Stonechats because of their partially migrant behavior. If time-constraints on molt depended on the onset of migration, molt timing should be more relaxed for the resident fraction of partially migrant populations. Therefore, I expected to find heterogeneity in Zugunruhe and corresponding differences in molt timing among Irish Stonechats. However, all birds displayed clear Zugunruhe patterns that closely resembled those found in obligatory short-distance migrant Central European Stonechats. This unexpected result is in contrast to studies on other captive partially migrant passerines where the migrant and resident fractions were clearly distinct. The consistent expression of Zugunruhe suggests that Irish Stonechats are genotypical migrants, and that actual migration is triggered or suppressed by additional factors. The unusual behavior of Irish Stonechats implies a more differentiated approach to the regulation of partial migration if the results are corroborated and alternative explanations can be excluded.

In migrant Irish Stonechats the timing of Zugunruhe was strongly influenced by hatching date. The onset of migratory restlessness correlated significantly with molt timing. Although many birds showed low amounts of nocturnal activity even before molt, coinciding with the time of juvenile dispersal, restlessness rose sharply after molt peak but before the plumage was completely renewed. I introduced a new technique for analyzing activity patterns that is based on time-series methods. It determines the onset and termination of core Zugunruhe by employment of a simple algorithm. The method reduced the risk of an observer-dependent bias in determining Zugunruhe timing, especially in birds with noisy patterns of nocturnal restlessness. The timing of Zugunruhe thus determined was in good accordance with field observations and with results from ringing recovery analyses.

Introduction

Precise timing of postjuvenile molt in migrant passerines presumably enables young to finish molt before they leave their breeding grounds. This hypothesis rests on the assumptions that departure time is inflexible and that overlapping migration and molt is avoided (Jenni and Winkler 1994; Swaddle and Witter 1997; Hedenström 1999). An

examination of the relationship between molt and migratory timing in captive birds can help test these assumptions. Although late hatched birds molt at younger ages or shorten molt they compensate only partly for their seasonal tardiness (Jenni and Winkler 1994; cf. Chapters 2 and 3; Helm and Gwinner 2003). Migrants have several choices to solve the remaining time conflict between molt and migration. One choice is an overlap between migration and molt, which has been shown to occur in some birds, among them Stonechats (Jenni and Winkler 1994; Flinks 1999). An alternative solution is a delay of outward migration. The two alternatives lead to different predictions for the time relationship between molt and migration in captive birds. If they solve the time conflict by overlapping molt and migration, the overlap should increase with increasing time pressure (i.e., later hatching date). The correlation between molt completion and initiation of migratory activity should then be low. Conversely, if birds solve the time conflict by delaying migration I expect a close correlation between the two activities and no time effects on the overlap between molt and migration. The coupling of molt and migration has so far been shown for populations but not in individual birds (e.g., Hall and Fransson 2001; Pulido and Coppack, pers. comm.). One purpose of the present chapter is hence to closely investigate the relationship between the two successive life-cycle stages.

A corollary of the hypothesis that postjuvenile molt is timed precisely to prepare for migration is that in birds that do not migrate molt may be timed differently and perhaps less rigidly. It still remains to be seen if time-constrained migrants differ from residents in the timing of molt (Snow 1969). This question can be best addressed in a partially migrant population. In contrast to the obligatory migrant Stonechat populations studied in Chapters 2 and 3, the British Stonechat is a partial migrant. From ringing recoveries it is clear that those individuals of *S.t. hibernans* that do migrate can cover long distances of up to 2000 km (Van Hecke 1965b; Chapter 5). Therefore, one should expect the migrant fraction of the population to avoid overlaps between molt and migration and to time seasonal activities more rigidly than the resident fraction. I therefore analyze nocturnal activity of young British Stonechats kept in laboratory registration cages and relate their timing of migratory restlessness (Zugunruhe) to that of molt.

The data on migratory restlessness in British Stonechats can also help address open questions about their migratory status (Chapter 5). Although there seems to be consensus that the subspecies is partially migrant, the relative proportion of migrants is still debated. In other partially migrant species such as the Robin (*Erithacus rubecula*, Biebach 1983), the Blackcap (*Sylvia atricapilla*, Pulido et al. 1996, 2001), and the European Blackbird (*Turdula merula*, Schwabl and Silverin 1990) migrants and residents showed distinct nocturnal restlessness patterns in captivity. Such migratory dimorphism (Lack 1943) has been interpreted to support the genetical hypothesis of bird migration, and high heritabilities for migratory propensity have indeed been reported (Biebach 1983, Pulido et al. 1996; 2001). I

estimate the proportion of migrants among captive British Stonechats and search for possible differences among families. Stonechats used in this study originate from a coastal Irish population reported as a wintering site by Lack (1986). In the vicinity Stonechats have been closely studied in the field from 1997 to 1999 (Cummins 2002). Since coastal habitats are preferred by Stonechats in winter (Lack 1986; Cummins 2002), I expected the nestlings from coastal habitats to show low migratory propensity. I compare patterns and timing of nocturnal restlessness of British Stonechats to those of obligatory migrant European Stonechats.

Furthermore, differential patterns have been proposed for migrant bird populations, and for Stonechats in particular (Chapter 5). Here I test for endogenous components of differential migration by comparing migratory restlessness of the sexes and among the first and the second fall migration of individuals recorded over two years.

A key assumption in analyses of Zugunruhe is that it can be properly related to the patterns of migration in freeliving conspecifics (Berthold et al. 1972; Berthold 1973). The relationship between nocturnal restlessness of caged birds and actual migration is not always straightforward (e.g., Gwinner and Schwabl-Benzinger 1982). The identification of Zugunruhe can be difficult because captive birds may show bouts of nightly activity for various reasons (Berthold 1988b). Therefore, a methodological concern is an identification of relevant Zugunruhe that reduces the possible bias introduced by the observer's judgment. An additional intent of the present chapter is the development of a simple algorithm that makes use of a large amount of information to identify the times of onset and completion of Zugunruhe corresponding to the timing of migration in freeliving conspecifics.

Material and methods

Birds and methods

35 Stonechats from seven nests were collected as nestlings in Ireland in May of 1999 (hatched between 11 and 20 of May; median: May 16; see General methods), 23 of which were kept under natural day length conditions. Two birds died before molt and migratory restlessness began. Four Irish Stonechats that hatched in captivity in 2000 as offspring of these birds were also analyzed. For two young hatched in 2001 only data on molt were available. Because aviary offspring hatched at different times and under different circumstances (hatching dates between May 9 and June 14), I left their data out of analyses of family effects.

All birds studied in the current chapter were kept under simulated natural day length. Postjuvenile body molt was assessed as described in the General methods section. The analysis of nocturnal activity data with time-series methods is detailed below. The derived data on molt and Zugunruhe timing were normally distributed (KS-test, p in all

cases >0.25). I analyzed them using REML analyses, paired t-tests, and correlation and regression methods. Family effects were analyzed as described in the General method section. In all analyses of family effects, hatching data were included as a covariate to avoid inflation of inter-family differences by calendar effects.

For comparison, I show Zugunruhe data from European Stonechats that hatched between April 24 and July 17 of 1999 and 2000. The data are means of nocturnal restlessness of 34 first year birds, among them 20 males and 14 females.

Analysis of nocturnal restlessness

Zugunruhe data were collected with infrared sensors as described in the General methods section. I analyzed the nightly number of ten-minute intervals with migratory activity during the first fall and spring migration of young Stonechats. In addition, for some birds data of their second fall migration were available. The patterns of nocturnal restlessness were too unsteady for a straightforward identification of migratory onset and completion. To derive estimates of migratory timing that were consistent among birds and independent of the eye of the investigator, I employed filtering techniques derived from time series analyses (Diggle 1990; W. Zucchini, pers. comm.).

Because time-series methods necessitate complete series of data, a first step of analysis consisted in scrutinizing the data and interpolating missing values. Nocturnal restlessness recording started between August 8 and 22. To allow for a homogenous sample I only used restlessness data beginning August 20. The fact that registration of one bird started two days later necessitated the interpolation of two data points as the mean of the three subsequent days. In some cases, activity values of either one night or of two consecutive nights were missing. I replaced them by the mean of the two preceding and the two succeeding values (number of interpolated data points for all three migratory seasons: 20 single values and 18 double values).

For the determination of onset, completion, and duration of Zugunruhe the series of nightly measurements were first subdivided into time blocks that corresponded to the overall migratory season of the subspecies (see Chapter 5). Nocturnal activity from August 20 to December 31 was studied for timing of fall migration ("outward migration" from breeding; Berthold 2001). Data from January 1 to April 30 were scanned for the timing of spring migration ("return migration" to breeding grounds; Berthold 2001). In the leap year of 2000 data were studied until April 29 so that the same number of days was considered in all years.

Using the completed series of nocturnal restlessness, I first tested if nocturnal restlessness could be interpreted as Zugunruhe. To that purpose, I compared mean restlessness during migratory seasons to that before and after migration. Representative data segments were for fall migration: the last decades of August (pre-migratory), October

(migratory), and December (wintering), and for spring migration: the last decades of December (overwintering), February (migratory), and April (breeding grounds). Analyses were carried out with repeated measures REML over decade means of all birds.

Subsequently, to distinguish migrants from residents I tested for the presence of significant Zugunruhe for each individual bird. I determined by autocorrelation analyses whether changes in nocturnal restlessness differed from white noise (Box-Ljung testing; series length between 130 and 135 values). All birds with significant changes of restlessness were considered migrants.

During spring migration, one bird showed insufficient levels of restlessness to determine migration onset and was left out of the analysis. Another bird died after February 28 but it had clearly initiated spring Zugunruhe at that time. Spring restlessness was different from fall restlessness in that some birds continued to be active well beyond the date at which their wild conspecifics terminate migration. This is a common phenomenon for caged birds and has been termed "summer restlessness" (Gwinner and Czeschlik 1978; Berthold 1988b). Because of this difficulty, I determined only the onset of spring restlessness. For nine birds (five males, four females) nocturnal restlessness was registered for the second fall migration periods. Of these, two birds were well into nocturnal activity when the registration started. Because they may have displayed summer restlessness, their data on second fall Zugunruhe onset were omitted.

For all remaining birds, I extracted estimates for onset, completion, and duration of migratory restlessness. The search algorithm consisted of two steps. I first employed a smoothing filter and secondly an edge detector to identify migratory timing (Diggle 1990; W. Zucchini, pers. comm.). The series of nightly restlessness were smoothed over 15 days using a moving average filter. For each day t_0 , the restlessness data (x) of the preceding and the consecutive week were averaged. The daily values were multiplied by weights that decreased with distance from the mean day t_0 . Weights were simple numbers from 1 to 8, assigned using the following equation for the moving average (MA) on day t_0 :

$$\text{MA}(x(t_0)) = (1 \cdot x(t_{0-7}) + 2 \cdot x(t_{0-6}) + 3 \cdot x(t_{0-5}) + 4 \cdot x(t_{0-4}) + 5 \cdot x(t_{0-3}) + 6 \cdot x(t_{0-2}) + 7 \cdot x(t_{0-1}) + 8 \cdot x(t_0) + 7 \cdot x(t_{0+1}) + 6 \cdot x(t_{0+2}) + 5 \cdot x(t_{0+3}) + 4 \cdot x(t_{0+4}) + 3 \cdot x(t_{0+5}) + 2 \cdot x(t_{0+6}) + 1 \cdot x(t_{0+7})) / 64.$$

The smoothed series was scanned to locate the timing of the most pronounced increase ("onset") and decrease ("completion") of nocturnal restlessness by an edge detector filter (ED) over 21 values (10 preceding and consecutive nights, respectively). For each value, the 10 preceding and the 10 consecutive values were added with reversed signs according to the equation:

$$\text{ED}(x(t_0)) = -\text{SUM}(x(t_{0-10}) \dots x(t_{0-1})) + \text{SUM}(x(t_{0+1}) \dots x(t_{0+10})).$$

The resulting series for the edge detector had a clearly defined maximum indicating the time of strongest increase in migratory restlessness ("onset") and a minimum indicating the time of strongest decrease ("completion"). Duration of Zugunruhe was calculated by

subtracting the date of onset from the date of end of nocturnal restlessness. The data used for further statistical analysis are the Julian dates onto which onset and completion fell. As an augmentary condition I required date of onset to precede the date of completion. This was necessary to avoid confusion due to the transition between fall and spring migration. Date of onset had to fall into the first half of the data space (earlier than date 299 = October 26 in fall, and day 60 = February 29 or March 1 in spring).

Due to the filtering, the theoretical time window into which the dates for onset and end of migratory activity could fall ranged from September 6 and December 14 in the fall and January 6 to April 13 in the spring. The methodology focuses on the timing of core migration. Because the edge detector determines the timing of the greatest increase and decrease of nocturnal activity smaller bouts of nocturnal restlessness that may precede or follow the core part of activity are likely to be cut off.

Results

Postjuvenile molt

Young Irish Stonechats initiated their postjuvenile molt at a median age of 81 days and spent on average 64 days molting (Table 4.1; Fig. 4.1). Variation coefficients were lower for molt onset, peak and completion (CV=8.34; CV=6.24 and 7.86, respectively) than for molt duration (CV=14.16). All three measures of molt timing were significantly correlated

Table 4.1

Summary statistics for postjuvenile molt and migratory restlessness in Irish Stonechats. The statistics specify sample size, mean, standard deviation, and extreme values. For molt and Zugunruhe timing, means refer to Julian dates whereas for duration, means indicate the number of days taken. In addition, median ages and interquartile ranges are included for comparison with the data in Chapter 2 and are specified for the timing of postjuvenile molt and first fall migratory activity.

	n	mean date	mean Julian / days \pm <i>std</i>	minimum- maximum	Median age \pm <i>IR</i>
molt onset	26	Aug. 9	221.2 \pm 9.18	205 – 243	81 \pm 9
molt peak	27	Sept. 9	251.7 \pm 7.51	238.5 – 269.5	113 \pm 11
molt completion	27	Oct. 11	284.0 \pm 7.24	273 – 300	147 \pm 13
molt duration	27		62.8 \pm 8.90	45 – 80	64 \pm 11
onset 1. fall migr.	25	Sept. 30	272.6 \pm 10.79	249 – 294	134 \pm 16
end 1. fall migr.	25	Oct. 24	297.2 \pm 7.16	285 – 321	160 \pm 9
duration 1. fall migr.	25		24.6 \pm 9.78	15 – 49	
onset 1. spring migr.	24	Jan. 31	31.2 \pm 8.70	15 – 58	
onset 2. fall migr.	7	Sept. 29	272.5 \pm 9.64	258 – 289	
end 2. fall migr.	9	Oct. 19	291.6 \pm 13.91	262 – 306	
duration 2. fall migr.	7		23.8 \pm 8.87	12 – 35	

with each other (onset and peak; $r = 0.74$; $n = 26$; $p = 0.000$; onset and end; $r = 0.63$; $n = 26$; $p = 0.001$; peak and end; $r = 0.85$; $n = 27$; $p = 0.000$). Molt duration was significantly related to the peak ($r = 0.53$; $n = 26$; $p = 0.005$) and end of molt ($r = 0.81$; $n = 26$; $p = 0.000$). There was no correlation between molt onset and its duration ($r = 0.05$; $n = 26$; $p = 0.815$), indicating that a longer molt was related to a slow rate of molt, and not to its late beginning.

There were no effects of sex on molting age (REML; $p > 0.1$ for onset, peak and duration of molt; $p = 0.09$ for molt completion). The date of hatching exerted a significant influence on all molt timing parameters (Table 4.2). The later a bird hatched, the younger the age at which it molted, and the shorter it took for it. The calendar effect increased over the course of molt and had its strongest bearing on the age at molt completion, both in terms of the steepness of the slope and of the proportion of variance explained (r^2) by hatching date. Families molted at similar times when differences in hatching date were accounted for.

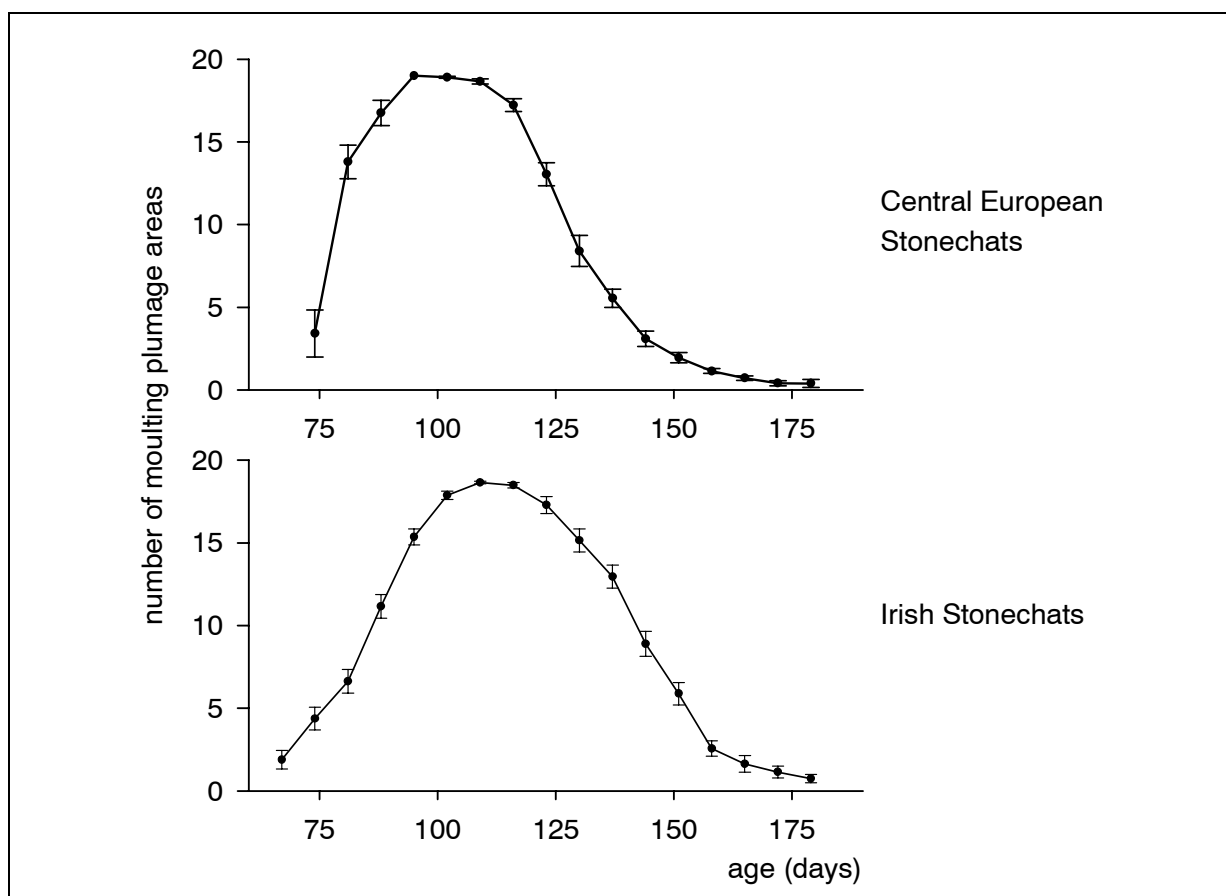


Figure 4.1

Postjuvenile molt in Irish and Central European Stonechats. The ordinate shows how many of the 19 plumage areas were in molt (mean ± SE). The abscissa gives the age of birds at that time.

There were no significant family differences in the dates on which birds molted (REML; at $df=5$; $p>0.3$ for all molt timing measures). The duration of molt showed some tendency of differences between families but they were not significant (Wald statistics= 10.24; at $df=5$; $p=0.069$).

Figure 4.1 compares molt timing in Irish Stonechats to that of European Stonechats. Both populations initiated molt at similar ages but European Stonechats renewed their plumage more quickly. Presently, the data are insufficient for a thorough statistical comparison between the subspecies because of confounding effects of hatching date.

Table 4.2

Calendar effect on molt timing in Irish Stonechats. The statistics are derived from linear regression and specify sample size, percentage of explained variance, slope \pm standard error, t, and the corresponding significance levels.

	n	r ²	slope \pm SE	t	p value
onset	26	15.9	-0.301 \pm 0.126	-2.40	0.025
peak	27	40.4	-0.461 \pm 0.107	-4.32	<0.001
completion	27	58.6	-0.889 \pm 0.144	-6.15	<0.001
duration	27	40.6	-0.591 \pm 0.139	-4.25	<0.001

Nocturnal restlessness in Irish Stonechats

Prevalence of Zugunruhe

Irish Stonechats showed pronounced patterns of nocturnal activity (Fig. 4.2). A comparison between three representative decades, one premigratory, one migratory, and one postmigratory, rendered highly significant changes in restlessness (repeated measures REML analysis of decade means; first fall (25 birds): Wald statistics = 174.91; $df = 2$; $p<0.001$; first spring (23 birds): Wald statistics = 49.94; $df= 2$; $p<0.001$; second fall (nine birds): Wald statistics = 6.90; $df = 2$; $p=0.032$). Nocturnal restlessness was significantly elevated during migratory seasons and can thus be interpreted as Zugunruhe.

For all individual birds, white noise could be excluded as underlying the seasonal changes in Zugunruhe. For all birds autocorrelation in the first fall and spring was highly significant (for one bird $p=0.048$; all other birds $p = 0.000$). In the second fall, white noise of Zugunruhe could be significantly excluded in eight of nine birds (Box-Ljung: $p < 0.001$). In one bird, the autocorrelation rho of Zugunruhe was too low to be significant ($\rho = 0.1$; $p=0.27$). However, this bird alternated between nights of high restlessness and nights with almost no activity. The partial autocorrelation for a time lag of two days in the bird was

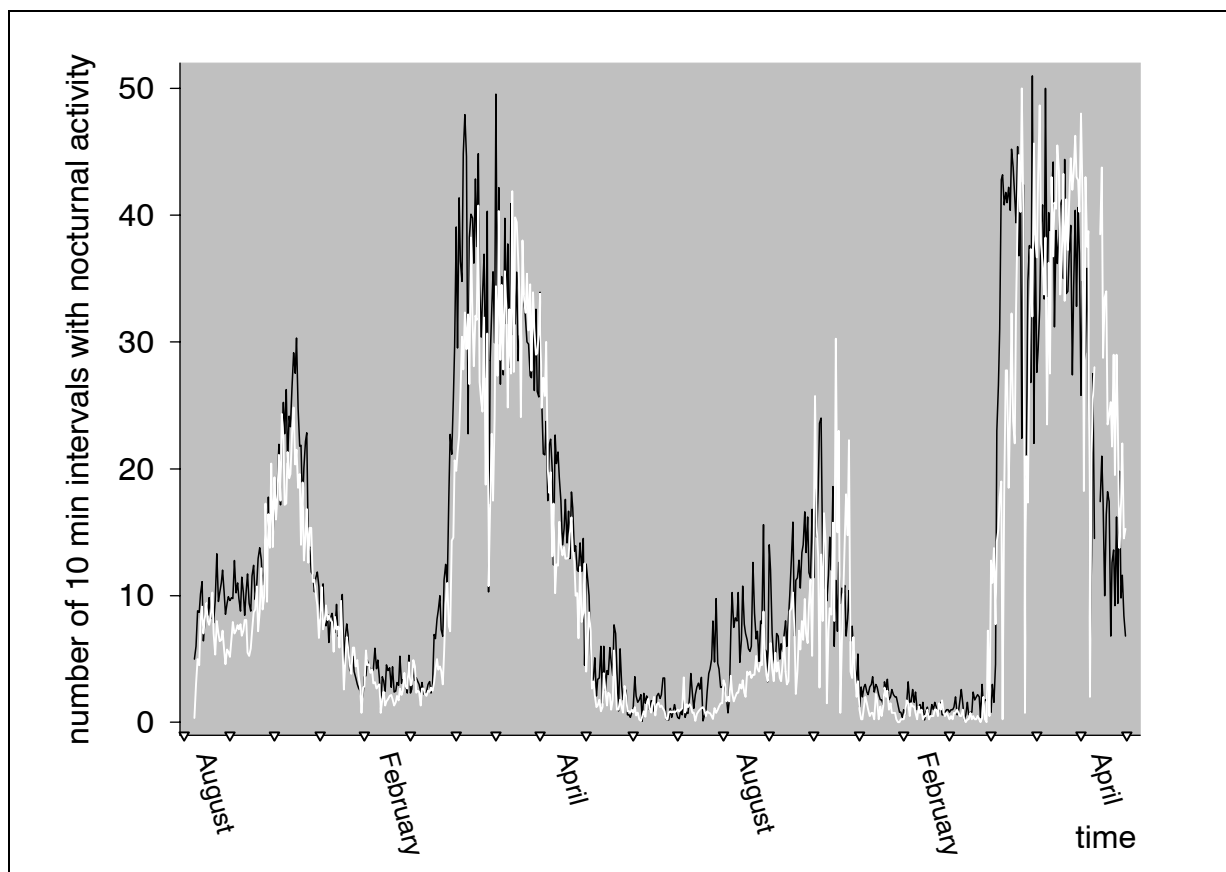


Figure 4.2

Zugunruhe in male and female Irish Stonechats over two years. The ordinate shows mean nocturnal restlessness of all simultaneously recorded birds, given as the number of 10-minute intervals with nightly activity; the abscissa gives the time in the year (starting on August 1, 1999); black line: *Zugunruhe* of males; white line: *Zugunruhe* of females.

very high (0.47) and greatly exceeded the confidence limits. When tested over the smoothed data, the *Zugunruhe* was highly significantly autocorrelated ($\rho = 0.99$; $p=0.000$). Thus, all birds were classified as migrants based on their *Zugunruhe* patterns.

Determination of Zugunruhe onset and completion using edge detectors

The patterns of nocturnal activity in Stonechats were nervous and often had no clear zero baseline. To avoid observer bias, I consistently applied edge detectors to determine *Zugunruhe* onset and end. The properties of the edge detector were such that it estimated onset and completion dates separately for each bird as the times of the strongest increase or decrease of its activity. In birds that expressed pronounced nocturnal activity and fairly low baseline levels, the edge detector estimates of onset and end of nocturnal restlessness coincided with straightforward methods such as applications of thresholds (e.g., Figs. 4.3A and 4.4A). However, for birds that only hesitantly developed migratory activity there is no straightforward definition of onset (e.g., Figs. 4.3B and 4.4B). The edge

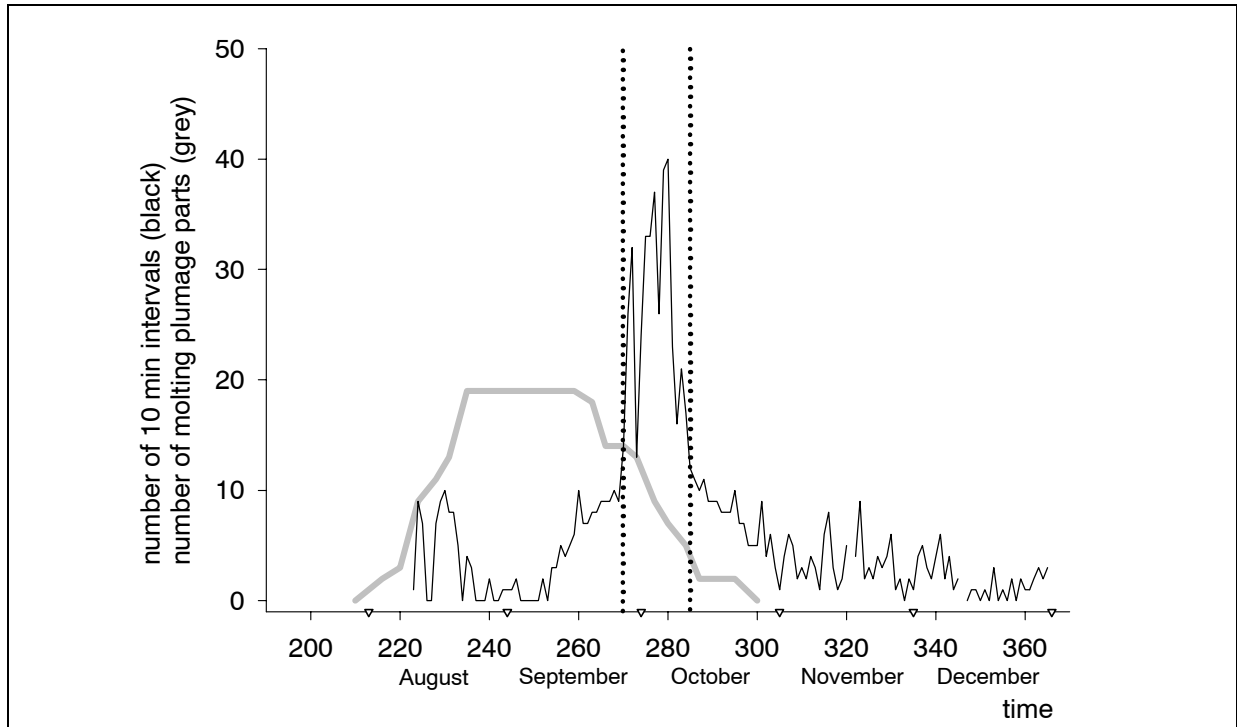


Figure 4.3A

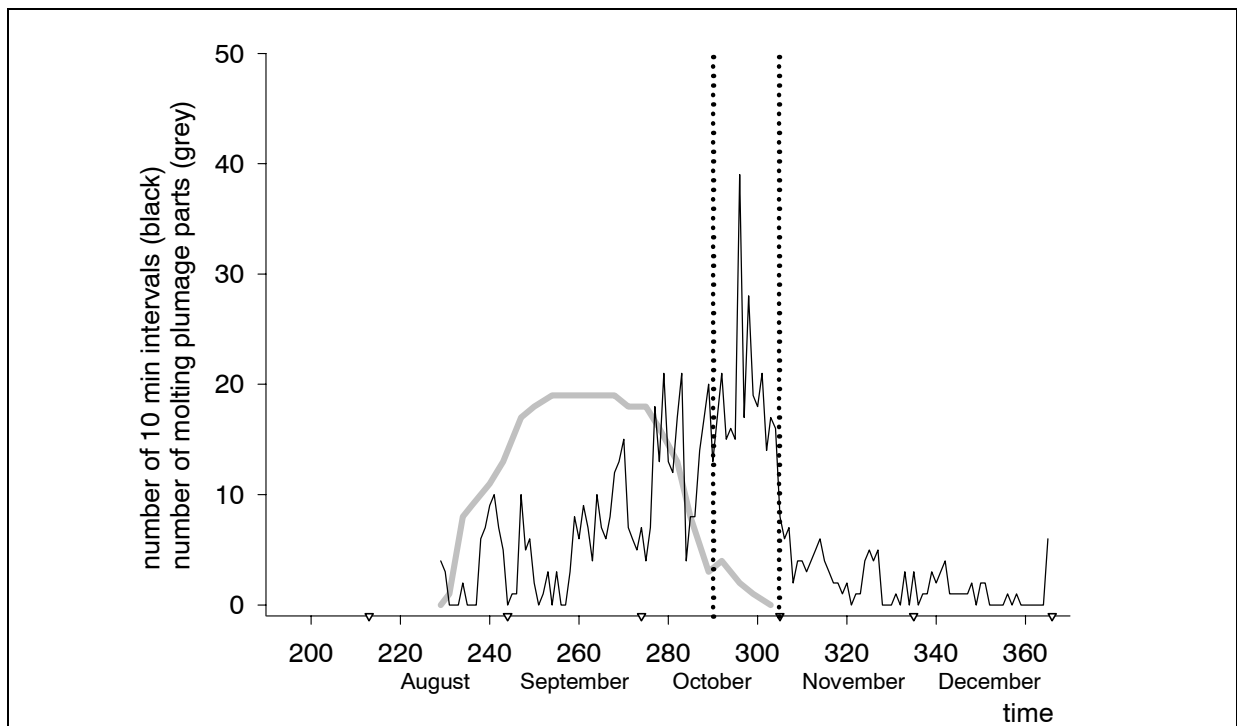


Figure 4.3B

Individual examples for the relationship between molt and Zugunruhe. Migratory restlessness of the first fall (black line) and postjuvenile molt (grey line) are plotted as in Figs. 4.1 and 4.2; dotted vertical lines indicate the dates of onset and completion of core migration as determined by the edge detector. A: a bird displaying a clearcut beginning of migratory activity; B: a bird with extremely unsteady nocturnal activity patterns.

