# Michael Raess

Annual Timing and Life-History Variation in Free-Living Stonechats
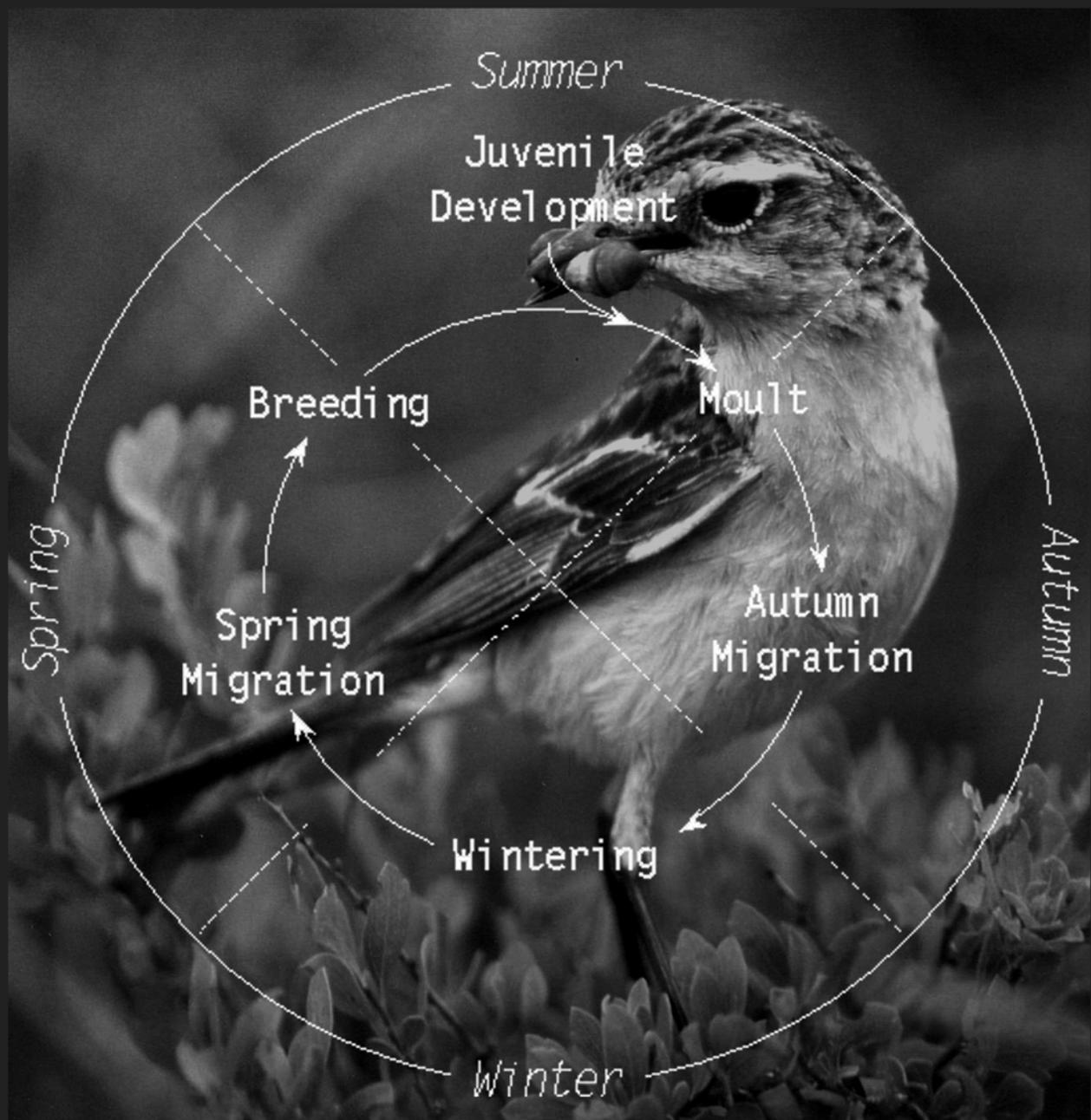
Cover picture: Female Siberian stonechat, *Saxicola torquata maura*

Photo: Peter Romanov

ANNUAL TIMING AND LIFE-HISTORY VARIATION IN FREE-LIVING STONECHATS

Dissertation

der Fakultät für Biologie

der Ludwigs-Maximilians-Universität

München

vorgelegt von

Michael Räß

München, Oktober 2005

Ich versichere hiermit ehrenwörtlich, dass

1. ich die vorliegende Dissertation selbständig und ohne unerlaubte Hilfe angefertigt habe,
2. ich nicht bereits anderweitig ohne Erfolg versuchte, eine Dissertation einzureichen oder mich einer Doktorprüfung zu unterziehen,
3. ich die Dissertation weder ganz noch in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt habe.

München, den 24.10.2005

Michael Räß

To Ebo Gwinner († 07-Sep 2004) and my son Janis (* 10-Feb 2005)

Мы, друзья, перелетные птицы,
Только быт наш одним нехорош:
На земле не успеешь жениться,
А на небе жены не найдешь!

Потому, потому, что мы [мигранты],
Небо наш... небо наш родимый дом.
Первым делом, первым делом [наши крылья]
- Ну, а девушки? - А девушки потом.

Мелодия - *В. СОЛОВЬЕВА-СЕДОГО*
Текст - *А. ФАТЬЯНОВА* (кроме [...])

```
We are, my friends, migratory birds,
There's only one bad thing about it:
On earth you got no bride,
And in the skies you don't find one either!

Because, because we are migrants,
And the sky's, yes the sky's our birthplace,
Our wings are the first thing we care for
- And the girls? - The girls come thereafter.

        After a song by V. Soloviev-Sedoy (melody)
        and A. Fatyanova (text)
```

1 Contents

1   INTRODUCTION - THEMES AND CONCEPTS

Natur! … Sie schafft ewig neue Gestalten; was da ist, war noch nie; was war, kommt nicht wieder - alles ist neu und doch immer das alte. Wir leben mitten in ihr und sind ihr fremd. Sie spricht unaufhörlich mit uns und verrät uns ihr Geheimnis nicht. Wir wirken beständig auf sie und haben doch keine Gewalt über sie.

Nature! … She is ever shaping new forms: what is, has never yet been; what has been, comes not again. Everything is new, and yet nought but the old. We live in her midst and know her not. She is incessantly speaking to us, but betrays not her secret. We constantly act upon her, and yet have no power over her.

Johann Wolfgang von. Goethe, Essay 'Die Natur' 1782; Translation by T.H. Huxley

The enormous variety of forms and patterns put forth by nature has always awed and fascinated mankind and served as a source of inspiration, in art as well as in science. While we might never see the full picture, as Goethe reminds us, generations of scientists have nevertheless set out to tackle nature's secrets in small steps. This process has led to the formulation of the concepts and hypothesis that form the basis of our current research. In this chapter I want to introduce some of the underlying themes and concepts of this thesis.

Lifetime reproductive success

Any organism, irrespective of its reproductive rate and total output, has to compete with other members of its species/population over reproductive success; the ultimate measure of its fitness is the number of reproducing offspring it produces during its life in relation to the rest of the population. Within populations there is considerable variation in lifetime reproductive success. Within any given generation of ten different bird species compiled by Newton (1989, 1995), only about a quarter of the individuals reproduce successfully (*Fig. 1.1*). On average 6% of the

individuals of one generation produce more than 50% of the next generation (Newton 1989, 1995).

Reproduction bears costs in terms of increased mortality and thus each reproductive bout reduces the probability to produce offspring in the future (Bell & Koufopanou 1986). For a semelparous organism, potential costs of reproduction are not relevant. As it will anyway die afterwards, it can put all its remaining effort into offspring production. Any reproductive decision in an iteroparous organism, however, has to take into account the relationship between the reproductive value of the given attempt and the residual reproductive value of future attempts. Hence, there exists a trade-off between current and future reproduction (Williams 1966, Roff 1992, Stearns 1992).
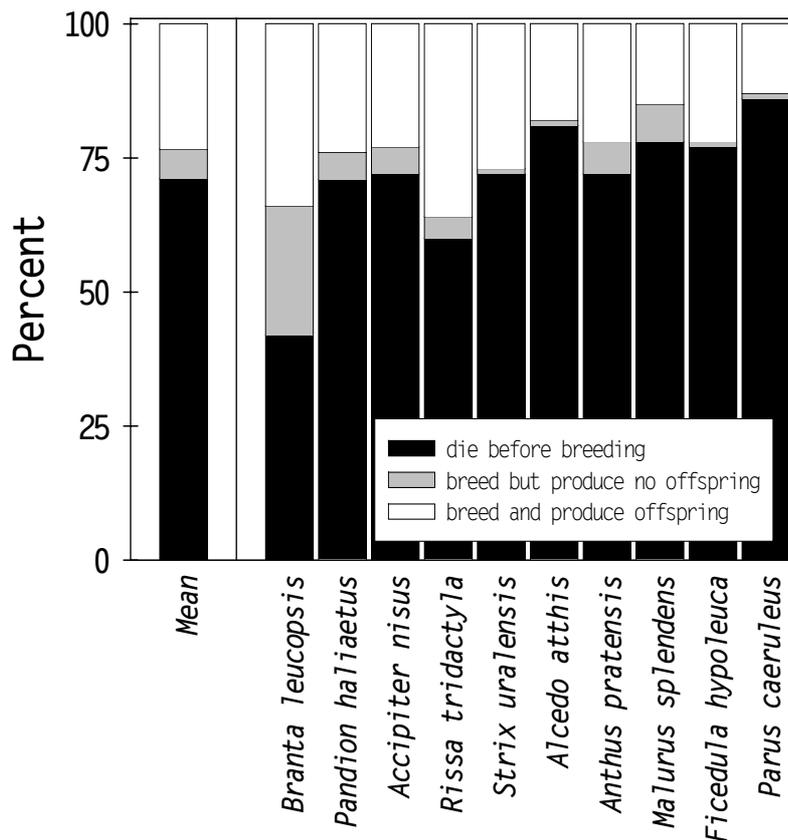
Fig. 1.1. The percentage of birds within a generation that either dies before reproducing, breeds but fails to produce young, or reproduces successfully during their lifetime (after Newton 1989, 1995).

Life-history stages and life-history cycles

Higher organisms usually do not reproduce continually, but alternate between reproductive and nonreproductive states. These states can be further subdivided into *life-history stages*, such as the developmental, hibernating, or senescence periods (e.g. Jacobs & Wingfield 2000, Wingfield 2004). The gross temporal organisation of these life-history stages is usually determined by the availability of the external resources required in each stage. Resources often fluctuate in a cyclic way, as seen in the temperate zones with their pronounced seasonality, but also in the periodically alternating wet and dry seasons in the tropics. Correspondingly, the life-history stages of organisms relying on resources with a predictable periodic availability are organised in regular cycles. *Fig. 1.2.* depicts the *annual cycle* of a north-temperate migratory passerine. This cycle can be decomposed into regularly occurring life-history stages, which can often be further divided into sub-stages.
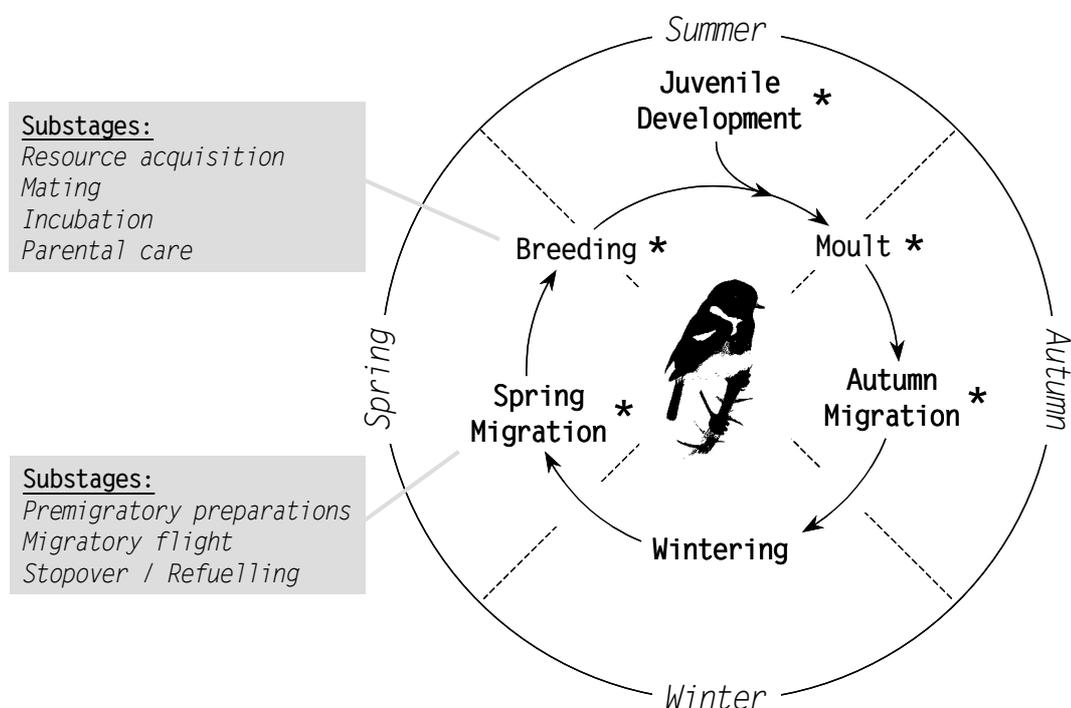
Fig. 1.2. Schematic of the annual cycle of the stonechat, a migratory passerine breeding in the north-temperate zone. The cycle consists of a sequence of life-history stages, which each can be typically divided into substages. Asterisks denote the life-history stages treated in this thesis.

If, however, the environmental fluctuations are unpredictable, as e.g. in Darwin finches on the Galapagos Islands which rely on the irregularly occurring rainy seasons (Hau et al. 2004), then the transitions between life-history stages occur opportunistically, i.e. whenever the conditions are favourable (Hahn et al. 1995, 1997, Hau et al. 2004).

The reproductive window

Seasonal reproduction is a common phenomenon in birds inhabiting the temperate zones (Baker 1938, Lack 1968, Murton & Westwood 1977, Gwinner 1986, 1996, 2003). But also in areas of less pronounced seasonality, like the tropics, environmental cycles like rainy and dry seasons create periods more suitable for reproduction than others (Murton & Westwood 1977, Gwinner & Dittami 1990, Gwinner & Scheuerlein 1998, 1999, Hau 2001). Avian reproduction is particularly sensitive to environmental fluctuations, because birds are relatively small, have high metabolic rates, produce nutrition-rich eggs and, when raising altricial young, have to provide large amounts of nutrients to their fast-growing offspring. The environmental conditions usually restrict breeding to a certain time period, the *reproductive* or *breeding window*. Within this window there exists an optimal time for offspring production, i.e. a time when the highest reproductive output can be achieved with the lowest costs in terms of adult mortality. Before or after this optimal date reproductive success and adult survival decrease, usually due to a decrease of the productivity of the environment (Perrins 1970, Drent & Daan 1980, Daan et al. 1986, Nilsson 1999).

The degree of seasonality of the environment varies strongly with latitude. One end of the extreme is represented by the arctic and antarctic regions with very short summers and long winters and photoperiods that range from zero to 24 hours of daylight; the other end by the equatorial regions with almost no seasonal variation in photoperiod and ambient

temperatures (although precipitation may vary, see above). Seasonality is, however, also strongly influenced by other factors, such as altitude or oceanic and continental influences. Therefore the length of the breeding window varies with latitude, but may differ also considerably between regions that share the same latitude.

Timing cues

When birds are held in constant ligth-dark cycles, they usually express robust *circannual* (i.e. nearly annual) rhythms of gonadal growth and regression, moult, migratory restlessness, and the body mass changes associated with moult and migration (Gwinner 1986, 2001, 2003). This indicates that these processes are controlled by an endogenous timing system. Baker (1938) differentiated between ultimate and proximate factors that determine the onset of a life-history stage. Avian reproduction is ultimately determined by the food availability for the offspring. This information may, however, not be available at the time when the reproductive stage has to be initiated. Most birds shut down their reproductive physiology during the nonbreeding stages (Murton & Westwood 1977, Gwinner 1986, Wingfield & Moore 1987, Wingfield & Farner 1993, Dawson et al. 2001). The activation from the regressed state has to occur weeks in advance of actual breeding, in migrants in the winter quarters or during migration, when an assessment of local conditions in the breeding area is not possible. Birds therefore need other, proximate, cues that allow them to anticipate the conditions most favourable for reproduction (Gwinner 1986, Wingfield et al. 1992). Most birds breeding in the temperate and arctic zones exploit the photoperiod as the main proximate cue that synchronises their endogenous timing mechanisms (Gwinner 1986, Juss 1993, Dawson et al. 2001, Gwinner 2003), because increasing daylengths reliably indicate the coming of spring and summer.

In the tropics photoperiod changes little over the year. Therefore other timing cues, e.g. the onset of rains, have been considered more important than photoperiod. However, Gwinner and Dittami (1990) found that also strictly tropical birds can express stable endogenous cycles of gonadal development, moult, and migratory behaviour under constant conditions, indicating the envolvement of endogenous timing mechanisms like in higher latidudes. Furthermore, tropical birds can anticipate conditions favourable for breeding (Wikelski et al. 2000). Recent findings suggest that endogenous clocks can use also tropical photoperiods as zeitgebers, either by measuring minute changes in photoperiod (Hau et al. 1998), or by exploiting regular variation in other characteristics, such as light intensity (Gwinner & Scheuerlein 1998).

Photoperiod is a reliable predictor of general seasonal changes; it contains, however, no information about the local conditions at a given time. Birds use therefore additional cues that allow a fine-tuning of reproductive and other annual activities. In the temperate zones, ambient temperature is an important supplementary timing cue used by many bird species. The increase in spring temperatures in the recent past (e.g. IPCC 2001, Luterbacher et al. 2004) has therefore led to a change of average laying dates (e.g. Crick et al. 1997, Forchhammer et al. 1998, McCleery & Perrins 1998, Stevenson & Bryant 2000, Both et al. 2004). Reproductive timing can also be fine-tuned by the availability of breeding opportunities and mating partners (e.g. Gwinner et al. 1987).

Allocation of time and resources

Birds invest a large amount of time and energy into reproduction: females produce large energy-rich eggs, males often adorn elaborate secondary sexual traits reflecting the resources they were able to muster to produce them (Hamilton & Zuk 1982, Hill 1991, Folstad & Karter 1992, Andersson 1994), furthermore they may engage in fierce male-male contests

over territories and mates, and both sexes usually invest a lot into parental care. Decisions over the reproductive timing and the amount of reproductive investment are therefore usually condition-dependent (Drent & Daan 1980).

Performance during the nonreproductive life-cycle stages does not directly contribute to fitness through offspring production, but contributes to future reproductive success. Analogous to the reproductive window there exist also optimal timeframes for other seasonal tasks such as moult or migration, which both take up a lot of time and energy (Alerstam & Lindström 1990, Lindström et al. 1993, Klaassen 1995, Biebach 1996, Klaassen 1996, Murphy 1996, McWilliams et al. 2004).

To optimise their life-history cycles, birds have to make two kinds of decisions: (1) *when should they initiate* a life-history stage, and (2) *how much time (and resources)* should they devote to it, i.e. when should they initiate the next stage. These questions are particularly relevant when more than one life-history stage draw on the same temporal patch of resources, because the time windows with optimal conditions overlap.

Outline of the thesis

For this thesis I investigated two populations of the stonechat *Saxicola torquata* that differ in the temporal organisation of their annual cycles. Based on the concepts developed above I expect that these differences affect how the animals *perform within* a given life-history stage, and how they *integrate* the different stages into their annual cycle. It is therefore important that the different life-history stages I studied - migration, breeding, juvenile development, and moult (*Fig. 1.2.*) - are not examined in isolation. Due to the trade-off between current and future reproduction, optimal performance in each stage depends also on the other stages in the annual cycle.

Chapter 2 outlines the basic biology of stonechats in general, and of the two populations that are the focus of this thesis, Siberian stonechats breeding in Kazakhstan and European stonechats breeding in Slovakia.

Siberian stonechats are long-distance migrants, whereas European stonechats are short-distance migrants. *Chapter 3* compiles available information on migratory routes, phenology, and speed of migration in the two subspecies.

In *Chapter 4* I investigate whether the differences in migratory distance and hence time spent on migration are reflected in the state of reproductive development in stonechat males arriving in Kazakhstan and Slovakia.

Chapter 5 deals with the effect of the length of the breeding window on reproductive timing, the number of broods, and breeding synchrony in Siberian and European stonechats. Differences in the breeding performance of the two populations are discussed in the light of reproductive investment and local conditions. A short report on facultative polygyny in the Siberian stonechats is given.

Differences in the number of broods and reproductive investment between Siberian and European stonechats may be reflected in the levels of sex hormones. *Chapter 6* deals with the seasonal profiles of gonadal steroids in males and females of the two populations. The results of simulated territorial intrusion experiments are implicated with circulating androgen levels of male stonechats.

Chapter 7 investigates whether Siberian and European stonechats differ in their glucocorticoid response to a standardised handling stress protocol. The results are discussed in the context of current hypothesis on baseline and stress-induced glucocorticoid levels.

Chapter 8 treats population differences in the length of the prenatal period and the rates of postnatal increase in body mass and body size and the effect of calendar date and hatching category (core nestling or runt nestling) on these measures. The pattern of postjuvenile moult in Siberian stonechats is reported.

Finally, in *Chapter 9* I investigate how reproductive timing of Siberian stonechats affects the patterns of postnuptial feather replacement and the overlap between breeding and moult.

References

Alerstam, T. & Lindström, A. (1990). Optimal bird migration: the relative importance of time, energy, and safety. *In* E. Gwinner (Ed.), *Bird Migration: Physiology and Ecophysiology*, pp. 331-351. Springer-Verlag, Berlin.

Andersson, M. (1994). *Sexual selection*. Princeton University Press, Princeton, NJ.

Baker, J. R. (1938). The evolution of breeding seasons. *In* G. R. de Beer (Ed.), *Evolution: Assays on Aspects of Evolutionary Biology*, pp. 161-177. Oxford University Press, London.

Bell, G. & Koufopanou, V. (1986). The cost of reproduction. *Oxford Surveys in Evolutionary Biology*: 83-131.

Biebach, H. (1996). Energetics of Winter and Migratory Fattening. *In* C. Carey (Ed.), *Avian Energetics and Nutritional Ecology*. Chapman & Hall, New York.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Jarvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P. A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Torok, J., Winkel, W., Wright, J., Zang, H. & Visser, M. E. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 271: 1657-1662.

Crick, H. Q. P., Dudley, C., Glue, D. E. & Thompson, D. L. (1997). UK birds are laying eggs earlier. *Nature* 388: 526.

Daan, S., Dijkstra, C., Drent, R. & Meijer, T. (1986). Food supply and the annual timing of avian reproduction. *In* H. Ouellet (Ed.), *Acta XIX Congressus Internationalis Ornithologici*, pp. 391-407. University of Ottawa Press, Ottawa.

Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. (2001). Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* 16: 365-380.

Drent, R. H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.

Folstad, I. & Karter, A. J. (1992). Parasites, bright males and the immunocompetence handicap. *American Naturalist* 139: 603-622.

Forchhammer, M. C., Post, E. & Stenseth, N. C. (1998). Breeding phenology and climate. *Nature* 391: 29-30.

Gwinner, E. (1986). *Circannual rhythms*. Springer Verlag, Heidelberg.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology* 199: 39-48.

Gwinner, E. (2001). Bird migration: its control by endogenous clocks. *In* D. Baltimore, R. Dulbecco, F. Jacob & R. Levi-Montalcini (Eds.), *Frontiers of Live*, Vol. 4: The Living World, pp. 193-206. Academic Press, New York.

Gwinner, E. (2003). Circannual rhythms in birds. *Current Opinion in Neurobiology* 13: 770-778.

Gwinner, E. & Dittami, J. P. (1990). Endogenous reproductive rhythms in a tropical bird. *Science* 249: 906-908.

Gwinner, E. & Scheuerlein, A. (1998). Seasonal changes in day-light intensity as a potential zeitgeber of circannual rhythms in equatorial Stonechats. *Journal fuer Ornithologie* 139: 407-412.

Gwinner, E. & Scheuerlein, A. (1999). Photoperiodic responsiveness of equatorial and temperate-zone stonechats. *Condor* 101: 347-359.

Gwinner, H., Gwinner, E. & Dittami, J. P. (1987). Effects of nestboxes on LH, testosterone, testicular size, and the reproductive behavior of male European starlings in spring. *Behaviour* 103: 68-82.

Hahn, T. P., Boswell, T., Wingfield, J. C. & Ball, G. F. (1997). Temporal flexibility in avian reproduction: Patterns and mechanisms. *In* V. Nolan, Jr., E. D. Ketterson & C. F. Thompson (Eds.), *Current Ornithology*, Vol. 14, pp. 39-80. Plenum Press, New York, London.

Hahn, T. P., Wingfield, J. C., Mullen, R. & Deviche, P. J. (1995). Endocrine bases of spatial and temporal opportunism in Arctic-breeding birds. *American Zoologist* 35: 259-273.

Hamilton, W. D. & Zuk, M. (1982). Heritable true fitness and bright birds - a role for parasites. *Science* 218: 384-387.

Hau, M. (2001). Timing of breeding in variable environments: Tropical birds as model systems. *Hormones and Behavior* 40: 281-290.

Hau, M., Wikelski, M., Gwinner, H. & Gwinner, E. (2004). Timing of reproduction in a Darwin's finch: temporal opportunism under spatial constraints. *Oikos* 106: 489-500.

Hau, M., Wikelski, M. & Wingfield, J. C. (1998). A neotropical forest bird can measure the slight changes in tropical photoperiod. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 265: 89-95.

Hill, G. E. (1991). Plumage coloration is a sexually selected indicator of male quality. *Nature* 350: 337-339.

IPCC (2001). *Third Assessment Report of the Intergovernmental Panel on Climate Change IPCC (WG I & II)*. Cambridge University Press, Cambridge.

Jacobs, J. D. & Wingfield, J. C. (2000). Endocrine control of life-cycle stages: A constraint on response to the environment? *Condor* 102: 35-51.

Juss, T. J. (1993). Neuroendocrine and neuronal changes associated with the photoperiodic control of reproduction. *In* E. P. Sharp (Ed.), *Avian Endocrinology*, pp. 47-59. Journal of Endocrinology, Ltd., Bristol.

Klaassen, M. (1995). Moult and basal metabolic costs in males of two subspecies of stonechats: The European Saxicola torquata rubicula and the East African S. t. axillaris. *Oecologia* 104: 424-432.

Klaassen, M. (1996). Metabolic constraints on long-distance migration in birds. 199: 57-64.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen, London.

Lindström, A., Visser, G. H. & Daan, S. (1993). The energetic cost of feather synthesis is proportional to basal metabolic-rate. *Physiological Zoology* 66: 490-510.

Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M. & Wanner, H. (2004). European Seasonal and Annual Temperature Variability, Trends, and Extremes Since 1500. *Science* 303: 1499-1503.

McCleery, R. H. & Perrins, C. M. (1998). Temperature and egg laying trends. *Nature* 391: 30-31.

McWilliams, S. R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology* 35: 377-393.

Murphy, M. E. (1996). Energetics and nutrition of molt. *In* C. Carey (Ed.), *Avian Energetics and Nutritional Ecology*, pp. 158-198. Chapman & Hall, New York.

Murton, R. K. & Westwood, N. J. (1977). *Avian Breeding Cycles*. Clarendon Press, Oxford.

Newton, I. (1989). *Lifetime reproduction in birds*. Academic Press, London.

Newton, I. (1995). The contribution of some recent work on birds to ecological understanding. *Journal of Animal Ecology* 64: 675-696.

Nilsson, J.-A. (1999). The fitness consequences of the timing of reproduction. *In* N. J. Adams & R. H. Slotow (Eds.), *Proc. 22 Int. Ornthol. Congr., Durban*, pp. 234-247. BirdLife South Africa, Johannesburg.

Perrins, C. M. (1970). The timing of birds breeding seasons. *Ibis* 112: 242-255.

Roff, D. A. (1992). *The Evolution of Life Histories: Theory and analysis*. Chapman & Hall, New York.

Stearns, S. C. (1992). *The Evolution of Life-Histories*. Oxford University Press, Oxford.

Stevenson, I. R. & Bryant, D. M. (2000). Avian phenology: climate change and constraints on breeding. *Nature* 406: 366-367.

Wikelski, M., Hau, M. & Wingfield, J. C. (2000). Seasonality of reproduction in a neotropical rain forest bird. *Ecology* 81: 2458-2472.

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.

Wingfield, J. C. (2004). Allostatic load and life-cycles: Implications for neuroendocrine control mechanisms. *In* J. Schulkin (Ed.), *Allostasis, homeostasis, and the costs of physiological adaptation*, pp. 302-342. Cambridge University Press, Cambridge, UK.

Wingfield, J. C. & Farner, D. S. (1993). Endocrinology of reproduction in wild species. *In* D. S. Farner, J. R. King & K. C. Parkes (Eds.), *Avian Biology*, Vol. 9, pp. 163-327. Academic Press, London/San Diego.

Wingfield, J. C., Hahn, T. P., Levin, R. & Honey, P. (1992). Environmental predictability and control of gonadal cycles in birds. *Journal of Experimental Zoology* 261: 214-231.

Wingfield, J. C. & Moore, M. C. (1987). Hormonal, social and environmental factors in the reproductive biology of free-living male birds. *In* D. Crews (Ed.), *Psychobiology of Reproductive Behaviour: An Evolutionary Perspective*, pp. 149-175. Prentice-Hall, New York.

2 CHARACTERISATION OF THE STUDY SPECIES AND THE STUDY SITES

2.1 Summary

In this chapter, I present a short overview of the taxonomic position, the geographical distribution, and the general biology of Siberian and European stonechats. This is followed by a description of the general characteristics of the study areas and the specific study sites in Kazakhstan and Slovakia. Capture data from the two populations is presented. Differences in body size and wing length of Siberian and European stonechats may be related to different migratory strategies. Within populations, differences between the sexes in body mass and visible fat reserves occur in the context of egg formation and incubation.

2.2 The stonechat *Saxicola torquata*

2.2.1 Phylogenetic status and geographical distribution of the stonechat

The stonechat belongs to the genus *Saxicola* in the family of Muscicapidae in the order of Passeriformes (Ripley 1964, Sibley & Monroe 1990). The genus *Saxicola* contains 12 species (more, if *Saxicola torquata* is split, see below), all of which are small (10-20 g) insectivorous, more or less sexually dimorphic birds that occur in the Palearctic and Afrotropis (Urquhart 2002). The common stonechat *Saxicola torquata* has the most extended breeding range among these species, it can be found in Asia, Europe, and Africa (Dement'ev & Gladkov 1954, Cramp 1988, Glutz von Blotzheim & Bauer 1988, Urquhart 2002)(*Fig. 2.1.*).

The taxonomical status of the common stonechat is under discussion. Traditionally seen as one species containing about 25 subspecies (Dement'ev & Gladkov 1954, Cramp 1988, Glutz von Blotzheim & Bauer 1988), more recent molecular evidence suggests that the *Saxicola torquata* complex can be split into at least three true species (Wittmann et al. 1995, Wink et al. 2002a, Wink et al. 2002b). The issue is as yet unresolved, because, as Urquhart (2002) points out, not all of the former *torquata* subspecies have been included in the analysis. The picture that emerges from the phylogenetic analysis, however, is that the common stonechat complex can be split into (1) a *European stonechat* (termed *S. rubicola* by Urquhart and *S. torquata* by Wink et al.), (2) a *Siberian stonechat* (*Saxicola maura*), and (3) an *African stonechat* (termed *S. torquata* by Urquhart, *S. axillaris* by Wink et al.), each of which contains several subspecies.