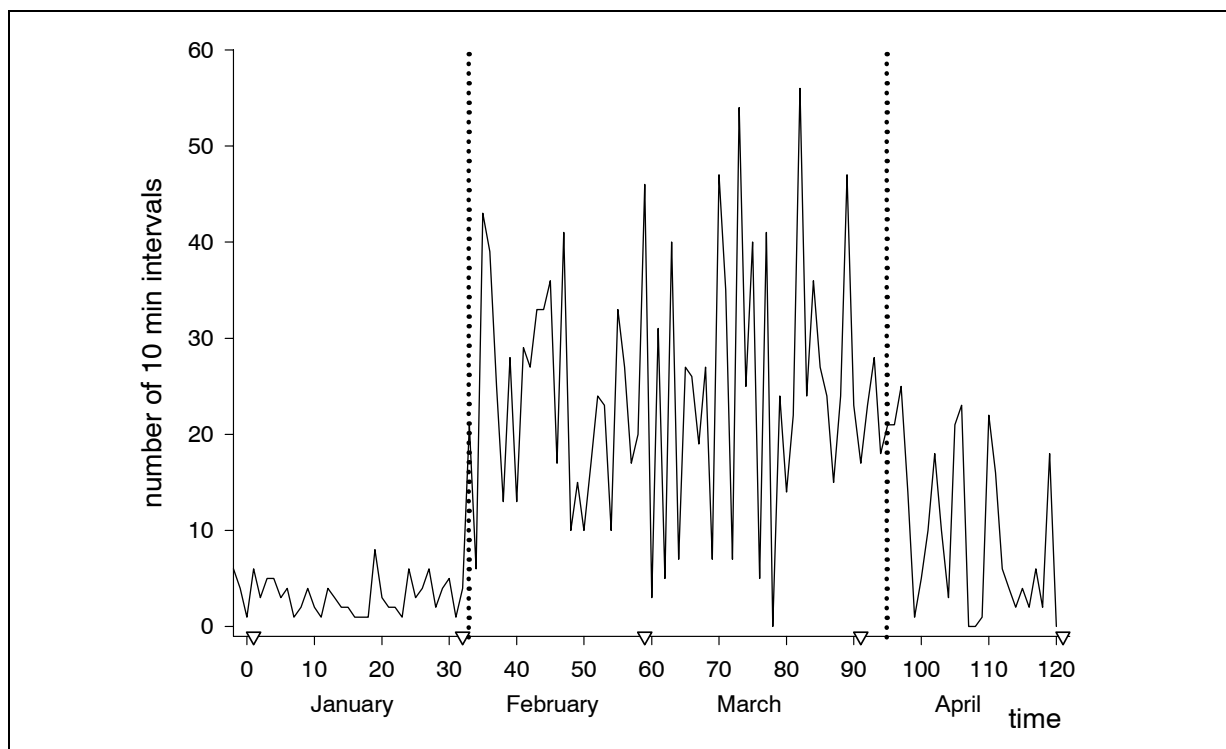


Figure 4.4A

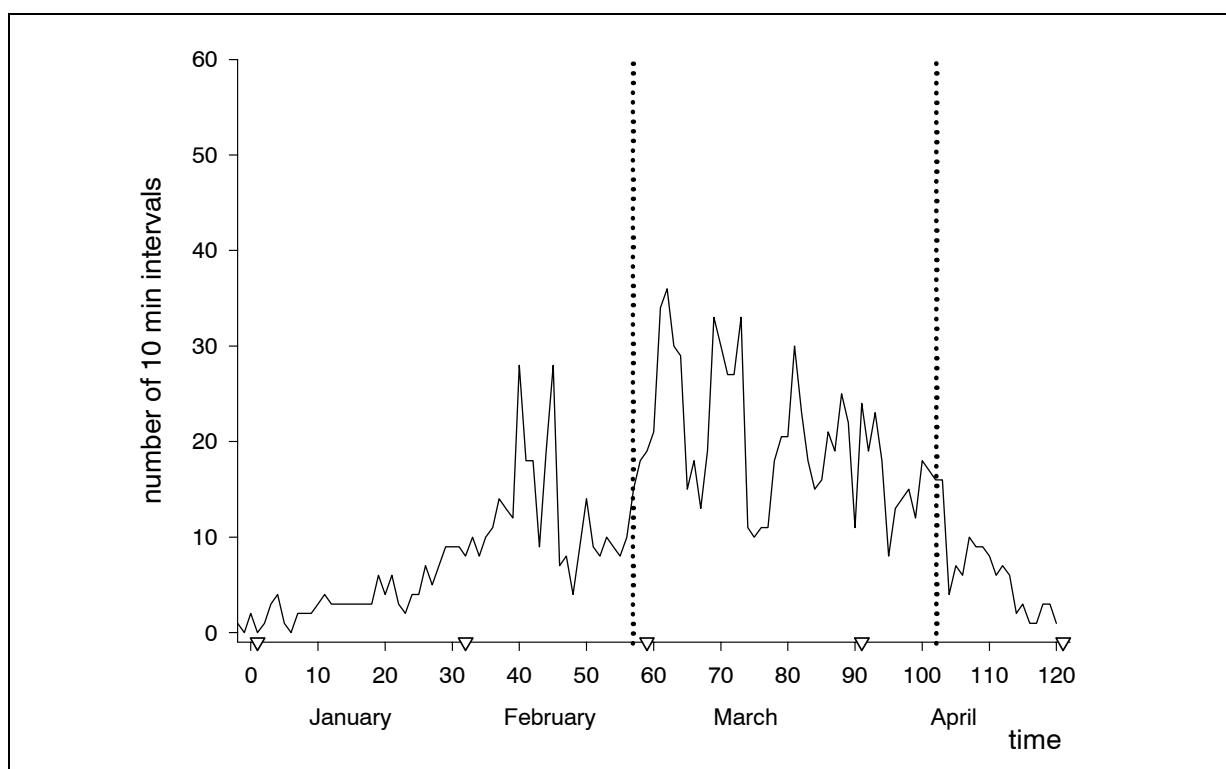


Figure 4.4B

Individual examples of spring Zugunruhe, plotted as in Fig. 4.3. A: a bird displaying a clearcut beginning of migratory activity; B: a bird with extremely unsteady nocturnal activity patterns.

detector estimated the onset of activity consistently. However, it selected the strongest and not the first activity increase as the onset of migratory restlessness. Therefore, compared to an observer the edge detector estimated hesitantly developing Zugunruhe as beginning relatively late. Hence, a bird's hesitancy to initiate migratory restlessness is confounded with Zugunruhe timing.

Timing of core migratory restlessness

Young Stonechats started to show some nocturnal restlessness in early August when the registration began (Fig. 4.2), at ages between 65 to 80 days. Typically, the first peak of restlessness dropped in late August. In most birds nocturnal activity was low from late August to late September coincident with most intense molt. A few birds maintained some amount of restlessness throughout molt (Fig. 4.3). All birds started core migratory activity after the peak of molt between mid September and mid October. The dates for onset and completion of core Zugunruhe estimated by the edge detector are shown in Table 4.1. Core fall Zugunruhe ceased between the second half of October and mid November. Variation coefficients for migratory timing were low for migration completion (CV=2.41) and for migratory onset (CV=3.96) but very high for the duration of migration (CV=39.74).

In the spring, restlessness was resumed by most birds in late January and early February. Typically, nightly activity rose sharply and was more intense than fall activity (Fig. 4.4). In many birds, restlessness ceased in late March and early April but in some it continued well into May. The nine birds for which migratory restlessness was also measured in the second fall migratory period showed similar activity patterns as in their first fall period. There was a small peak of activity in August, a slight depression in late August and September, and core migratory restlessness from late September to October. In the second autumn birds started migration at almost the same time as in the first fall (Table 4.1), finished it slightly earlier (mean first fall: 297.2; mean second fall: 291.6), but took approximately the same amount of time for it (mean first fall: 24.6; mean second fall: 23.8). Paired t-tests for migratory timing in these birds showed no significant differences between the years (for all measures $p > 0.3$).

Within birds, correlations indicated that some timing parameters were coupled. During the first fall, Stonechats that initiated migratory restlessness late also finished it late (correlation between onset and completion of Zugunruhe: $r = 0.66$; $n = 25$; $p = 0.025$). Nevertheless, a delayed onset of restlessness was partially compensated for by a negative correlation between migratory onset and duration. The later a bird started to migrate the less time it took for it ($r = -0.50$; $n = 25$; $p = 0.011$). These relationships were of similar magnitude during the second fall migration but due to the small sample size not significant (correlation between onset and completion: $r = 0.56$; $n = 7$; $p = 0.194$; onset and duration: $r = -0.51$; $n = 7$; $p = 0.241$). Between different migratory seasons, the durations of first and

Table 4.3

Calendar effect on Zugunruhe timing in Irish Stonechats. The statistics are the same as in Table 4.2.

	n	r²	Slope ± SE	t	p value
onset	24	26.4	-0.670 ± 0.216	-3.10	<0.005
completion	24	58.8	-0.881 ± 0.148	-5.94	<0.001

second year fall restlessness were weakly but non-significantly correlated ($r = 0.44$; $n = 7$; $p = 0.336$). In addition, those birds that had completed Zugunruhe late in their first fall finished it earlier in their second fall ($r = -0.79$; $n = 9$; $p = 0.011$). There was no correlation between times of spring and fall restlessness.

Calendar effects on the age of fall Zugunruhe onset and completion were pronounced (Table 4.3). Later hatched young started and finished migration at significantly younger ages than those hatched earlier in the season. In contrast, there were no effects of hatching date on the duration of fall Zugunruhe and on the initiation of spring restlessness ($p = 0.965$).

Family effects did not significantly influence the timing of Zugunruhe onset (Wald statistics=4.86; at $df=5$; $p=0.433$). The date of completion of migratory restlessness showed a tendency of family differences (Wald statistics=10.04; at $df=5$; $p=0.074$). Duration differed significantly among families (Wald statistics=12.72; at $df=5$; $p=0.026$). There was no indication of family effects on the interval between molt completion and initiation of Zugunruhe, i.e., the overlap between molt and migration (Wald statistics=2.22; at $df=5$; $p=0.818$). The initiation of spring migratory restlessness was also unaffected by family group (Wald statistics= 5.30; at $df=5$; $p=0.380$). There was no evidence of other factors influencing Zugunruhe timing. Among first year birds, there were no significant sex effects

Table 4.4

Comparison of Zugunruhe timing between the sexes. Results of two-sample t-tests for differences in migratory restlessness timing for the first fall and spring migration.

	onset 1. fall.		end 1. fall.		duration 1. fall.		onset 1. spring.	
	female	male	female	male	female	male	female	male
n	10	11	10	11	10	11	9	11
mean	269.6	270.8	296.8	296.3	27.20	25.45	34.33	29.27
t	-0.27		0.15		0.40		1.22	
p	0.788		0.882		0.694		0.240	

on migratory timing during the two first migratory periods (Table 4.4). Figure 4.2 shows means for the sexes separately. From the curves it looks as if males were active earlier in their second fall but the means of the second year are based on only nine Stonechats in total.

Temporal correlations between molt and migratory restlessness

Irish Stonechats overlapped migratory activity with the late stages of postjuvenile molt. Core Zugunruhe started after the peak of postjuvenile molt and before its completion. The time interval between onset of migratory restlessness and molt completion was unaffected by the time of hatching. Late hatched birds did not save time by overlapping molt and migration more than early hatched young (linear regression; $p=0.396$). The interval between molt and migration was significantly related to onset and duration of migratory restlessness: birds with a long interval (i.e., little overlap between the two activities) started core Zugunruhe later ($r = 0.81$; $n = 24$; $p=0.000$) and spend less time displaying Zugunruhe ($r = -0.58$; $n = 25$; $p=0.002$) than those that overlapped molt and migration more.

Onset of migratory restlessness was significantly correlated with molt beginning ($r = 0.50$; $n = 24$; $p=0.012$), molt peak ($r = 0.68$; $n = 25$; $p=0.000$) and molt completion ($r = 0.70$; $n = 25$; $p=0.000$). The later a bird molted the later it started its core migratory period. Onset of Zugunruhe was negatively correlated with molt duration: the longer the molt, the later Zugunruhe began ($r = -0.50$; $n = 25$; $p=0.011$). On average, core migratory restlessness began 21 days after molt peak and 11 days before molt completion (Table 4.1). Similarly, the age at completing migration was significantly correlated with the age at completing molt ($r = 0.77$; $n = 25$; $p=0.000$). The duration of fall migration was not related to the timing of molt.

Comparison with migratory restlessness of European Stonechats

Figure 4.5B shows the mean nocturnal activity of entirely migratory European Stonechats. The overall patterns of migratory restlessness between the two subspecies look very similar. Like the Irish, European Stonechats started their first fall Zugunruhe with a period of low nocturnal activity and a subsequent strong increase. In spring, nocturnal restlessness started rapidly and peaked more sharply than in the autumn. Closer inspection revealed that the migratory restlessness was timed differently between the subspecies. The activity of Irish Stonechats preceded that of European Stonechats (Figs. 4.5 and 4.6). While core migratory restlessness of the Irish occurred in mid October, European Stonechats showed the most restlessness in the first half of November. Similarly, spring migratory restlessness in the Irish started in late January, almost a month before that of European Stonechats.

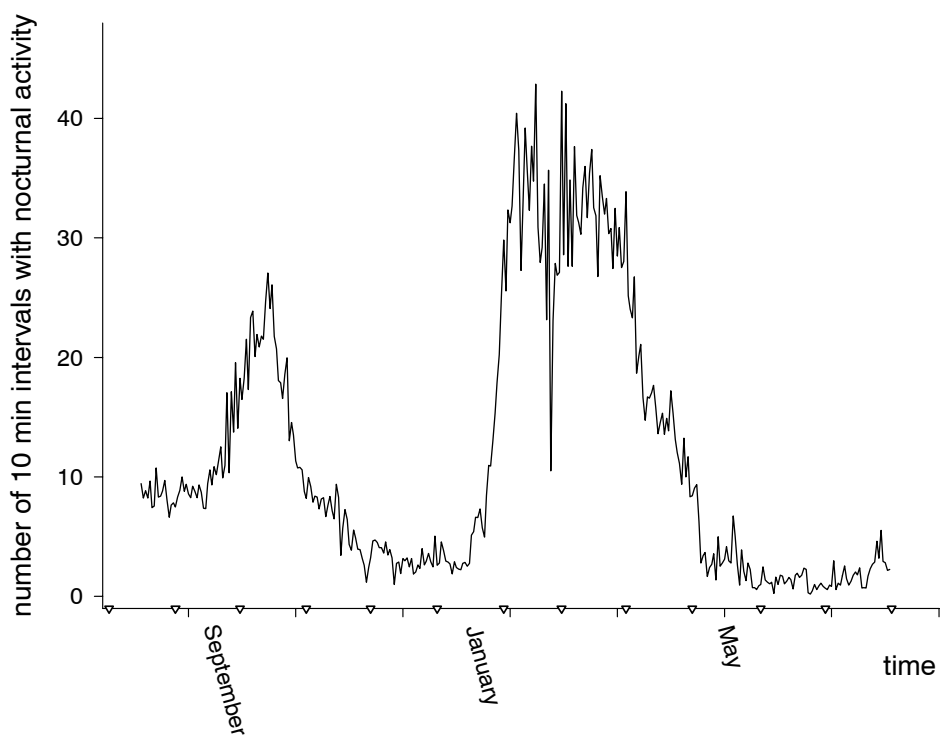


Figure 4.5A

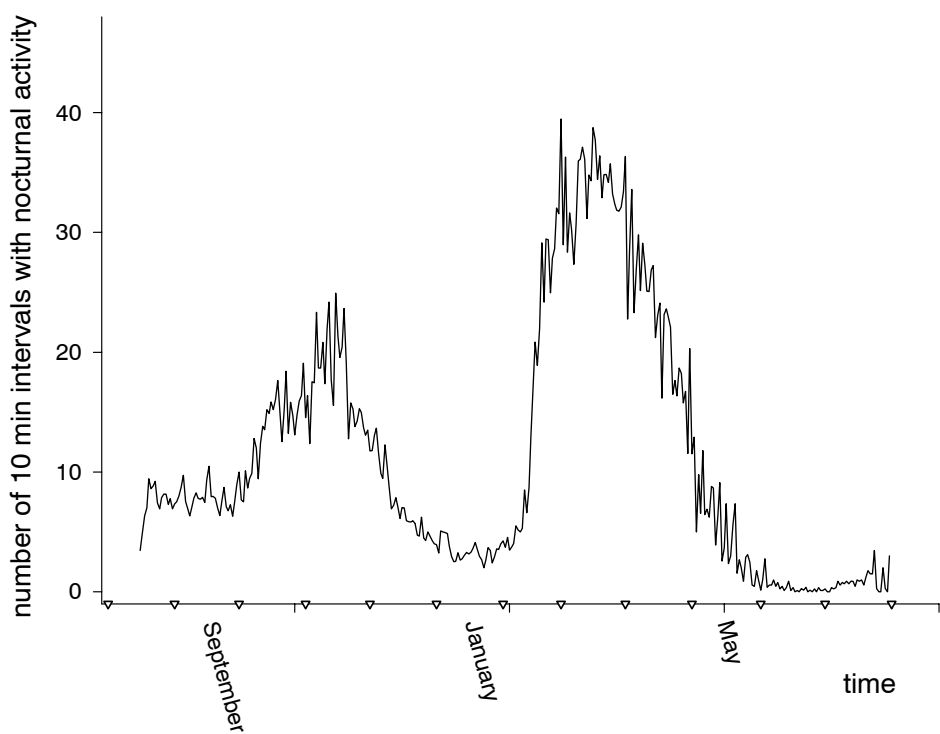


Figure 4.5B

Nocturnal restlessness of Irish and European Stonechats. Data are plotted over one year as in Fig. 4.2 but sexes are pooled. A: Irish Stonechats; B: European Stonechats.

Discussion

Timing of postjuvenile molt and migratory restlessness

Postjuvenile molt in most birds overlapped with low levels of nocturnal restlessness. Low-level postbreeding Zugunruhe will be discussed below. The birds avoided overlaps between intensive molt and core migratory activity. Zugunruhe rose sharply after peak molt and before its completion. The onset of Zugunruhe was closely correlated with molt timing. Under increasing time pressure, Irish Stonechats advanced and accelerated molt to compensate for late hatching but they did not increase the overlap between molt and Zugunruhe. The close coupling of both activities and lack of major overlaps between molt and Zugunruhe suggest that the timing of migration indeed depends on molt timing, and in particular on time of molt completion. The relationship between molt and migration in Stonechats supports the hypothesis that molt needs to be timed precisely to enable young to migrate in time, and that molt thus serves as a time buffer in the annual cycle (Noskov and Rymkevich 1999; Helm and Gwinner 2003). A similarly high correlation between molt completion and the beginning of migratory restlessness has so far only been observed in the Blackcap, *Sylvia atricapilla* (Pulido and Coppack, pers. comm.).

Differences between families in timing were not pronounced in Irish Stonechats. During both molt and fall Zugunruhe the timing of initiation was entirely unaffected by family patterns. For fall migration and to a questionable degree for molt, the duration differed slightly among families. There were no family differences in the interval between molt completion and Zugunruhe, in contrast to the situation in Blackcaps (Pulido and Coppack, pers. comm.). If these results are confirmed by more extensive studies, British Stonechats would differ from the other populations and from other passerines by the lack of family differences in timing (e.g., Larsson 1996; Widmer 1999; Brown and Brown 2000; Pulido et al. 2001; cf. Chapters 2 and 3). By implication, these birds might respond to changing time-environments by plasticity rather than by evolutionary change. Selection for different time strategies would be unlikely to result in fast evolutionary changes.

Further testing the relationship between molt and migratory timing by comparing resident and migrant Irish Stonechats was precluded by their uniformly migratory behavior. In comparison to obligatory migrant European Stonechats, young Irish Stonechats initiated their postjuvenile molt at similar ages (Fig. 4.1; Table 4.1). However, Irish Stonechats molted more slowly than European Stonechats (median ages in European Stonechats: onset 84; peak 101.5; completion 134; duration 48 days, respectively; cf. Chapters 2, 3). On average, they were 14 days older when they finished molt and took 16 days longer for it than European Stonechats. These differences may be partly due to the slightly later hatching date of European Stonechats (on average 11 days) that may have accelerated their molt. If a slower molt in Irish than European Stonechats stands the test of more data it would support the hypothesis of a more time-constrained molt in obligatory migrants.

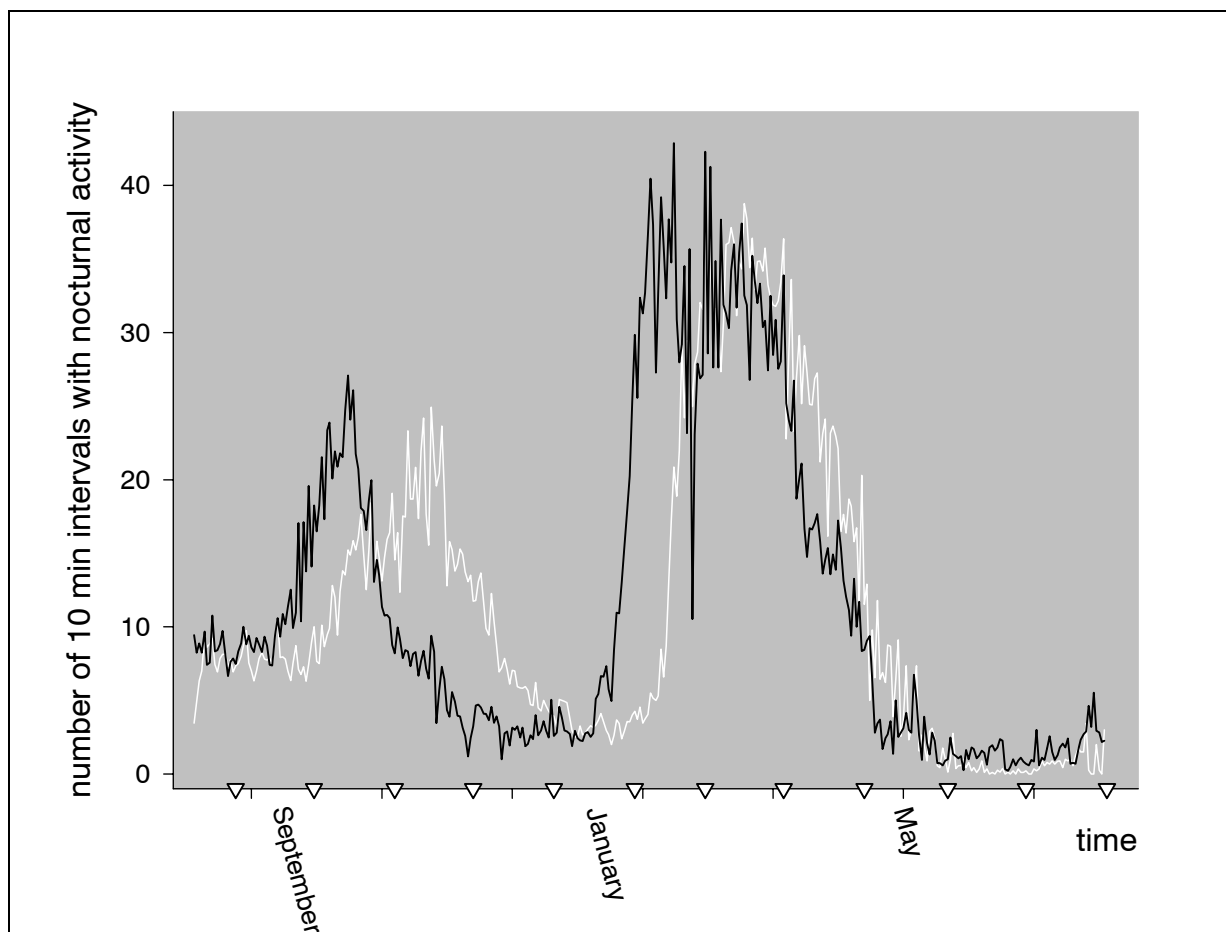


Figure 4.6

Zugunruhe in Irish and European Stonechats. Data are plotted as in Fig. 4.2 but sexes are pooled; black line: *Zugunruhe* of Irish Stonechats; white line: *Zugunruhe* of European Stonechats.

Molt timing of the captive Stonechats occurred at similar times as in the field. On average, molt of the captive birds started on August 9, peaked on September 9, and ended on October 11. In freelifving conspecifics it reportedly occurs between July and September (Ginn and Melville 1983). The slightly later molt timing in the captive Stonechats studied here may be related to their relatively late hatching date. Local Irish birds initiated their clutches between March 18 and July 13 (Cummins 2002). The captive Stonechats were collected as nestlings in mid May and were probably from second clutches. Although the calendar effect reported above (Table 4.2) accelerates molt timing in late hatched young its magnitude is too small to fully compensate for the late hatching date.

Incidence of migratory restlessness

The most surprising result of the study was the consistent prevalence of migratory restlessness in all Irish Stonechats. The data show clearly that the captive Irish Stonechats behaved entirely migratory. Unlike in other captive partial migrants a distinction between

residents and migrants was not possible (Biebach 1983; Pulido et al. 1996; 2001; Schwabl and Silverin 1990). The patterns and amount of Zugunruhe in Irish Stonechats closely resembled those of the obligatory migratory European Stonechats (Figs. 4.5, 4.6). One of the key assumptions in studying captive birds is that Zugunruhe reflects migration. The amount of Zugunruhe has been shown to be correlated with the distance flown by freelifving conspecifics (Gwinner 1968; Berthold et al. 1972; Berthold 1973). If this correlation were true in Stonechats, the captive Irish birds would have migrated as far as the Europeans. Migrants of both subspecies can winter in roughly the same region but for British Stonechats such long flown distances figure as extremes of the wintering distribution (cf. Chapter 5, Fig. 4.7). Therefore, captive Irish Stonechats differed from predictions for partial migrants in both incidence and amount of Zugunruhe, and behaved entirely like obligatory migrant European Stonechats.

There are three main possible interpretations of this surprising result. The first one is that solely migratory individuals from Ireland were sampled. This is unlikely since *S.t. hibernans* is considered largely resident. In particular in coastal regions where the birds were collected outward migration is presumably negligible. Cummins (2002) reported reductions in adult density from summer ($1.45/\text{km}^2$) to winter ($1.21/\text{km}^2$). Male densities fell from $0.73/\text{km}^2$ to $0.66/\text{km}^2$ in winter, those of females from $0.71/\text{km}^2$ to $0.55/\text{km}^2$. Overall, 85% of the summer density was found in winter and in addition, mortality needs to be taken into account. The birds studied here originated from six families and were all migrants. In contrast, assuming a resident proportion of 85%, the expected number of migrant families would have been one. Chances of sampling no migrant families are 0.003 percent (Chi square test; Chi square=8.57; df=1). However, it is possible that the migratory tendency of the population is underestimated because migrant local birds are replaced by winter immigrants.

A second interpretation is that most or all British Stonechats move, if only locally. There is equivocal anecdotal support for this assumption (cf. Chapter 5; Witherby et al. 1938-41; E. Urquhart, pers. comm.). Some observers stated that on the heaths no pairs overwintered on their breeding territories (Hughes 1975; cf. Clark and Eyre 1993). These birds may have overwintered nearby since after severe winters severely reduced their return numbers. Other observers reported that birds were residents, established "winter territories which were merely extensions of their breeding territories", and that young birds wintered close to their natal sites (Parrinder and Parrinder 1945; Thomson 1956; Johnson 1961; Phillips 1967; Gibbons et al. 1993; Callion 2002). The different observations may be related to local differences. Ringing recoveries (Chapter 5) suggest that about half of the British Stonechats migrate and the others move locally. However, if it is true that the amount of Zugunruhe reflects migratory distance local movements cannot explain the data presented here.

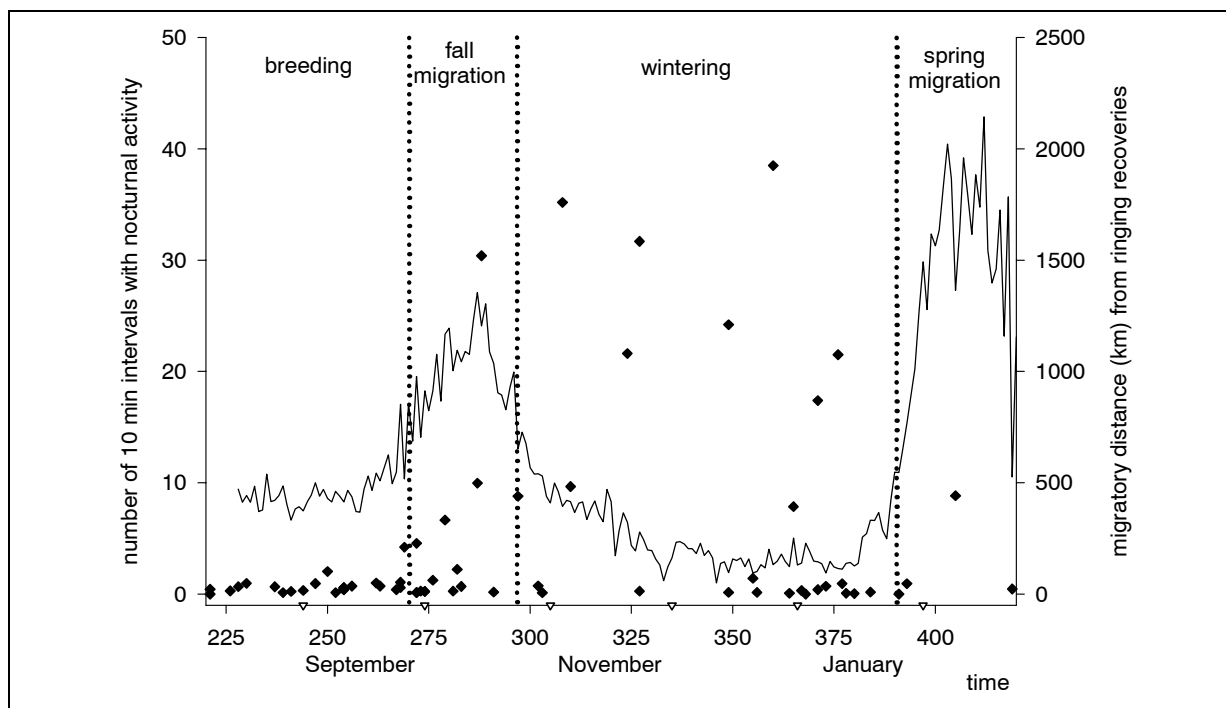


Figure 4.7A

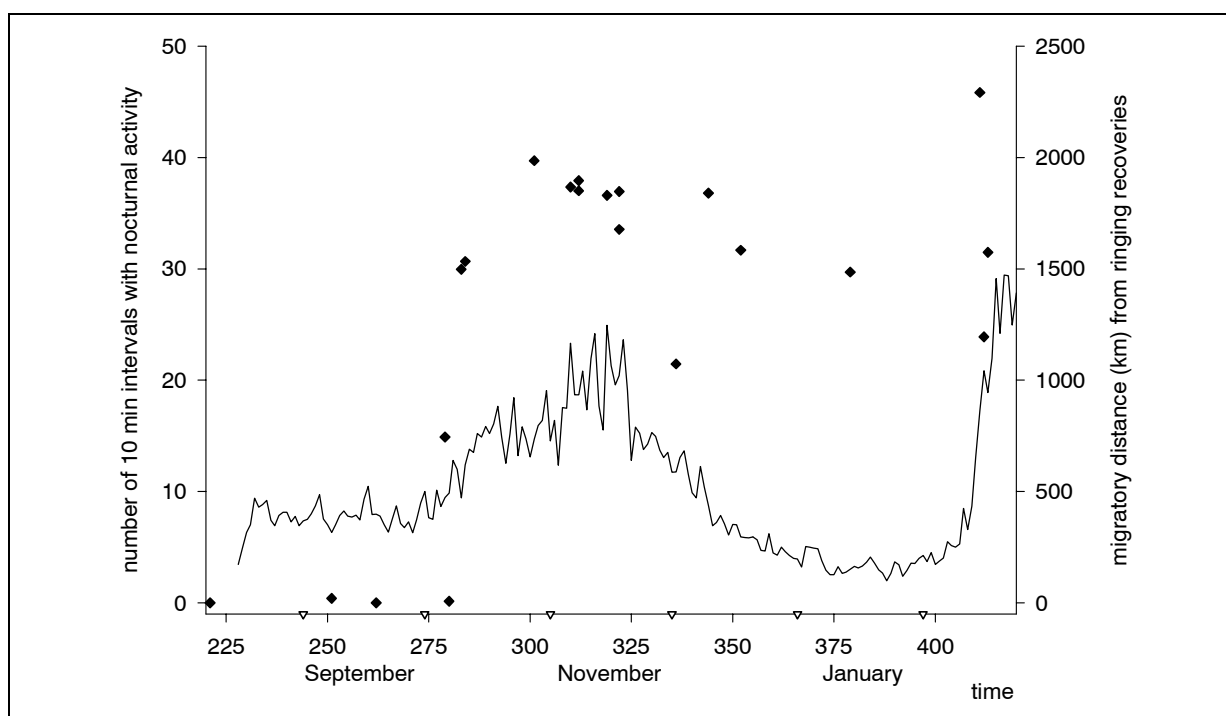


Figure 4.7B

Zugunruhe and migration. Mean nocturnal restlessness (black line) is plotted over one year as in Fig. 4.5; migratory distances (black diamonds) are the flown distances of first year birds derived from ringing recoveries (see Chapter 5); the abscissa gives time of the year in months and as Julian date (in the second year, 365 days have been added to Julian date). A: Irish Stonechats; for temporal orientation, the approximate timing of life cycle phases is indicated as text; B: European Stonechats.

The third and most likely interpretation is that Irish Stonechats are genotypically full migrants but that under natural conditions the migratory urge is suppressed in parts of the population (Lack 1943; Berthold 2002). I will use this interpretation as the working hypothesis but data from captive Stonechats that are known to be residents are necessary to fully exclude alternative interpretations.

A monomorphic genotypical disposition to migrate in partially migrant Irish Stonechats contrasts with results from three other passerine species (Robin, *Erithacus rubecula*, Biebach 1983; Blackcap, *Sylvia atricapilla*, Pulido et al. 1996, 2001; European Blackbird, *Turdula merula*, Schwabl and Silverin 1990) where migrant and resident fractions of a population were discernible in captivity. If Irish Stonechats are genotypical migrants but migration occurs in part of the population only there need to be factors that elicit or suppress migration (Lack 1943; Schwabl and Silverin 1990). A decisive role of environmental factors for migration is in apparent contradiction to the genetical theory of bird migration (Pulido et al. 1998; Berthold 2001). However, a threshold model for migration may explain results from other species as well as the novel pattern in Irish Stonechats. It is likely that a threshold for eliciting Zugunruhe in a bird is affected by environmental factors. Genetic differences between migrants and residents as found in earlier studies could hence be based on family differences in migratory thresholds, i.e., reaction norms to environmental factors. Reaction norms of Irish Stonechats could be such that the captive situation elicits migratory urge in all individuals. Irish Stonechats may therefore be untypical migrants in that their reaction norms of migratory behavior differ from those of other species studied in captivity.

It is presently unclear which factors suppress or trigger migration in Irish Stonechats. Differential migration within populations have been related to sex, age, and dominance of individuals (Lack 1943; Kalela 1954). The data on Irish Stonechats show no differences in migratory behavior between age groups and the sexes. Although a higher incidence of migration in first year compared to older Stonechats has been suggested (cf. Chapter 5) neither the captivity data nor the ringing recoveries yield any support for it. Similarly, in both datasets the sexes behaved the same. Hence, differences between the sexes and age groups may be absent in Stonechats, a feature that may be related to their pairwise wintering behavior (cf. Chapter 5). In British Stonechats local environmental and social factors may be decisive in eliciting or suppressing migration.

Timing of core migratory restlessness

Core fall migratory restlessness of first year Irish Stonechats began when molt receded, on average on September 30. It ended at a mean date of October 24, in good accordance with field observations. Autumn movements are reported to start between July and mid-August and cease from late October to early November (Hughes 1975; Cullen and

Jennings 1986; Urquhart 2002). Field observations suggest that postbreeding movements, coincident with low Zugunruhe during molt in captive Stonechats, may be related to local movements whereas the timing of core migratory restlessness coincides with overseas migration. Lighthouse and observatory reports indicate concentrations along Southern coasts and overseas movements from mid-September until early November (Kennedy et al. 1954; Van Hecke 1965b; Munkejord 1981; Riddiford 1982). Based on the literature Callion (2002) stated that "true migration" commenced in September after molt and break-up of the breeding pairs. Witherby et al. (1938-41) report emigration of Irish Stonechats in October and early November.

In the spring, migratory restlessness started on January 31. The early spring Zugunruhe also corresponded well with field observations. Migrants reportedly return to their breeding grounds starting in early February (Hughes 1975; Clark and Eyre 1993; Callion 2002). Lighthouse and passage data suggest that overseas migrants arrive in late February and March (Kennedy et al. 1954; Van Hecke 1965b; Cullen and Jennings 1986; Urquhart 2002). The early return is in accordance with early territorial activity and song in late January, and of reproductive activities in early March (Lack 1986; Urquhart 2002). For the Irish population studied here, clutch initiation started on March 18 and thus earlier than in European Stonechats (Glutz and Bauer 1988; Flinks, pers. comm.). The early return of British Stonechats may be related to their partially migrant behavior. Migrants started breeding later than residents and therefore often produced one less clutch (Parrinder and Parrinder 1944; Johnson 1971; Cramp et al. 1988). Hence, selective pressure on migrants to return quickly is presumably high. The earlier initiation of fall Zugunruhe in British compared to European Stonechats may be partly related to their overall earlier hatching date.

The close correspondence between the dates of onset and completion of Zugunruhe with field data suggests that overall, core Zugunruhe in Irish Stonechats reflects their migratory behavior. Figure 4.7 relates Zugunruhe of captive Stonechats to the distance flown by freelifving conspecifics (Chapter 5). Increases of Zugunruhe roughly parallel the distance flown by migrant Stonechats. Field observations and ringing recoveries also indicate that employment of the edge detector method succeeded in identifying the sections of nocturnal restlessness relevant for core migration. Ringing recoveries corroborate the interpretation that sporadic early bouts of restlessness coincide with small-scale postbreeding movements whereas core Zugunruhe cooccurred with considerable flown distances (Chapter 5; Fig. 4.7).

Postbreeding nocturnal restlessness

In most Irish Stonechats, low levels of nocturnal restlessness preceded molt or coincided with it. Some birds showed restlessness from the earliest registration in August, at ages of approximately 70 days). It is possible that they reflect dispersal restlessness (Berthold 1988b). In freelifving British Stonechats, juvenile dispersal starts in June (Clark and Eyre 1993; Callion 2002) and increases over August and early September. The movements start out locally but later some birds make for the coast (Clark and Eyre 1993; Callion 2002). Two ringing recoveries (Chapter 5) confirm early movements: in July, two young aged 70–80 days were recovered c. 50 km from their nesting site. Greig-Smith (1979) has argued that during their first three months of life young Stonechats choose between two strategies of movement: while part of the population stays close to parental territories, others move considerable distances of up to 300 km. Individual patterns of restlessness in captive Stonechats (Fig. 4.3 A versus B) might reflect such differences. Coincident with the time of dispersal, young Stonechats aggregate to small molting flocks which preferably move to the coast (Urquhart 2002). In a colour-ringed British Stonechat population, five flocks did not comprise any siblings (J. Callion, pers. comm.). The young were observed between July 30 and September 23 and had moved between 2 and 35 km from their natal site. Such movements may therefore be molting migrations and simultaneously enhance dispersal and genetic exchange (Clark and Eyre 1993; Callion 2002). Gwinner and Schwabl-Benzinger (1982) reported early juvenile *Zugunruhe* in two species of Flycatchers. They interpreted it differently for the two species. Based on ringing recovery data, restlessness coincided with local juvenile dispersal in Pied Flycatchers (*Ficedula hypoleuca*). In Collared Flycatchers (*F. albicollis*) it coincided with directed migration to Mediterranean refuelling and molting areas ("Zwischenzug"; Schüz 1951). The two interpretations may be mutually non-exclusive and both pertain to Stonechats.

Early nocturnal activity has also been reported for Reed Warblers (*Acrocephalus scirpaceus*) by Mukhin and colleagues (1999a, b; Bulyuk et al. 2000; Chernetsov and Mukhin 2001). In most caged birds they observed sporadic bouts of *Zugunruhe* at ages of 25–40 days during the early stages of molt. After the end of molt nocturnal restlessness was expressed clearly. However, in a small fraction of immatures, *Zugunruhe* was not observed until molt was largely completed. These data corresponded to captures of freelifving Reed Warblers. Most young dispersed at ages of 35 to 40 days while a minority remained on site until molt receded (Chernetsov and Mukhin 2001). Hence, postfledging *Zugunruhe* was interpreted as an endogenously controlled nocturnal dispersal restlessness. In other studies, molting Reed warblers of all age groups were found on migration (Herremans 1990). Therefore, the behavior observed by Mukhin and colleagues may not be confined to juvenile dispersal.

In captive Irish Stonechats adults also showed Zugunruhe during late summer, coincident with molt in the field (ranging from late July until early October; Snow 1969; Riddiford 1981; Ginn and Melville 1983). Since migratory timing did not differ between age groups, postbreeding Zugunruhe is not exclusive to juvenile dispersal. Postbreeding movements of young and adult Stonechats may serve similar ends. In a British Stonechat population, incoming birds of both age groups caused a turnover between late August and October (Johnson 1971; Phillips 1976; Lack 1986). Some birds secured winter territories but even those that continued to migrate may have benefited. Löhrl (1959; 1962) has shown that Collared Flycatchers returned for breeding to the location where they had carried out postjuvenile molt. Local knowledge and the temporary establishment of a territory can enhance a bird's prospects for the next breeding season, as has been shown for Dusky Warblers, *Phylloscopus fuscatus* (Forstmaier 2002; cf. Kalela 1954). Reed et al. (1999) have proposed that "prospecting" for future breeding sites in late summer may be particularly advantageous for time-constrained migrants.

Chapter 5

Movements of Stonechats from central Europe and the British Isles (*S.t. rubicola* and *hibernans*): results from ringing recoveries

Summary

Captive birds may act differently than their freeliving conspecifics. Hence, studies of caged birds, in particular of migration, may be severely biased. Here, I address this caveat by a comprehensive analysis of all currently available ringing recoveries of Stonechats. The ringing analysis aims to reassess the migratory behavior of Stonechats in Europe which had last been studied in depth in 1965. Several questions remained unresolved, and in addition, changes in migratory behavior may have occurred. Since then, the number of available ringing recoveries has increased by more than 700% to 675 records. The recovery analyses concentrate on three focal populations, including birds ringed on the British Isles, in Belgium and the Netherlands, and in Germany. Ringing recoveries of British Stonechats indicate that the time patterns of Zugunruhe observed in captive Irish Stonechats correspond closely to that of their freeliving conspecifics. However, in contrast to the entirely migratory behavior of captive birds, less than half (41.7%) of the recovered British Stonechats overwintered far enough from the breeding grounds to be considered migrants. According to ringing records, Stonechats from Belgium and the Netherlands behaved entirely migratory, just like German Stonechats. None of the populations showed changes in migratory behavior over time as has been reported for other species. There was no evidence for differential migration in Stonechats. Their migratory behavior was homogenous both among the sexes and between first-year and older birds.

Introduction

Bird migration patterns have changed over time, and during the last decades, rapid modifications have been observed (e.g., Sutherland 1998; Bairlein and Winkel 2001; Berthold 2001). A genetic basis to at least some of these changes is likely in view of evidence both from the field (e.g., Brown and Brown 2000) and from laboratory experiments (Berthold et al. 1992; Berthold and Pulido 1994; Pulido et al. 1996). A well known example for rapid genetic change of migratory behavior is the Blackcap (*Sylvia atricapilla*). An increasingly larger proportion of this species has moved its wintering quarters from the Mediterranean to the British Isles. The novel pattern has included a directional change of migratory route which has been shown to be genetic (Berthold et al. 1992), a change of distance flown, and, due to the shortened route, of the timing of migration. Although this might be an extreme example, migratory behavior can no longer be assumed to remain constant over the years.

In Stonechats, the migratory status was last assessed in depth by Van Hecke (1965a,b). Since his analysis the number of available ringing recoveries has increased by more than 700% to 675 records. There is reason to expect that changes in Stonechat migratory behavior may have occurred. Based on more frequent sightings the long-distance migrating eastern subspecies have been suspected to show novel migratory patterns to central and western Europe (e.g., Robertson 1977; Pfeifer 2000). For partially migrant British Stonechats a possible reduction of migratory behavior as a consequence of climatic change has been predicted (Callion 2002; Urquhart 2002). The rationale is that if migratory propensity is genetically determined, the proportion of residents could be expected to increase if mild winters prevail (Dhondt 1983; Callion 2002; Urquhart 2002). *Therefore, one goal of this study is to check if in central and western Europe changes in Stonechat migratory behavior have occurred.*

Since the ringing recovery study by Van Hecke (1965a,b), Stonechat migratory behavior has been subject of debate. Zink (1973) stated that European Stonechats *S.t. rubicola* should be considered partial migrants: southern and western population overwinter and the others migrate short-distances. For the subspecies *S.t. hibernans* which breeds on the British Isles and in western Europe, the case seems less clear. Vaurie (1959) called it resident and many other authors regarded it as "basically a sedentary species in Britain and Ireland", with only "a few birds" migrating south (Thomson 1956; Johnson 1971; Lack 1986). Van Hecke (1965a, b, based on 93 recoveries and counts in Belgium and NL) considered British Stonechats "largely resident with some movement abroad". Zink (1973) rejected the view that British Stonechats were mostly resident, pointing out regular movement as far as north Africa. In their recent reviews, Callion (2002) and Urquhart (2002) stated that overall the majority of British birds were residents and only a minority migrated. However, they pointed out that on a finer local scale seasonal movement among British Stonechats may be more frequent (Cramp et al. 1988; Cummins 2001; Callion 2002; Urquhart 2002). Therefore, the British population as a whole may show some migratory tendency. The more northern populations appear to be more likely to move to milder regions such as the coast (Van Hecke 1965; Callion 2002; Urquhart 2002). This tenet is based on a gradient in winter densities that increase along the coast and drop further inland (Lack 1986; Gibbons et al. 1993). The confusion over the British Stonechat's migratory status may arise from such regional differences or from different interpretations of their wintering behavior.

There is also disagreement about the migratory status of Stonechats from Belgium and the Netherlands. It is not clear if Dutch and Belgian Stonechats are fully distinct from *S. t. hibernans* (Cramp et al. 1988; Walker 2001). There is anecdotal evidence of juvenile dispersal from the British Isles to Belgium (Van Hecke 1965b and J. Callion, pers. comm.). Stonechats overwinter regularly in the Netherlands and Belgium. Van Hecke (1965a) and

Dhondt (1983) have differed in their interpretation of overwintering birds. While Van Hecke (1965a) suggested that Stonechats wintering in Belgium were migrants originating from the British Isles, Dhondt (1983) has questioned this view and suggested that the Stonechats wintering in Belgium and the Netherlands were resident local birds. *A second goal of my study is to reassess the migratory status of British, Dutch and Belgian Stonechats.*

Some migratory populations, in particular partial migrants, show heterogeneity in their migratory behavior. In an early study of ringing recoveries from the British Isles Lack (1943) proposed that differential migration patterns were typical of partial migrant populations. Depending on age and sex, parts of the population may migrate longer distances, at different times, and to a larger proportion than others. In particular, Lack suggested that females migrated further than males, and young birds further than adults, a view that has found wide support (Kalela 1954; Cristol et al. 1999). Cristol et al (1999) found the evidence for differential migration so compelling that they suggested to ask "How can we explain species in which classes migrate the same distance?". For Stonechats, sex divisions are less likely than in other birds because they typically overwinter in heterosexual pairs (Gwinner et al. 1994; Roedl 1994; 1999). An age division of migrant Stonechats has found anecdotal support. Johnson (1961, 1971) reported from Jersey that the majority of local young left the island over winter. Because incoming winterers were all young, arriving between late August and early October, he concluded that first year Stonechats were more likely to migrate. Riddiford (1981) suggested that Stonechat passage records at Dungeness bird observatory on the south east coast of Britain consisted predominantly of juveniles, some of which were erroneously aged as adults. His observation of fall aggregations along the Channel supports Van Hecke's (1965b) claim that Stonechats use "springboard locations" before crossing open water. Similarly, Bueno (1991) observed more juveniles than adults in Gibraltar during the fall passage and suggested that the young concentrated there to move on to north Africa because their proportions dropped after December. *Therefore, the third focus of this chapter is a search for evidence of differential migration in Stonechats.*

Because of the spatial heterogeneity of Stonechat migratory behavior, detailed analyses concentrate on birds from three regions of specific interest with sufficient ringing recoveries. One such area is the British Isles including Channel Islands which is the central breeding range of *S. t. hibernans*. The second area is the Netherlands and Belgium where the breeding population presumably belongs to *S.t. rubicola* but the migratory status is still debated. The third focal region is Germany with its completely migratory population of *S.t. rubicola*. Thus, I compare ringing recoveries of an alleged partial migrant population to a possibly mixed population and an obligatory short distance migrant population.

Material and methods

Until the beginning of 2002 the BTO and the EURING ringing schemes have compiled 675 ringing recoveries. A single local recovery of a Stonechat from Asia has been excluded from the dataset. Data of all other recoveries are combined in some figures and analyses. The more detailed analyses concentrate on birds from the three focal regions.

Ringing and recovery data are heterogenous in their temporal and spatial accuracy and in the information content they convey. I used details of ringing records to select recoveries that were sufficiently accurate for the respective use in analyses. In Figures 5.1 and 5.2 all ringing information is depicted, irrespective of accuracy of information. For detailed analyses and in all other figures, only data were used that met the following requirements: For temporal accuracy I excluded birds if their finding conditions were specified as "not freshly dead" or if their finding details involved captivity of more than 24 hours. Ringing and finding time had to be accurate to within one week. If the accuracy was less than within three days data were used only if birds were found alive so that total time accuracy was ascertained to be within \pm one week of recovery. For spatial accuracy birds were excluded if moved by humans or other circumstances; data were rounded to full km. In total, data for 609 out of 674 recoveries were sufficiently accurate to allow for thorough analyses. The number of birds ringed in the three focal populations and recovered with sufficient accuracy were 109 in the Netherlands and Belgium, 189 in Britain, and 111 in Germany. The most accurate information was for birds ringed as nestlings because the place of origin was known exactly and age was approximated to within two weeks. The other two age categories were immatures for which the year but not the place of birth was known, and adult. The category sex was used if either reported by the ringer or the finder or if both agreed.

To analyze partial migration, it was necessary to classify birds as migrants or residents, respectively. The definitions of "migrant" and "resident" are crucial as they determine the assessment of migratory status. As suggested by Lack (1943), birds were classified as "residents" if they were present on the breeding grounds at the time when migrants were recovered at their respective wintering sites. By implication, the assignment of migratory status depends on the demarcation between breeding and wintering grounds. For British birds, a frequently used criterium for migration is whether or not they leave the British Isles in winter (Urquhart, pers. comm.). However, there are drawbacks of this definition. Firstly, it applies only to Britain and cannot be used for other populations, such as for the Belgian and Dutch Stonechats. Secondly, wintering movements of Stonechats within Britain would be excluded by definition. Distances flown within the British Isles can be longer than those to the continent. Therefore, I use the criterium of wintering within Britain in the discussion but for analyses derive a definition from the recovery data.

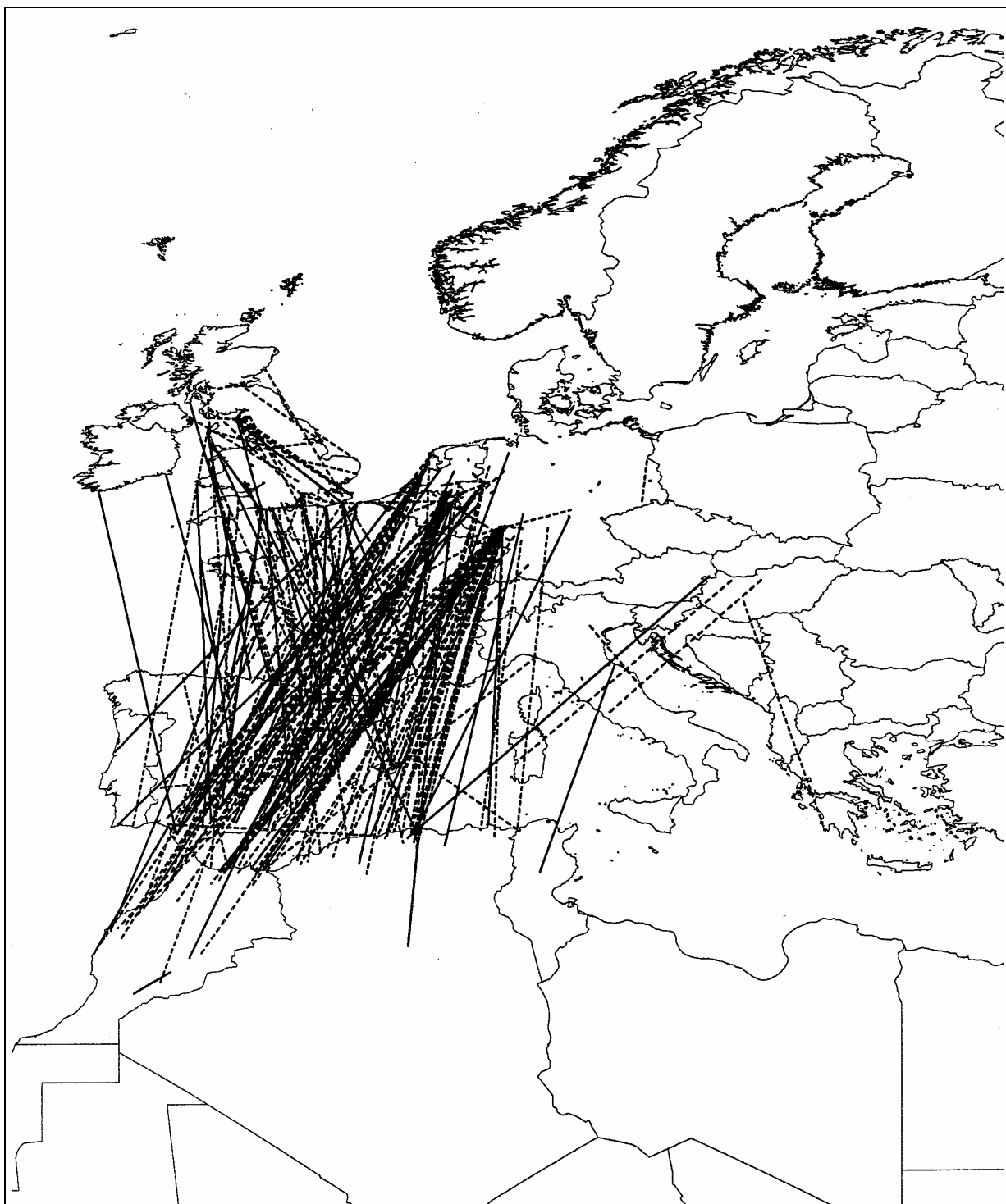


Figure 5.1

Ringing recoveries of all Stonechats. Lines connect ringing and recovery sites. Solid lines indicate recoveries from the same migratory period, dashed lines show recoveries after the current migratory period.

I assume that there is a visible divide between residents and migrants in the distances travelled. Birds that are recovered in winter closer to home than the divide are regarded as residents, and those that flew further are considered migrants (see Results).

The recoveries were related to the Stonechats' seasonal activities according to the literature (Callion 2002; Urquhart 2002). The breeding season was assumed to last from April until August, and wintering to take place between November and January. Because the number of winter recoveries was small, summer and winter movements could not be analyzed in detail. Therefore, movements of birds recovered from February to May were classified as "spring migration" (homeward migration, Berthold 2001) whereas the distances flown by birds recovered from June to January were classified as being part of "fall migration" (outward migration, Berthold 2001). This leaves some ambivalence due to overlap between seasonal activities, especially between the end of the breeding season and early postbreeding movements. Birds ringed at that time could be either still at their breeding grounds or may have already moved some distance. However, inspection of the data from focal populations (see below; Fig. 5.8) showed that movements in August occurred at local scales so that the spatial deviation from the actual breeding site is presumably small. The maps are divided into the time on the breeding grounds (from February until May); wide-sense postbreeding movements (June to September); and presence on wintering grounds (October to January).

To investigate changes in migratory behavior over time, I divided the data set into two time-slots. The main climb of global temperature started approximately in 1980 (Houghton et al. 2001). Therefore, I assigned recoveries until 1979 to one group and more recent recoveries to a second. This cut-off point yielded roughly equal group sizes. I analyzed changes in the proportion of migrants and in the distance flown by non-parametric and ANOVA over ranks, as suggested by Conover and Iman (1981). Analyses of data were performed over the loxodromic (minimal) distance flown and over the proportion of migrants. Loxodromic distance was preferred because it amounts to straight lines on the geographical mercator-representation used here. The data were calculated with programs written by Wolfgang Fiedler, Radolfzell. Maps were produced using GIS Arc View 3.0.

Results

General patterns

The 675 records of ringing recoveries have been collected over 70 years. The earliest record is of a bird ringed and recovered in Great Britain in 1923. The first foreign recovery was of bird ringed in Germany in 1930 and recovered in the same year in Spain. The majority of data accumulated between 1950 and 2000. Stonechats were banded and recovered in 16 countries, respectively. Ringing and recovery countries were Algeria, Belgium, France, Germany, Great Britain, Ireland, Italy, Morocco, Poland, Spain, Switzerland, The Netherlands, Tunisia, and the Asiatic part of the former Soviet Union. Austria and Hungary were only among the banding nations, and Greece and Portugal were only among

the recovery nations (see Figs. 5.1 and 5.2). The greatest time difference between ringing and recovery was of a bird ringed as an immature in Spain in August of 1969 and recovered there in April of 1982. No details about the finding circumstances were given but 12 years of age appears unlikely for a northern hemisphere passerine. Cramp et al. (1988) report the oldest ringed Stonechat as having been six years of age. The next two oldest Stonechats were seven and six years old, respectively, and thus closer to the maximum in the literature. The longest minimal (loxodrome) distance was 2450 km flown by a bird ringed as an immature in the Netherlands on August 27 1964 and found freshly dead only twelve days later in Morocco (Figs. 5.1 and 5.2). Overall, the continental Stonechat populations migrated in south-westerly directions and wintered around the Mediterranean Sea and on the islands. Five records from the Italian north Adriatic coast further indicate passage across the Mediterranean islands. The British population tended to migrate more south and south east than the continental birds.

Recovery rates of Stonechats have been low, as in other passerines. Overall, of 135,599 Stonechats ringed in Europe and the Mediterranean region 746 have been recovered. These totals are minimum estimates because numbers were not available from all schemes, and if present were often not up to date. The overall proportion of recovered birds (from schemes that have reported both numbers) is 0.56%. The recovery proportions vary widely between regions. For the focal areas of this chapter, they are lowest in Germany (for all three banding stations: ringed 26 444, recovered 64; recovery rate 0.42%) and much higher for the British Isles (27 433 ringed; 201 recovered; recovery rate 0.73%; Clark et al. 2001). The highest recovery rates were reported by Van Hecke (1965b), ranging from 0.88% in the Netherlands to 1.2% in Belgium, and they have since then remained stable. Until 1998, 1.3% of the Stonechats ringed through Arnhem have been recovered. The differences between the recovery rates are not influenced by the relative proportions of ringed pulli and adults. Pulli were 78.7% of the ringed birds in Britain (Clark et al. 2001) and 77.5% of the birds ringed by the Radolfzell scheme (representing the vast majority of birds ringed in Germany).