In this study we investigated two stonechat populations: a population of the western (*see below*) Siberian stonechat (former subspecies *S. t. maura*) in northern Kazakhstan, and a population of the European stonechat (former subspecies *S. t. rubicola*) in Slovakia. Throughout this text, I will refer to them as Siberian stonechats and European stonechats, and as their taxonomic status is not fully resolved, I will regard them as different populations of the common stonechat.
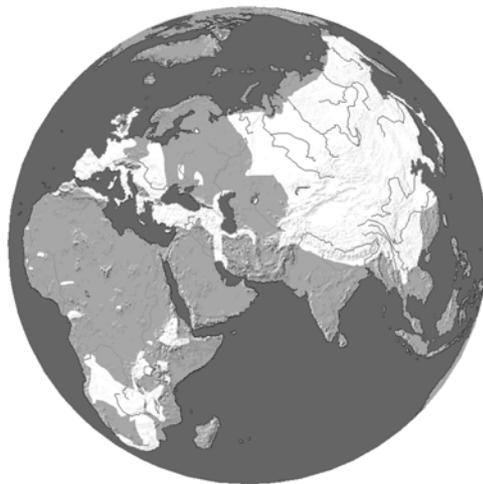
Fig. 2.1. The breeding range of the common stonechat complex (light areas). Adapted from Dement'ev and Gladkov (1954), Kuz'mina (1970), and Urquhart (2002).

2.2.2   The geographical distribution of the Siberian stonechat

The breeding range of the Siberian stonechat encompasses the Asian part of Russia, Western and Central Siberia, and parts of Central Asia, Mongolia and China (*Fig. 2.2.*). To the east of these areas extends the breeding range of the eastern Siberian stonechat subspecies *S. t. stejnegeri*, which is not considered in this thesis.

The wintering areas are located in northern Pakistan and India, and the Arabian Peninsula (*Fig. 2.2.*). Thus, over a large part of its range, the Siberian stonechat is a long-distance migrant, which covers distances of up to 6000 km and more and has to avoid or overcome prominent mountain ranges such as the Tien-Shan Mountains or the Himalayas on their way (see Chapter 3 of this thesis).
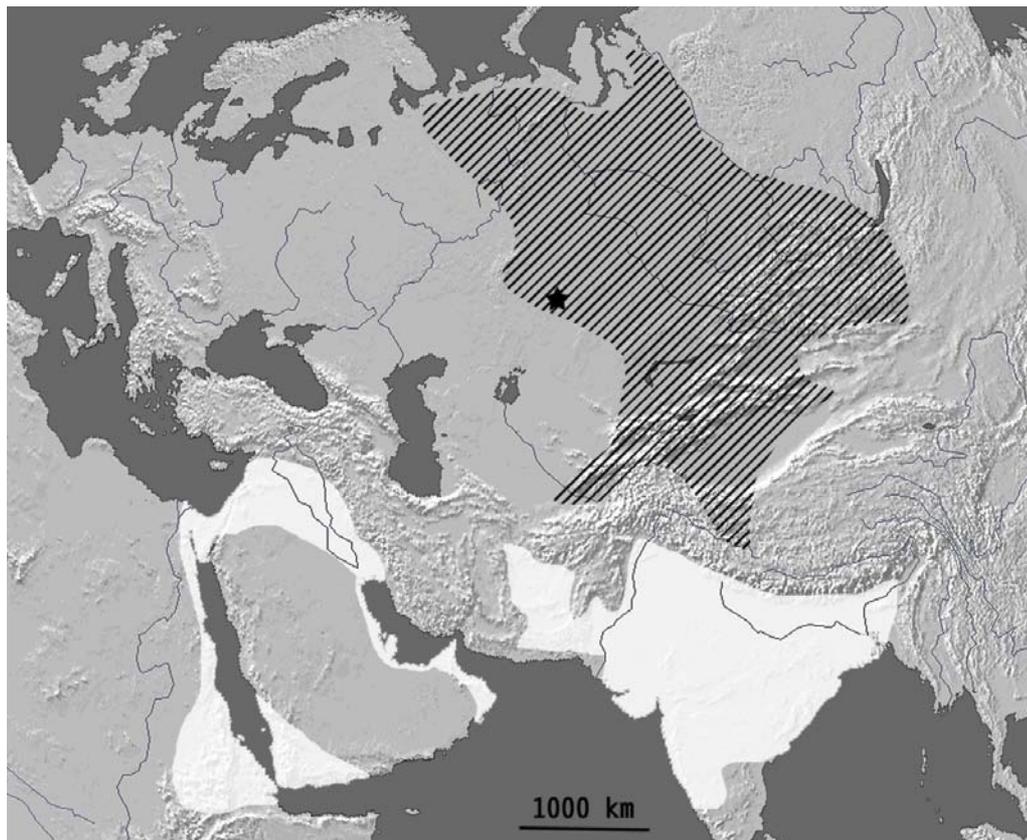
Fig. 2.2. The breeding range (hatched area) and the wintering range (light area) of the Siberian stonechat. The star indicates the position of my Central Asian study area. Adapted from Dement'ev and Gladkov (1954), Kuz'mina (1970), and Urquhart (2002).

2.2.3 The geographical distribution of the European stonechat

The European stonechat breeds all over Europe, but is rare in the northern Alps, central Germany, Denmark and Scandinavia. Its breeding distribution stretches east to Poland and Ukraine, and south to Turkey, northern Morocco, Algeria and Tunisia (*Fig. 2.3.*). European stonechat populations can be year-round residents, partial migrants or obligatory migrants. Wintering areas are the Mediterranean part of Europe and northern Africa and the Middle East (*Fig. 2.3.*). Thus, migratory European stonechats usually cover short distances of less than 2000 km (see Chapter 3 of this thesis).
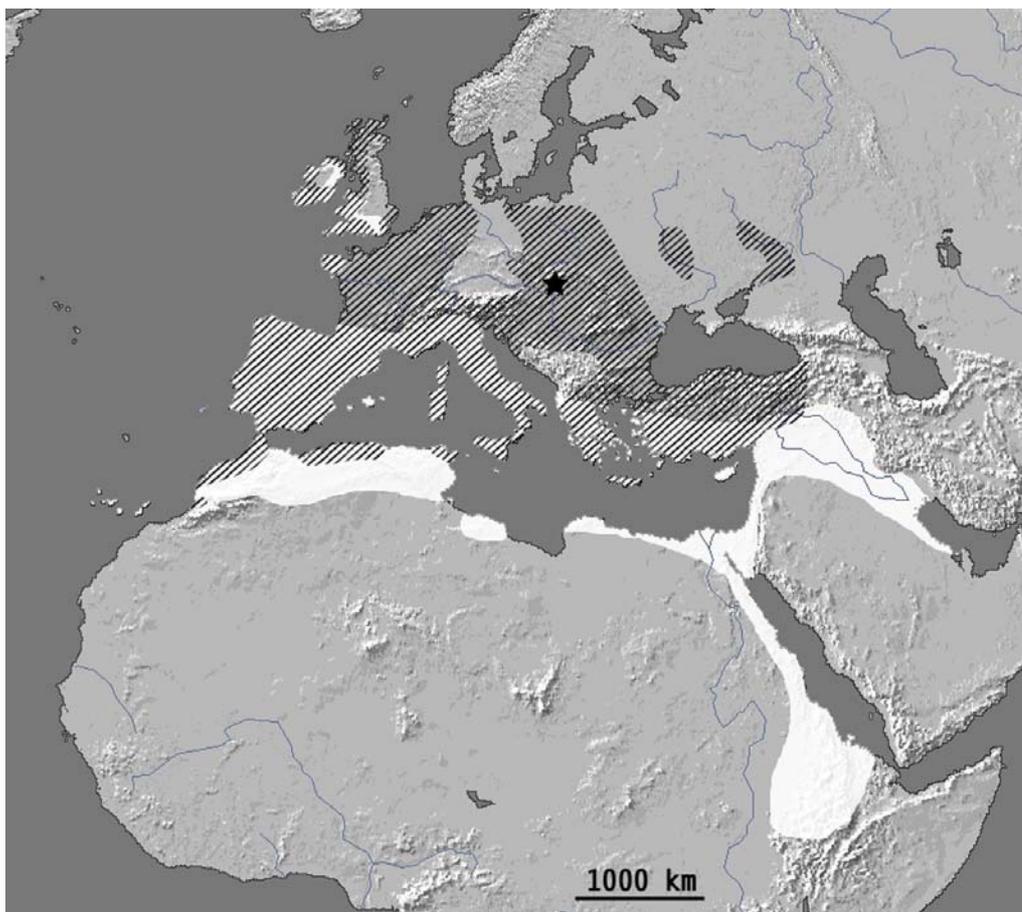
Fig. 2.3. The breeding range (hatched areas) and wintering range (light areas) of the European stonechat. The star indicates the location of my East European study area (after Urquhart 2002).

2.2.4   General biology of the stonechat

Stonechats are birds of the open habitats, they prefer areas with low vegetation, such as steppes, loose scrubland, heathland, meadows, and wasteland. They generally prefer habitats with low moisture, but eventually use the dryer parts (or the drying-up parts, see Gwinner et al. 1998) of moors. Stonechats are comparably conspicuous birds, as they hunt their prey, small insects, spiders, and other invertebrates, from elevated perches that provide a good view-point on the surrounding vegetation. Stonechats establish territories in the breeding and nonbreeding seasons. Furthermore, in sedentary as well as in migratory birds, males and females frequently defend a territory together in autumn and winter (Gwinner et al. 1994, Rödl 1995). Stonechats are socially monogamous. However, occasional facultative polygyny has been described in European stonechats (Johnson 1961), and is described for Siberian stonechats in this thesis (see Chapter 5). The number of breeding attempts depends on the length of the breeding season and varies between one and five in different populations. The females lay clutches of three to seven greenish-blue eggs into nests built into the ground vegetation. Nests built aboveground into bushes or trees are very rare. Only the females incubate, but both sexes feed the young. The rate of extra-pair fertilisations is not known. After breeding, stonechats carry out a complete post-nuptial moult on their breeding grounds.

2.3   Characterisation of the study areas

My study areas are both located in the temperate zones of the northern hemisphere. Photoperiods are similar, daylengths at the solar eclipses, when photoperiods differ the most, are 29 minutes longer in summer and 29 minutes shorter in winter in Kazakhstan (*Fig. 2.4.*).
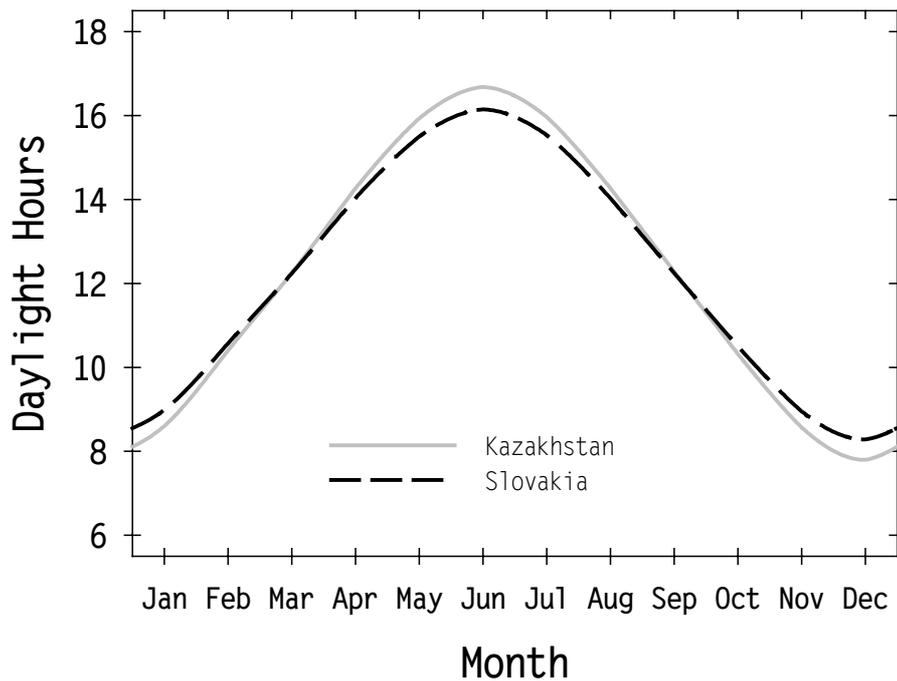
Fig. 2.4. Photoperiodic conditions in my study areas in Kazakhstan and Slovakia. Daylengths at the solar eclipses differ by 29 Minutes.

2.3.1 Kazakhstan

Kazakhstan is a country of steppes, semi-deserts and deserts, which cover more than 90% of its landmass. It is located in Central Asia and has common borders with Russia in the North, China in the south-east, and Kyrgyzstan and Turkmenistan in the south. Part of its western border is made up by the Caspian sea. With a surface area of over 2.7 million square kilometres, it is the fourth largest country in Asia. This vast area is populated by 15.1 million people, therefore the population density is only 5.6 inhabitants per square kilometre. Most of Kazakhstan is flat, but two prominent mountain ranges extend onto Kazakh territory: The Altai Mountains in the east with elevations around 2500-3000 m (highest elevation: *Gora Belukha* 4506 m, Kazakhstan), and the Tien-Shan and Ala-Tau Mountains in the south with elevations around 4000-5000 m (highest elevation: *Khan Tangiri*

Shyngy 6995 m, borderland of Kazakhstan, Kyrgyzstan and China). The overall climate is continental, with hot summers and severe winters.

Approximately 500 bird species can be encountered in Kazakhstan, either as residents or as summer or winter guests (Kuz'mina 1970, Gavrilov 1999). The Siberian stonechat is a common breeding migrant. It is most abundant in the steppe zones in the north of Kazakhstan and in the foothills of the Altai, Tien-Shan and Ala-Tau mountain ranges in the east and south east. It has been found breeding up to an elevation of 3200 m in the south-east (Shnitnikov 1949). Although it penetrates into the semi-deserts in central Kazakhstan, it is absent in the deserts of the south and south-west of the country (Kuz'mina 1970, Gavrilov 1999).

2.3.2   The Kazakh study site

Our Central Asian study area is located in the administrative region of Kostanay in northern Kazakhstan (52°N, 64°E), close to the town of Dokuchaevka (now Karamendy) and the *Naurzumskij gosudarstvenij zapovednik* (Naurzum State Nature Reserve)(*Fig. 2.5.*). The area belongs bio-geographically to the the *Kazakh Steppe*, the world largest dry steppe region, which covers most of northern Kazakhstan (Lavrenko et al. 1991, Chibilev 1998, Ponomarenko 2000).

The *Kazakh Steppe* is characterised by large tree-less plains and gentle hill plateaus (*melkosopochniki*, low hilly structures - generally not exceeding 200 m elevation - with gentle forms, that are products of erosion processes prevailing in the *Kazakh Steppe* region). Typical are dry steppe plant formations with *Stipa* feathergrasses, *Festuca* and *Koeleria* grasses, and *Artemisia* sagebrushes as predominant species. Patches of steppe are covered by small shrubs, mainly *Spiraea*, *Caracana*, *Amygdalus*, and *Lonicera* (Lavrenko et al. 1991, Chibilev 1998, Ponomarenko 2000).

In the 1950s, Khrushchev initiated the '*Virgin Lands Campaign*' to transform the steppes of Central Asia, which were by then mainly used for cattle grazing by nomadic herdsmen, into the granary of the Soviet Union (Chibilev 1998). About 60% of the Kazakh steppe were ploughed for grain

cultivation, and fertilizers and pesticides were employed. This had a profound impact on the original steppe biocenoses (Fedorenko et al. 1981, Belik 1997, Chibilev 1998). The town of Dokuchaevka was an administrative and logistical centre for the 'Virgin Lands Campaign' in that area. The use of the pesticide DDT in the 1970s caused a steep decline in the populations of passerines breeding in the vicinity of Dokuchaevka. These populations recovered from the 1980s on, when DDT was no longer used (Alexander Moiseev, pers. communication). Since the 1990s, after the disintegration of the Soviet Union and the independence of Kazakhstan, agricultural activities and the use of chemicals decreased drastically, and the area around Dokuchaevka is now mainly used for cattle grazing and hay harvesting.