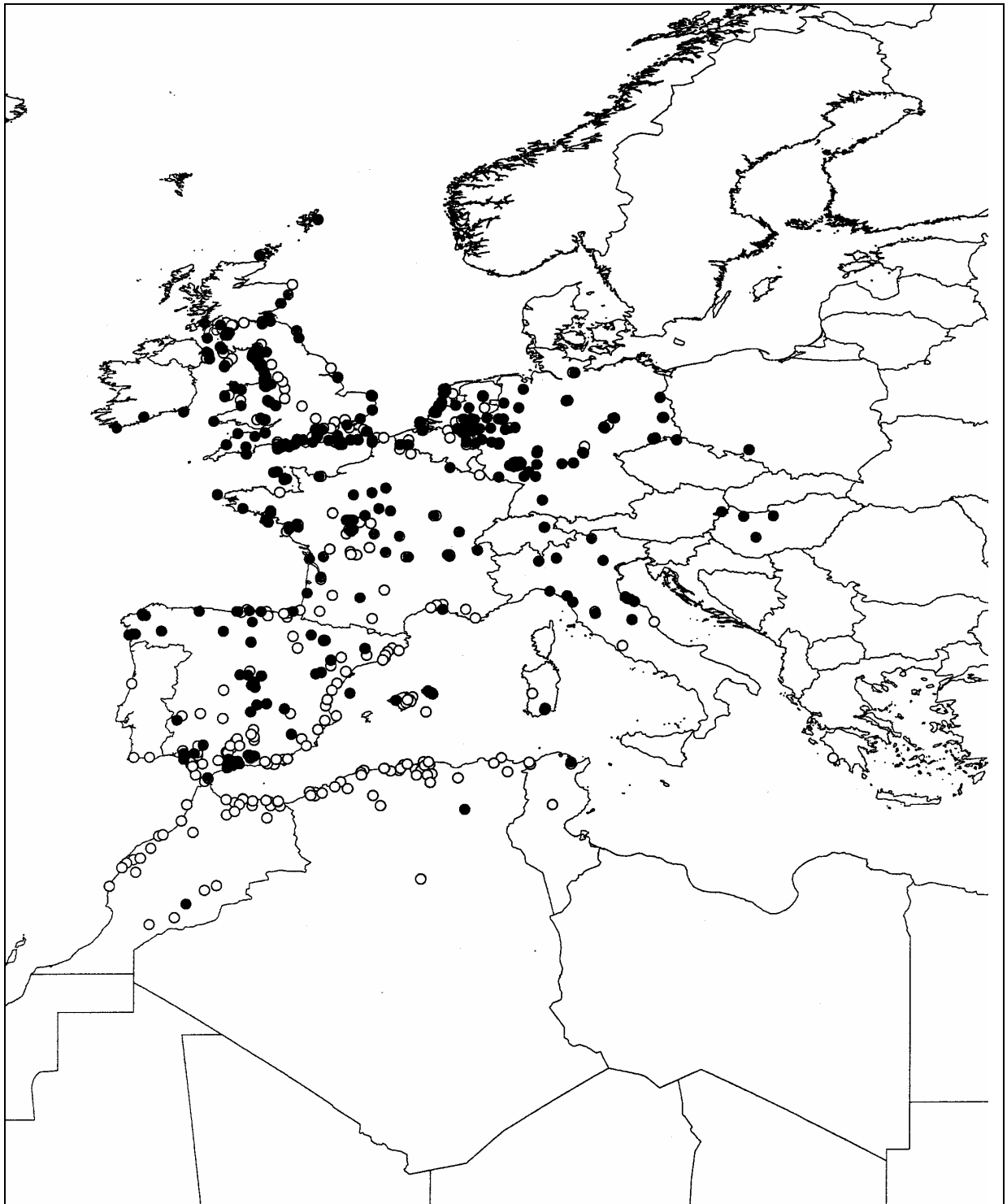


Figure 5.2

Ringing and recovery sites of all Stonechats. Full circles indicate ringing and open circles recovery sites.

Comparison of the three focal populations

Temporal and spatial patterns

The migratory patterns of Stonechats from the three focal regions largely confirm the results by Van Hecke (1965b). Stonechats from Britain migrated in southerly and south-easterly directions (Figs. 5.3A). In contrast, Stonechats from Belgium, the Netherlands and Germany flew mostly westward (Figs. 5.3B, C). The recoveries can be better interpreted if subdivided by month of recovery (Figs. 5.4 – 5.6). Figure 5.4 shows the recoveries of birds ringed in the focal regions during the early part of the breeding season. During February, many of the migrants were still recovered at the most distant wintering sites but some had already approached their breeding sites. In March, all German and British Stonechats had returned to their native countries but some of the Dutch and Belgian birds were still far from the breeding grounds (Fig. 5.4A, B, C). From April until July, all recoveries were found near the breeding sites (Figs. 5.4 and 5.5A, B, C). In August movement was local (see below; Fig. 5.8) and in September some Stonechats from the Netherlands and Belgium emigrated. From November until January migrants were presumably at their wintering grounds (Fig. 5.6A, B, C).

During wintering, differences between the populations in migratory behavior became obvious. The two continental populations were very similar to each other. They wintered further from the breeding grounds than British Stonechats and their wintering area was more coherent. Dutch and Belgian Stonechats wintered mostly in southern Spain and western north Africa, whereas German recoveries tended to be located more easterly. For British Stonechats, many wintering recoveries came from the British Isles, confirming the status of the population as partially resident. Migrants wintered from southern England to north Africa with no evidence of stopping over or wintering in the Netherlands and Belgium. To date, there are only two recoveries of British ringed Stonechats in Belgium and the Netherlands. Both were found breeding in the summer in Belgium and thus had dispersed there (Van Hecke 1965b; John Callion, pers. obs.).

To assess the proportion of migrants, the distribution of recovery distances from the breeding grounds among overwintering British Stonechats is plotted in Fig. 5.7. There is a clear peak at short distances: of 36 winter recoveries, 20 birds had travelled less than 100km and one bird was recovered after 107 km. The distance flown by the other 15 winter recoveries ranged between 392 km to 1925 km. Apparently, the migrant population wintered over a vast range of distances. The two largest divides in the distribution of flown distances were between 107 km and 392 km, and between 531 and 869 km, respectively. Since the distance range of the second gap is unambiguously within the wintering range of British Stonechats I've chosen the first divide to delineate residents and migrants. The bird

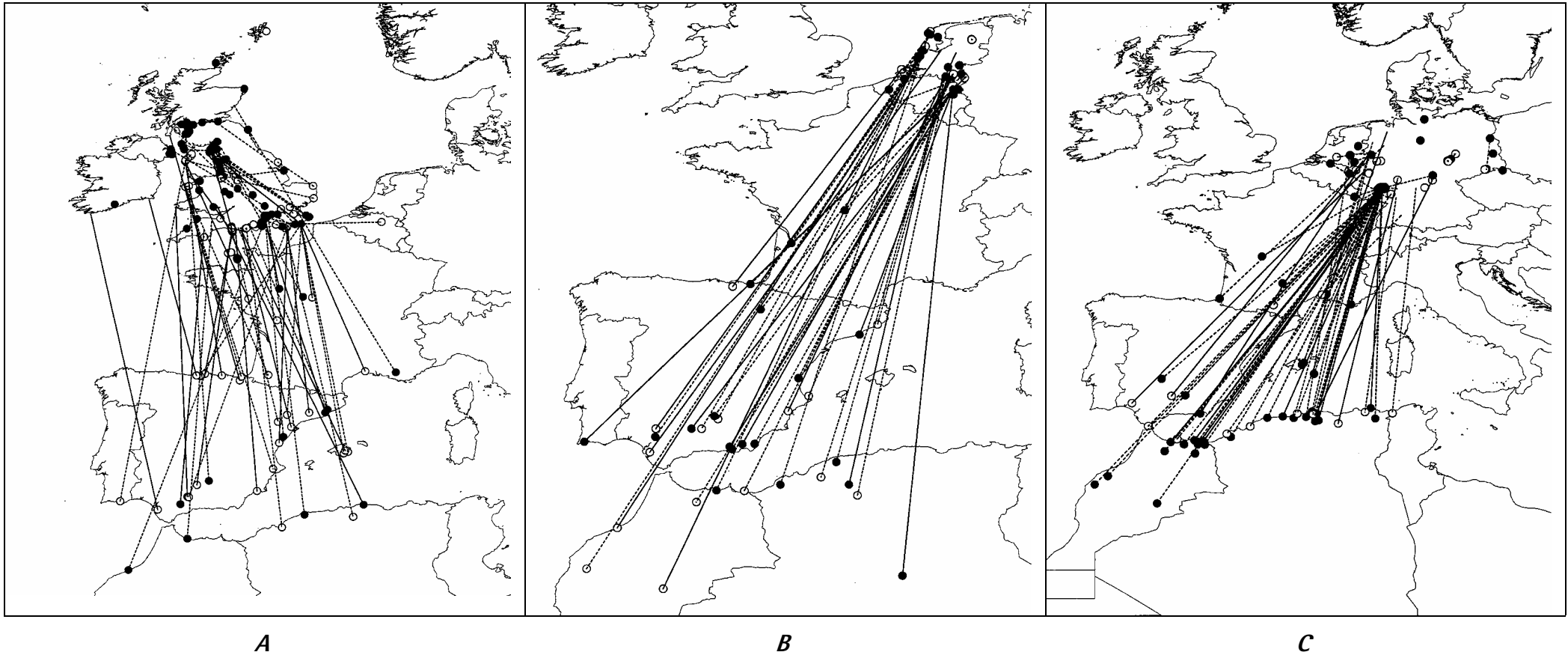


Figure 5.3

Recovery locations of Stonechats from the focal regions. Full circles indicate recoveries from birds ringed as nestlings, and open circles those from birds ringed as immatures or adults; lines as in Fig. 5.1. A: British Stonechats; B: Dutch and Belgian Stonechats; C: German Stonechats.

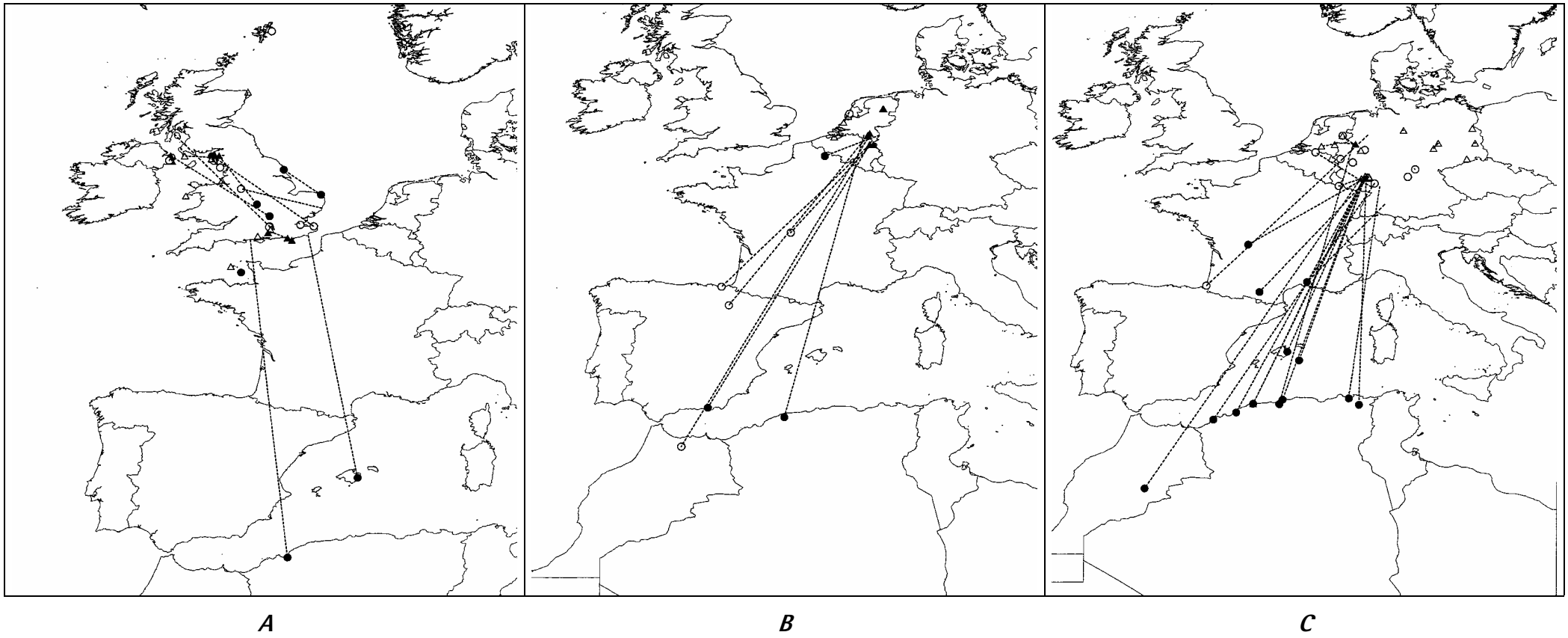


Figure 5.4

Recovery locations during the early breeding season. Months are plotted separately by different symbols: filled circles February; open circles March; filled triangles April; open triangles May; lines as in Fig. 5.1. A: British Stonechats; B: Dutch and Belgian Stonechats; C: German Stonechats.

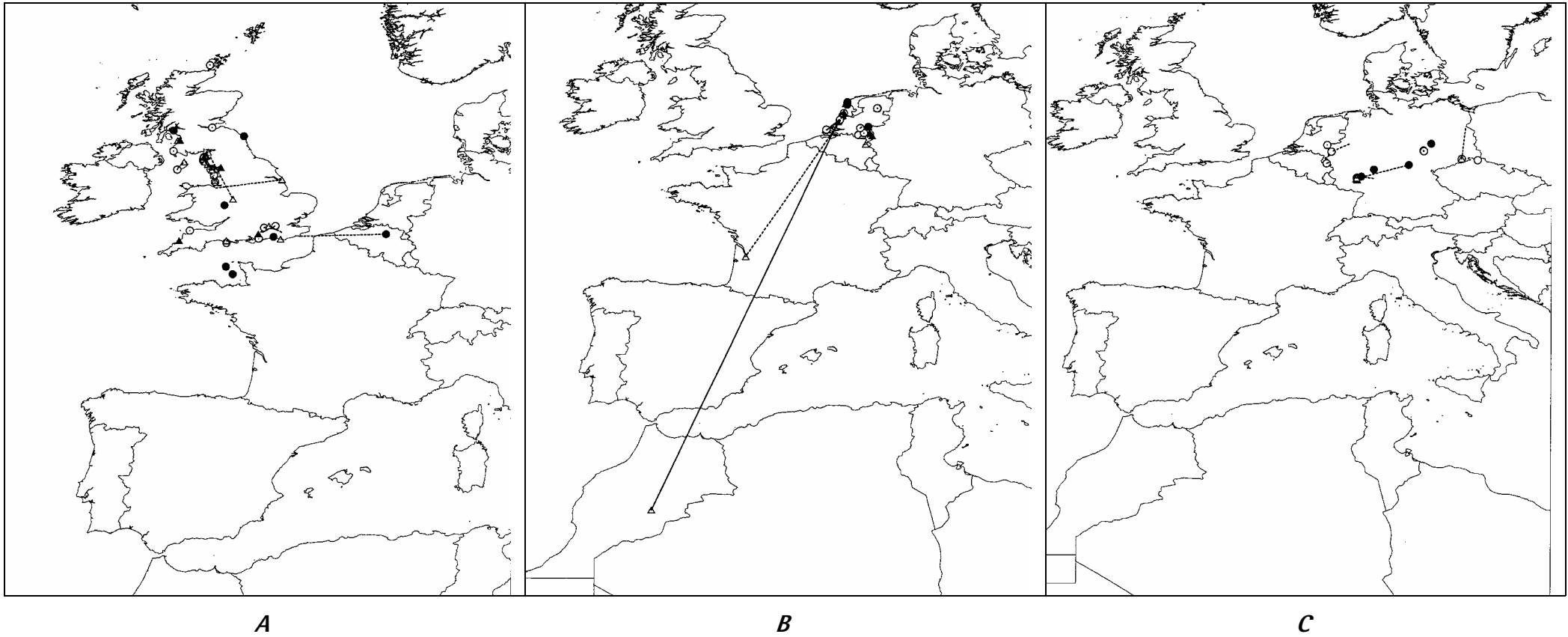


Figure 5.5

Recovery locations during late breeding and postbreeding movements. Months are plotted separately by different symbols: filled circles June; open circles July; filled triangles August; open triangles September; lines as in Fig. 5.1. A: British Stonechats; B: Dutch and Belgian Stonechats; C: German Stonechats.

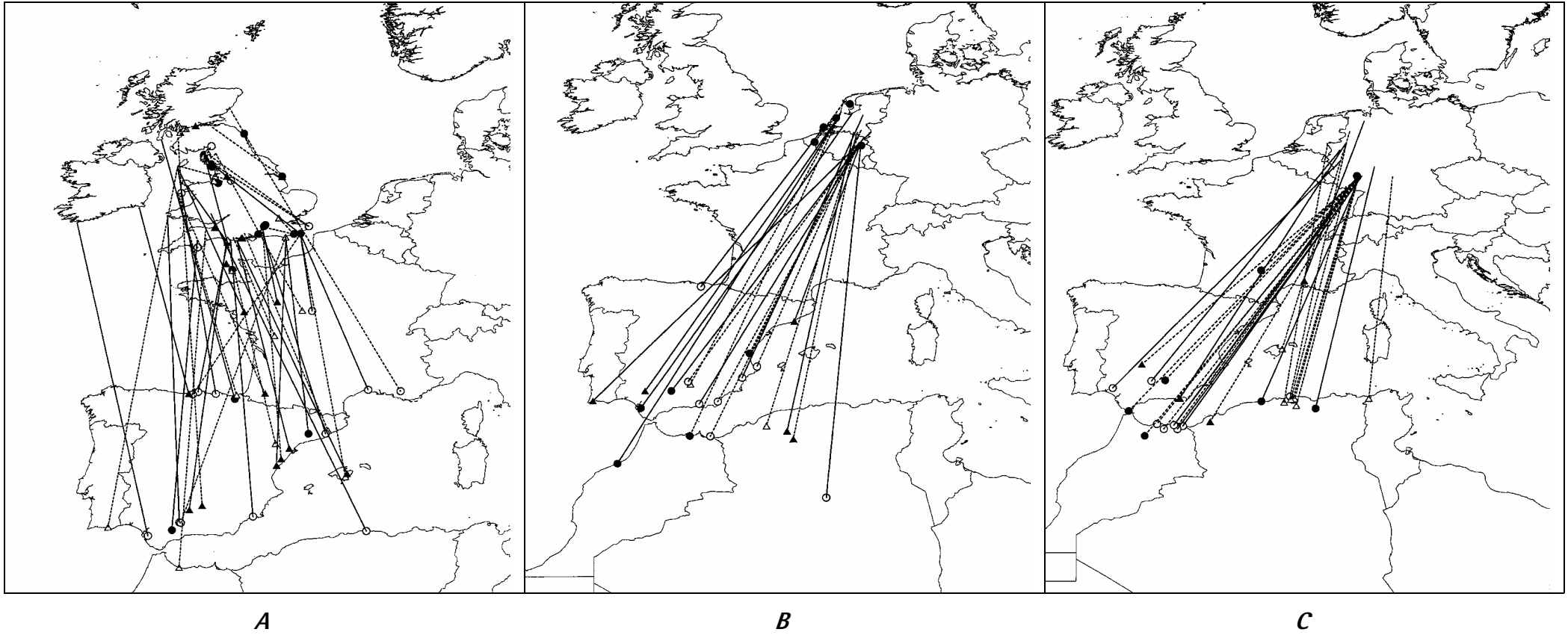


Figure 5.6

Recovery locations outside the breeding season. Months are plotted separately by different symbols: filled circles October; open circles November; filled triangles December; open triangles January; lines as in Fig. 5.1. A: British Stonechats; B: Dutch and Belgian Stonechats; C: German Stonechats.

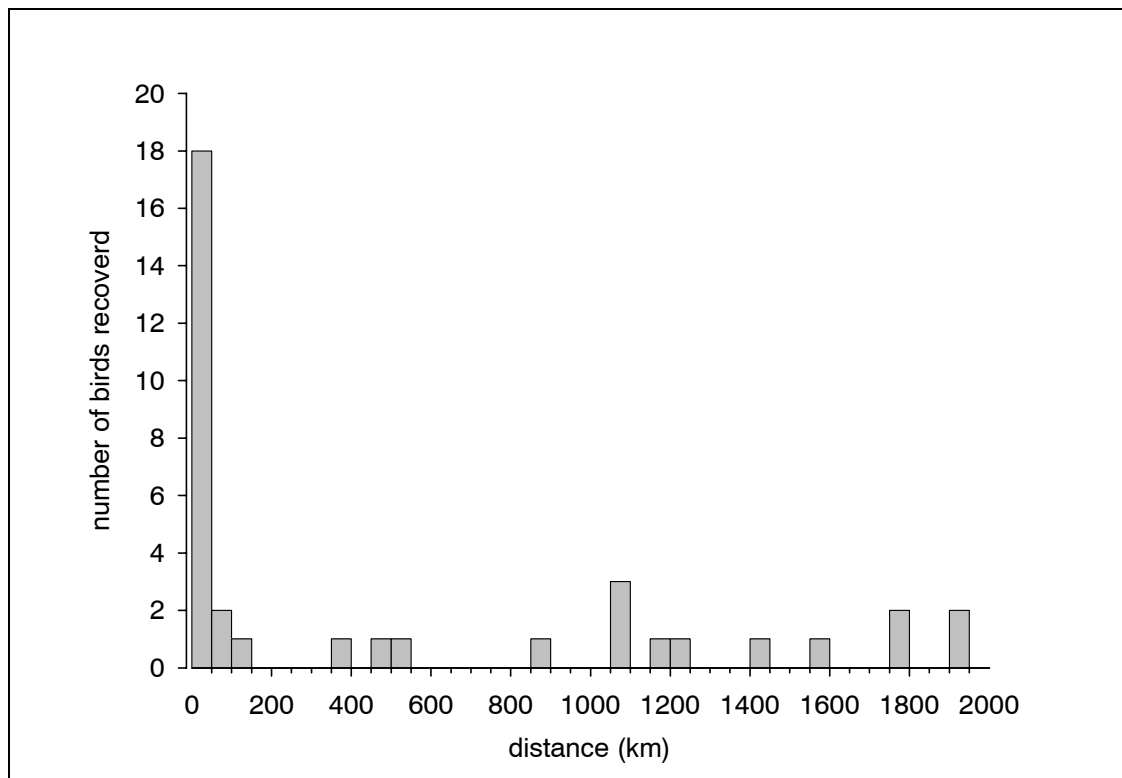


Figure 5.7

Wintering locations of British Stonechats. Distribution of distances flown by birds ringed in the breeding season and recovered between November and January. The graph shows the frequency of recoveries for intervals spanning 50km.

that flew 107.2 km was recovered in Britain whereas the next one, 392.3 km away, was found in France. Only one bird that travelled further (482.6 km) was still recovered in Britain. Using the gap between 107 km and 392 km for a cut-off point rendered an overall migrant proportion of 41.7%. The alternative criterium for migrants as the proportion of birds that left Britain yielded a slightly lower migrant percentage of 38.9%. For the Dutch and Belgian population and German Stonechats, no residents could be identified. For better temporal and spatial resolution, I plotted the distance flown against the month of recovery (Fig. 5.8). From April to August, all Stonechats were present within 250 km of their breeding sites. Migrants started to leave in September and returned in February and March. Only the British population remained close to the breeding grounds. All recoveries of German, Dutch and Belgian birds between November and January were further than 1000 km from the breeding grounds.

Statistically, there was a significant difference in migratory distance between the migrants of the three focal areas (ANOVA: $F(1;42)=5.432$; $p=0.008$). British Stonechats flew significantly shorter distances than Dutch and Belgian (Tukey's HSD post-hoc test; $p=0.009$) and German Stonechats (Tukey's HSD: $p=0.044$; see Table 5.1 for the median distance flown).

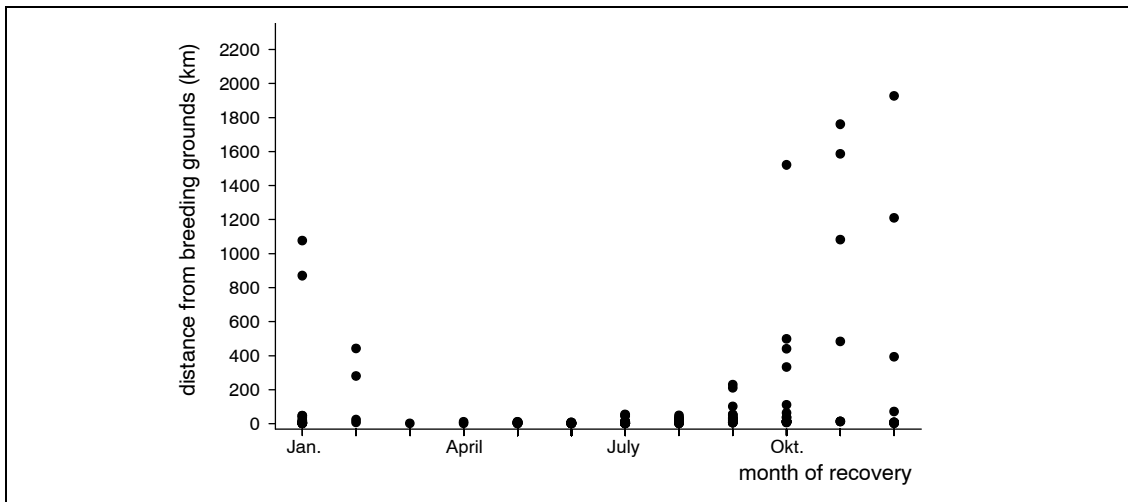


Figure 5.8A

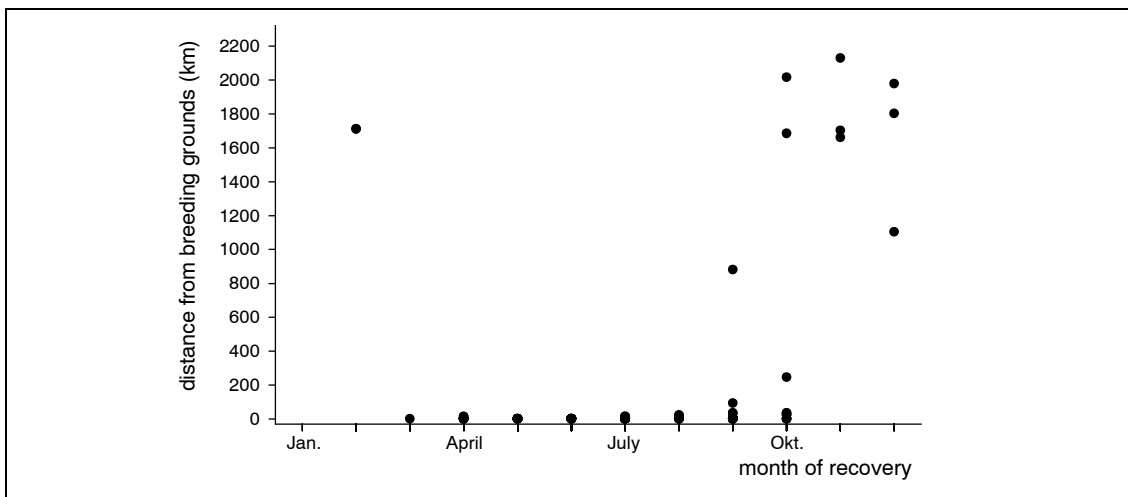


Figure 5.8B

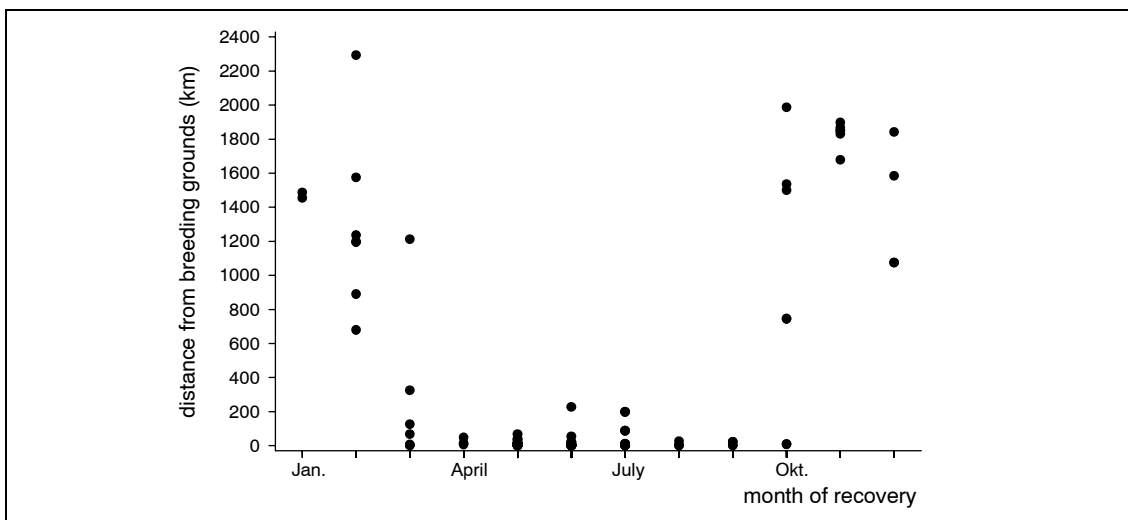


Figure 5.8C

Distance from breeding grounds over the year. The ordinate gives loxodromic distance from the ringing site, the abscissa shows the month of the year. A: British Stonechats; B: Dutch and Belgian Stonechats; C: German Stonechats.

Table 5.1

Distance (rounded to full km) between ringing site in summer (April to August) and recovery site in the winter (November to January) of Stonechats of three focal populations.

population	n	median	minimum	maximum
NL and Belgium	13	1788	1102	2129
Germany	17	1702	1073	1897
all British	36	52	0	1925
British residents only	21	13	0	107
British migrants only	15	1190	392	1925

The most accurate information is on birds ringed as nestlings. Table 5.2 shows the distance travelled by young of the focal populations during their first year of life. During July

Table 5.2

Distance from hatching site. The table gives loxodromic distance rounded to full km (median; number of birds ringed; minimum to maximum) between nesting and recovery site for Stonechats of the focal populations during their first year of life.

Month	NL and Belgium			Germany			British Isles		
	median	n	range	median	n	range	median	n	range
1	—	—	—	1485	1	1485 – 1485	17	12	0 – 1076
2	1711	2	1710 – 1711	1574	3	1195 – 2292	280	3	23 – 442
3	816	2	597 – 1034	124	3	66 – 1211	23	4	14 – 466
4	13	5	0 – 46	14	3	5 – 46	21	4	0 – 57
5	0	1	0	5	9	0 – 13	4	42	0 – 9
6	0	2	0 – 0	—	—	—	0	03	0
7	0	4	0 – 1	5	2	0 – 10	1	14	0 – 53
8	9	2	4 – 13	0	1	0	19	11	0 – 48
9	5	8	0 – 881	10	2	0 – 21	29	20	6 – 228
10	245	5	22 – 2014	1498	5	7 – 1986	36	13	6 – 1520
11	1703	3	1660 – 2129	1849	6	1677 – 1897	1081	5	13 – 1760
12	1802	3	1102 – 1978	1584	3	1073 – 1841	71	7	4 – 1925

and August young from continental populations were recovered in the vicinity of their nesting sites (maximum 10 km) whereas British Stonechats had dispersed to greater distances (maximum 53 km). Emigration of the young started in September, and between November and February, all recoveries from the two continental populations were further than 1000 km from the ringing sites. For British Stonechats where information is best,

postfledging movements are shown in detail (Fig. 5.9). In July, two young birds had already moved c. 50 km, at ages of c. 70 and 80 days. Apart from these birds, movements remained short (up to c. 25 km) until mid August. Long movements began in the second half of September.

Differential migration

Figure 5.10 shows the wintering distribution of sexes for the three populations. In Fig. 5.11, the winter recovery sites can be compared between first year and older birds. From the maps there is no indication for differential migration patterns based on age or sex in any of the populations. I compared the distance flown to wintering sites between first year and older birds within the three focal populations and found no effect of age (ANOVA: $F(1;28)=0.326$; $p=0.725$; no interactions between age group and subspecies). Nor were there any effects of hatching date of first year birds on the distance flown (linear regression, n.s.). For an assessment of differences between the sexes, the sample size was very small because most birds had been ringed as nestlings and hence were unsexed by the ringers. Non-parametric testing revealed no differences between six females and four males of the focal populations in the distance to the wintering sites (Mann-Whitney $U=9.00$; $Z=-0.64$; $p=0.610$).