The Naurzum Nature Reserve was established in 1931 to protect insular remnants of coniferous and deciduous forests (which belong to the *Forest Steppe* zone further north), lakes and wetlands, which are important staging areas during bird migration, and pristine steppe habitats that were never used for agriculture. The *zapovednik* (nature reserve) today encompasses 87,700 hectares. Due to the diversity of habitats, the nature reserve is home to about 690 plant species, 320 species of vertebrates, and 160 species of breeding birds, including 21 species of birds of prey (Zaugolnova 1977, Bragin & Bragina 1999, Katzner et al. 2003).

The climate in the area is strongly continental. The average temperature is below zero degrees for five months from November till March. The lowest temperatures are measured in January, the mean temperature for this month is -17.9°C. July is the hottest month with an average temperature of 20.4°C. The average annual precipitation is 298 mm, 40% of the annual amount falls from June to August (IRI 2004)(*Fig. 2.7.*).

For our investigations we established three study plots that contained between 10 and 25 breeding pairs each. They were located in secondary grasslands used for cattle grazing and hay-making (*A, B*) on the ridge of the *melkosopochnik* on which Dokuchaevka is located, or on primary *Festuca-Artemisia* steppe close to the nature reserve (*C*)(*Fig. 2.5.*).

Typical breeding birds that shared these habitats with the stonechat are grey partridge *Perdix perdix*, quail *Coturnix coturnix*, short-eared owl *Asio flammeus*, skylark *Alauda arvensis*, white-winged lark *Melanocorypha leucoptera*, yellow wagtail *Motacilla flava*, tawny pipit *Anthus campestris*, wheatear *Oenanthe oenanthe*, isabelline wheatear *O. isabellinus*, grasshopper warbler *Locustella naevia*, whitethroat *Sylvia communis*, lesser whitethroat *S. curruca*, barred warbler *S. nisoria* (the *Sylvia* warblers occurred only in the secondary grasslands, where the vegetation contained higher bushes), booted warbler *Hippolais caligata*, and red-headed bunting *Emberiza bruniceps*. The study plots in the secondary grasslands contained boggy ponds formed by melt water and surrounding bush thickets, which attracted Merlin *Falco columbarius*, bluethroat *Luscinia svecica*, magpie *Pica pica*, rook *Corvus frugileus*, and tree sparrow *Passer montanus*.

All three plots were within the range of the birds of prey nesting in the steppe and forest zones of the *zapovednik*. Birds of prey that were regularly observed hunting small passerines include pallid harrier *Circus macrourus*, Montagu's harrier *C. pygargus*, marsh harrier *C. aeruginosus*, sparrowhawk *Accipiter nisus*, kestrel *Falco tinnunculus*, lesser kestrel *F. naumanni*, red-footed falcon *F. vespertinus*, merlin, and hobby *F. subbuteo*.

Among the terrestrial predators threatening stonechats or their clutches were steppe polecat *Mustela eversmanni*, Eurasian badger *Meles meles*, red fox and steppe fox *Vulpes vulpes* and *V. corsac*, and steppe viper *Vipera ursini*, and in addition domesticated dogs and pigs from close settlements.

We carried out our studies in Kazakhstan from May to September 1999, April to September 2000, and June to September 2001.

Fig. 2.5. (Next page) The Central Asian study area is located in the *Kazakh Steppe* zone (light area), close to the village of Dokuchaevka and the Naurzum Nature Reserve (the borders of the Reserve are indicated by the white hatched line). Three study plots (A, B, C), contained each between 25 and 50 breeding pairs of Siberian stonechats.

Kazakhstan

Kazakh Steppe

250 km

5000 m

A

B

C

Dokuchaevka

Naurzum Nature Reserve
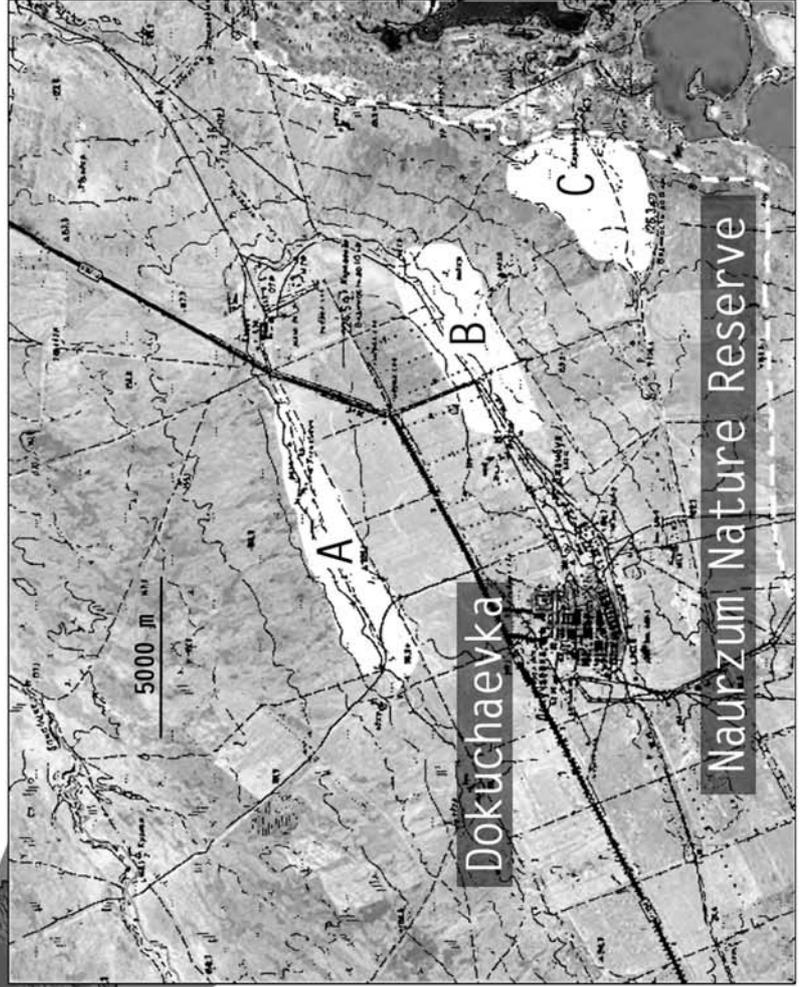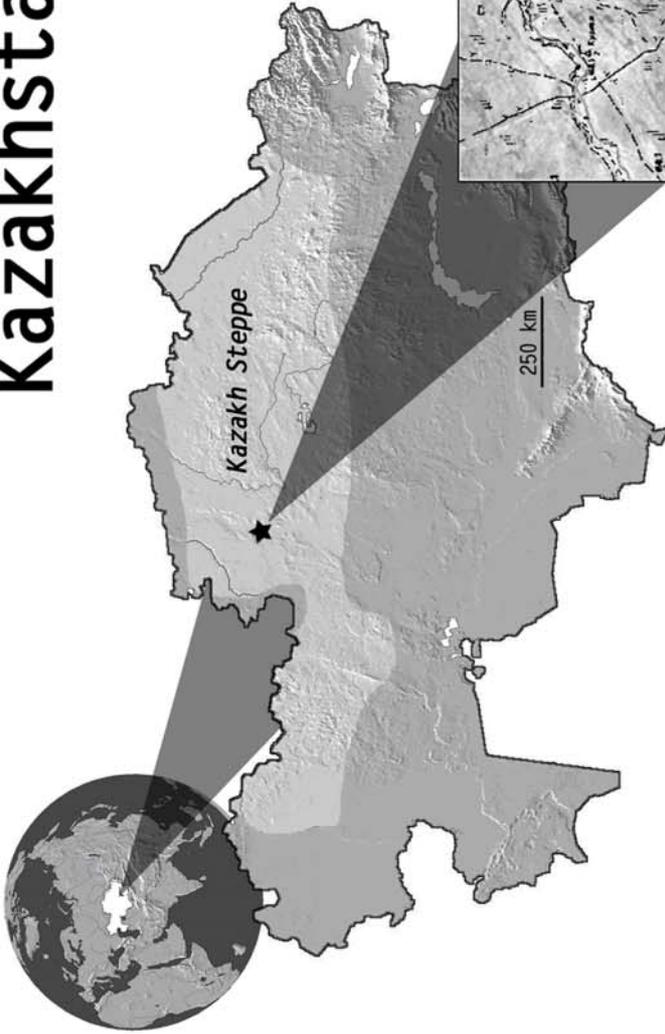
2.3.3 Slovakia

Slovakia is located in Eastern Europe and borders on Poland in the north, Ukraine in the east, Hungary in the south and Austria and the Czech Republic in the west. It is characterised by forests and mountains. More than 40% of the area of 48.8 thousand square kilometres is covered by forests, 15% lie above an elevation of 800 m. Slovaks distinguish several different mountain ranges with elevations from 1500 to 2600 m (highest elevation: Gerlachovský štít 2655 m, High Tatra Mountains), all belonging to the Carpathian Mountains that stretch from the Czech Republic to Romania and Yugoslavia. Only the south-westerly and south-easterly portions of Slovakia open up towards Austria and Hungary into the Pannonian basin.

Slovakia has 5.4 million inhabitants, the population density is 111.0 inhabitants per square kilometre. The climate is generally temperate, with mild summers and mild winters, however temperature and precipitation are strongly influenced by elevation. Arable land is limited to the plains and the bottoms of the valleys; therefore agriculture in these areas is usually intensive, involving a pronounced use of agrochemicals. The transition from the agricultural co-operatives of the socialist area to private ventures did not bring about a strong reduction of the area under cultivation or of the use of pesticides and fertilizers. Therefore, except in the protected areas, wildlife in Slovakia faces similar problems as in the rest of Central Europe (Heath & Evans 2000).

The avifauna in Slovakia comprises about 340 species, 220 of which are breeding birds (Danko et al. 2002). The European stonechat is an abundant breeding migrant throughout Slovakia. It nests up to an elevation of 950 m. Some rare incidents of overwintering of stonechats in Slovakia have been reported (Danko et al. 2002).

Fig. 2.6. (Next page) The European study site is located in central Slovakia, in the Pol'ana region, which belongs to the western Carpathian Mountain area. The study plots (*A, B, C, D*) were situated between the city of Zvolen, the village of Očová and the Pol'ana Biosphere Reserve.
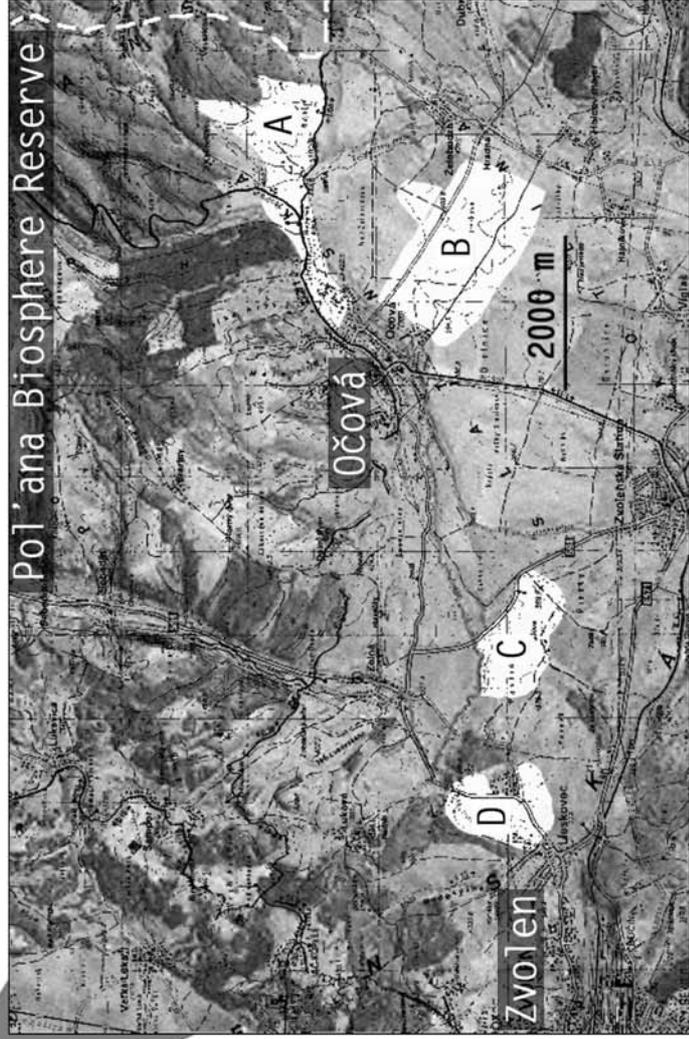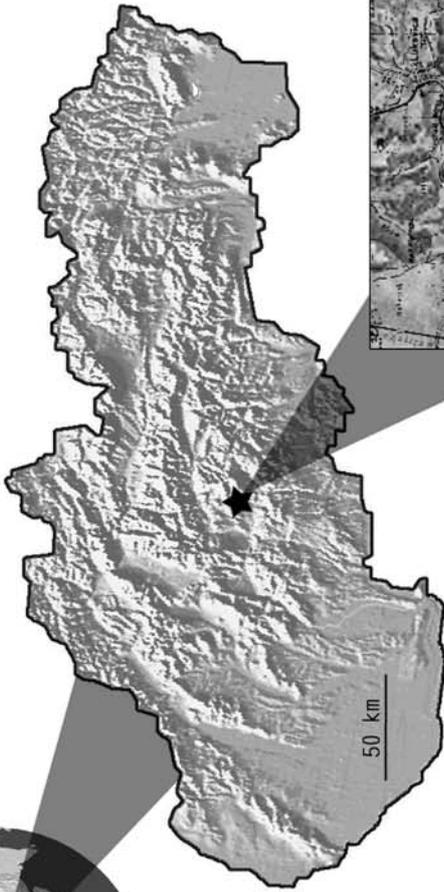
2.3.4 The study site in Slovakia

We conducted our study on the European stonechat in central Slovakia, close to the city of Zvolen and the Pol'ana Biosphere Reserve (49°N, 19°E) (*Fig. 2.6.*). The area belongs biogeographically to the *Carpathian Montane Forest* Ecoregion. This area is characterised by different forest types in different altitudes: Deciduous forests (predominantly *Quercus* species) are typical for low elevations and in the foothills of the mountains. Mixed forests of European beech *Fagus sylvatica*, sycamore *Acer pseudoplatanus*, Norway spruce *Picea abies* and silver fir *Abies alba* grow in the montane zones between 400 and 1100 m. The alpine zones above 1100 m are dominated by Norway spruce, and above 1500 m the mountain pine *Pinus mugo* prevails (DMEER 2000, Perzanowski 2001).

The climate in the area is continental with mild summers and winters. The average temperatures of March to November lie above zero degrees. The warmest month is July with 18.2°C mean temperature, the coldest month is January with -3.8°C on average. The annual precipitation amounts to 687 mm (IRI 2004) (*Fig. 2.7.*).

The Pol'ana UNESCO Biosphere Reserve close to our study sites comprises 20,000 hectares with the erosive caldera of the Pol'ana volcano (active 12 million years ago) in the centre. The reserve was established in 1990 to manage abandoned or extensively used pastures and grasslands and the montane flora and fauna of the Pol'ana Mountain. The avifauna is particularly rich, with 144 species of which 121 nest in the area.