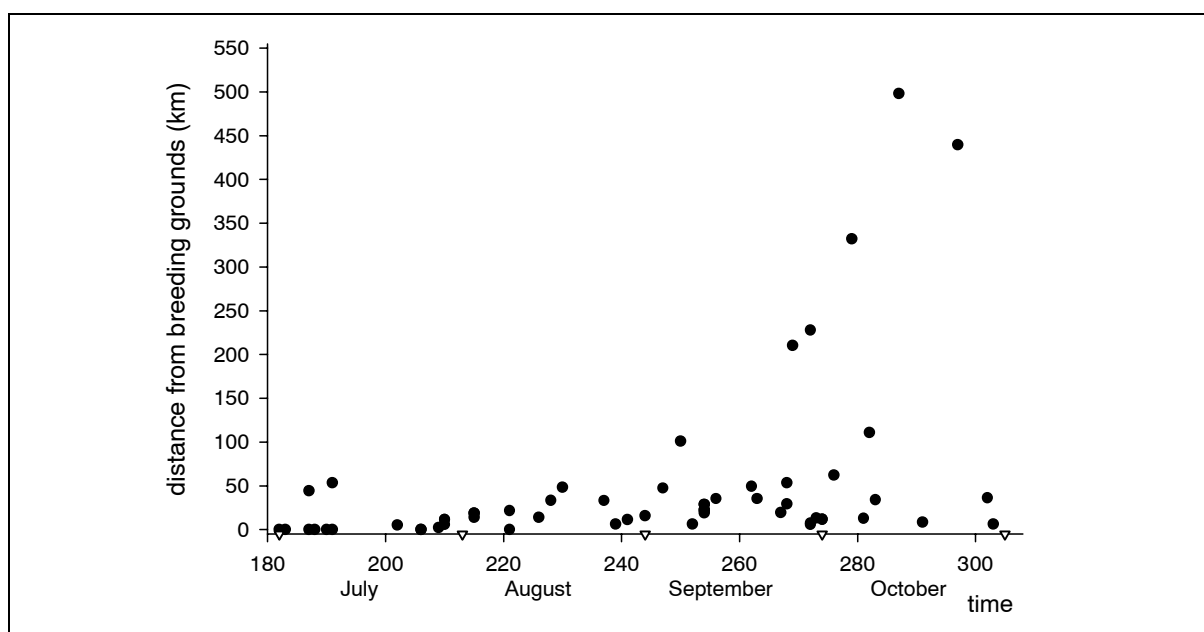


Figure 5.9

Postfledging movements of British Stonechats. The graph shows distance from the ringing site in relation to time of recovery from July to October (magnified detail from Fig. 8; see there for details); note that the distance flown by one bird recovered after 1520km on October 15 is not plotted.

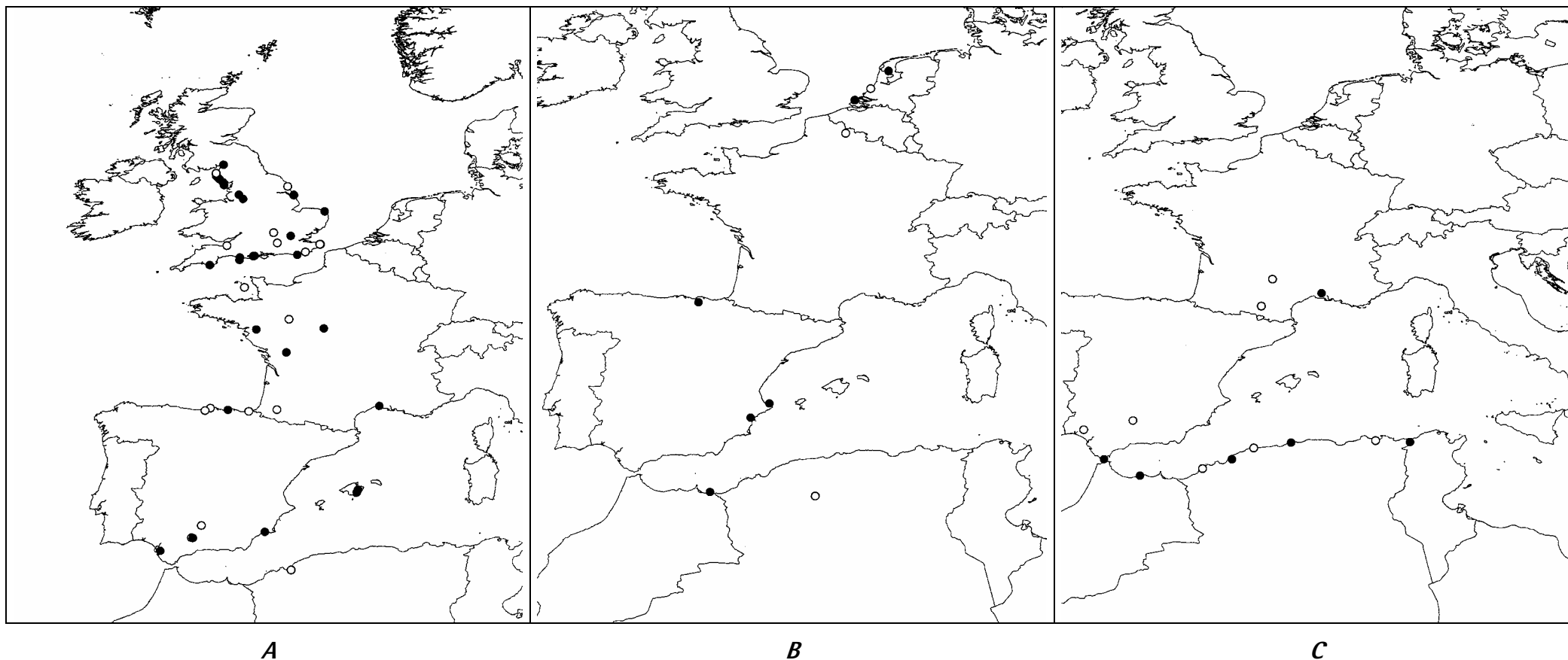


Figure 5.10

Wintering locations by sex. Full circles indicate recoveries of males, and open circles of females from the focal regions between November and January. A: British Stonechats; B: Dutch and Belgian Stonechats; C: German Stonechats.

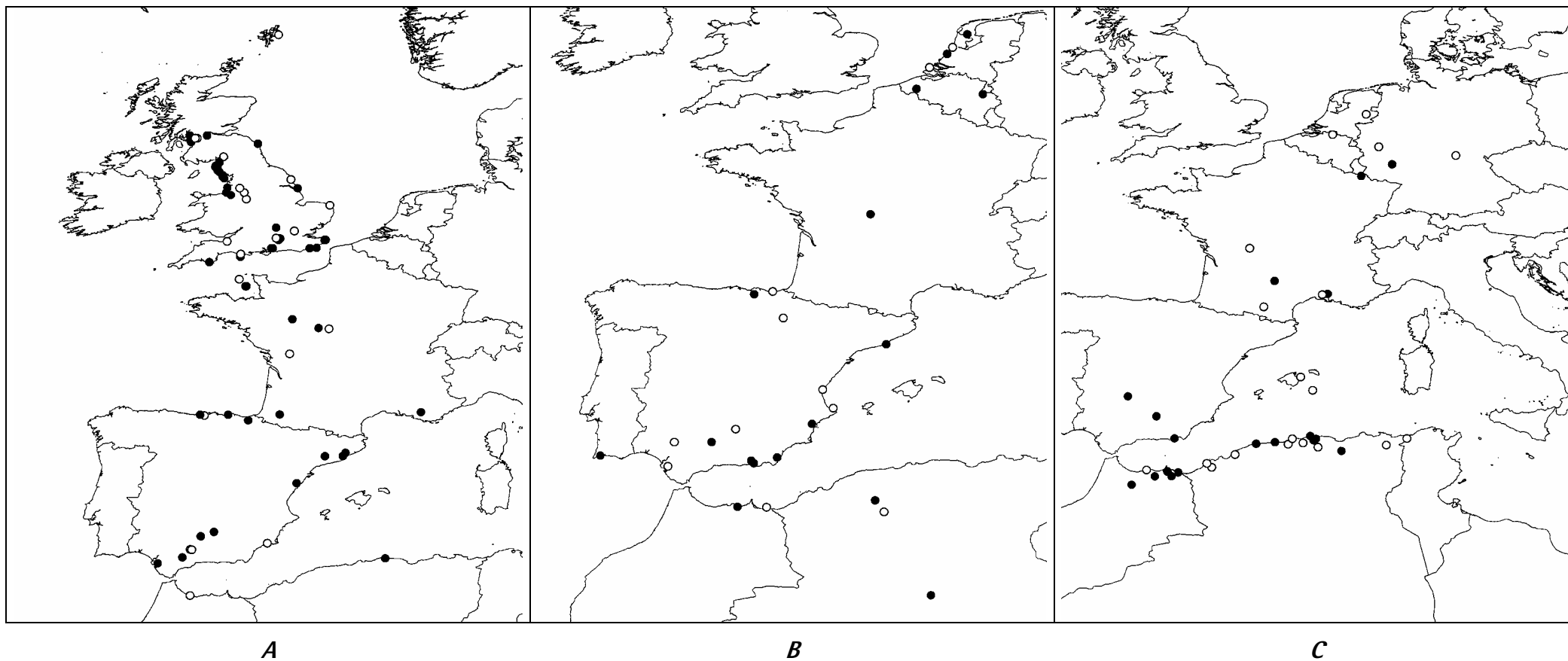


Figure 5.11

Wintering locations by age group. Full circles indicate recoveries of first year birds, and open circles recoveries from older birds between November and January. A: British Stonechats; B: Dutch and Belgian Stonechats; C: German Stonechats.

Time trends

I tested for changes in migratory behavior of Stonechats in two ways: firstly, I checked if migratory distance decreased over time by comparing the distance from the breeding grounds of birds recovered in the winter months. For all Stonechats ringed in the three focal areas during the breeding season, loxodromic distance to the wintering sites from the breeding grounds had not changed (ANOVA: $F(1;39)=0.306$; $p=0.583$). The populations differed from each other ($F(2;39)=4.057$; $p=0.025$) but not in their behavior over time (interaction between time slot and subspecies: $F(2;39)=1.724$; $p=0.192$). A closer look at British Stonechats revealed the same tendency: among migrants, there was no indication of a shortening of migratory distance (Mann-Whitney $U=18.00$; $Z=-1.061$; $p=0.289$). Similarly, the proportion of residents increased slightly but not significantly since 1980 (likelihood ratio= 2.728 ; $df=1$; $p=0.19$). Until 1979, nine of 17 birds were migrants, whereas since 1980, only six of 19 Stonechats overwintered far from the breeding site.

Discussion

Although the amount of data has increased sevenfold since Van Hecke's (1965b) analysis the overall patterns of Stonechat migration have not markedly changed. Migratory directions and the ringing and recovery locations very much resemble those shown by Van Hecke (1965b). However, based on the much extended data, some unambiguous answers can be given to open questions. There is no indication to date of recent changes in migratory behavior in Stonechats.

The partially migratory status of British Stonechats was confirmed but the migrant proportion of 42% was higher than suggested in the recent literature. Even if the criterium for migrants as those that leave Britain is applied, a large percentage (38.9%) migrated. This proportion may underestimate the true migratory propensity of the population because British recoveries may be more likely than those from countries with less popular interest in birds. As in other partial migrants, the migratory distance of British Stonechats was lower than in the entirely migrant Belgian, Dutch, and German populations, but some birds did fly as far as their conspecifics. For those British birds that migrated, the preferred direction seemed to differ from the continental Stonechats. Whereas continental Stonechats migrated mainly to southwestern and southern wintering quarters, the preferred direction of British Stonechats appears to be south-south-east (Glutz and Bauer 1988). Belgian and Dutch migrants have been recovered further west than central European Stonechats, leading to suggestions that the birds fly directly south across the Mediterranean. Captures of central European Stonechats on Mediterranean Islands, mostly on Majorca, and passage data from the Italian Adriatic coast also indicate flights across the Mediterranean (Van Hecke 1965b; Glutz and Bauer 1988).

A higher proportion of migrants than previously assumed and maximal overwintering distances that are close to those of continental Stonechats accord to the result of Chapter 4 that migratory behavior is pronounced in Irish Stonechats. The timing of migration in both, British and European Stonechats also parallels the behavior of captive birds (Chapter 4, Fig. 4.7). However, it is yet unclear why in captivity all Irish Stonechats showed migratory urge while the migrant proportion expected from ringing recoveries should be around 40%.

The migratory status of the Belgian and Dutch population, judged from ringing recoveries, is clearly migrant. The dates of foreign recoveries of local Stonechats and the distances flown indicate that local birds emigrate in winter (Fig. 5.8B). There are no differences in migratory behavior to German Stonechats. The convincingly migrant behavior is surprising in view of two records of breeding dispersal of British Stonechats to Belgium (Van Hecke 1965b; J. Callion, pers. comm.). The origin of birds wintering in Belgium and the Netherlands remains obscure because so far, no ringed Stonechats have been recovered in winter in these countries. Van Hecke's (1965a) suggestion that overwintering birds originated from the British Isles has still not found support.

Dhondt's (1983) hypothesis that local birds overwinter in Belgium appears unlikely upon closer inspection of ringing recoveries. The argument was based on local recoveries but these birds were exclusively found in October while migrants were still near their breeding sites (Fig. 5.8; cf. Cramp et al. 1988; Glutz and Bauer 1988). In addition, Dhondt (1983) suggested that the number of overwintering Stonechats was reduced after cold winters and may therefore indicate natural selection. His data do not sufficiently support this conclusion because alternative interpretations are possible. Dhondt's argument could be strengthened if he had shown that after cold winters overwintering Stonechats are significantly more reduced than the breeding population. But even then, an unambiguous interpretation of the results would be hard because there is no indication that breeding and wintering Stonechats belong to the same population. Presently, there is therefore no evidence that Belgian and Dutch Stonechats are partial migrants and that changes in the numbers of overwintering birds may be caused by natural selection.

There is no support for any differential migration patterns in Stonechats. In all three focal populations, the sexes and age classes behaved alike, in keeping with the lack of endogenous differences in captive Irish Stonechats (Chapter 4). Identical migratory behavior of the sexes may be facilitated by the fact that Stonechats, unlike most migrants, winter in pairs (Johnson 1961, 1971; Roedl 1994, 1999; Urquhart 2002). The occasional reports of differences in migratory phenology of age groups may be due to other factors. Firstly, they are based on coastal observations. An age differential of migrants along coasts with a predominance of young birds has been reported in many cases and has been termed "coastal effect" by Ralph (1974, 1978). Aggregations of young birds along coasts have been

related to disorientation and lack of experience. Therefore, a greater proportion of young along coasts cannot be taken as evidence for differential migration. Secondly, if age differences in migratory behavior exist in Stonechats they may be due to age-related survival. Roedl (1994, 1999) studied pair territoriality of Stonechats wintering in Israel and estimated that roughly 30% of the birds, mostly juvenile males, did not find partners. They were significantly more likely to vanish from the wintering grounds under difficult environmental conditions (Rödl 1999). Therefore in Stonechats, differential migration may occur sporadically as a behavior-mediated density effect under difficult conditions (Kalela 1954). Behavioral data corroborate this idea. Migrating Stonechats show social tendencies (Van Hecke 1965; Clark and Eyre 1993; Flinks 1999; Urquart 2002) but aggression in captive European Stonechats reportedly rose endogenously and sharply after core migratory activity but before Zugunruhe stopped (König et al. 2002). The actual success of a Stonechat to secure a pair territory and its resulting access to food sources might hence determine whether or not it moves on (Kalela 1954; Gwinner et al. 1988; Schwabl and Silverin 1990).

Chapter 6

Reproductive timing in European and Siberian Stonechats (*S.t. rubicola* and *maura*) and its implications for hybridization of the two subspecies

Summary

The two migrant subspecies, Siberian and European Stonechats, differ in reproductive timing, related to the European Stonechats' shorter migratory journey and longer breeding season. Both have expanded their breeding ranges and started hybridization. The relative success of crossbreeding pairs depends in part on the subspecies' ability to synchronize their breeding cycles. Therefore, I tested the persistence of reproductive timing of both subspecies under identical condition. Individually caged birds of the two subspecies differed from each other in the timing of gonadal growth. In aviaries, crossbreeding birds were exposed to a mate with a different reproductive schedule. Siberian Stonechats of both sexes did not synchronize to the longer breeding season of their European mates. Reproductive success, defined here as the number of fertile clutches per pair, was therefore dramatically reduced in crossbreeding Stonechats. The costs of hybridization were high for the population with the longer breeding season, i.e., European Stonechats. Crossbreeding European males fathered fewer clutches because Siberian females initiated egg-laying later. Crossbreeding European females suffered high infertility of clutches prior to the Siberian breeding season. The study shows that in contrast to some other species Stonechats have rigidly programmed breeding cycles. Differences in reproductive timing may add to detrimental effects of range expansions and hybridization when populations with rigid endogenous programs meet.

Introduction

Like other animal species (Wuethrich 1999; Thomas and Lennon 1999; Berthold 2001; Pimm 2001) Stonechats are reportedly changing their ranges. As a consequence, new distribution patterns and concomitant hybridization additionally threaten this bird species of European conservation concern (Tucker and Heath 1994; Wuethrich 1999; Allendorf et al. 2001). European and British Stonechats are suffering population declines in Western Europe but are extending their breeding range to the northeast, while Siberian Stonechats are expanding westwards (Vaurie 1959; Cramp et al. 1988; Pfeifer 2000; Urquhart 2002). In 1997 the first hybridization between *S.t. maura* and *S.t. rubicola* was observed on Heligoland (Pfeifer 2000), indicating an incipient contact zone between the formerly fully separated subspecies. Four young were successfully raised. The two Stonechat subspecies have evolved distinct seasonal schedules (cf. Introduction; Cramp et al. 1988; Urquhart 2002). European and British Stonechats are multi-clutched over a long breeding season

from March to July, while Siberian Stonechats usually lay a single clutch between mid-May and June. If the timing of reproduction were rigidly fixed, crossbreeding should be confined to the short period from mid-May through June when the subspecies' breeding cycles overlap. Timing differences between the subspecies could thus impair hybridization through prezygotic isolation (Turelli et al. 2001).

The purpose of this chapter is to test the rigidity of reproductive timing in Stonechats. Avian reproduction is possible only during population-specific breeding seasons when the gonads are enlarged and active (Murton and Westwood 1977). It has been shown that while in some bird species reproductive activity is rigidly controlled, it is timed more flexibly in others (e.g., Berthold 1969; Hahn et al. 1997). The time window during which breeding is possible can be extended beyond the normal breeding time by appropriate supplemental cues. Social stimuli such as the presence of a mate in breeding condition have advanced breeding (e.g. in anatids, Davies et al. 1969) or sustained reproductive activity in birds (Runfeldt and Wingfield 1985; cf. Hahn et al. 1992, 1997). In contrast, earlier studies in African Stonechats suggest rigidly programmed annual cycles and no effects of mate presence in birds kept in indoor boxes (Gwinner 1991; Gwinner et al. 1995b). Here, I test the rigidity of reproductive timing in Stonechats in the presence of a mate in breeding condition. Because of the different breeding timing of the subspecies, Siberian Stonechats can be exposed to a European mate that is in breeding condition before the time during which they usually breed. To investigate whether timing differences impair reproduction, European and Siberian Stonechats were therefore bred and crossbred in large outdoor aviaries. Simultaneously, gonadal cycles were monitored.

A first experiment was designed to test whether the gonadal cycles of males of the two subspecies differed from each other under identical conditions in captivity, corresponding to the subspecies differences in reproductive cycles of free-living birds. Because laparotomies might interfere with breeding repeated measurements during the breeding season were taken of birds kept individually in inside registration cages. Comparative measurements of aviary males were taken at the beginning and end of one breeding season.

In a second experiment, Stonechats were matched into mixed and same-subspecies pairs, allowed to breed, and monitored for their reproductive success. By experimentally matching birds into same-subspecies and mixed pairs, I excluded the possibility of mate choice that in the field may limit hybridization. However, matching of pairs may mimic the situation in a hybridization zone at the margin of a species range where access to a breeding partner of the same subspecies is limited. Among European passerine birds, there has been compelling support for Hubbs's principle stating that hybridization should occur most frequently where one of the (sub-)species involved is rare (Randler 2002). Furthermore, evidence is increasing that under the time pressure typical for birds at

northerly latitudes, mate choice may be constrained and counteracted by selection for early breeding (e.g., Alatalo et al. 1986; Gowaty 1997; Veen et al. 2001).

Material and methods

From 1998 until 2001, two experiments were conducted with European and Siberian Stonechats. Birds were either collected as nestlings in Austria and Kazakhstan or were offspring from pairs held in institute aviaries as described in the General method section. Firstly, gonad size was measured in 35 individually caged Stonechats (*S.t. maura*: ten females, 13 males; *S.t. rubicola*: five females, seven males) by laparotomy (Gwinner et al. 1995) at approximately monthly intervals. Measurements during the breeding season were taken on individually caged birds to minimize interference with breeding activities in the aviaries. Onset and end of the testicular and follicular cycle were defined as the first and last dates on which birds had gonadal sizes equal to or above a threshold value (females: 0.8 mm; males: 1.5 mm). For statistical analysis, I compared the proportion of birds of each subspecies in reproductive condition by likelihood-ratio testing. Tests were carried out over the late February, early April, late May, June and July measurements. In January all birds were below, and in early May above the threshold values.

To check for possible effects of individual caging on gonadal size, control measurements of subsamples of aviary males were taken at the beginning and end of one breeding season. At the very beginning of the breeding season of 2002 males were checked on April 4 (n=17; six Siberian and 11 European males). This was three weeks after the birds were paired up and moved from individual cages into outdoor aviaries. At the end of the breeding season of 2001, flight feather molt and testes sizes of males were simultaneously assessed (July 15, n=22; nine Siberian and 13 European males). Since testis size and molt score were closely negatively correlated ($r=-0.90$; $p=0.000$; $n=22$), statistical testing was carried out over testes sizes only. Among the 22 males, 12 were mated to a female of their own subspecies and ten to a conspecific belonging to the other subspecies. Nine of the 22 males had been successful breeders. Chi-square tests were conducted to test if breeders and non-breeders were evenly distributed over the parent constellations. There were no significant associations between male subspecies, breeding status, and subspecies of the female mate. Therefore, testes sizes were analyzed in a full factorial 3-way ANOVA with subspecies, breeding status, and subspecies of the female mate as fixed factors. After a first run of the ANOVA, all factors that were clearly non-significant ($p>0.1$) were eliminated and the ANOVA was recalculated.

In the second experiment, 79 pairs of European and Siberian Stonechats were bred in large outdoor aviaries in Seewiesen, Germany. After wintering indoors, the birds were kept in aviaries from approximately mid March until molt in late summer. They were paired into the four parent constellations so that approximately 20 pairs of each of the two subspecies

and the two mixed-subspecies constellations were allowed to breed. Aviaries were checked for breeding activity at intervals of five days or less. Clutch initiation was calculated assuming daily laying. The calculated date of the first deposited egg represented the laying date of a given clutch. Hatched young were hand-raised from an age of five to seven days. Infertile clutches were left to be incubated until eggs were removed about one week after the calculated hatching date.

The fertility of eggs was determined by hatching success and by candling all eggs over a bright light (LED Lenser). Clutches were defined as fertile if at least one egg hatched or if embryonic development was visible. For the purpose of this chapter, I defined reproductive success as the number of fertile clutches laid by a breeding pair. The definition of fertility is complicated by the fact that undeveloped eggs do not preclude sperm presence or very early embryonic mortality (Kempnaers et al. 1999). Therefore, I cannot exclude the possibility that clutches defined as "infertile" had actually been fertile but stopped development at a very early stage of incubation (Carter et al. 2000). To assess the proportion of undeveloped clutches that had been fertilized, 67 eggs from 14 unhatched clutches laid over the breeding season of 2002 were screened for the presence of sperm. Eggs were studied by investigations of stained perivitellar membranes as described by Kempnaers et al. (1999).

The data were grouped into two data sets, one accumulating reproductive events for each breeding pair over the entire breeding season ($n=54$). These data were used to compare the numbers of clutches and fertile clutches per pair between parent groups. In the other data set each clutch was treated as a unit ($n=83$) to compare the proportion and timing of fertile clutches between parent groups. Statistical methods included likelihood-ratio testing of nominal data (fertility status), derivation of Kendall's tau b for ordinal data (number of clutches, number of eggs), and two-factorial ANOVA analysis of the timing of egg laying. In the ANOVA, one laying date (Julian date = 203) qualified as an outlier according to Dixon's criterion (Sokal and Rohlf 1995; $p<0.05$) and was left out of the analysis.

Results

Among the caged birds, individuals of the two sexes were largely synchronous. Small differences between the sexes in Siberian Stonechats were not significant. European Stonechats developed gonads earlier than Siberian Stonechats: in late February, all European but none of the Siberian Stonechats had initiated gonadal growth (Fig. 6.1A; $n = 36$; likelihood-ratio 45.8 on $df = 1$; $p = 0.00$). From early April gonads were enlarged in all Siberian males and in 7 out of 10 Siberian females. Gonads regressed below threshold values in the first caged males in late May and in females in June. Until the end of the breeding season, there were no further subspecies differences. Hence, in Siberian

Stonechats gonadal growth started later but reproductive activity lasted as long as in European Stonechats. These results were partially confirmed by measurements of aviary males. In early April all European but only half of the six Siberian males in outdoor aviaries had initiated gonadal growth.

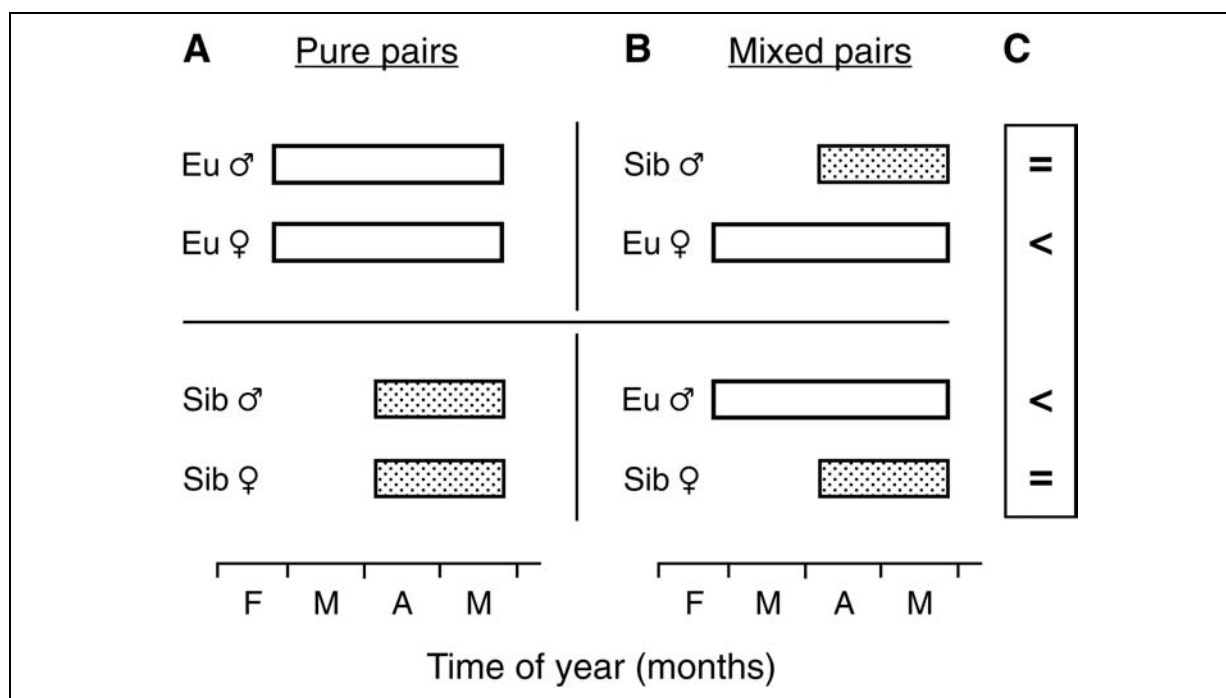


Figure 6.1

Timing of active gonads in Stonechats. Timing of enlarged gonads of individually caged European (open bars) and Siberian (shaded bars) Stonechats in experiment 1. Bars indicate the times of the year when mean testis size and mean size of the largest ovarian follicle were above a threshold level of 1.5 mm and 0.8 mm respectively. Arrangement of bars predicts the matching of reproductive timing in (A) same-subspecies pairs and (B) mixed pairs; (C) predicts reproductive success of males and females in mixed pairs compared to that in same-subspecies pairs (= same success; < reduced success).

Gonadal growth in Siberian males was far behind that of European males, as indicated by their significantly smaller testis size (mean \pm std: Siberian = 1.62 ± 0.44 ; European = 4.28 ± 0.4 unpaired t-test; $t = -12.01$; $df = 15$; $p = 0.00$). Therefore, the subspecies differences shown in caged birds were confirmed, but gonadal growth occurred later in outdoor aviaries, at least in Siberian Stonechats.

At the end of the breeding season on July 15, testes of aviary males were still large whereas males in institute cages had reduced them to non-reproductive condition (Fig. 6.2). In contrast to caged birds, aviary males of the two subspecies differed from each other at the end of the breeding season. Whereas most Siberian males had halved their testes size and all had initiated molt, testes were much larger and molt scores lower in European

males (Fig. 6.2; ANOVA of testis size: subspecies: F-ratio = 10.930; df = 1; 17; p = 0.004). Males mated to females of the same subspecies had larger testes than those in mixed pairs (F-ratio = 7.22; df = 1; 17; p = 0.016), and this was true for males of both subspecies (no interactive effects between male subspecies and identity of the breeding partner). Successful breeding had no influence on testis size. There was a tendency for breeders to have large testes independent of the subspecies of the breeding partner while non-breeders had large testes only when mated to a female of the same subspecies (interaction of breeding status and mate subspecies: F-ratio = 3.87; df = 1;17; p = 0.066). In comparison to the caged individuals, the reproductive season lasted longer in paired male Stonechats of both subspecies in outdoor aviaries. In addition, in July European males had larger gonads than Siberian males, indicating that the breeding season began earlier and ended later in European Stonechats.

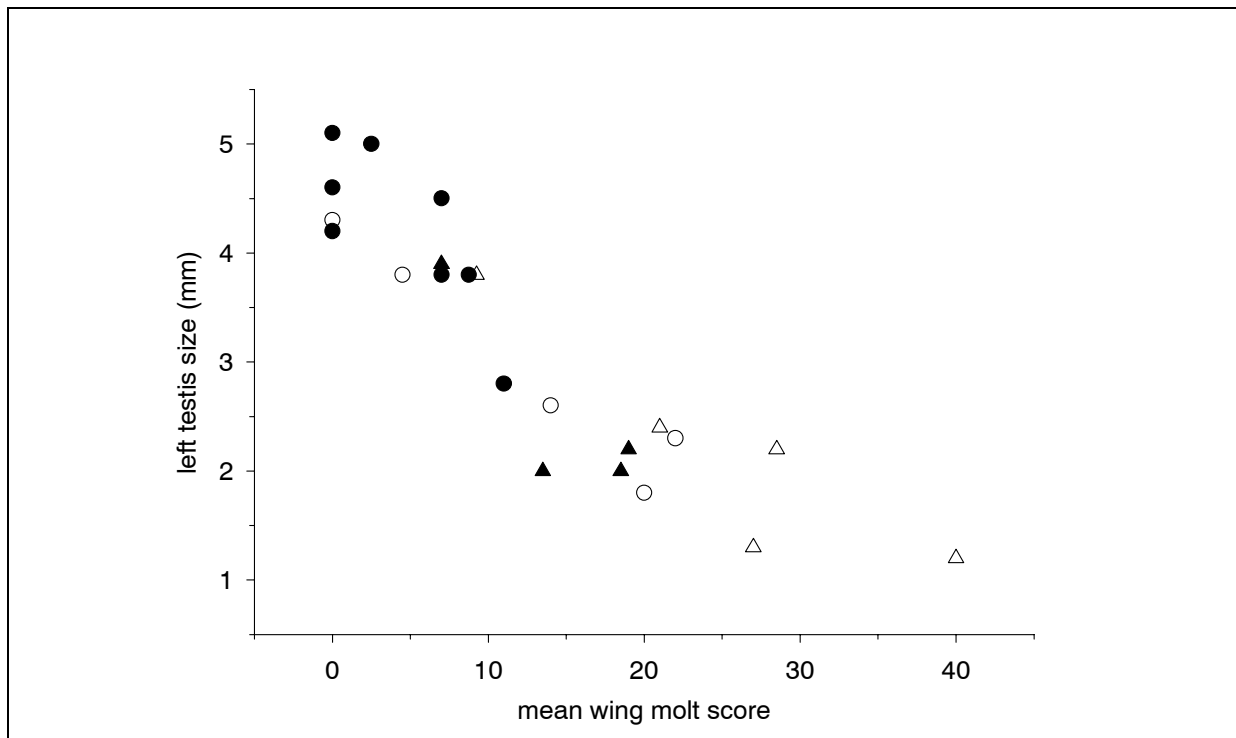


Figure 6.2

Testis size and flight feather molt late in the breeding season. The abscissa shows wing molt score of aviary males at the end of the breeding season (July 15); the ordinate gives the size of the left testis on the same day; different symbols indicate male subspecies (circles: European males; triangles: Siberian males) and the subspecies of the mating partner (filled symbols: same subspecies; open symbols: crossbreeding).

On the basis of the timing differences a mismatch between the reproductive cycles of the breeding partners in mixed pairs was predicted (Fig. 6.1B). For the mate of the subspecies with the longer reproductive period (i.e., the European Stonechat), the mismatch

early in the breeding season should result in reduced reproductive success (i.e., fewer fertile clutches per pair). This prediction was tested in a second experiment, in which a total of 79 pairs of all four parent constellations were bred in aviaries. 70.9 % of the pairs laid eggs. 83 clutches were classified as either fertile or infertile. They were laid by nine Siberian and 15 European pairs, and by 13 crossbreeding Siberian and 15 crossbreeding European females. Viable offspring of both sexes hatched from all parental constellations.

The females laid eggs at the times typical of their respective subspecies (Fig. 6.3). As a consequence of the earlier onset of their breeding season, the European females laid more clutches than the Siberian females (Kendall's tau $b = 0.34$; $n=52$; $p=0.00$). Accordingly, males of both subspecies fathered more clutches when mated to European females than when mated to Siberian females. In crossbreeding European males the difference in the number of clutches was significant (Kendall's tau $b = 0.48$; $n=28$; $p=0.00$) whereas in crossbreeding Siberian males it was not. The fertility of clutches depended strongly on the parental subspecies (Fig. 6.4). In same-subspecies pairs, most clutches were fertile (Siberian: 76.9%; European: 71%). In contrast, in mixed pairs clutch fertility was dramatically affected by the parent constellation (likelihood-ratio = 13.55; $df=1$; $p=0.00$). In comparison to same-subspecies pairs, the proportion of fertile clutches dropped markedly in crossbreeding *S.t. rubicola* females (36%; likelihood-ratio = 6.97; $df=1$; $p=0.01$; Fig 6.3A vs. C). In crossbreeding *S.t. maura* females the percentage of fertile clutches rose (non-significantly) to 92.9% (Fig. 6.3B vs D). Together, the differences in number and fertility of clutches reduced the reproductive success of mixed pairs (average: 0.79 fertile clutches per pair) compared to that of same-subspecies pairs (average: 1.22 fertile clutches per pair). Hence, hybridization lowered reproductive success significantly (Kendall's tau $b = -0.26$; $n=51$; $p=0.03$).

An analysis of lay dates revealed significant differences between the subspecies, with an overall earlier lay date in European (mean date: 15 May) than Siberian females (mean date: 21 May). This is consistent with the timing differences in the gonadal cycles of the birds in experiment 1 (Fig. 6.1). Figure 6.3 also shows a tendency of females to lay eggs later in the season when paired with a male of their own subspecies. The parent groups also differed in the timing of their respective infertile clutches: Same-subspecies pairs (Fig. 6.3A, B) laid infertile clutches mostly late in the season whereas in crossbreeding European females infertile clutches peaked early in the laying period (Fig. 6.3C). The difference in the timing of infertile clutches was statistically expressed by the significant interaction between fertility and parent constellation (ANOVA of laying dates: parent group: F-ratio=5.26; $df=1;74$; $p=0.00$; fertility: F-ratio=2.59; $df=1;74$; $p=0.11$; interaction of fertility and parent group: F-ratio=4.41; $df=3;74$; $p=0.01$). In addition to this time-related early infertility there was also a persistent infertility component in crossbreeding European Stonechats.

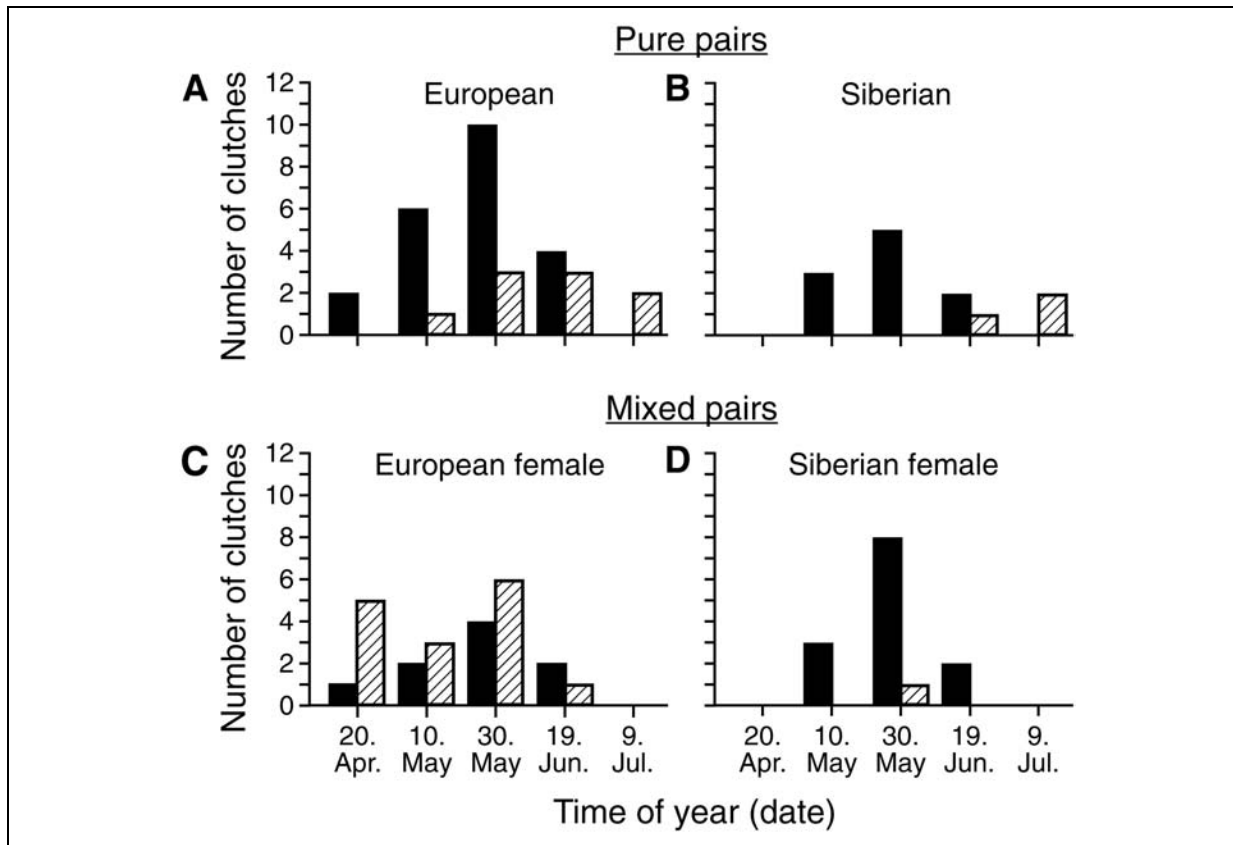


Figure 6.3

Timing of egg laying in Stonechats. The abscissa gives the mean dates of successive 20-day intervals within which clutches were initiated. Bars show number of fertile (black) and infertile (hatched) clutches of the four parent constellations (A-D).

Inspection of eggs laid in the breeding season of 2002 indicated the absence of sperm in most undeveloped eggs, as judged from the perivitellar membrane. Among 67 eggs from 14 unhatched clutches, embryonic mortality was found in three eggs of a single clutch, and sperm was present in one additional egg. In the remaining 63 eggs, no sperm was detected.

Discussion

Hybridization of Stonechat populations lowered their reproductive success significantly. The results of this chapter provide strong evidence that this reduction was caused by rigid reproductive timing that differed between the subspecies. Females of both subspecies laid eggs at the times typical of their subspecies, regardless of the subspecies of their mate. Therefore, females were not synchronized to the reproductive condition of their partner.

European females mated to Siberian males were multiclutched, but egg fertility was dramatically reduced. The occurrence of infertile clutches was not an artefact of aviary breeding because overall, the proportion of fertile clutches was similar to that of fertile

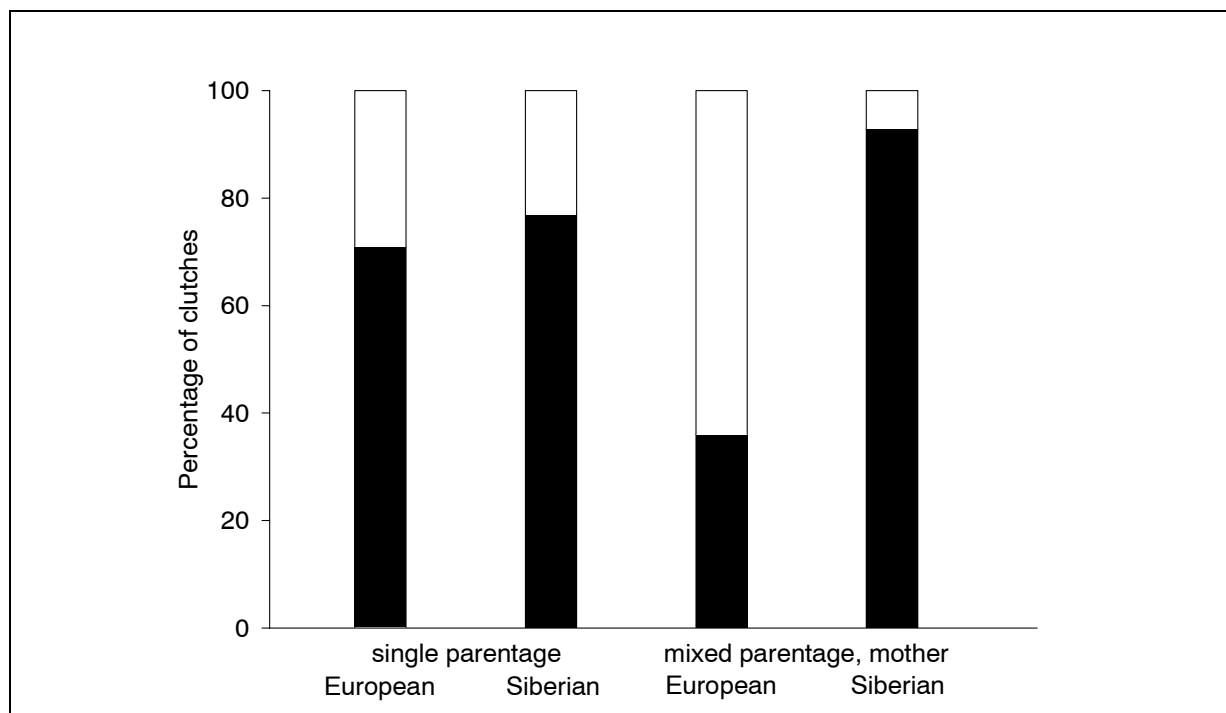


Figure 6.4

Clutch fertility in relation to parent constellation. The histograms show the proportion of fertile (black) compared to that of infertile clutches (white) for each of the four parent constellations.

eggs in the field (ranging between 5% and 30%; Johnson 1971; Rogacheva 1998; Urquhart 2002). Field studies showed a tendency of the proportion of unhatched eggs to increase in late clutches, presumably caused by a seasonal decline in fertility (Johnson 1971). Although the aviary data for European and Siberian Stonechats refer to fertility of clutches rather than eggs, the proportions and seasonal trends of fertility are in good correspondence with the field data. In same-subspecies breeding pairs, infertile clutches occurred late in the breeding season. Molt and testes sizes of aviary males in mid July suggest that male fertility may have been reduced when females laid late clutches. Sexual conflict over the termination of the breeding season has been shown in other species, e.g. in Flycatchers (*Ficedula albicollis* and *F. hypoleuca*) where males started molt early while females still allocated their energy to reproduction, risking an overlap of molt and migration (Hemborg and Lundberg 1998; Hemborg and Merilä 1998; Slagsvold 1999). In contrast to same-subspecies breeding pairs, clutch fertility in crossbreeding European females dropped to 36%. The distinct peak of infertile clutches occurred at the beginning of the breeding period when their Siberian mates were predicted to have inactive gonads. Since inspection of unhatched eggs indicated the absence of sperm, i.e. "infertility" was prezygotic, I propose that it originated from insufficient synchronization of males. The results of this chapter suggest that both breeding partners were not synchronized, and that the mismatch

between them predicted from the gonad cycles of caged birds (Fig. 6.1A) had deleterious consequences.

These results confirm earlier studies that have shown rigid endogenous circannual programs for reproduction in Stonechats (Gwinner 1991; Gwinner et al. 1995b). However, even in Stonechats there appears to be a small amount of flexibility in response to supplemental timing cues. Males caged individually indoors initiated gonadal growth earlier than those living with a mate in outdoor aviaries, possibly due to lower ambient temperatures outside (Maney et al. 1999). Furthermore, in the aviary experiments, Stonechats of both sexes reduced their reproductive activities earlier when paired with a mate of the other subspecies. It is possible that due to conflicting demands before migration the maintenance of reproductive condition is sensitive to social stimuli. The earlier molt in crossbreeding males suggests that the time gained by early termination of the breeding season is used for a presumably competing seasonal activity (Slagsvold 1999). The difference to earlier results from African Stonechats that have demonstrated little flexibility, e.g. with respect to the presence of a mate, may be related to differences between populations or to the experimental setup. Outdoor aviaries presumably provide much better breeding conditions than the boxes used in the earlier study (Gwinner et al. 1995b).

In contrast to the small adjustments of reproductive timing in Stonechats, other species - like the European starling (*Sturnus vulgaris*; Berthold 1969; Gwinner 1975) and some opportunistic breeders (Hahn et al. 1997) - can adjust their reproductive timing to supplemental cues such as climatic conditions or the breeding state of their mate. In geese, crossbreeding of species with different reproductive timing did not change the lay dates of females, but males fathered successful clutches up to one month before their usual breeding time (Davies et al. 1969). Oestradiol treatment that artificially extended the breeding condition of freelifing female Song sparrows, *Melospiza melodia*, delayed the completion of reproductive activities of their mates by up to three months. In such species, detrimental effects of different reproductive windows may be compensated by social synchronization between breeding partners.

Although the aviary data presented here cannot be directly applied to the situation in the field, they provide strong experimental evidence that rigid differences in reproductive timing can play a key role in counteracting hybridization. Although the costs reported here were detrimental, they probably underestimated real costs because they only accounted for reduced reproductive success. In addition, crossbreeding European females wasted reproductive effort by the production of infertile eggs. Recent studies have pointed out that egg production has larger costs for females than previously assumed and can lead to significant fitness reductions (Slagsvold and Dale 1996; Visser and Lessels 2001; Cottam et al. 2002; Kullberg et al. 2002). Furthermore, the reproductive value of eggs is thought to

decline as the season progresses (Daan et al. 1989), and this tendency has been confirmed for British Stonechats (Cummins 2002). Therefore, the sole survival of late clutches in crossbreeding European Stonechats of both sexes presumably further reduced reproductive success via lower offspring survival chances. Taken together, endogenous breeding programs provided by a circannual rhythmicity may thus severely constrain gene flow. If populations with different rigidly controlled breeding cycles crossbreed, the timing differences between them can waste reproductive effort at the expense of populations with the longer breeding season. Hence, timing differences between hybridizing populations can contribute to the decline of endangered species. Detrimental effects of unsynchronized populations may differ between bird species, depending on the relative rigidity of their timing programs.

Outlook:

Implications for timing under changing seasonal conditions

Stonechats, like other organisms, are faced with the challenges of human activities. In this outlook section, I review main effects of climate change that pertain to seasonal activities of birds. Based on the results of my dissertation, I make predictions about the possible ways in which Stonechats could respond to challenges posed by changes in seasonality.

Evidence is ample that seasonal conditions are changing in response to anthropogenic influences on the environment. Climate change is predicted to be exacerbated over the next decades (Houghton et al. 2001). The Intergovernmental Panel for Climate Change (IPCC) regularly assesses and predicts effects of human activities on the global climate. The most recent report lists several aspects of climate change that may severely affect seasonal timing. Overall, global temperatures have risen by approximately 0.6°C (Houghton et al. 2001). The beginning of the growing season has advanced, and, to a lesser degree, autumnal events have been delayed, amounting to an extension of the growing season at least in temperate zones (e.g., Menzel and Fabian 1999). Precipitation has increased and a tendency for more frequent occurrences of extreme events has been noted. As a consequence, there is greater variation in the weather (Easterling et al. 1997, 2000; Houghton et al. 2002; Frich et al. 2002; Gitay et al. 2002). Observed changes have been spatially and temporally heterogeneous, differing in their geographical patterns and in the distribution over the year (Easterling et al. 1997, 2000; Watson et al. 1997; Frich et al. 2002). The spatial and temporal heterogeneity of changes further reduces the predictability of the climate, especially for mobile organisms like birds.

These changes have severe consequences for animals and plants (cf. Hughes 2000; Penuelas and Filella 2001; McCarthy et al. 2001; Gitay et al. 2002; Walther et al. 2002). Hughes (2000) classified observed effects on organisms into four groups: those on physiology, on distributions, on phenology, and on adaptation. All four groups of effects can bear on seasonal timing in birds. Changes in temperature and precipitation may directly modify seasonal schedules through physiological mechanisms, e.g., temperature-dependent gonadal maturation, or by interpretation of weather information as supplementary cue (e.g., Wingfield et al. 1992; Maney et al. 1999; Visser and Lambrechts 1999; Jacobs and Wingfield 2000). A higher frequency of extreme events can act as modifying information and thereby also change schedules (Wingfield et al. 1992). Birds alter their timing behavior in response to indirect effects of increasing temperature and precipitation, such as a seasonal advance in phenology of their habitats. Phenological changes in the growing season have been tracked by some bird species but not by others.

An earlier initiation of the growing season has prompted some species to breed earlier. Depending on the main food source for raising young and the width of their reproductive window, birds breeding earlier could either complete reproduction earlier in the year or add clutches and hence extend their breeding season. Multi-brooded species that do not depend on specialized food sources are those most likely to take advantage of the delayed onset of autumnal events by initiating additional clutches. Changing lay dates lead to different phase relationships between seasonal activities and day length. Hatchlings and breeding parents are hence exposed to different photoperiodic conditions.

Novel distribution patterns have already been discussed in the context of Chapter 6 (e.g., Wuethrich 1999; Thomas and Lennon 1999; Allendorf et al. 2001; Berthold 2001; Pimm 2001). Effects of climate change on adaptation have also been demonstrated in birds (e.g., Berthold et al. 1992; Brown and Brown 2000). Evolutionary modifications of time programs have been related to continuously changing selection differentials (e.g., Van Noordwijk et al. 1995) as well as to massive selection events following severe weather (Grant and Grant 1993; Brown and Brown 1995). Catastrophic events (e.g., James 1956) can lead to particularly rapid evolutionary change, provided that additive genetic variation of the trait is high.

Consequences of an increasing spatial and temporal heterogeneity of the climate may be severe for seasonal timing but are hard to predict. For instance, in the Netherlands spring temperatures rose late, but not early in the season, whereas in England the increase in spring temperatures was consistent, leading to different timing responses among Great tits of the two countries (Visser et al. 1998; Stevenson and Bryant 2000). Migrant species may be particularly vulnerable to such local differences in climate change patterns. Greater unpredictability of the weather may generally favour flexible timing strategies. If unpredictability is distributed non-randomly over the year it may affect life-cycle stages differentially. In addition, the impact of unpredictability may differ over the year, affecting birds most markedly during sensitive times of the annual cycle.

Taken together, Stonechats are faced with multiple challenges of climatic change. So far, modifications of their breeding range and novel hybridization patterns have been reported (e.g., Pfeifer 2000; Urquhart 2002; cf. Chapter 6). Increasing observations of Siberian Stonechats could be based on new migratory patterns of the Eastern populations (Cramp et al. 1988). For the migratory propensity of British Stonechats, possible changes have been predicted but not yet been observed (Callion 2002; Urquhart 2002). Field observations of Stonechats in Northern Germany suggest that first broods may occur earlier in the year but these tendencies still need to be confirmed (H. Flinks, pers. observation). The results of my dissertation about life cycle timing in captive Stonechats can be applied for inferences about possible consequences of and adjustments to modified seasonal conditions.

In the following section I summarize results of my dissertation that may bear on the Stonechat's response to changing climatic conditions in the left-hand column. In a parallel column to the right I juxtapose the results by their possible implications for the Stonechats' responses to climate change.

Main results of the study

Implications for responses to climate change

Chapter 1: growth

Stonechat populations differed in the dynamics of growth parameters but differences were not clearly related to seasonal pressure. Fluctuating asymmetry differed neither among populations nor between birds exposed to different time-constraints. Final sizes of the wing but not tarsus were reduced under time-constraints.

Growth rate in Stonechats varies between populations and may be modified by selection. Novel seasonal conditions are unlikely to markedly affect the time course and precision of growth. In contrast, if Stonechats hatch successively later in the breeding season photoperiodic responses such as diminished wing length could compromise recruitment chances of the young.

Chapter 2: postjuvenile molt

Molt served as a timing buffer regulated by day length. The way in which photoperiod affected molt timing was population-specific. Unlike African and European conspecifics, Siberian Stonechats molted much faster and no earlier under time-constraints. Although the populations modified molt timing differently, all completed molt earlier under short day length. In addition to phenotypic plasticity molt timing was heritable in a population-specific way. h^2 was high for duration in Siberian and onset and peak of molt in African and European Stonechats.

If young hatch later in the year, photoperiodic responses would modify molt timing. Hatching later in the year should advance molt in European Stonechats and accelerate it in Siberian Stonechats. Such phenotypic plasticity may allow late breeders to partially catch up in development with earlier breeders, but presumably at high fitness costs for offspring and parents. The magnitude of fitness costs may also depend on climate change, e.g. on conditions during molt late in the season. In addition, selection could successively modify the overall timing and duration of molt, but in different ways for the populations.

Chapter 3: selecting for molt timing

High h^2 of molt timing was corroborated by selection experiments in European Stonechats. There was some indication for a correlated change in reaction norms to day length at the photoperiodically most sensitive time, molt onset.

Under changed environmental conditions selection may affect molt timing by modifications of the photoperiodic response mechanism. Correlated responses of other photoperiodically driven mechanisms, further modifying timing behavior are conceivable.

Chapter 4: migration and molt

In Irish Stonechats migratory restlessness was closely related to molt peak and completion, suggesting that changes in the timing of one activity affect that of the other. Timing aspects of both molt and Zugunruhe but not of the time interval between them were heritable. There was no calendar effect on the interval between the two activities. – All studied Irish Stonechats were genotypical migrants, in contrast to other partially migrant species where residents and migrants differ in captivity. Nor did the sexes or age groups differ in Zugunruhe timing. A consolidation of these results by exclusion of alternative interpretations should renew an interest in environmental factors that suppress or trigger migration.

Late-hatched young that molt later may also delay migration, which in turn may increase mortality risks, especially if unpredictable weather becomes more frequent. Stonechats are unlikely to compensate for delays by modifying the interval between molt and migration. Effects of climate change on partial migrants are harder to predict in species in which migration is triggered by environmental factors than in those with a mainly genetical regulation. For species with environmental control of migration, research should aim to identify likely factors that favour or suppress migration.

Chapter 5: ringing recoveries

The field data on migratory timing but not on the proportion of migrants support the results from captive Stonechats. The seasonal distribution of recovery distances suggests graded movements in late summer and a possible overlap between molt and local movements. In British Stonechats, there is no indication of differential migration of the sexes or age groups. No time-trends in the occurrence and extent of migration were detected.

Studies on migratory timing in captive birds can indeed reveal realistic patterns that correspond to those in free-living conspecifics. In contrast, captivity results about migratory propensity may not be realistic in all species. In British Stonechats neither the distance of migration nor the proportion of migrants has changed over the last decades. There is no evidence for current changes in migratory behavior.

Chapter 6: reproductive timing

Reproductive timing of European and Siberian Stonechats is rigidly controlled. Siberian Stonechats took no advantage of favourable conditions early in the breeding season, even when offered a mate in breeding condition. Crossbreeding of birds with different reproductive windows did not result in an extended breeding season. Instead, European Stonechats with a longer breeding window wasted reproductive effort and suffered drastic reductions of reproductive success. Whereas Stonechats seem to be largely immune to social stimulation, the timing of their readiness to breed differed between individually caged birds and those paired up in outdoor aviaries.

Siberian Stonechats take no immediate advantage of earlier breeding seasons. An extension of the reproductive window in Stonechats therefore is unlikely to occur quickly. If range expansions of Stonechats and hybridization increase, costs of rigid reproductive timing may markedly reduce reproductive success of populations with longer breeding cycles. An introgression of Siberian Stonechats into the breeding range of European Stonechats is more likely than its opposite. In general, when populations with different breeding schedules meet, those with the longer breeding season may suffer time-related costs. However, an extended growing season may favour populations with longer reproductive windows, and lead to long-term adjustments of breeding seasons.

The above juxtaposition suggests that for some aspects of climate change, possible responses of Stonechats can be predicted from studies of their timing behavior. Stonechats rely in their annual timing strongly on endogenous programs that coordinate their responses to environmental cues (Gwinner 1999). The results of the dissertation show that the environmental cue predominantly used by Stonechats are changes in day length. Day length provides "initial predictive information" (Wingfield et al. 1992) independently of climatic change. In contrast to Stonechats, other species make greater use of immediate environmental information for correct timing of their activities (Wingfield et al. 1992; Hahn et al. 1992, 1997).

The Stonechat's reliance on day length cues becomes problematic because the phase relationship between day length and climatic conditions is changing rapidly as part of climatic change. In relying on photoperiodic information, Stonechats may incur two kinds of costs: they can only make limited use of advantageous conditions, and at the same time pay costs of hastened development regulated by their timing program, such as shortened wings or rapid molt, that may no longer be necessary in view of more clement outside conditions. Therefore, judged by their timing system, Stonechats are expected to be overall slow respondents to novel seasonal conditions. For instance, the lack of observable change in migratory propensity of Stonechats may be based on their rigid programs. Their

migratory behavior may be less quickly modified by selection than that of other species, e.g., the Blackcap (Berthold et al. 1992; Pulido et al. 1996; Berthold 1998). Similarly, changes in the timing of breeding in Stonechats may be slow in tracking phenology changes because the reproductive window appears to be rigidly programmed and hence unlikely to be rapidly modified (Gwinner 1999).

However, the above predictions for possible responses of Stonechats to climate change were based exclusively on studies of their timing behavior. Effects of climate change depend on a suite of characteristics of an organisms' life history, e.g. on main food sources and the degree of specialization, and on complex interactions with other climate-related changes (e.g., Hughes 2000; Walther et al. 2002). Therefore, other characteristics of Stonechats may enable them to steadily extend their breeding season in response to a longer growing season, despite their rigidly controlled reproductive cycles. In contrast to other species like Great Tits, *Parus major*, that rely for breeding on outbursts of specific food species (e.g., Van Noordwijk et al. 1985) Stonechats have relatively flexible foraging strategies and feed their young a variety of arthropod taxa (e.g., Greig-Smith and Quicke 1983; Rödl 1994; Rödl and Flinks 1996; Cummins 2002).

Within the limits set by their rigid reproductive windows, Stonechats have been shown to add clutches if conditions are favourable (König and Gwinner 1995). Differences between populations in the number of clutches have been reported on relatively fine local scales (cf. Gwinner 1999; for Siberian Stonechats cf. Dementiev and Gladkov 1968; for African Stonechats cf. Scheuerlein 2002). These differences further suggest that the length of the breeding season may be adjusted under changing selection pressure, provided that counteracting disadvantages do not proceed at a faster rate. Therefore in Stonechats, I would predict that an extended growth season may provide opportunities for slowly extending the breeding season.

By implication, Stonechats would then breed under new photoperiodic conditions, leading to possible responses that may impose costs like those mentioned above. The responses to day length differed between the populations but it is likely that within birds, a common photoperiodic mechanism may simultaneously affect various seasonal activities. Therefore, for accurate predictions we need a still deeper understanding of the mutual interdependence of seasonal activities. On the basis of the rich information about Stonechats further steps in this direction could be promising. One future focus could be searching for consistent patterns of photoperiodic response mechanisms within populations throughout the annual cycle. Another, probably related, approach, would be searching for genetical correlations between the timing of different life cycle stages (Price and Langen 1992). Furthermore, investigations of populations in which seasonal timing is loosened may be fruitful. These themes will be further developed in the concluding section below.

Conclusions

The purpose of my dissertation was to contribute to a better understanding of seasonal timing in birds. As outlined in the introduction, several mechanisms are known by which birds adjust their schedules to stay in time. Some populations display a great amount of phenotypic plasticity that allows them to accommodate immediately to timing challenges. A number of cues that regulate the plasticity of timing have been suggested and were classified into different categories (Wingfield et al. 1992; Visser and Lambrechts 1999). Day length provides reliable "initiative predictive" information as a calendar that informs birds of the time in the year. In addition, other timing cues are related to immediate environmental information, e.g., to weather conditions (i.e. supplementary information) or to the availability of mates (synchronizing information). Modifying information regulates responses to unforeseeable events (Wingfield et al. 1992). Furthermore, learning has been suggested as an efficient tool to accommodate schedules to environmental conditions (e.g., Gwinner 1999).

The amount of plasticity of timing responses and the relative importance of different cues has been related to the temporal conditions under which populations live (Wingfield et al. 1992; Hahn et al. 1992, 1997; Visser and Lambrechts 1999). Some species, for example White-crowned sparrows (*Zonotrichia leucophrys*), varied greatly from each other in the plasticity of reproductive timing and in the cues they used (e.g., Wingfield et al. 1992; Maney et al. 1999). While arctic populations relied strongly on photoperiodic information, temperate subspecies responded in addition to supplementary information. Micro-evolutionary fine-tuning of timing strategies to local conditions has been suggested and in part supported by quantitative genetic analyses (e.g., Silverin et al. 1993; Lambrechts et al. 1996; Merilä and Sheldon 2001; Pulido and Berthold 2002). Advances in conceptual thinking have helped dissolve a formerly perceived dichotomy between "rigid endogenous programs" and "plastic responses" (Lambrechts and Dias 1993; Schlichting and Pigliucci 1998; Gwinner 1999; Gwinner and Helm 2002). Instead, endogenous timing programs are now seen as "periodically changing dispositions to respond to environmental cues" (Gwinner 1999).