We studied European stonechats at four different spots in the vicinity of Zvolen and the village of Očová, each containing between 5 and 20 breeding pairs. The study plots either comprised meadows (*A, C*), or the slopes and ditches alongside country roads (*B, D*) (*Fig. 2.6.*).
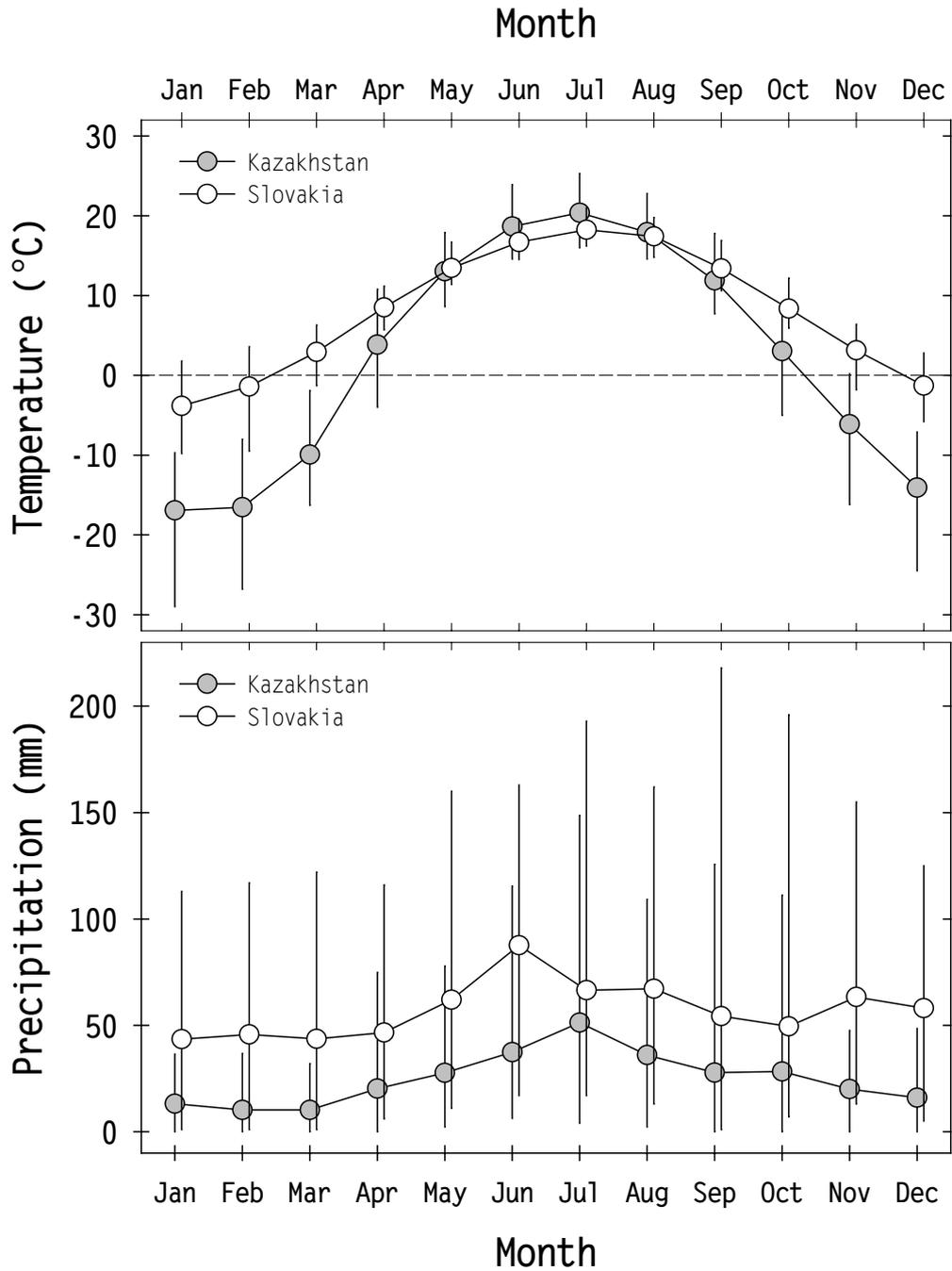
Fig. 2.7. The annual distribution of temperature and precipitiation in the breeding areas of Siberian and European stonechats. The points show monthly mean data, averaged over the period from 1902 to 1993 for the meteorological station in Kustanay, Kazakhstan, and over the period from 1951 to 1990 for the meteorological station in Sliac, Slovakia. The vertical lines show the ranges of the monthly means (Data source: IRI 2004).

The most common birds occurring in the same habitats were kestrel, sparrowhawk, pheasant *Phasianus colchicus*, cuckoo *Cuculus canorus*, skylark, meadow pipit *Anthus pratensis*, tree pipit *A. trivialis*, pied wagtail *Motacilla alba*, winter wren *Troglodytes* troglodytes, dunnock *Prunella modularis*, Robin *Erithacus rubecula*, whinchat *Saxicola rubetra*, black redstart *Phoenicurus ochruros*, wheatear, blackbird *Turdus* merula, fieldfare *T. pilaris*, grasshopper warbler, whitethroat, blackcap *Silvia atricapilla*, red-backed shrike *Lanius collurio*, jay *Garrulus glandarius*, magpie, European starling *Sturnus vulgaris*, tree sparrow, linnet *Carduelis* cannabina, goldfinch *C. carduelis*, green finch *C. chloris*, and yellowhammer *Emberiza citrinella*.

Among the potential avian predators on stonechats or their clutches were sparrowhawk, kestrel, red-backed shrike, jay and magpie. Potential terrestrial predators were the red fox, members of the mustelid family, the smooth snake *Coronella austriaca*, and domestic cats and dogs. Among the potential predators on the researchers was the brown bear *Ursus arctos* from the close Pol'ana Biosphere Reserve.

We conducted our studies in Slovakia from March to May 2001 and from March to August 2002.

2.4   A comparison of measures of body size and condition in Siberian and European stonechats

2.4.1 Methods

Field methods and measures

Basis of our regular monitoring of territorial and reproductive activities in our population was a large number of individually marked stonechats. In Kazakhstan we colour-banded 161 individuals as adults, 78 individuals as juveniles outside of the nest, and 368 individuals as nestlings. In Slowakia we colour-banded 94 individuals as adults and 138

individuals as nestlings. Adults and juveniles were either caught with mealworm-baited spring traps, or with mist nets. Nestlings were banded one or two days prior to the presumed date of fledging.

Each of these birds was banded with an aluminium ring from the Vogelwarte Radolfzell (Kazakh birds) or the Slovakia Bird Ringing Centre (Slovak birds), and with a unique combination of two coloured plastic bands. The position of the aluminium ring on the left or right foot in combination with an additional colour band above the aluminium ring coded for the capture year and whether a birds was marked as nestling, juvenile, or adult.

The following measures were taken from each bird: *(1)* body mass was determined to the nearest of 0.25 g with a PESOLA spring balance; *(2)* Subcutaneous fat reserves were estimated according to a fat score that ranges from *1 = no visible fat reserves* to *5 = maximal fat stores*; *(3)* total wing length and the length of the 8th primary were determined to the nearest of 1 mm using rulers with elbow or pin at the zero-end; (4) tarsus length was determined to the nearest of 0.1 mm with a calliper, following the method depicted in Fig. 18A in Svensson (1992).

Definition of the breeding cycle stages

Body mass and fat stores are related to distinct phases in the breeding seasons of Siberian and European stonechats. These *breeding cycle stages*, which will also be used in the description of seasonal patterns of circulating gonadal and adrenal steroids (Chapter 6 and 7 of this thesis), are defined as follows:

Snow: A 3-day period during early arrival in Slovakia with low ambient temperatures and snow cover; *Arrival*: The birds do not establish territories and do not react aggressively towards conspecifics and a stuffed specimen; *Territorial*: Birds are only seen singly or in pairs, territories are defended against conspecifics and birds react aggressively towards a stuffed specimen; no breeding activities; *Egg*: Egg formation, laying and incubation of the first clutch; courtship, copulations and nest-

building can be observed during this stage; *Nestling*: the period from hatching to fledging, food is provisioned into the nest; *Fledgling*: the period from the fledging of the young until they gain independence, food is provisioned outside of the nest, later the young are only guarded and defended; *Moult:* the period of feather replacement. The suffix *1* denotes the first clutch in both populations, the suffix *2* replacement clutches in Kazakhstan, and replacement clutches, second clutches, and third clutches in Slovakia. Note that stages can overlap: birds in Kazakhstan initiate moult during the fledgling stage; while in Slovakia females lay and incubate the second clutch, the male cares for the fledglings of the first clutch. The chronology of the breeding cycle stages in Kazakhstan and Slovakia is shown in *Fig. 2.8*.
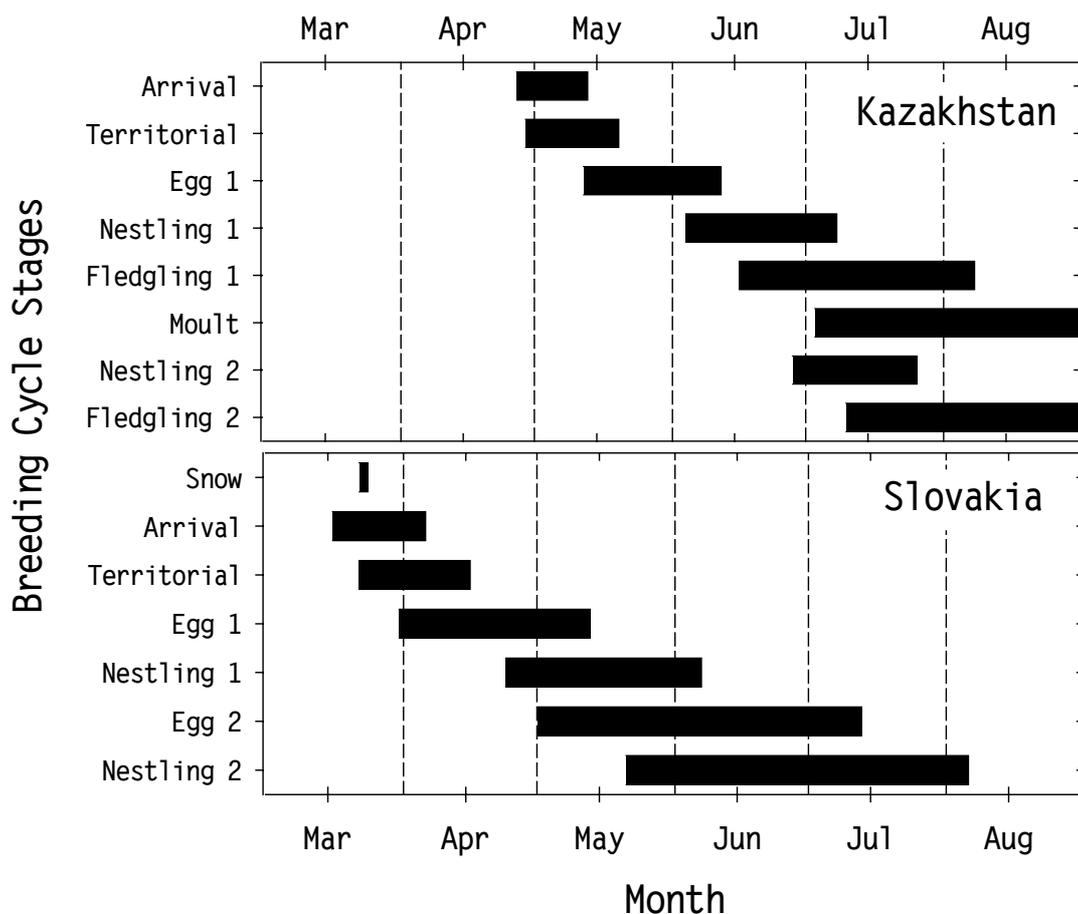
Fig. 2.8. The onset and duration of the breeding cycle stages in Kazakhstan and Slovakia. Note that stages for which no banding data was available, e.g. that the *Egg 2* stage in Kazakhstan, are not shown.

Statistical analysis

Except for tarsus length, the measures of body size and body condition were not consistently normally distributed in the two sexes and the two populations. Hence, all comparisons, including tarsus length, were carried out with Mann-Whitney-U tests (if the sample size for both groups was larger than 5) and relationships between variables were explored with Spearman's rank correlations.

Table 2.1. A comparison of measures of size and condition between Siberian and European stonechats and between the sexes within the populations.

		Males			Female			Total			Comparison between Sexes	
		mean	SD	N	mean	SD	N	mean	SD	N	U	p
Body Mass	Kazakhstan	12.67	0.73	81	13.05	1.27	80	12.86	1.04	161	2853.5	.189
(g)	Slovakia	14.80	0.82	49	16.08	1.25	49	15.44	1.23	98	487.0	.001
	Comparison between Populations						U	780.5				
							p	.001				
Fat Score	Kazakhstan	2.17	0.78	81	2.16	0.97	81	2.16	0.88	162	3224.0	.845
	Slovakia	2.46	1.01	49	2.89	0.97	49	2.67	1.01	98	888.5	.022
	Comparison between Populations						U	5731.0				
							p	.001				
Wing	Kazakhstan	68.06	1.15	50	66.74	1.18	35	67.52	1.33	85	350.0	.001
(mm)	Slovakia	65.67	1.10	38	64.09	1.13	33	64.94	1.36	71	185.5	.001
	Comparison between Populations						U	554.0				
							p	.001				
Primary 8	Kazakhstan	51.89	1.08	45	50.77	1.25	33	51.42	1.27	78	377.5	.001
(mm)	Slovakia	49.41	1.02	33	48.18	1.07	33	48.80	1.21	66	230.0	.001
	Comparison between Populations						U	368.5				
							p	.001				
Tarsus	Kazakhstan	21.48	0.58	70	21.40	0.44	77	21.44	0.51	147	2232.5	.072
(mm)	Slovakia	22.49	0.76	49	22.51	0.56	49	22.50	0.66	98	1195.0	.969
	Comparison between Populations						U	1302.5				
							p	.001				
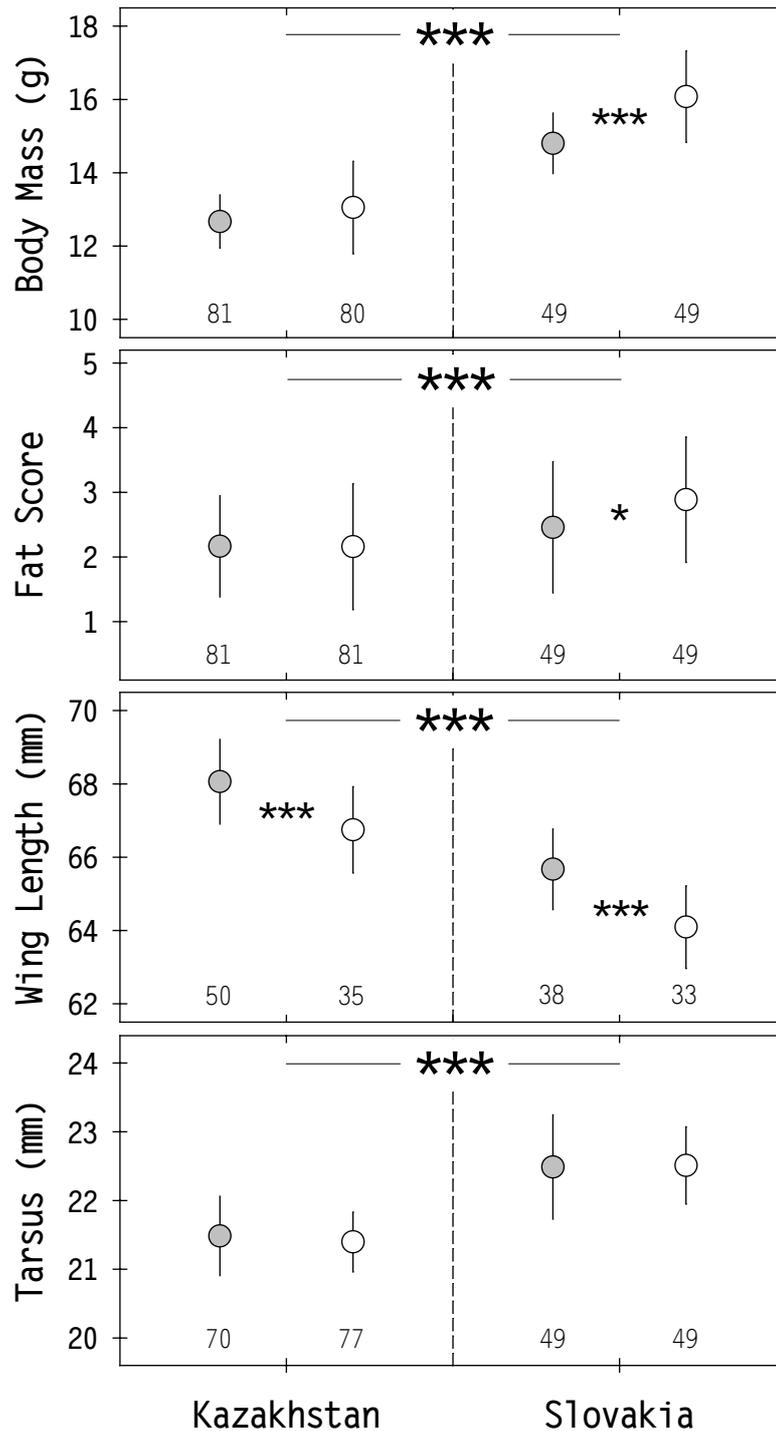
Fig. 2.9. A comparison of body mass, fat scores, and the size measures wing length and tarsus length in males (closed symbols) and females (open symbols) of Siberian and European stonechats. For the comparison between populations the data of the sexes was combined. The asterisks flag significant differences revealed by Mann-Whitney-U tests.(Values for the 8th primary are not shown because of the high correlations with the total wing lengths, cf. *Table 2.1.*).

2.4.2   Results

Adult Siberian stonechats had on average significantly lower body masses than adult European stonechats. The same was true for the amount of visible fat reserves. Siberian stonechats had smaller tarsi than European stonechats, however the total wing length and the length of the 8th primary were larger in the Kazakh birds (*Table 2.1., Fig. 2.9.*). Body mass and fat scores differed significantly between the sexes in European stonechats (both measures being higher in the females), but did not differ between the sexes in the Siberian stonechats. In both populations males had longer wings and 8th primaries than the females. Tarsus length did not differ between the sexes (*Table 2.1., Fig. 2.9.*).

Total wing lengths and lengths of the 8th primary were significantly correlated in all groups (Spearman's rank correlation coefficients for Kazakh males, Kazakh females, Slovak males, and Slovak females: 0.63, 0.80, 0.80, 0.71; in all cases $p < 0.01$). However, total wing length and length of the 8th primary were not correlated with tarsus length, and none of these size measures was correlated with body mass.

Body mass and visible fat reserves varied in the course of the breeding season in Siberian and European stonechats, however in both populations the variation was higher in females than in males (*Figs. 2.10. and 2.11.*). In the Siberian stonechats, fat scores in females were significantly higher during territorial establishment ($U = 55.5, p < 0.05$) and egg production and incubation ($U = 45.0, p < 0.01$). Female body mass was significantly higher during egg production and incubation (Mann-Whitney-U test: $U = 10.0, p < 0.01$). Males had higher body masses and fat scores during moult, however the sample size in this group was to low to test the difference statistically (*Fig. 2.10.*). In the European stonechats, females had significantly higher body masses during territorial establishment ($U = 22.5, p < 0.01$) and egg production and incubation ($U = 1.0, p < 0.01$) and significantly higher fat scores during territorial establishment ($U = 35.5, p < 0.01$). Both, body mass and fat scores were higher in females during egg formation and incubation of the second clutch,

however sample size was too low to test statistically (*Fig. 2.11.*). During a short period of low ambient temperatures and snow cover at the time of arrival both sexes had low body masses and high fat scores (*Fig. 2.11.*).
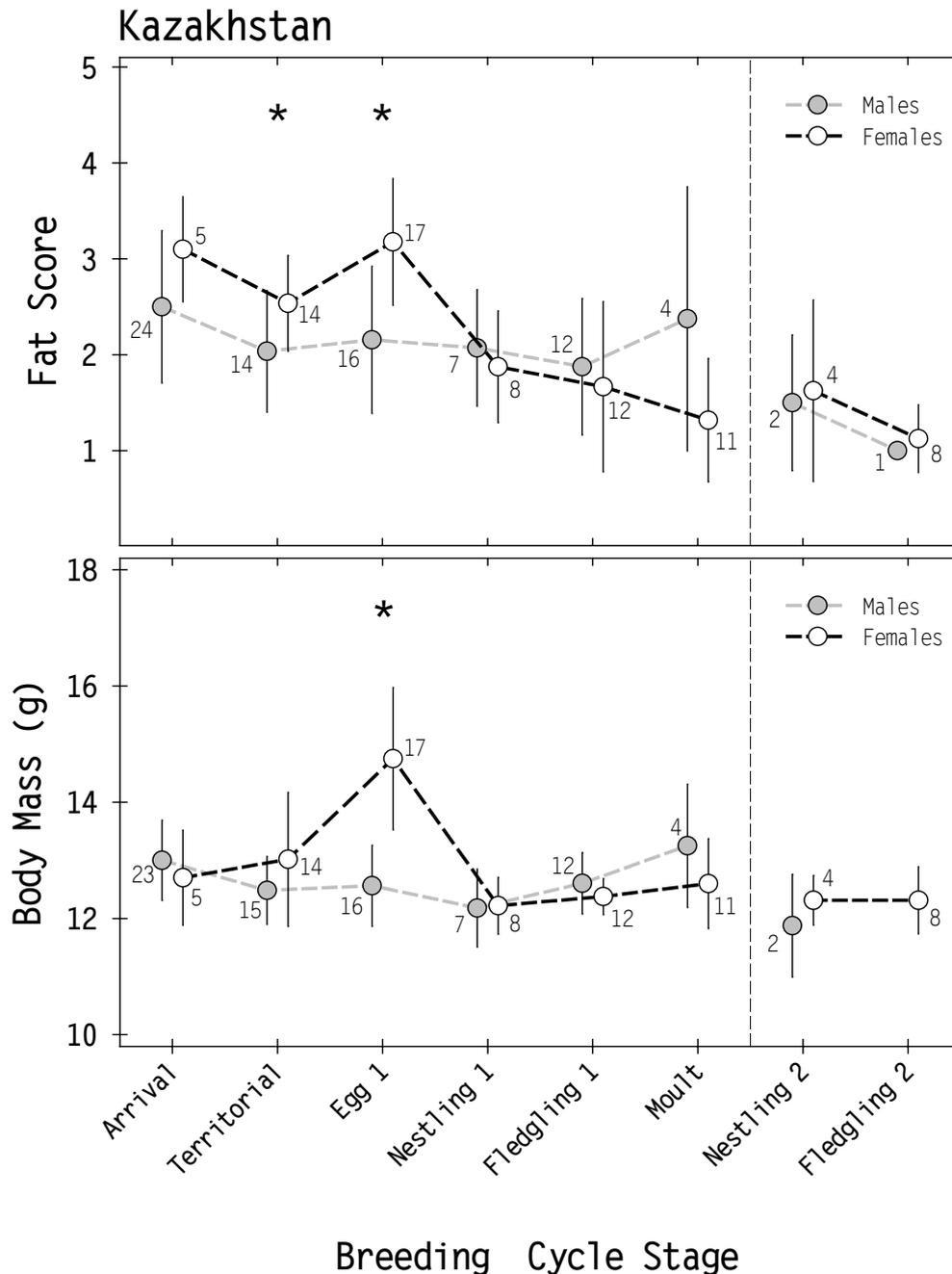
Fig. 2.10. Body mass and visible fat reserves of Siberian stonechats in the course of the breeding season. Means and standard deviations for males and females are shown, asterisks flag significant differences between the sexes, the sample sizes are indicated.
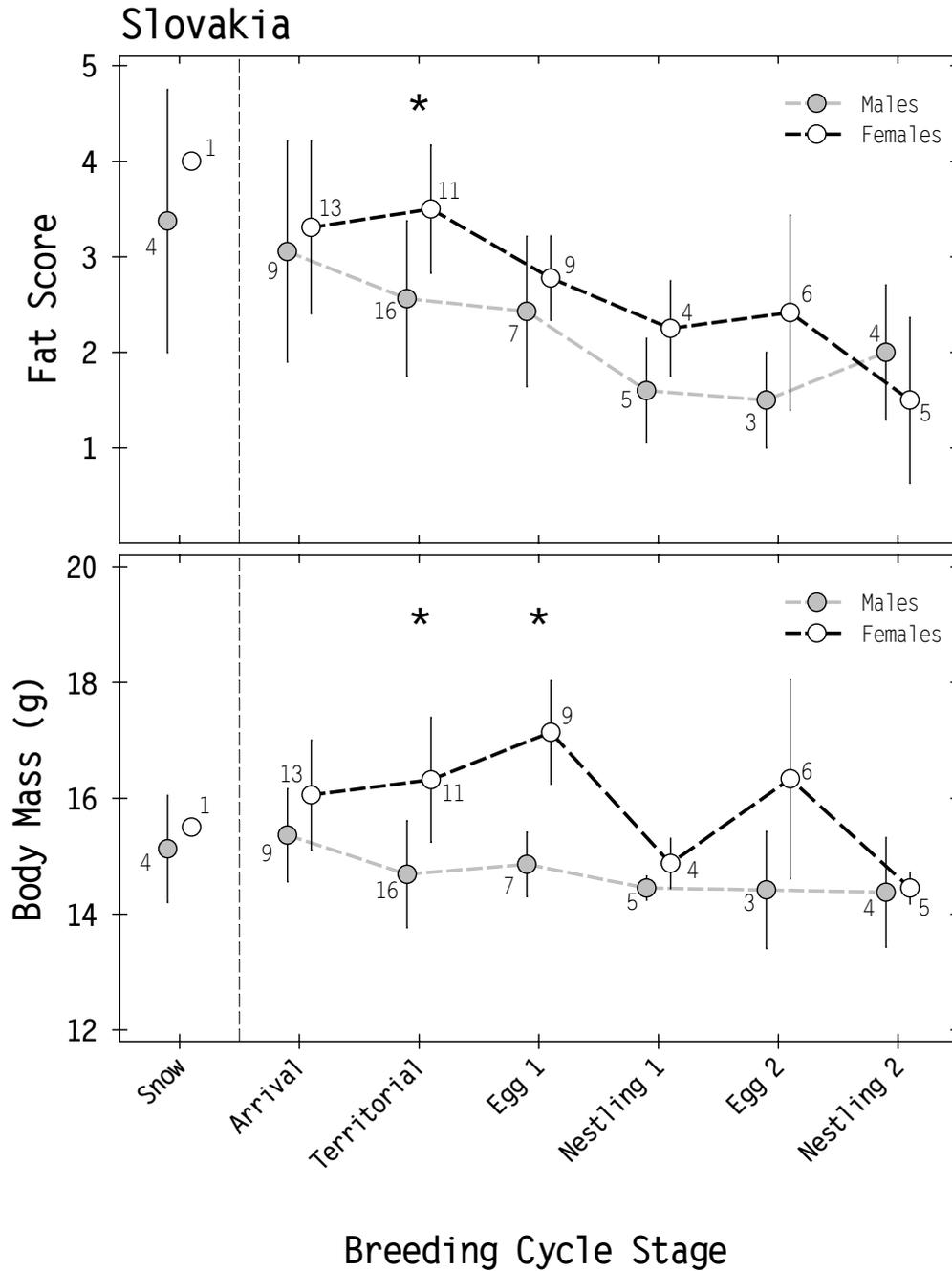
Fig. 2.11. Body mass and visible fat stores of European stonechats in the course of the breeding season. Means and standard deviations for males and females are shown, asterisks flag significant differences between the sexes, the sample sizes are indicated.

2.4.3 Discussion

Stonechats from Kazakhstan had smaller measures of body mass and tarsus length when compared to birds caught in Slovakia. These results corroborate the general view that the Siberian subspecies of the stonechat is smaller than the European subspecies (Cramp 1988, Glutz von Blotzheim & Bauer 1988, Urquhart 2002). Both populations breed on similar latitudes, thus the differences in body size cannot be explained by Bergmann's rule (which would predict a larger body size in the more northerly populations). Differences in body size may rather relate to the migratory strategy, long-distance migrants being smaller (and therefore lighter) than short-distance migrants.

Wing length, besides being dependent on general body size, is strongly affected by the predominant flight mode (soaring flight, flapping flight, …) (Brown 1963, Viscor & Fuster 1987) and migratory distance (Marchetti et al. 1995, Calmaestra & Moreno 2001). Accordingly, the wings were larger in the long-distance migrating birds from Kazakhstan than in the short-distance migrants from Slovakia, even though the Kazakh birds have smaller body sizes.

Wing length was sexually dimorphic in both populations, with males having longer wings than females. This may indicate that migratory strategies differ between the sexes (Morbey & Ydenberg 2001, Kissner et al. 2003). The wintering grounds of males may be located more distantly from the breeding areas than those of the females (Holberton & Able 2000). However, at least in the European stonechats this seems unlikely. Banding records do not suggest divergent wintering areas of the stonechat sexes (van Hecke 1965, Zink 1973, Helm 2002). On the wintering grounds males and females form pairs that jointly defend territories (Gwinner et al. 1994, Rödl 1995, 1999). In captive European stonechats the sexes do not differ in the amount of migratory restlessness (Helm & Gwinner, unpubl. results). Much less is known about the wintering areas and the nonbreeding ecology of the Siberian stonechats (see Chapter 3 of this thesis), and therefore a relation between separate wintering areas and differences in wing lengths

cannot be ruled out here. However, also in captive Siberian stonechats the sexes do not differ in the amount of migratory restlessness (Helm & Gwinner, unpubl. results).

An alternative explanation for larger wings in males may be selection on flight speed. In stonechats as in many other passerines, males establish territories on the breeding grounds and are later joined by females. Therefore males may benefit more by arriving early than females, and this may drive the evolution of sexual dimorphism in wing length (Francis & Cooke 1986, Lozano et al. 1996, Morbey & Ydenberg 2001). During my study periods males preceded females in spring by not more than one day. As males are generally easier to spot (they have brighter plumage and behave more conspicuously), I cannot rule out that both sexes arrived at the same time in my study areas.

Despite the sexual size dimorphism in wing length, the sexes did not generally differ in body mass or tarsus lengths. While on average in both populations females were heavier than males, this can mainly be explained by sex differences during the periods of egg formation and incubation, when the mass of the developing ovum adds to the female body mass. Furthermore, females increase their body stores to meet the increased demand of nutrients during egg formation and to prepare for the period of restricted feeding during incubation. This explains also the differences in the amounts of visibly stored fat during the territorial and egg stages between the sexes.

2.5   References

Belik, V. P. (1997). Nekotorye posledstviya ispolzovaniya pestitsidov dlya stepnykh ptits Vostochnoj Evropy [Some consequences of pesticide use for steppe birds in Eastern Europe]. *Berkut* 1-2: 70-82.

Bragin, E. A. & Bragina, T. M. (1999). Gnesdovaja fauna ptits Naurzumskogo zapovednika [Breeding bird fauna in the Naurzum Nature Reserve]. *In* C. A. Bukreev (Ed.), *Territorialnye Aspekty Okhrany Ptits v Crednej Azii i Kazakhstane [Territorial Aspekts of Bird Conservation in Central Asia and Kazakhstan]*, Moskow.

Brown, R. H. J. (1963). Flight of birds. *Biological Reviews of the Cambridge Philosophical Society* 38: 460.

Calmaestra, R. G. & Moreno, E. (2001). A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in passeriformes. *Ardea* 89: 407-416.

Chibilev, A. A. (1998). *Stepi Severnoj Evrazij [The Steppes of Northern Eurasia]*, Ekaterinburg.

Cramp, S. (1988). *Handbook of the birds of Europe, the Middle East and North Africa*, Vol. 5. Oxford University Press, Oxford.