In my dissertation, I compared timing mechanisms among four populations of Stonechats, probed for flexibility and rigidity, and explored the mutual interdependence of life cycle stages. The results, together with earlier studies about Stonechats, generally support our understanding of avian timing mechanisms. Yet by revealing characteristics and perhaps idiosyncracies of annual timing in Stonechats they caution against quick generalizations and indicate a diversity of strategies used by birds to stay in time. A consistent result was that the Stonechats' schedules are precisely controlled by endogenous

programs. These timing programs function as reaction norms to photoperiodic information and allow for differentiated responses to temporal challenges. *Saxicola torquata* appears to differ from some other passerine species so far studied in the strength of photoperiodic control over its seasonal behavior. There was no evidence that birds modified their schedules in response to favourable conditions (e.g., a mate in breeding condition).

The studies presented here suggest that major components of the annual cycle differ in the rigidity of their timing programs. Postjuvenile molt showed the greatest amount of temporal flexibility. Through phenotypic plasticity it served as a buffer in the annual cycle. Early hatched young took time to initiate molt or change their plumage at relaxed rates whereas offspring from late clutches partially compensated for their seasonal delay by an earlier or faster molt. The buffer function of molt was regulated by photoperiod via reaction norms to day length. Thus, Stonechats can respond instantaneously to a cue that conveys seasonal pressure, i.e., hatching late in the year (Chapters 1, 2, 3).

The timing of postjuvenile molt in Irish Stonechats was closely correlated to the onset of migratory restlessness (Chapter 4). Like molt, Zugunruhe timing was adjusted in response to day length, as indicated by strong effects of hatching date. The correlation between both activities suggests that adjustments of molt timing may affect the timing of migration. In the field, migratory departure times may depend on additional factors but observations and ringing recoveries suggest a close temporal association between Zugunruhe and Stonechat migration (Chapters 4 and 5). The consistently migratory behavior of partially migrant Irish Stonechats opens up interesting questions. The behavior of captive birds suggests that genotypically the strict temporal organization of migrants is retained in all birds. If these results are consolidated by more rigid testing, the implication would be that the migratory program of Irish Stonechats can be overridden by other cues. If so, Irish Stonechats may provide opportunities to study how underlying rigid endogenous programs may be loosened by relevant environmental cues. It is still unclear how such modifications would affect other life cycle stages, e.g., the subsequent reproductive cycle.

Reproductive timing was studied in Siberian and European Stonechats. The persistence of differences between the populations in captivity again indicated local adjustments through selection (Chapter 6). But in contrast to molt and probably migration, the flexibility of breeding cycles appeared to be low. European and Siberian Stonechats advanced and completed gonadal development slightly earlier in inside cages. However, Siberian Stonechats in outdoor aviaries bred no earlier in the milder European climate than their freeliving conspecifics in Kazakhstan. In contrast to many other species, Stonechats seemed to be highly insensitive to social cues for the timing of reproduction. They were so oblivious to the condition of their mates that they incurred dramatic costs of wasted reproductive effort and reduced reproductive success. The lack of social synchronization

could possibly be related to rigid photoperiodic control of their breeding seasons. Within natural populations, breeding mates would then be sufficiently synchronized with each other by their responses to day length. Currently, there are no data to resolve this question for Stonechats.

Growth and development of Stonechats also appeared to be rigidly controlled (Chapter 1). So far, there is no compelling evidence that the rate of growth is adjusted in response to seasonal pressure. Populations differences in growth rate accorded only in part to predictions based on the seasonal pressure of their temporal habitats. Similarly, judged by patterns of fluctuating asymmetry, developmental processes were not disturbed by time-pressure conveyed by short day length. However, migrating Stonechat populations under time-pressure selectively shortened the size of the 8th primary (a proxy for wing length) while keeping tarsus size undiminished. The reduction of wing size appears to be based on a programmed response to photoperiod because the birds received unlimited food and were kept under constant temperatures. As reduced wing span is likely to raise energetic costs of flight, it is a remarkable price paid by migrants to stay in time.

The comparison of life cycle schedules showed that all four populations relied on photoperiodic cues. The timing strategies differed among populations, but there is no evidence that endogenous programs lose their impact for birds under relaxed seasonal conditions, or that the populations differ in the kinds of timing cues they use. However, inter-population differences in schedules suggest micro-evolutionary tailoring to local conditions. This is best illustrated by the way in which molt buffers the annual cycle in different populations (Chapter 2). For instance, the weak photoperiodic response of African Stonechats to short day length is likely to be related to their native photoperiodic conditions near the equator. Siberian Stonechats did not advance molt onset under time-constraint. In the field, they breed and initiate molt around midsummer when day length changes are small. In contrast, Siberian Stonechats dramatically increased the rate of molt under short day length, in keeping with the fact that day length changes increase rapidly over molt. In multi-clutched European Stonechats, young hatch and molt under very different day lengths. They advance molt onset dramatically in response to photoperiodic time pressure. Therefore, the populations' magnitude of photoperiodic response corresponds to the importance of photoperiod as a timing cue in their native temporal environments. The observation that photoperiodic responses of the populations differed even between substages of molt (e.g., onset vs. duration) reveals a surprisingly fine temporal resolution of local timing strategies.

The interpretation of fine-tuned photoperiodic reaction norms is supported by first results from selection experiments for molt timing. Preliminary evidence indicated a correlated response of reaction norms to selection and further suggests evolvability of responses to day length (Chapter 3). High heritability of molt timing may therefore be

based on heritable responses to photoperiod. Family differences in photoperiodic responses have also been observed in split-brood experiments (Chapter 2).

Taken together, evidence for the evolvability of timing mechanisms, and the fact that Stonechats successfully inhabit a wide range of temporal habitats, suggest that their rigid endogenous timing programs enable them to meet the challenges of various fluctuating environments. But Stonechats also incur costs of their rigid timing programs. Three examples are provided by this study: the lack of flexibility in breeding time that counteracts social synchronization among breeding partners and keeps birds from taking advantage of favourable breeding conditions early in the season; reduced wing-length when day length indicates time pressure despite undiminished access to food; and an acceleration of molt rate that in other species reportedly reduced feather quality. These examples indicate disadvantages of a pre-programmed seasonal organization. The disadvantages are exacerbated if selective pressures change rapidly so that formerly successful time strategies may become maladaptive. There is little evidence for the Stonechat' use of other information that could serve as supplemental cues for timing. The predominant reliance of their timing system on photoperiodic cues may prove disadvantageous for Stonechats in times of fast (anthropogenic) change (cf. Outlook section). In contrast to present changes in ambient temperature and phenology of the birds' habitats, day length is not affected by climatic change. As a consequence, the phase relationship between phenology and timing cues changes, and Stonechats suffer "information constraints" (Visser and Lambrechts 1999; cf. Introduction). Formerly reliable programs may then be misleading and impose unnecessary costs on Stonechats.

Evolutionary accommodation of timing occurs less directly and on a slower time scale than phenotypic plasticity. Adjustments of schedules through micro-evolutionary processes are likely to take place in Stonechats, and since maladaptive timing has high fitness costs, timing programs could theoretically be modified rapidly. However, micro-evolutionary adjustments cannot be taken for granted. Results of my dissertation indicate two caveats in assuming an unquestioning optimalization perspective. Firstly, quantitative genetic analyses have shown that heritabilities were highly patterned, being high for some timing parameters but not for others. Therefore, "genostasis", a shortage of additive genetic variance in some traits (Bradshaw 1991), could limit the direction or rapidity of micro-evolutionary adjustments. Secondly, correlated responses to selection based on genetical correlations between life cycle stages are likely to occur (Price and Langen 1992). Preliminary evidence suggests that selection on molt timing may affect photoperiodic reaction norms. If photoperiodic responses of seasonal activities involved a common mechanism, selection may simultaneously affect several parts of the timing system. Adverse side-effects, such as the costs of time-keeping illustrated above, may then inflate the costs of a photoperiodic organization.

Therefore, timing programs of Stonechats may respond more slowly to time challenges than those of other species like for instance the Blackcap (Pulido et al. 1996, 2002). The results for Stonechats and the outlook on possible schedule modifications suggest that climate change will likely affect bird species or even populations differentially. They also indicate that changing selection pressures influence various components of the life cycle simultaneously. Overall effects depend on many characteristics of an organisms' life history, including its feeding strategies and degree of specialization (e.g., Hughes 2000; Sol and Lefebvre 2000; Walther et al. 2002). Therefore, for accurate predictions we need a still deeper understanding of timing processes and mutual interdependence of seasonal activities. This very complexity – still a daunting task – can best be approached by detailed studies of model organisms, such as the Stonechat. Further research on schedules of this bird promises insights about possible modifications of pre-programmed timing systems. Three aspects appear particularly promising for further studies: quantitative genetic research should be extended to simultaneous consideration of the entire annual cycle. Knowledge of genetic correlations is a prerequisite for predictions of responses to selection, and of an understanding of the evolution of timing strategies in general.

Secondly, research should aim at identifying physiological mechanisms that underly timing strategies. One approach suggested by results of my dissertation is investigating consistency of photoperiodic responses within birds. To that purpose, timing responses throughout the annual cycle should be explored and related to each other. A better mechanistic knowledge of responses to day length is a key to understanding functions and limitations of timing systems.

Finally, in view of fluctuating weather conditions and increasing unpredictability, research on seasonal timing could focus on ways by which rigid temporal programs can be relaxed. Because of their strictly photoperiodic organization Stonechats are a particularly promising subject for such studies. So far, we have only limited information about timing flexibility in the absence of time constraints. African Stonechats as residents are probably under less pressure than other populations but their equatorial origin makes their responses to photoperiod hard to interpret. Studies on African residents could be supplemented by research on a completely resident population that, unlike African Stonechats, lives under seasonally changing photoperiodic conditions. Results may indicate to which extent the impact of photoperiodic information is loosened under relaxed conditions. Such studies could be carried out, e.g., on Mediterranean or South African Stonechat populations. Similarly, among partially migrant Irish Stonechats it is yet unclear how seasonal behavior of residents is organized. Because the decision of a bird to migrate has huge impact on its seasonal schedule partial migrants are prime candidates to investigate the integration of rigid and flexible components in endogenous timing programs. An identification of cues that override internal rhythms (such as migratory urge) could reveal hierarchies among

information systems and mechanisms that organize seasonal timing. These steps may allow further progress in attempts at understanding the adaptive significance of endogenous timing programs.

Acknowledgements

In completing this dissertation, I owe a huge debt to Ebo Gwinner whose confidence and support made this endeavour possible under most unusual circumstances. It was a joy to work together and to fuel each other's enthusiasm. Helga Gwinner, with her persistent encouragement, creative mind and reliable friendship, deserves just as much gratitude. Many colleagues in the Max-Planck Research-Centre for Ornithology were greatly helpful, supportive, and patient, especially Heidrun Albrecht, Ingrid Schwabl, Raimund Barth, Lisa Trost, and Willi Jensen. My fellows Elisabeth Yohannes, Jesko Partecke and Ulf Bauchinger were consistently encouraging and supportive. Etienne Vermeirssen, Kim Carter and Anja Kahles helped investigating eggs, and Bart Kempnaers and Francisco Pulido gave stimulating comments regarding Stonechat breeding experiments.

Heiner Flinks, Theunis Piersma, John Wingfield, Marilyn Ramenofsky, John Rappole, Lukas Jenni, Les Underhill, Peter Berthold and Marcel Visser inspired the work by their comments about Stonechats and discussions of ornithology. Irene Tielemann, in her parallel course, invigorated my efforts from close distance. The work on Irish Stonechats profited from insights of Ewan Urquhart, John Callion, Oscar Merne, Kathy Freeman and John O'Halloran. John Callion and Ewan Urquhart also shared unpublished material with me and enhanced the analysis of ringing recoveries. Nigel Blake's fantastic photography brings out the best of Stonechats.

I gratefully acknowledge the British Trust for Ornithology (BTO), Thetford, UK, for providing their ringing recovery data. The BTO Ringing Scheme is funded by a partnership of the BTO, the Joint Nature Conservation Committee, Duchas the Heritage Service – National Parks and Wildlife (Ireland) and the ringers themselves. Likewise, I thank the organizers of the EURING database, Rinse Wassenaar, Wolfgang Fiedler, and all contributing ringing schemes and bird ringers for their banding efforts and for providing recovery data. Wolfgang Fiedler also contributed to analyzing ringing recoveries, in particular with the software package GIS. I thank Richard Palmer for his thoughtful discussions of fluctuating asymmetry and his commitment to critical thinking. Walter Zucchini has patiently introduced me to time-series techniques. Richard Palmer, Walter Zucchini, and Les Underhill have helped a lot by sharing mathematical insights and hand-written software programs with me.

Most cordially I thank my friends, especially Emily Wheeler, for their nurturing friendship and all they keep offering. My efforts and joy were fuelled by quiet forest walks, inspiring discussions, and fragrant loaves of oven-warm bread.

Finally, the project of this dissertation was backed by huge family support. My father's enthusiasm had nurtured the interest in nature as well as in academic work. I thank Gertrud Helm, Gisela Bender and Pia Starck for making my worktime a pleasure for the children. I'm grateful to my brother Leonhard for his untiring help with illustrations, final polishing, and affectionate interest. Finally, Tim, Lotte, Edda and Matthias provided the spirited space in which the whole undertaking took place. In particular, I thank my children for the countless pictures of birds and dragonflies that flag my study, making me smile with each line I type.

References

- Alatalo, R., A. Lundberg and C. Glynn. 1986. Female pied Flycatchers choose territory quality and not male characteristics. *Nature* 323:152–153.
- Allendorf, F.W., R. Leary, P. Spruell, and J.K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. *Trends Ecol. Evol.* 16:613–622.
- Arnold, S. J. 1994. Multivariate inheritance and evolution: a review of concepts. pp 17–48 in Boake, C. (ed.). *Quantitative genetic studies of behavioral evolution*. University of Press, Chicago.
- Bairlein, F., and W. Winkel. 2001. Birds and climate change. in: Lozán, J., H. Graßl, and P. Hupfer (eds.) *Climate of the 21st Century: Changes and Risks – Scientific facts*. GEO (Hamburg):278–282.
- Balmford, A., I. Jones, and A. Thomas. 1993. On avian asymmetry: evidence of natural selection for symmetrical tails and wings in birds. *Proc. R. Soc. Lond. B* 252:245–251.
- Berthold, P. 1969. Über Populationsunterschiede im Gonadenzyklus europäischer *Sturnus vulgaris*, *Fringilla coelebs*, *Erithacus rubecula* und *Phylloscopus collybita* und deren Ursachen. *Zool. Jb. Syst.* 96:491–557.
- Berthold, P. 1973. Relationships between migratory restlessness and migration distance in six *Sylvia* species. *Ibis* 115:594–599.
- Berthold, P. 1988a. The control of migration in European warblers. *Proc. 19th Int. Orn. Congr.* Ottawa. (1986):215–249.
- Berthold, P. 1988b. Unruhe-Aktivität bei Vögeln: eine Übersicht. *Vogelwarte* 34:249–259.
- Berthold, P. 1998. Bird migration: genetic programs with high adaptability. *Zoology* 101:235–245.
- Berthold, P. 2001. *Bird Migration. A general survey*. 2nd ed. Oxford Univ. Press, 253 pp.
- Berthold, P. 2002. *Control of bird migration*. 2nd ed. Chapman and Hall, London.
- Berthold, P., and W. Friedrich. 1989. Die Federlänge: Ein neues nützliches Flügelmaß. *J. Orn.* 30:11–21.
- Berthold, P., and F. Pulido. 1994. Heritability of migratory activity in a natural bird population. *Proc. R. Soc. Lond. B* 257:311–315.
- Berthold, P., E. Gwinner, and H. Klein. 1970. Vergleichende Untersuchung der Jugendentwicklung eines ausgeprägten Zugvogels (*Sylvia borin*) und eines weniger ausgeprägten Zugvogels (*S. atricapilla*). *Vogelwarte* 25:297 – 331.
- Berthold, P., E. Gwinner, H. Klein, and P. Westrich. 1972. Beziehungen zwischen Zugunruhe bei Gratengrasmücke und Mönchsgrasmücke (*Sylvia borin* and *S. atricapilla*). *Z. Tierpsychol.* 30:26–35.
- Berthold, P., A. Helbig, G. Mohr, and U. Querner. 1992. Rapid microevolution of migratory behavior in a wild bird species. *Nature* 360:668–670.
- Biebach, H. 1983. Genetic determination of partial migration in the European Robin, *Erithacus rubecola*. *Auk* 100:602–606.

- Björklund, M. 1996. The effect of male presence on nestling growth and fluctuating asymmetry in the Blue Tit. *Condor* 98:172–175.
- Boag, P., and A. Van Noordwijk. 1987. Quantitative genetics. pp. 45–78 in Cooke, F., and P.A. Buckley (eds.). *Avian genetics. A population and ecological approach*. Academic Press, London.
- Boake, C. 1994. Evaluation of applications of the theory and methods of quantitative genetics to behavioral evolution. pp. 305–325 in Boake, C. (ed.). *Quantitative genetic studies of behavioral evolution*. University of Chicago Press, Chicago.
- Boon, P. 1999. *Day length and growth*. Ph. D. thesis University of Groningen.
- Bosque, C., and M. Bosque. 1995. Nest predation as a selective factor in the evolution of developmental rates in altricial birds. *Amer. Nat.* 45:234–260.
- Both, C., and M.E. Visser. 2001. Adjustment to climate change is constrained by arrival date in a long distance migrant bird. *Nature* 411:296–298.
- Bradshaw, A.D. 1987. Comparison: its scope and limits. *New Phytol.* 106:3–21.
- Bradshaw, A.D. 1991. Genostasis and the limits to evolution. *Phil. Trans. R. Soc. Lond. B* 333:289–305.
- Bradshaw, W.E., and C. Holzapfel. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci.* 98:14509–14511.
- Brown, C., and M. Brown. 2000. Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behav Ecol Sociobiol.* 47:339–345.
- Brown, L. H., and P. Britton. 1980. *The Breeding Seasons of East African Birds*. Nairobi, The East Africa Natural History Society.
- Bueno, J. 1991. Migracion e invernada de pequenos Turdinos en la Peninsula Iberica. II. Collalba Gris *Oenanthe oenanthe* Tarabilla Nortena, *Saxicola rubetra* y Tarabilla Comun *Saxicola torquata*. *Ardeola* 38:117–129.
- Bulyuk, V., A. Mukhin, V. Fedorov, A. Tsvey, and D. Kishkinev. 2000. Juvenile dispersal in Reed Warblers (*Acrocephalus scirpaceus*) at night. *Avian Ecol. Behav.* 5:45–61.
- Callion, J. 2002. Stonechat. in Wernham, C.V., M.P. Tom, J.H. Marchant, J.A., Clark, G.M. Siriwardena, and S.R. Baillie (eds.). *The Migration Atlas: Movements of the Birds of Britain and Ireland*. T. and A.D. Poyser, London.
- Carbonell, R., and J. Telleria. 1998. Increased asymmetry of tarsus-length in three populations of Blackcaps *Sylvia atricapilla* as related to proximity to range boundary. *Ibis* 140:331–333.
- Carter, K.L., B.C. Robertson, and B. Kempnaers. 2000. A differential DNA extraction method for sperm on the perivitelline membrane of avian eggs. *Mol. Ecol.* 9:2149–2154.
- Chernetsov, N., and A. Mukhin. 2001. Possible endogenous basis of juvenile dispersal in the reed warbler (*Acrocephalus scirpaceus*). *Ring* 23:173–177.
- Clark, J., and J. Eyre (eds.). 1993. *Birds of Hampshire*. Hampshire Ornithological Society Over Wallop England.
- Clark, J., C. Wernham, D. Balmer, S. Adams, B. Griffin, J. Blackburn, D. Anning, and L. Milne. 2001. Bird ringing in Britain and Ireland in 1999. *Ring and Migr.* 20:239–288.

- Clarke, G. 1995. Relationships between developmental stability and fitness: Application for conservation biology. *Cons. Biol.* 9:18–24.
- Clarke, G. 1998. The genetic basis of developmental stability. IV. Individual and population asymmetry parameters. *Heredity* 80:553–561.
- Colwell, R.K. 1974. Predictability, constancy, and contingency of periodic phenomena. *Ecology* 55:1148–1153.
- Conover, W., and R. Iman. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. *Am. Statistician* 35:124–133.
- Cottam, M., D. Houston, G. Loble, and I. Hamilton. 2002. The use of muscle protein for egg production in the Zebra Finch *Taeniopygia guttata*. *Ibis* 144:210–217.
- Cramp, S., et al. (eds) 1988. *Handbook of the birds of Europe, the Middle East and North Africa, Vol 5*. Oxford University Press, Oxford.
- Crick, H., C. Dudley, D. Glue, and D. Thomson. 1997. UK birds are laying eggs earlier. *Nature* 388:526.
- Cristol, D., M. Baker, and C. Carbone. 1999. Differential migration revisited. Latitudinal segregation by age and sex class. pp. 33–88 in: Nolan, V., Ketterson, E., and C. Thompson (eds.). *Current Ornithology* Vol. 15. Kluwer, New York, Boston.
- Cullen, J., and P. Jennings. 1986. *Birds of the Isle of Man*. Bridgen Publ., Douglas UK.
- Cummins, S. 2001. *The ecology of the Stonechat, Saxicola torquata*. Ph. D. thesis, University college Cork, Ireland.
- Daan, S., C. Dijkstra, R. Drent, and T. Meijer. 1989. Food supply and the annual timing of avian reproduction. pp 392–407 in Quillet, H. (ed.). *Acta XIX Congressus Internationalis Ornithologici*, Vol. I. University of Ottawa Press, Ottawa.
- Davies, C., H. Fischer, and E. Gwinner. 1969. Die Brutzeiten einiger Gänsearten und ihrer Bastarde in identischen Bedingungen. *Oecologia* 3:266–276.
- Dawson, A., S. Hinsley, P. Ferns, R. Bonser, and L. Eccleston. 2000. Rate of molt affects feather quality: a mechanism linking current reproductive effort to future survival. *Proc. R. Soc. Lond. B* 267:2093–98.
- Dementiev, G., and N. Gladkov. 1968. *The birds of the Soviet Union*. [English translation]. Israel Program for Scientific Translations, Jerusalem.
- Dhondt, A. 1973. Postjuvenile and postnuptial molt in a Belgian population of Great tits *Parus major* with some data on captive birds. *Gerfaut* 63:187–209.
- Dhondt, A. 1981. Postnuptial molt of the Great tit in southern Sweden. *Ornis Scand.* 12:127–133.
- Dhondt, A. 1983. Variations in the number of overwintering Stonechats possibly caused by natural selection. *Ring and Migr.* 4:155–158.
- Diggle, P. 1990. *Time Series: a biostatistical introduction*. Oxford University Press, New York.
- Dingle, H. 1990. The evolution of life histories. pp. 267–289 in Wöhrmann, K. and S.K. Jain (eds.). *Population biology. Ecological and evolutionary viewpoints*. Springer Verlag, Berlin.

- Dingle, H. 1994. Genetic analyses of animal migration. pp 145–164 in: Boake, C. (ed.). *Quantitative genetic studies of behavioral evolution*. University of Chicago Press, Chicago.
- Dingle, H. 1996. *Migration. The biology of life on the move*. Oxford University Press, Oxford.
- Dittami, J., and E. Gwinner 1985. Annual cycles in the African stonechat *Saxicola torquata axillaris* and their relationship to environmental factors. *J. Zool. Lond. (A)* 207:357–370.
- Dufour, K., and P. Weatherhead. 1998. Bilateral symmetry and social dominance in captive male red-winged blackbirds. *Behav. Ecol. Sociobiol.* 42:71–76.
- Dukes, J., and H. Mooney. 1999. Does global change increase the success of biological invaders? *Trends Ecol. Evol.* 14:135–139.
- Easterling, D., G. Meehl, C. Parmesan, S. Changnon, T. Karl, and L. Mearns. 2000. Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074.
- Easterling, D., B. Horton, P. Jones, T. Peterson, T. Karl, D. Parker, M. Salinger, V. Razuvayev, N. Plummer, P. Jamason, and C. Folland. 1997. Maximum and minimum temperature trends for the globe. *Science* 277:364–367.
- Falconer, D. S., and T. F. C. Mackay. 1996. *Introduction to quantitative genetics*. 4th ed. Longman, London.
- Fiedler, W. 1998. *Der Flugapparat der Mönchsgrasmücke (Sylvia atricapilla)*. Unpubl. dissertation, University of Tübingen.
- Flinks, H. 1999. Muster, Intensität und zeitliche Aspekte der postjuvenilen Mauser beim Schwarzkehlchen (*Saxicola torquata*). *Vogelwarte* 40:11–27.
- Forstmeier, W. 2002. Benefits of early arrival at breeding grounds vary between males. *J. Anim. Ecol.* 71:1–9.
- Frich, P., L. Alexander, P. Della-Marta, B. Gleason, M. Haylock, A. Klein Tank, and T. Peterson. 2002. Observed coherent changes in climatic extremes during the second half of the twentieth century. *Climate Research* 19:193–212.
- Garland, T., and S. Adolph. 1994. Why not to do two-species comparative studies. Limitations on inferring adaptation. *Phys. Zool.* 67(4):797–829.
- Gebhardt-Henrich, S., and H. Richner. 1998. Causes of growth variation and its consequences for fitness. pp. 324–339 in: Starck, J.M., and R.E. Ricklefs (eds.). *Avian growth and development*. Oxford University Press, New York.
- Gibbons D., Reid, J. and R. Chapman. 1993. *The new atlas of breeding birds in Britain and Ireland, 1988–1991*. TandAD Pyser, Calton UK.
- Ginn, H.B., and D.S. Melville. 1983. *Molt in Birds*. BTO, Tring.
- Gitay, H., A Suárez, R. Watson, and D. Dokken (eds). 2002. *Climate Change and Biodiversity*. IPCC, Geneva, Switzerland, 85 pp.
- Glutz von Blotzheim, U. N., and K.M. Bauer (eds.). 1988. *Handbuch der Vögel Mitteleuropas*, 11. Aula, Wiesbaden.
- Gowaty, P. 1997. Principles of females' perspectives in avian behavioral ecology. *Journ. Av. Biol.* 28:95–102.

- Grant, B., and P. Grant. 1993. Evolution of Darwin's finches caused by a rare climatic event. *Proc. R. Soc. Lond. B* 251:111–117.
- Greig-Smith, P. 1979. *The behavioral ecology of the Stonechat (Saxicola torquata)* D. Phil. Thesis. Sussex University.
- Greig-Smith, P. 1985. Weight differences, brood reduction, and sibling competition among nestling Stonechats *Saxicola torquata* (Aves: Turdidae). *J.Zool. Lond. (A)* 205:453–465.
- Greig-Smith, P., and D. Quicke. 1983. The diet of nestling Stonechats. *Bird Study* 30:47–50.
- Groeters, F. R., and H. Dingle. 1987. Genetics and maternal influences on life history plasticity in response to photoperiod by milkweed bugs (*Oncopeltus fasciatus*). *Am. Nat.* 129:332–346.
- Gwinner, E. 1968. Circannuale Periodik als Grundlage des jahreszeitlichen Funktionswandels bei Zugvögeln. Untersuchungen am Fitis (*Phylloscopus trochilus*) und am Waldlaubsänger (*P. sibilatrix*). *J. Ornithol* 109:70–95.
- Gwinner, E. 1975. Die circannuale Periodik der Fortpflanzungsaktivität beim Star (*Sturnus vulgaris*) unter dem Einfluß gleich- und andersgeschlechtiger Artgenossen. *Z. Tierpsychol.* 38:34–43.
- Gwinner, E. 1986. *Circannual rhythms. Endogenous annual clocks in the organization of seasonal processes*. Springer, Berlin Heidelberg.
- Gwinner, E. 1991. Circannual rhythms in tropical and temperate-zone stonechats: a comparison of properties under constant conditions. *Ökol. Vögel (Ecol. birds)* 13:5–14.
- Gwinner, E. 1999. Rigid and flexible adjustments to a periodic environment: Role of circadian and circannual programs. pp. 2366–2378 in: Adams, N., and R. Slotow (eds.). *Proc. 22nd Int. Orn. Congr. Durban*. Johannesburg, BirdLife South Africa.
- Gwinner, E., and H. Biebach. 1977. Endogene Kontrolle der Mauser und Zugdisposition bei südfinnischen und südfranzösischen Neuntöttern (*Lanius collurio*). *Vogelwarte* 29:56–63.
- Gwinner, E., and D. Czeschlik. 1978. On the significance of spring migratory restlessness in caged birds. *Oikos* 30:364–372.
- Gwinner, E., and J. Dittami. 1985. Photoperiodic responses in temperate zone and equatorial stonechats: a contribution to the problem of photoperiodism in tropical organisms. pp. 279–294 in Follett, B.K., S. Ishii, and A. Chandola (eds.). *The Endocrine System and the Environment*. Japan Sci. Soc. Press, Tokyo/ Springer-Verlag, Berlin.
- Gwinner, E., and J. Dittami. 1990. Endogenous reproductive rhythms in a tropical bird. *Science* 249:906–908.
- Gwinner, E., and B. Helm. 2002. Circannual and circadian contributions to the timing of avian migration. pp 81–95 in: Berthold, P., E. Gwinner, and E. Sonnenschein (eds.). *Avian Migration*. Springer Verlag Heidelberg.
- Gwinner, E., and I. Schwabl-Benzinger. 1982. Adaptive temporal programming of molt and migratory disposition in two closely related long-distance migrants, the Pied Flycatcher (*Ficedula hypoleuca*) and the Collared Flycatcher (*Ficedula albicollis*). pp. 75–89 in Papi, F., and H. Wallraff (eds.). *Avian Navigation*. Springer, Berlin.