Danko, S., Darolová, A. & Krištín, A. (2002). *Bird distribution in Slovakia*. Veda, vydavateľstvo Slovenskej akadémie vied, Bratislava.

Dement'ev, G. P. & Gladkov, N. A. (1954). *Birds of the Soviet Union*, Vol. Volume VI. Gosudarstvenno Izdatstelstvo Sovetskaya Nauka, Moskow.

DMEER (2000). *Digital Maps of European Ecological Regions*. http://dataservice.eea.eu.int, European Environmental Agency.

Fedorenko, A. P., Rogatko, I. V., Spynu, E. I. & Akoronko, S. L. (1981). Accumulation of organochlorine pesticides in animals of nature reserves of the USSR [Russian]. *Vestnik Zoologii* 6: 67-70.

Francis, C. M. & Cooke, F. (1986). Differential timing of spring migration in wood warblers, *Parulinae*. *Auk* 103: 548-556.

Gavrilov, E. I. (1999). *Cpravochnik po ptizam respubliki Kazakhstan [Guide to the Birds of the Kazakh Republik]*. Author/Publisher, Almaty.

Glutz von Blotzheim, U. & Bauer, K. M. (1988). *Handbuch der Vögel Mitteleuropas*, Vol. 11. Aula-Verlag, Wiesbaden.

Gwinner, E., König, S., Rödl, T. & Scheuerlein, A. (1998). Ausbreitung des Schwarzkehlchens in Oberbayern: eine Brut im Landkreis Starnberg. *Avifaunistischer Informationsdienst Bayern* 5: 82-83.

Gwinner, E., Rödl, T. & Schwabl, H. (1994). Pair territoriality of wintering stonechats: Behaviour, function and hormones. *Behavioral Ecology and Sociobiology* 34: 321-327.

Heath, M. F. & Evans, M. I. (Eds.). (2000). *Important bird areas in Europe: Priority sites for conservation*. BirdLife International, Cambridge, UK.

Helm, B. (2002). Seasonal timing in different environments: comparative studies in Stonechats. Ph.D. thesis, Ludwig-Maximilians-Universität München, Germany.

Holberton, R. L. & Able, K. P. (2000). Differential migration and an endocrine response to stress in wintering dark-eyed juncos (Junco hyemalis). *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 1889-1896.

IRI (2004). *NOAA NCDC GCPS MONTHLY STATION*. http://ingrid.ldgo.columbia.edu/SOURCES/.NOAA/.NCDC/.GCPS/.MONTHLY/.STATION.cuf/, International Research Institute For Climate Prediction.

Johnson, E. D. (1961). The pair relationship and polygyny in the Stonechat. *British Birds* 54: 213-225.

Katzner, T. E., Bragin, E. A., Knick, S. T. & Smith, A. T. (2003). Coexistence in a multispecies assemblage of eagles in Central Asia. *Condor* 105: 538-551.

Kissner, K. J., Weatherhead, P. J. & Francis, C. M. (2003). Sexual size dimorphism and timing of spring migration in birds. *Journal of Evolutionary Biology* 16: 154-162.

Kuz'mina, M. A. (1970). Rod Chekan [Genus Saxicola], *Ptitsy Kazakhstana [The birds of Kazakhstan]*, Vol. Volume 3, pp. 557-570, Almaty.

Lavrenko, E. M., Karamysheva, Z. V. & Nikulina, R. I. (1991). *Stepi Evrazii [The Steppes of Eurasia]*. Nauka, St. Petersburg.

Lozano, G. A., Perreault, S. & Lemon, R. E. (1996). Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. *Journal of Avian Biology* 27: 164-170.

Marchetti, K., Price, T. & Richman, A. (1995). Correlates of wing morphology with foraging behavior and migration distance in the genus *Phylloscopus*. *Journal of Avian Biology* 26: 177-181.

Morbey, Y. E. & Ydenberg, R. C. (2001). Protandrous arrival timing to breeding areas: a review. *Ecology Letters* 4: 663-673.

Perzanowski, K. (2001). *Carpathian montane forests*. http://www.worldwildlife.org/science/ecoregions/palearctic.cfm., World Wildlife Fund.

Ponomarenko, S. (2000). *Kazakh steppe*. http://www.worldwildlife.org/science/ecoregions/palearctic.cfm, World Wildlife Fund.

Ripley, S. D. (1964). Turdinae. *In* E. Mayr & R. A. Paynter, Jr (Eds.), *Check-list of the birds of the world*, Vol. 10, pp. 13-227. Museum of Comparative Zoology, Cambridge, Mass.

Rödl, T. (1995). The wintering of territorial stonechat pairs *Saxicola torquata* in Israel. *Journal fuer Ornithologie* 136: 423-433.

Rödl, T. (1999). Environmental factors determine numbers of over-wintering European Stonechats *Saxicola rubicola* - A long term study. *Ardea* 87: 247-259.

Shnitnikov, V. N. (1949). *Ptitsy Semirechya [Birds of Semirechie]*. House of the Academy of Science of the USSR, Moscow-Leningrad.

Sibley, C. G. & Monroe, B. L., Jr (1990). *The distribution and taxonomy of the birds of the world*. Yale University Press, New Haven.

Svensson, L. (1992). *Identification Guide to European Passerines*, Fourth ed. Rosersberg, Stockholm.

Urquhart, E. (2002). *Stonechats: A guide to the genus Saxicola*. Christopher Helm, London.

van Hecke, P. (1965). The migration of the west-european Stonechat, *Saxicola torquata* (L.), according to ringing data. *Le Gerfaut* 55: 146-194.

Viscor, G. & Fuster, J. F. (1987). Relationships between morphological parameters in birds with different flying habits. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 87: 231-249.

Wink, M., Sauer-Guerth, H. & Gwinner, E. (2002a). Evolutionary relationships of stonechats and related species inferred from mitochondrial-DNA sequences and genomic fingerprinting. *British Birds* 95: 349-355.

Wink, M., Sauer-Guerth, H., Heidrich, P., Witt, H.-H. & Gwinner, E. (2002b). A molecular phylogeny of stonechats and related turdids. *In* E. Urquhart (Ed.), *Stonechats: A guide to the genus Saxicola*, pp. 22-30. Christopher Helm, London.

Wittmann, U., Heidrich, P., Wink, M. & Gwinner, E. (1995). Speciation in the stonechat (Saxicola torquata) inferred from nucleotide sequences of the cytochrome-b gene. *Journal of Zoological Systematics and Evolutionary Research* 33: 116-122.

Zaugolnova, L. B. (1977). Analysis of ceno populations as a method of studying anthropogenic effects on a phytocenosis. *Botanicheskii Zhurnal (Leningrad)* 62: 1767-1779.

Zink, G. (1973). *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel*, Vol. 1. Vogelwarte Radolfzell, Möggingen.

3   MIGRATIONS OF EUROPEAN AND SIBERIAN STONECHATS

3.1   Summary

The analysis of stonechat migrations has so far focused on the western European populations, in part because most ringing data stems from these areas. Here I report the results of a literature survey on the migrations of eastern European and Siberian stonechats (ringing recovery data and local passage dates). Most European stonechats banded in eastern Austria, Hungary, Slovakia, and the Czech Republic winter in North Africa (Tunisia, Algeria). They migrate about 1500 km and spend about 20 days on their spring movements and 30-40 days during autumn. Hence I estimate a higher speed for spring than for autumn migration. This is in line with other studies on the migration speed in European passerines. For the Siberian stonechats no banding data exists. Passage data suggest that Siberian stonechats arrive in spring in Central Asia from the south-west, either coming from North Africa (Sudan) or from southern Asia (India/Pakistan) circumventing the high Asian mountain ranges on their way. From there they move on north-westward and north-eastward into the Central Asian and western Siberian breeding ranges. The autumn migrations retrace this pattern backwards, however the movements are less synchronised than during spring. Within Central Asia and Western Siberia spring migration proceeds at the same speed as (or even slower than) autumn migration. Local climatic conditions may constrain the progression of the spring movements in this area. Outside Central Asia and western Siberia the birds seem to migrate faster, especially in spring, with the result that over the whole migratory distance also in the Siberian stonechats the speed of migration is higher in spring than in autumn.

3.2   Introduction

Migration has enabled birds to extend their breeding range into areas that are highly productive in spring and summer, but would not support them during winter. This is apparent in the arctic regions which attract millions of breeding birds during their short summers. However, it applies as well to most northern temperate areas, where only a minority of bird species can find enough food (usually seeds or berries) and can thus tolerate the harsh winter conditions (Forsman & Monkkonen 2003, Sol et al. 2005). The diet of stonechats consists almost exclusively of insects and other small invertebrates (Rödl & Flinks 1996, Urquhart 2002). Due to this selectivity year-round resident stonechats occur only in areas with relatively mild winters such as the British Islands, the Iberian Peninsula and the Mediterranean (Cramp 1988, Glutz von Blotzheim & Bauer 1988, Urquhart 2002). The remaining populations of the European and Siberian stonechat are migratory. Like other migratory birds they move thousands of kilometres twice a year, negotiate obstacles like oceans, deserts and mountain ranges, and return to their wintering and breeding sites with great temporal and spatial accuracy. This would be impossible without a series of distinct specialisations.

Before they start their annual movements, migratory birds accumulate large body reserves in the form of subcutaneous fat stores (Bairlein & Gwinner 1994, Biebach 1996, McWilliams et al. 2004), a process that requires intensified foraging and metabolic changes (Deviche 1995, Holberton 1999, Landys et al. 2004). During long-distance flights, the masses of some internal organs such as gastrointestinal tract, heart and liver, and the size of skeletal muscles decrease significantly, supposedly to reduce metabolic flight costs and release protein as additional flight fuel (Bauchinger & Biebach 1998, Biebach 1998, Bauchinger & Biebach 2001). Gross wing morphology is affected by the mode of migration (e.g. soaring flight or flapping flight), however both between and within species additional variation in relation to the migratory distance is observed

(Brown 1963, Viscor & Fuster 1987, Marchetti et al. 1995, Monkkonen 1995, Calmaestra & Moreno 2001).

Many diurnal birds become nocturnal during migration, flying during the night and resting or refuelling during the day. This shift in the circadian activity patterns is mediated by a change in the secretory pattern of the pineal hormone melatonin (Gwinner et al. 1993, Gwinner 1996, Gwinner et al. 1997). The high degree of spatial and temporal precision required to return year after year to the same breeding, stopover, and wintering sites (Mikkonen 1983, Nolan & Ketterson 1991, Cantos & Telleria 1994, Merom et al. 2000, Hansson et al. 2002, Hoover 2003) is achieved by employing a multitude of navigational systems: visual and olfactory cues, polarised light, geomagnetic and celestial compasses (Berthold et al. 2003, Wiltschko & Wiltschko 2003, Cochran et al. 2004, Wallraff 2004, Mouritsen & Ritz 2005). The spatial information that feeds out of these systems requires a complex neuronal representation with the ability to integrate the continuous changes that come about as the bird moves onward (Bingman & Able 2002). The migratory mode also influences other aspects of cognition such as memory formation: long-distance migrants store spatial memory longer than nonmigrants (Mettke-Hofmann & Gwinner 2003).

The ability to migrate has a genetic basis. Several features such as migratory disposition, the direction of movements or the timing of migratory activities are heritable (Brown & Brown 2000, Pulido et al. 2001, Berthold et al. 2003). This does not imply, however, rigid programming. Breeding and wintering ranges can shift rapidly when local conditions change (Sutherland 1998, Berthold 2001). Birds in partially migrating species either migrate in autumn or stay in their breeding areas and sometimes individuals or age-classes switch between these migratory modes in consecutive years (Berthold 2001). Although this flexibility is to a certain degree based on phenotypic plasticity, there is also evidence for the involvement of rapid microevolutionary changes (Berthold et al. 1990, 1992).

The migratory schedule is tightly interlocked with other annual tasks such as reproduction or moult (Gwinner 1986, 1996, McNamara et al. 1998, Gwinner 2001, 2003). Hence, variation in migratory behaviour, between populations or over time (as e.g. caused by the recent climatic changes, Butler 2003, Cotton 2003, Hüppop & Hüppop 2003, Jenni & Kéry 2003, Hubalek 2004, Vähätalo et al. 2004, Mills 2005, Stervander et al. 2005) will affect (and will be constrained by) the temporal and physiological requirements of other seasonal tasks. The differences in the migratory behaviour of Siberian and European stonechats are a recurrent theme in this thesis. While Chapter 2 summarises information on the breeding and wintering distributions of Siberian and European stonechats that form the basis of the differences in the migratory behaviour between the two populations, subsequent Chapters investigate how this affects reproductive physiology (Chapter 4), reproductive phenology and performance (Chapter 5), patterns of circulating gonadal steroids and glucocorticoids (Chapters 6 and 7), juvenile development (Chapter 8), and adult postnuptial moult (Chapter 9).

In the current chapter I compile available information on the migrations of (eastern) European and Siberian stonechats. The migrations of the (western) European stonechats have been analysed in detail (van Hecke 1965, Zink 1973, Helm 2002), but comprehensive information about the migrations of Siberian stonechats is scarce, despite a wealth of local accounts in the (mostly Russian) literature. With this chapter I try to close this gap. The migrations of Siberian stonechats are therefore dealt with in particular depth.

3.3   Material and Methods

3.3.1   Timing and orientation of migrations, migratory distances

For the European stonechats ringing recoveries are available. For information on wintering locations and migratory distances of eastern European stonechats, I used a subset of the data summarised in Helm (2002),

together with an additional record from Kubán & Matoušek (1999) and currently unpublished data communicated by B. Helm et al. These data cover all ringing recoveries of European stonechats banded eastward of the 15th meridian that were recovered more than 200 km from the ringing site. For the Siberian stonechats no recovery data was available.

Additional information on stonechat migrations was compiled from handbooks on palearctic birds (Dement'ev & Gladkov 1954, Kuz'mina 1970, Hudec & Cerný 1983, Paz 1987, Cramp 1988, Glutz von Blotzheim & Bauer 1988, Rogacheva 1992, Shirihai 1996, Danko et al. 2002), a monograph on stonechats (Urquhart 2002), and Russian articles containing information on the migrations of Siberian stonechats (Shnitnikov 1949, Toropova & Eremchenko 1979, Chernyshov 1982, Egorov 1985, Erokhov & Gavrilov 1993, Blinova & Blinov 1997, Karyakin et al. 1999, Tsybulin 1999, Stakheev 2000).

Several geographical names used in these publications are no longer in use, either because they are outdated (*"Semirechya"*), or have changed in the course of the disintegration of the USSR and the formation of the Central Asian Republics and the Russian Federation. Some geographical names exist several times in different places. Areas that could not be located with certainty were not included into the data set. Some sources cover rather large areas (e.g. "Trans-Uralia", Blinova & Blinov 1997) and do not always specify from where in the area the information originates. In these cases I took roughly the centre of the area as reference point.