- Gwinner, E., J. Dittami, and H. Gwinner. 1983. Postjuvenile molt in East African and Central European Stonechats (*Saxicola torquata axillaris*, *S. t. rubicola*) and its modification by photoperiod. *Oecologia* 60:66–70.
- Gwinner, E., S. König, and C. S. Haley 1995a. Genetic and environmental factors influencing clutch size in equatorial and temperate zone stonechats (*Saxicola torquata axillaris* and *S. t. rubicola*): an experimental study. *Auk* 112(3):748–755.
- Gwinner, E., S. König, and M. Zeman. 1995b. Endogenous gonadal, LH and molt rhythms in tropical stonechats: effect of pair bond on period, amplitude, and pattern of circannual cycles. *J. Comp. Physiol. A* 177:73–79.
- Gwinner, E., T. Rödl, and H. Schwabl. 1994. Pair territoriality of wintering Stonechats: behavior, function and hormones. *Behav. Ecol. Sociobiol.* 34:321–327.
- Gwinner, E., H. Schwabl, and I. Schwabl-Benzinger. 1988. Effects of food-deprivation on migratory restlessness and diurnal activity in the garden warbler (*Sylvia borin*). *Oecologia* 77:321–326.
- Gwinner, E., V. Neusser, E. Engl, and D. Schmidl. 1987. Haltung, Zucht und Eiaufzucht afrikanischer und europäischer Schwarzkehlchen *Saxicola torquata*. *Gef. Welt* 111:118–120, 145 – 147.
- Hahn, T., T. Boswell, J. Wingfield, and G. Ball. 1997. pp. 39–80 in Nolan, V. E. Ketterson, and C. Thompson (eds.). *Current Ornithology*. Vol. 14. Plenum Press, New York.
- Hahn, T., J. Swingle, J. Wingfield, and M. Ramenofsky. 1992. Adjustments of the prebasic molt schedule in birds. *Ornis Scand.* 23:314–321.
- Hailman, J. P. 1986. The heritability concept applied to wild birds. *Current Ornithology* 4:71–95.
- Hall, S., and T. Fransson. 2000. Lesser Whitethroats under time-constraint molt more rapidly and grow shorter wing feathers. *J. Avian Biol.* 31:583–587.
- Hall, S., and T. Fransson. 2001. Wing molt in relation to autumn migration in adult Common Whitethroats *Sylvia communis communis*. *Ibis* 143:580–586.
- Hedenström, A. 1999. Aerodynamics of molt in birds: effects of wing gaps on flight performance. pp. 536–543 in: Adams, N., and R. Slotow (eds.). *Proc. 22nd Int. Orn. Congr. Durban*. Johannesburg, BirdLife South Africa.
- Helm, B. 1997. *Analyse der zeitlichen Organisation der Jugendmauser von afrikanischen (*Saxicola torquata axillaris*) und europäischen Schwarzkehlchen (*S. t. rubicola*)*. Diploma thesis, University of Tübingen.
- Helm, B., and H. Albrecht. 2000. Human handedness causes directional asymmetry in avian wing length measurements. *Anim. Behav.* (60):899–902.
- Helm, B., and E. Gwinner. 1999. Timing of postjuvenile molt in African (*Saxicola torquata axillaris*) and European (*Saxicola torquata rubicola*) stonechats: effects of genetic and environmental factors. *Auk* 116, 589–603.
- Helm, B., and E. Gwinner. 2001. Nestling growth and post-juvenile molt under a tight seasonal schedule in stonechats *Saxicola torquata maura* from Kazakhstan. *Avian Science* 1(1):31–42.

- Helm, B., and E. Gwinner. 2003. Molt timing as a buffer in the avian annual cycle. *in* Schodde, R. (ed.) *Proceedings of the 23. International Ornithological Congress Beijing 2002*; Acta Orn. Sinica.
- Helm, B., and M. Visser. 2003. Round table discussion: Integrating the avian annual cycle. *in* Schodde, R. (ed.) *Proceedings of the 23. International Ornithological Congress Beijing 2002*. Acta Orn. Sinica.
- Hemborg, C., and A. Lundberg. 1998. Costs of overlapping reproduction and molt in passerine birds: an experiment with the pied flycatcher. *Behav. Ecol. Sociobiol.* 43:19–23.
- Hemborg, C., and J. Merilä. 1998. A sexual conflict in collared flycatchers, *Ficedula albicollis*: early male molt reduces female fitness. *Proc. R. Soc. Lond. B* 265:2003–2007.
- Herremans, M. 1990. Body molt and migration overlap in reed warblers (*Acrocephalus scirpaceus*) trapped during nocturnal migration. *Gerfaut* 80:149–158.
- Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P. J. van der Linden, and D. Xiaosu (eds.) 2001. *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, UK. 944 pp.
- Houston, A., and J. McNamara. 1999. *Models of adaptive behavior. An approach based on state*. Cambridge University Press, Cambridge.
- Hovorka, M., and R. Robertson. 2000. Food stress, nesting growth, and fluctuating asymmetry. *Can. J. Zool.* 78:28–35.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* 15:56–61.
- Hughes, S. 1975. The distribution of the Stonechat in Sussex outside the breeding season. *Sussex Bird Rep.* 27:64–67.
- Humphrey, P., and K. Parkes. 1959. An approach to the study of molts and plumages. *Auk* 76:1–31.
- Jacobs, J., and J. Wingfield. 2000. Endocrine control of life-cycle stages: A constraint on response to the environment? *Condor* 102:35–51.
- James, P. 1956. Destruction of warblers on padre island, Texas, in May, 1951. *Wilson Bull.* 68:224–227.
- Jännes, H. 1990. Mustapäätaskun *Saxicola torquata* alalajien ja sukupuolen määrittämisestä sekä lajin esiintymisestä Suomessa. *Lintumies* 25:162–175.
- Järvinen, A. 1989. Body mass and winglength of nestling Redstarts *Phoenicurus phoenicurus* in a harsh northern environment. *Orn. Fenn.* 66:151–156.
- Järvinen, A., and J. Ylimaunu. 1986. Growth of nestling Pied Flycatchers *Ficedula hypoleuca* in northern Lapland. *Orn. Fenn.* 63:17–25.
- Jenni, L. and R. Winkler. 1989. The feather length of small passerines: a measure for wing-length in live birds and museum skins. *Bird Study* 36:1–15.
- Jenni, L., and R. Winkler. 1994. *Molt and ageing of European passerines*. Academic Press, London.

- Johansen, H. 1943. Die Vogelfauna Westsibiriens. Teil I und Literaturverzeichnis. *J. Ornithol.* 91:3–110.
- Johansen, H. 1954. Die Vogelfauna Westsibiriens. Teil II. *J. Orn.* 95:319–342.
- Johnson, E. 1961. The pair relationship and polygyny in the Stonechat. *Brit. Birds* 54(6):213–225.
- Johnson, E. 1971. Observations on a resident population of Stonechats in Jersey. *Brit. Birds* 64:201–213 and 267–279.
- Kalela, O. 1954. Populationsökologische Gesichtspunkte zur Entstehung des Vogelzugs. Über den Revierbesitz bei Vögeln und Säugetieren als populationsökologischer Faktor II. *Ann. Zool. Soc. Vanamo* 16(4):1–30.
- Keith, S., E. K. Urban, and C. H. Fry. 1992. *Saxicola torquata* (Linnaeus). Common Stonechat. Traquet patre. pp 494–500 in *The birds of Africa* Vol. 4. Academic Press, London.
- Kempnaers, B., B. Congdon, P. Boag, and R.J. Robertson. 1999. Extrapair paternity and egg hatchability in tree swallows: evidence for the genetic compatibility hypothesis? *Behav. Ecol.* 10:304–311.
- Kennedy, P., R. Ruttledge and C. Scroope. 1954. *The birds of Ireland*. Edinburgh: Oliver and Boyd.
- Klassen, M. 1994. Growth and energetics of tern chicks from temperate and polar environments. *Auk* 111:525–544.
- Klassen, M. 1995. Molt and basal metabolic costs in males of two subspecies of stonechats: the European *Saxicola torquata rubicola* and the East African *S. t. axillaris*. *Oecologia* 104:424–432.
- König, S., and E. Gwinner. 1995. Frequency and timing of successive broods in captive African and European stonechats *Saxicola torquata axillaris* and *S. t. rubicola*. *J. Avian Biol.* 26:247–254.
- König, S., E. Gwinner, and B. Helm. 2002. Programmed patterns of territorial aggression in first-year European and African Stonechats (*Saxicola torquata rubicola* and *S. t. axillaris*). *Ecol. Birds* 24:579–594.
- Kullberg, C., N. Metcalfe, and D. Houston. 2002. Impaired flight ability during incubation in the pied flycatcher. *J. of Av. Biol.* 33:179–183.
- Kuz'mina, M. 1970. Rod Chekan [Genus *Saxicola*]. pp. 557–570 in: *Ptitsy Kazakhstana* [Birds of Kazakhstan] Vol. 3. Alma Ata.
- Lack, D. 1943. The problem of partial migration. *Brit. Birds* 37:122–130, 143–150.
- Lack, D. 1946. *The life of the Robin*. 4th ed. Methuen, London.
- Lack, D. 1968. *Ecological adaptation for breeding in birds*. Methuen, London.
- Lack, P. 1986. *The atlas of wintering birds in Britain and Ireland*. T. and A.D. Poyser, London.
- Lambrechts, M.M., and P. Dias. 1993. Differences in the onset of laying between island and mainland Mediterranean Blue Tits *Parus caeruleus*: phenotypic plasticity or genetic differences? *Ibis* 135:451–455.

- Lambrechts, M.M., J. Blondel, M. Maistre, and P. Perret. 1997. A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. *Proc. Natl. Acad. Sci.* 94:5153–5155.
- Lambrechts, M.M., P. Perret, and J. Blondel. 1996. Adaptive differences in the timing of egg laying between different populations of birds result from variation in photoresponsiveness. *Proc. R. Soc. Lond. B* 263:19–22.
- Larsson, K. 1996. Genetic and environmental effects on the timing of wing molt in the barnacle goose. *Heredity* 76:100–107.
- Leary, R., and Allendorf, F. 1989. Fluctuating asymmetry as an indicator of stress: implications for conservation biology. *Trends Ecol. Evol.* 4(7) 214–17.
- Lens, L., and S. van Dongen. 1999. Evidence for organism-wide asymmetry in five bird species of a fragmented afroropical forest. *Proc. R. Soc. Lond. B* 266:1055–1060.
- Lens, L., S. van Dongen, S. Kark, and E. Matthysen. 2002. Fluctuating asymmetry as an indicator of fitness: can we bridge the gap between studies? *Biol. Rev.* 77:27–38.
- Lens, L., S. van Dongen, C. Wilder, T. Brooks, and E. Matthysen. 1999. Fluctuating asymmetry increases with habitat disturbance in seven bird species of fragmented afroropical forest. *Proc. R. Soc. Lond. B* 266:1241–46.
- Lind, J. 2001. Escape flight in molting Tree Sparrows (*Passer montanus*). *Functional Ecology* 15:29–35.
- Lindström, A., Visser, G. H., and S. Dn. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Phys. Zool.* 66:490–510.
- Loehrl, H. 1959. Zur Frage des Zeitpunktes einer Prägung auf die Heimatregion beim Halsbandschnäpper (*Ficedula albicollis*). *J. Ornithol.* 100:132–140.
- Loehrl, H. 1962. Weiterer Versuch zur Klärung der Heimat-Prägung. *J. Ornithol.* 103(4).
- Maney, D., S. Schoech, and J. Wingfield. 1999. Environmental endocrinology and the timing of reproduction: interaction of photoperiod and temperature. pp. 279–294 in: Adams, N., and R. Slotow (eds.). *Proc. 22nd Int. Orn. Congr. Durban*. Johannesburg, BirdLife South Africa.
- Mason, C. F. 1995. Long-term trends in the arrival dates of spring migrants. *Bird Study* 42:182–189.
- McCarthy, J., O. Canziani, N. Leary, D. Dokken, and K. White (eds.). 2001. *Climate Change 2001: Impacts, Adaptation & Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, UK. 1000 pp.
- McLaughlin, J., J. Hellmann, C. Boggs, and P. Ehrlich. 2002. Climate change hastens population extinctions. *Proc. Natl. Acad. Sci.* 99:6070–6074.
- Menzel, A., and P. Fabian. 1999. Growing season extended in Europe. *Nature* 397:659–660.
- Merilä, J. 1997. Expression of genetic variation in body size of the collared flycatcher under different environmental conditions. *Evolution* 51:526–536.
- Merilä, J., and B. Sheldon. 2001. Avian quantitative genetics. pp. 179–255 in: Nolan, V., and C. Thompson (eds.): *Current Ornithology Vol. 16*. Kluwer, New York, Boston.

- Møller, A. 1995. Developmental stability and ideal despotic distribution of blackbirds in a patchy environment. *Oikos* 72:228–234.
- Moreau, R. 1972. *The palaeartic-African bird migration systems*. Academic Press, New York.
- Mukhin, A. 1999a. Nocturnal restlessness and postjuvenile molt in reed warblers (*Acrocephalus scirpaceus*). *Ring* 21:150.
- Mukhin, A. 1999b. Nocturnal restlessness in caged juvenile reed warblers (*Acrocephalus scirpaceus*). *Avian Ecol. Behav.* 3:91–97.
- Munkejord, A. 1981. The Stonechat in western Norway south of 62°N 1973–1980. *Cinclus* 4:69–75.
- Murton, R.K., and N.J. Westwood. 1977. *Avian breeding cycles*. Clarendon, Oxford.
- Noskov, G A., and T.A. Rymkevich. 1985. Photoperiodic control of postjuvenile and postnuptial molts in passeriformes. pp. 930–934 in *Acta 18th Congressus Internationalis Ornithologicus, Moscow, 1982*.
- Noskov, G.A., T.A. Rymkevich, and N. Iovchenko. 1999. Intraspecific variation of molt: adaptive significance and ways of realisation. pp. 544–563 in: Adams, N., and R. Slotow (eds.). *Proc. 22nd Int. Orn. Congr. Durban*. Johannesburg, BirdLife South Africa.
- Palmer, R. 1994. Fluctuating asymmetry analyses: a primer. pp. 335–364 in: Markow, T. (ed.). *Developmental instability: its origins and evolutionary implications*. Kluwer Academic Publ., Dordrecht.
- Palmer, R. 2000. Quasireplication and the contract of error: lessons from sex ratios, heritabilities, and fluctuating asymmetry. *Annu. Rev. Ecol. Syst.* 31:441–480.
- Palmer, R., and C. Strobeck. 1986. Fluctuating asymmetry: measurement, analysis, patterns. *Ann. Rev. Ecol. Syst.* 17, 391–421.
- Palmer, R., and C. Strobeck. 2003. Fluctuating asymmetry analyses revisited. in: Polak, M. (ed.). *Developmental Instability (DI): Causes and Consequences*. Oxford University Press, Oxford.
- Parmesan, C. 1996. Climate and species' range. *Nature* 382:765–448.
- Parmesan, C., N. Ryrholm, C. Stefanescu, J. Hill, C. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, T. Tammaru, W. Tennent, J. Thomas, and M. Warren. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579–583.
- Parrinder, E.R., and D.E. Parrinder. 1945. Some observations on Stonechats in North Cornwall. *Brit. Birds* 38:362–369.
- Patterson, H. D., and R. Thompson. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrika* 58:545–554.
- Penuelas, J., and I. Filella. 2001. Responses to a warming world. *Science* 294:793–795.
- Pfeifer, G. 2000. Vorkommen und Ausbreitung des Schwarzkehlchens, *Saxicola torquata* Linnaeus 1766, in Schleswig-Holstein unter Einbeziehung der Bestandsentwicklung in den Nachbarländern. *Corax* 18:109–141.

- Phillips, J. 1967. Winter territory in the Stonechat. *Bird Study* 14:191–192.
- Phillips, J. 1976. Survival and local movement in young Stonechats. *Bird Study* 23:57–58.
- Piersma, T. 2002. Energetic bottlenecks and other design constraints in avian annual cycles. *Integ. and Comp. Bio.* 42:51–67.
- Piersma, T., and A. Lindström. 1997. Rapid reversible changes in organ size as a component of adaptive behavior. *Trends Ecol. Evol.* 12:134–138.
- Pimm, S. 2001. Entrepreneurial insects. *Nature* 411:531–32.
- Polak, M., and R. Trivers. 1994. The science of symmetry in biology. *Trends Ecol. Evol.* 9(4):122–24.
- Price, T., and T. Langen. 1992. Evolution of correlated characters. *Trends Ecol. Evol.* 7:307–310.
- Przybylo, R., B. Sheldon, and J. Merilä. 2000. Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J. Animal Ecology* 69:395–403.
- Pulido, F. 2000. *Evolutionary quantitative genetics of migratory restlessness in the Blackcap (Sylvia atricapilla)*. Tectum, Marburg.
- Pulido, F., and P. Berthold. 2002. Quantitative genetic analysis of migratory behavior. In: Berthold, P., E. Gwinner, and E. Sonnenschein (eds.). *Avian migration*. Springer, Berlin.
- Pulido, F., P. Berthold, and A. Van Noordwijk. 1996. Frequency of migrants and migratory activity are genetically correlated in a bird population: evolutionary implications. *Proc. Natl. Acad. Sci.* 93:14642–14647.
- Pulido, F., P. Berthold, G. Mohr, and U. Querner. 2001. Heritability of the timing of autumn migration in a natural bird population. *Proc. R. Soc. Lond. B* 268:953–959.
- Ralph, J. 1971. An age differential of migrants in coastal California. *Condor* 73:243–246.
- Ralph, J. 1978. Disorientation and possible fate of young passerine coastal migrants. *Bird Banding* 49(3):227–247.
- Randler, C. 2002. Avian hybridization, mixed pairing and female choice. *Anim. Behav.* 63:103–119.
- Reed, M., T. Boulinier, E. Danchin, and L. Oring. 1999. Informed dispersal. Prospecting by birds for breeding sites. pp. 189–259 in: Nolan, V., Ketterson, E., and C. Thompson (eds.): *Current Ornithology Vol. 15*. Kluwer, New York, Boston.
- Ricklefs, R.E. 1976. Growth rates of birds in the humid New World tropics. *Ibis* 118:179–207.
- Ricklefs, R.E., J.M. Starck, and M. Konarzewski. 1998. Internal constraints on growth in birds. pp. 266–287 in: Starck, J.M., and R.E. Ricklefs (eds.). *Avian growth and development*. Oxford University Press, New York.
- Riddiford, N. 1981. Cautionary notes on ageing Redwings and Stonechats. *Ringer's Bulletin* 5:120.
- Robertson, I. 1977. Identification and European status of eastern Stonechats. *Brit. Birds* 70:237–245.

- Robinson, D. L. 1987. Estimation and use of variance components. *Statistician* 36:3–14.
- Rödl, T. 1994. The wintering of territorial Stonechat pairs *Saxicola torquata* in Israel. *J. Ornithol.* 136:423–433.
- Rödl, T. 1999. Environmental factors determine the numbers of overwintering European Stonechats *Saxicola torquata rubicola* – a long term study. *Ardea* 87 (2):247–259.
- Rödl, T., and H. Flinks. 1996. Nutrition of Stonechats *Saxicola torquata* and Mourning Wheatears *Oenanthe lugens* wintering sympatrically in Israel. *Ecol. Birds* 18:107–126.
- Roff, D. 1997. *Evolutionary quantitative genetics*. Chapman and Hall, New York.
- Roff, D., and D. Fairbairn. 2001. The genetic basis of dispersal and migration, and its consequences for the evolution of correlated traits. pp 191–202. In: Clobert, C., J. Danchin, A. Dhont, and J. Nichols (eds.). *Causes, consequences and mechanisms of dispersal at the individual, population and community level*. Oxford University Press, Oxford.
- Rogacheva, H. 1998. *The birds of central Siberia*. Husum Druck (Husum).
- Runfeldt, S., and J. Wingfield. 1985. Experimentally prolonged sexual activity in female sparrows delays termination of reproductive activity in their untreated mates. *Anim. Behav.* 33:403–410.
- Scheuerlein, A. 2000. *Control of reproduction in a tropical bird, the Stonechat (Saxicola torquata axillaris)*. Aachen, Shaker Verlag. (Ph.D. Thesis, LM University München).
- Schlichting, C., and M. Pigliucci. 1998. *Phenotypic evolution. A reaction norm perspective*. Sinauer, Sunderland MA.
- Schüz, E. 1951. *Grundriss der Vogelzugskunde*. Parey, Berlin Hamburg.
- Schwabl, H., and B. Silverin. 1990. Control of partial migration and autumnal behavior. pp 144–155 in Gwinner, E. (ed.). *Bird migration: Physiology and ecophysiology*. Springer, Berlin Heidelberg New York.
- Serra, L., 1999. Does primary molt duration affect primary quality? The case of Grey Plover (*Pluvialis squatarola*). *Ring* 21:200.
- Serra, L., 2001. Duration of primary molt duration affects primary quality in Grey Plovers *Pluvialis squatarola*. *J. Av. Biol.* 32:377–380.
- Sillett, T., R. Holmes, and T. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288:2040–2042.
- Silverin, B., R. Massa, and K. Stokkan. 1993. Photoperiodic adaptation to breeding at different latitudes in great tits. *Gen. comp. Endocrinol.* 90:14–22.
- Slagsvold, T. 1999. Sexual conflict in birds with biparental care: share of care in small vs. large broods and late vs. early broods. pp. 2622–2638 in: Adams, N., and R. Slotow (eds.). *Proc. 22nd Int. Orn. Congr. Durban*. Johannesburg, BirdLife South Africa.
- Slagsvold, T., and S. Dale. 1996. Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. *Ecology* 77:461–471.
- Snow, D. W. 1969. The molt of British thrushes and chats. *Bird Study* 16:115–129.

- Sokal, R., and F. J. Rohlf 1995a. *Biometry*. 3rd ed. W.H. Freeman, New York.
- Sokal, R., and F. J. Rohlf 1995b. *Statistical Tables*. 3rd ed. W.H. Freeman, New York.
- Sol, D., and L. Lefebvre. 2000. Behavioral flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* 90:599–605.
- Starck, J.M., and R. E. Ricklefs. 1998. Data set of avian growth parameters. pp. 381–423 in: Starck, J.M., and R.E. Ricklefs (eds.). *Avian growth and development*. Oxford Univ. Pr., New York.
- Starck, J. M., S. König, and E. Gwinner. 1995. Growth of Stonechats *Saxicola torquata* from Africa and Europe: an analysis of genetic and environmental components. *Ibis* 137:519–531.
- Stearns, S. C. 1992. *The evolution of life histories*. Oxford University Press, Oxford New York.
- Stevenson, I., and D. Bryant. 2000. Climate change and constraints on breeding. *Nature* 406:366–367.
- Sutherland, W. 1998. Evidence for flexibility and constraint in migration systems. *J. Av. Biol.* 29:441–446.
- Svensson, L. 1992. *Identification guide to European passerines*. 4th ed. Stockholm: Rosersberg.
- Swaddle, J., and M. Witter. 1994. Food, feathers and fluctuating asymmetry. *Proc. R. Soc. Lond. B* 255:147–52.
- Swaddle, J., and M. Witter. 1997. The effects of molt on the flight performance, body mass and behavior of European starlings (*Sturnus vulgaris*): An experimental approach. *Can. Journ. Zool* 75:1135–46.
- Swaddle, J., M. Witter, I. Cuthill, A. Budden, and P. McCowen. 1996. Plumage condition affects flight performance in Commons Starlings: implications for developmental homeostasis, abrasion and molt. *J. Av. Biol.* 27:103–11.
- Teather, K. 1996. Patterns of growth and asymmetry in nestling Tree Swallows. *J. Av. Biol.* 27:302–310.
- Thomas, A. 1993. The aerodynamic costs of asymmetry in the wings and tail of birds: asymmetric birds can't fly round tight corners. *Proc. R. Soc. Lond. B* 254:181–189.
- Thomas, C., and J. Lennon. 1999. Birds extend their ranges northwards. *Nature* 399:213.
- Thomas, D., J. Blondel, P. Perret, M. Lambrechts, and J. Speakman. 2001. Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* 291:2598–2600.
- Thomson, A. 1956. The migrations of British Chats (*Oenanthe*, *Saxicola*, *Phoenicurus*) as shown by the results of ringing. *Brit. Birds* 49:63–73.
- Tucker, G.M., and M.F. Heath. 1994. *Birds in Europe: their Conservation Status*. Birdlife International, Cambridge.
- Turelli, M., N.H. Barton, and J.A. Coyne. 2001. Theory and speciation. *Trends Ecol. Evol.* 16, 330–343.

- Underhill, L.G. 1999. Avian demography: statistics and ornithology. pp. 61–70. *In*: Adams, N., and R. Slotow (eds.). *Proc. 22nd Int. Orn. Congr. Durban*. Johannesburg, BirdLife South Africa.
- Urquhart, E.D. 2002. *Stonechats*. Christopher Helm, London.
- Van Hecke, P. 1965a. De overwintering van de roodborsttapuit *Saxicola torquata rubicola* (L.), in België. *Gerfaut* 55:124–141.
- Van Hecke, P. 1965b. The migration of the west-european Stonechat, *Saxicola torquata* (L.), according to ringing-data. *Gerfaut* 55:146–194.
- Van Noordwijk, A. 1990. The methods of genetical ecology applied to the study of evolutionary change. Pages 291–319 *in* Wöhrmann, K., and S.K. Jain (eds.). *Population biology. Ecological and evolutionary viewpoints*. Springer, Berlin.
- Van Noordwijk, A., R. McCleery, and C. Perrins. 1995. Selection for the timing of great tit breeding in relation to caterpillar growth and temperature. *J. Anim. Ecol.* 64:451–458.
- Van Noordwijk, A., J. Van Balen, and W. Scharloo. 1981. Genetic variation in the Timing of reproduction in the Great Tit. *Oecologia* 49:158–166.
- Vaurie, C. 1959. *The birds of the palearctic fauna*. London, Witherby.
- Veen, T., T. Borge, S. Griffith, G. Saetre, S. Bures, L. Gustafsson and B. Sheldon. 2001. Hybridization and adaptive mate choice in flycatchers. *Nature* 411:45–50.
- Visser, M.E., and L.J. Holleman. 2001. Warmer springs disrupt the synchrony of Oak and Winter Moth phenology. *Proc. R. Soc. Lond. B* 268:289–294.
- Visser, M.E., and M. M. Lambrechts. 1999. Information constraints in the timing of reproduction in temperate zone birds: Great and Blue Tits. pp. 279–294 *in*: Adams, N., and R. Slotow (eds.). *Proc. 22nd Int. Orn. Congr. Durban*. Johannesburg, BirdLife South Africa.
- Visser, M.E., and C. M. Lessells. 2001. The costs of egg production and incubation in the Great Tit. *Proc. R. Soc. Lond. B* 268:1271–1277.
- Visser, M.E., A.J. Van Noordwijk, J. M. Tinbergen, and C. M. Lessells. 1998. Warmer springs lead to mis-timed reproduction in Great Tits (*Parus major*). *Proc. R. Soc. Lond. B* 265:1867–1870.
- Voelker, G., and S. Rohwer. 1998. Contrasts in scheduling of molt and migration in Eastern and Western Warbling vireos. *Auk* 115:142–155.
- Walker, D. 2001. Apparent continental Stonechats in England. *Birding World* 14:156–158.
- Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. Beebee, J. Fromentin, O. Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389–395.
- Watson, R., M. Zinyowera, and R. Moss (eds). 1997. *The Regional Impacts of Climate Change: An Assessment of Vulnerability. A Special Report of IPCC Working group II*. Cambridge University Press, UK. pp 517.
- Werschkul, D., and J. Jackson. 1979. Sibling competition and avian growth rates. *Ibis* 121:97–102.

- Widmer, M. 1999. *Altitudinal variation of migratory traits in the Garden warbler Sylvia borin*. Ph.D. thesis. University Zurich, Switzerland.
- Wingfield, J., T. Hahn, T. Levin, and P. Honey. 1992. Environmental predictability and control of gonadal cycles in birds. *J. Exp. Zool.* 261:214–231.
- Wink, M., H. Sauer-Gürth, and E. Gwinner. 2002. Evolutionary relationships of stonechats and related species inferred from mitochondrial-DNA sequences and genomic fingerprinting by ISSR-PCR. *Brit. Birds* 95:349–355.
- Witherby, H., F. Jourdain, N. Ticehurst, and B. Tucker. 1938–41. *The handbook of British birds*. Vol I–V. Witherby, London. .
- Wittmann, U., P. Heidrich, M. Wink, and E. Gwinner. 1995. Speciation in the stonechat (*Saxicola torquata*) inferred from nucleotide sequences of the cytochrome-b gene. *J. Zoo. Syst. Evol. Research* 33:116–122.
- Wuethrich, B. 1999. How climate change alters rhythms of the Wild. *Science* 287:793–795.
- Zink, G. 1973. Der Zug europäischer Singvögel. *Ein Atlas der Wiederfunde beringter Vögel*. Vol. 1. Vogelwarte Radolfzell, Möggingen.

List of publications in biology

- Helm B, Gwinner E (1999) Timing of postjuvencal molt in African (*Saxicola torquata axillaris*) and European (*Saxicola torquata rubicola*) stonechats: Effects of genetic and environmental factors. *Auk* 116:589-603.
- Helm B, Albrecht H (2000) Human handedness causes directional asymmetry in avian wing length measurements. *Animal Behavior* (60): 899-902.
- Helm B, Gwinner E (2001) Nestling growth and post-juvenile molt under tight seasonal schedule: Stonechats from Kazakhstan, *Saxicola torquata maura*. *Avian Science* 1(1):31-42.
- Gwinner E, Helm B (2002) Circannual and circadian contributions to the timing of avian migration. In: P. Berthold, E. Gwinner & E. Sonnenschein: *Avian Migration*. Springer Verlag Heidelberg, pp. 81-95.
- König, S, Gwinner, E, Helm, B (2002) Programmed patterns of territorial aggression in first-year European and African Stonechats (*Saxicola torquata rubicola* and *S. t. axillaris*). *Ecol. Birds* 24:579-594.
- Rappole, J, Helm B, Ramos, M (2003) An integrative framework for understanding the origin and evolution of avian migration. *J. Av. Biol.* 34:125-129.
- Helm, B (2003) Coping with extreme conditions: Are desert birds different? Tieleman, B.I. 2002. *Avian adaptation along an aridity gradient. Physiology, behavior, and life history*. Proefschrift Rijksuniversiteit Groningen, 367 pp. *Ardea*, in the press.
- Helm, B, and Visser, M (2003). Round table discussion: Integrating the avian annual cycle. In: Schodde, R. (ed.) *Proceedings of the 23. International Ornithological Congress Beijing 2002; Acta Orn.Sinica*, in the press.
- Helm, B, and Gwinner, E (2003). Molt timing as a buffer in the avian annual cycle. In Schodde, R. (ed.) *Proceedings of the 23. International Ornithological Congress Beijing 2002; Acta Orn. Sinica*, in the press.

Curriculum Vitae

Personal data

- Born • January 17, 1966; Königstein / Taunus, Germany
 Family • Married, three children: Tim (*1991), Lotte (*1992), Edda (*1995)
-

Education and academic life

- 1976-1983 • Melanchthon Gymnasium Nürnberg, classical education.
 1983-1984 • Exchange student in Holland, Michigan; US High-School diploma
 1986 • Abitur Melanchthon Gymnasium Nürnberg, majoring in Greek and English
 from 1986 • University of Tübingen, studies in biology and philosophy; research assistant at Max-Planck-Institute for Behavioral Physiology, Seewiesen; research and teaching assistant at the University of Tübingen, Institute for Behavioral Physiology
 1989-1990 • Exchange student at Tufts University, Medford Massachusetts; research assistant at the Department of German studies; visiting student at Harvard, Cambridge, Massachusetts.
 1990-1997 • University of Tübingen, graduate studies in zoology, plant-physiology, mathematics, and philosophy; teaching assistant at the Department of Philosophy
 1993-94 • Year abroad at the University of Pennsylvania, Philadelphia, Pennsylvania; research at the Quaker Peace Collection, Swarthmore College, Swarthmore Pennsylvania.
 1995 • University of Tübingen, master thesis in philosophy: "Reception of Nietzsche by the feminist movement of turn-of-the-century Germany".
 1997 • University of Tübingen and Max-Planck-Research Centre for Ornithology, Andechs; diploma thesis in biology: "Analysis of the temporal organization of postjuvenile molt in African and European Stonechats".
 1997 • Completion of MA in philosophy and diploma in biology 1997.
 1997-1998 • University of Jena, Germany; studies in philosophy, legal philosophy, and environmental law.
 since 1998 • Max-Planck-Research Centre for Ornithology, Andechs, and Ludwig-Maximilians-University, Munich: Ph-D student of Biology. Dissertation about seasonal timing in Stonechats.