The accuracy of information on the timing of migration differs considerably between the sources. Whereas some authors give exact dates and sometimes even mean dates over several years, others report only rough estimates such as "in the first half of May" or "till October". To account for these differences, all information was attributed to one of three 10-day periods of each month (*I* = 1. to 10. of a month, *II* = 11. to 20., *III* = 21. to end). If only the month was given, the second decade (*II*) was assigned.
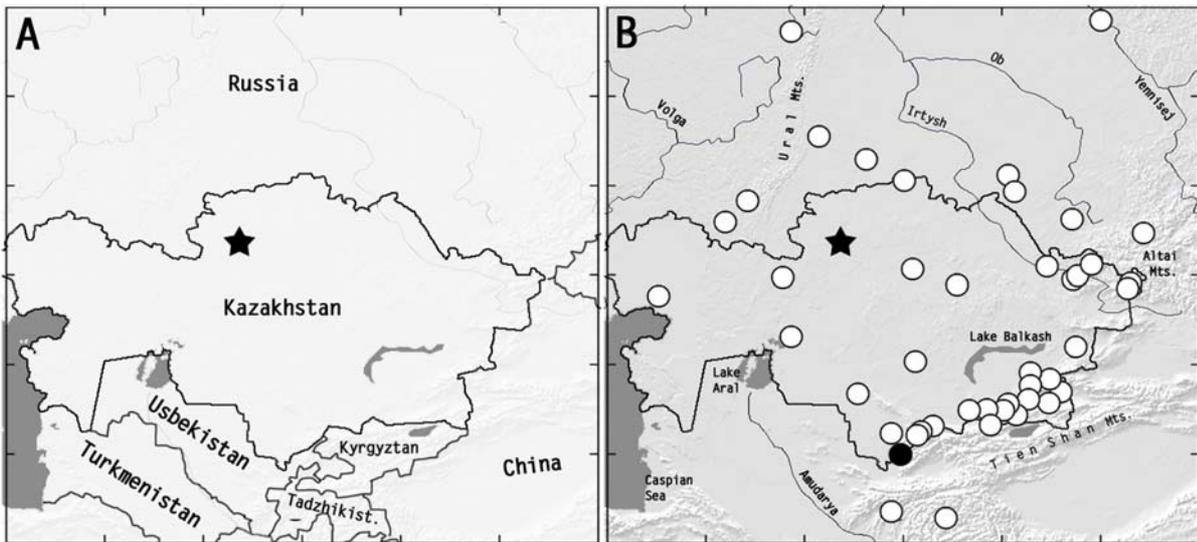
Fig. 3.1. The area in Central Asia and western Siberia for which data on the migrations of Siberian stonechats was compiled from the literature. *A:* The borders of Kazakhstan and neighbouring countries. *B:* The circles show the locations of the sites for which migration data was extracted. The filled circle indicates Tashkent (which was used as reference point for calculating migration speed), the star my study site. Important water bodies and mountain ranges are indicated.

3.3.2 Speed of migration

The time period a bird spends on migration consists mainly of stopovers and refuelling, with short periods of flight interspersed. Therefore, the speed of migration, which includes flight and stopover periods, is usually much lower than the maximal flight speed a bird can reach (Lindström & Alerstam 1992, Hedenström & Alerstam 1998). Estimates on individual migration speeds are derived from radio and satellite tracking studies (Cochran & Applegate 1986, Cochran 1987, Kjellen et al. 2001, Wikelski et al. 2003, Bowlin et al. 2005), but due to technical constraints the sample sizes are usually low. Alternatively, recoveries of ringed birds within one migratory period are used (Hilden & Saurola 1982, Ellegren 1993), but again, sample sizes are constrained by low recovery rates of banded birds. A more general picture of the speed of migration on the population or species level is obtained by using mean passage dates at different sites along the migratory route of a species (Ellegren 1990a,

Fransson 1995, Yohannes 2003). Estimates of migration speeds based on individual ringing recoveries and on population passage dates usually yield similar results (Ellegren 1990a, Fransson 1995).

There are no ringing recoveries within one migratory period for eastern European stonechats, therefore I combined the data on the mean passage dates from the literature (Glutz von Blotzheim & Bauer 1988, Urquhart 2002) with the migration distances from the ringing recoveries (*Table 3.1.*) to calculate the speed of migration. Birds do probably migrate along loxodromes, keeping their angle to the earth's magnetic field constant (but see Hake et al. 2001). Nevertheless, I compute shortest distances between breeding and wintering or passage sites (orthodromes), because even at long distances, orthodromatic and loxodromatic differences rarely differ by more than 5% (Imboden & Imboden 1972).

Table 3.1. Distances and durations of the migrations of Eastern European stonechats compiled from ringing recoveries and literature data.

Banding site	°N	°E	Recovery site	°N	°E	distance (km)	Autumn Migration Duration (days)[c]		Spring Migration Mean Duration (days)[c]	
							early	main	early	main
Czech Republic [A]	49	17	Italy	42	12	838	30	30-40	20	20
Czech Republic [A]	49	16	Italy	44	10	775	30	30-40	20	20
Slovakia [A]	48	18	Algeria	37	5	1634	30	30-40	20	20
Slovakia [B]	48	17	Tunisia	36	8	1532	30	30-40	20	20
Slovakia [A]	49	18	Tunisia	37	9	1535	30	30-40	20	20
Austria [A]	48	17	Algeria	37	4	1647	30	30-40	20	20
Hungary [A]	47	18	Greece	37	22	1105	30	30-40	20	20
Hungary [A]	48	18	Italy (Sardinia)	40	9	1127	30	30-40	20	20
Hungary [A]	48	19	Italy	42	13	815	30	30-40	20	20

[A] data communicated by B. Helm et al. (unpublished)
[B] Kubán & Matoušek 1999
[c] based on main passage dates from the literature, cf. section 3.4.1.

The speed of migration of Siberian stonechats within Central Asia and western Siberia was calculated using the data on the stonechat migrations compiled from the literature (*Table 3.2., Fig. 3.1.*). In spring, the first birds appeared in Tashkent, and in autumn the last birds disappeared from the same location. Hence migratory speed was estimated using Tashkent as the reference point from which difference and duration was calculated. Speed of migration was calculated separately for the early migration, main

passage, and late migration periods. Data on the timing of Siberian stonechat migrations outside Central Asia and western Siberia is scarce and not very precise. To get a rough estimate of migration speed for the whole migratory distance, I calculated the speed of migration for birds moving from Siberia (Sverdlovskaja oblast) to either Sudan or India.

3.4   Results and Discussion

3.4.1   The migrations of eastern European stonechats

European stonechats find suitable wintering areas all over the Mediterranean areas of southern Europe, northern Africa north of the Sahara and the Middle East (Chapter 2 of this thesis: *Fig 2.3.*). Ringing recoveries of birds banded in eastern Austria, the Czech Republic, Slovakia and Hungary indicate that most eastern European stonechats migrate to the south or south-west to wintering grounds in northern Africa (*Fig. 3.2.*). Three birds recorded in Italy may have been *en route* to destinations in Northern Africa, because all recoveries are from the western coast during the main autumn migration period in September and October. The mean distance (± standard deviation) between ringing and recovery sites is 1223 ± 368 km (1430 ± 246 km if the three Italian records are excluded).

According to the literature (Hudec & Cerný 1983, Paz 1987, Cramp 1988, Glutz von Blotzheim & Bauer 1988, Shirihai 1996, Danko et al. 2002, Urquhart 2002), the first birds start their autumn migration in late August, but the main migration period is later, between 15th September and 15th October in the Czech Republic, Slovakia and western Ukraine. The influx into the Mediterranean basin, coastal north Africa and the middle east starts in the end of September, but is greatest between mid-October and late November. The stonechats leave their wintering areas from mid-February on, but most birds start their movement to the breeding quarters between late February and early March. The first birds reach their breeding quarters in eastern Europe in the beginning of March. The bulk of arrivals

and passage migration occurs in mid to end March, however late arrivals occur until late April. On our study site in central Slovakia, the first birds arrived before the 10th of March, and all birds were still present in mid-August.
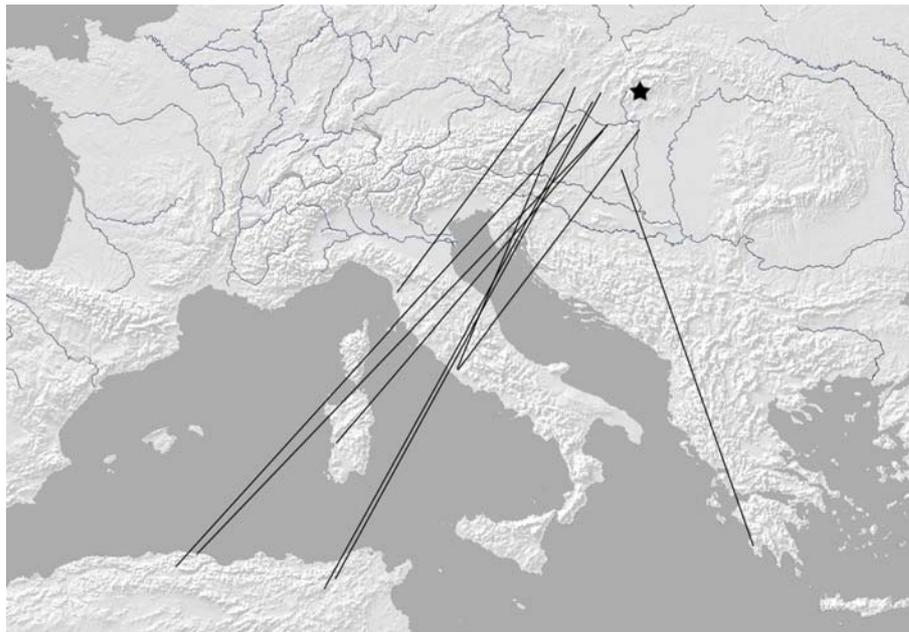
Fig. 3.2. Ringing recoveries of stonechats banded in eastern Europe. The lines connect ringing and recovery sites. The star indicates the position of the study site in Slovakia.

3.4.2   The migrations of Siberian stonechats

Siberian stonechats breed in a large area of western and central Siberia and Central Asia. They are long-distance migrants that overwinter in north-east Africa (Sudan, Ethiopia), the Middle East and the parts of the Arabian Peninsula, but mainly in southern Iran, Afghanistan, Pakistan and northern India (chapter 2 of this thesis: *Fig. 2.2.*). There is an increasing number of records of Siberian stonechats in Northern Europe, indicating that the subspecies is currently expanding its range (Robertson 1977, Glutz von Blotzheim & Bauer 1988, Urquhart 2002).

Table 3.2. The timing of spring and autumn migration of Stonechats in Central Asia and western Siberia. See text for further explanations.

Location	°N	°E	Spring			Autumn			Source
			start	main	end	start	main	end	
Pamirs	38	72				III-8			Dement'ev & Gladkov 1954
Tadshikistan	38	69	I-4	III-4	II-5	III-8		III-10	Dement'ev & Gladkov 1954
Tashkent	41	69	II-3	I-4	I-5	I-8	II-9	II-10	Kuz'mina 1970
Arys Station	42	69	III-4						Kuz'mina 1970
Aksu-Dzhabagly Nature Reserve	42	70	III-3			III-8	II-9	II-10	Kuz'mina 1970
Chokpak	43	71		I-4					Erokhov & Gavrilov 1993
Tokmak	43	75	I-4						Toropova & Eremchenko 1979
Dzhambul	43	71	II-3						Kuz'mina 1970
Almaty	43	77		II-4			I-9		Kuz'mina 1970
Kopa	44	76	II-4						Shnitnikov 1949
Chu Valley	44	74						III-9	Shnitnikov 1949
Chu Valley	44	74				III-8		I-10	Kuz'mina 1970
Chu-Ili Mountains	44	75	II-4						Kuz'mina 1970
Sorbulak Lake	44	77	I-4	III-4	II-5	II-8	I-9	I-10	Erokhov & Gavrilov 1993
Ili Passage Way	44	79	I-4						Shnitnikov 1949
Between Kugaly and Almaty	44	78	I-4						Shnitnikov 1949
Sharkent (Panfilov)	44	80	III-3						Shnitnikov 1949
Sharkent (Panfilov)	44	80		II-4	III-4	III-8		III-9	Kuz'mina 1970
Sharkent (Panfilov)	44	80	III-3						Dement'ev & Gladkov 1954
Dzhulek	44	66	II-4	III-4	I-5				Kuz'mina 1970
Bizhe	45	78	I-4			I-9	II-9	III-9	Kuz'mina 1970
Junggar Alatau	45	79	I-4						Kuz'mina 1970
Karatal Valley	45	78					III-9	I-10	Shnitnikov 1949
Betpak-Dala Desert	46	70					III-8	II-9	Kuz'mina 1970
Alakol' Plain	46	81					II-9		Shnitnikov 1949
Aralskoe More Station	47	62	III-4						Kuz'mina 1970
Karmanovo	48	52	II-4						Kuz'mina 1970
Alekseevka	48	86				III-8	I-9		Kuz'mina 1970
Markakol' Lake	49	86	I-5	II-5		I-9	II-9		Kuz'mina 1970
Katon-Karakgaj	49	86				II-9			Kuz'mina 1970
Kalba	50	82	III-4					II-9	Egorov 1985
Upper Irgiz River	50	60	III-4						Kuz'mina 1970
Karaganda	50	73	I-5		III-5			III-9	Kuz'mina 1970
Ust'-Kamenogorsk (Öskemen)	50	83					II-9		Kuz'mina 1970
Leninogorsk	50	84	II-5	III-5					Kuz'mina 1970
Semipalatinsk	50	80	II-4				II-9		Kuz'mina 1970
Kurgal'dzhino Lake	51	70	III-4			III-8	I-9	III-9	Kuz'mina 1970
Teletskoe Lake	51	88	I-5	III-5	I-6	III-7	III-8	III-9	Stakheev 2000
Chulyshman River	51	88	III-4						Dement'ev & Gladkov 1954
Dokuchaevka (Karamendy)	52	64	III-4	I-5	III-5				This Study
Orenburg	52	55	III-4	I-5	II-5				Kuz'mina 1970
Northern Altai	53	83	I-5	III-5			I-8		Tsybulin 1999
Southern Bashkiria	53	57	II-5	III-5		I-9			Dement'ev & Gladkov 1954
Northern Kulunda	54	78	I-5						Dement'ev & Gladkov 1954
Petropavlovsk	55	69	I-5	II-5					Kuz'mina 1970
Barabinskoj Forest-Steppe	55	78	I-5	II-5	I-6	I-8	III-8	III-9	Chernyshev 1982
Southern Trans-Uralian Steppe	56	66	I-5					III-8	Blinova & Blinov 1997
Sverdlovskaja Oblast	57	62	III-4	I-5		I-8	III-8	I-9	Karyakin et al. 1999
Pechora	62	57	II-5						Dement'ev & Gladkov 1954
Yennisej River	62	89	II-5	I-6					Rogacheva 1993

The proportion of Siberian stonechats that takes the longer route to the Middle East and north-east Africa is not known. A certain number of winter records in these areas may actually apply to individuals of Caucasian stonechat subspecies, which are not easy to distinguish from Siberian stonechats (Urquhart 2002). In Israel, some Siberian stonechats have been reported wintering in the Jordan Valley, but 99% of the Siberian stonechats caught on passage to Egypt and Sudan were first-year birds, suggesting that only inexperienced birds take this route (Shirihai 1996). Moreau (1972) speculated that of the passerines breeding in the Mid Palearctic, a greater proportion migrates directly down to southern Asia, and only a smaller proportion makes the longer voyage to Africa. This is supported by studies quantifying migration from the central Palearctic (Dolnik 1990, Bolshakov 2002).

Irrespective of whether they winter in Africa, the Middle East or south Asia, Siberian stonechats have to overcome a belt of deserts, semi-deserts, and mountains (*Fig. 3.3.*) which form an ecological barrier comparable to the Saharan desert (Moreau 1972, Dolnik 1990, Bolshakov 2002). Most prominent is the high elevation range formed by the Tien-Shan Mountains, Alay Mountains, Pamirs, Hindukush and Karakorum Mountains, and the Himalayas. Its southern part, the highland of Tibet, is particularly hostile to migrants, as Moreau (1972) points out:

"… between 75° and 90° E the exceedingly formidable mountain mass of Tibet interposes itself, some 800 km form north to south, averaging 4500 m above sea level, barren, tree-less and swept by appalling cross-winds. There is virtually no evidence from either observation or interference, that this block, flanked as it is on the south by the mighty Himalayas, is crossed by appreciable numbers of small birds …"

The majority of central Palearctic migrants avoids the areas with high elevation, particularly in spring when they are covered with snow. During this season therefore most migrants travel through the deserts and semi-deserts in the west of the mountains, which bloom at that time and therefore provide relatively favourable conditions (Dolnik 1990). In autumn the deserts and semi-deserts are dry, and birds avoid them by either passing them in the west (this may apply mostly to African

migrants)(Bolshakov 2002), or by travelling over the lower Central Asian mountain ranges, which during this time provide better conditions than in spring (Dolnik 1990).
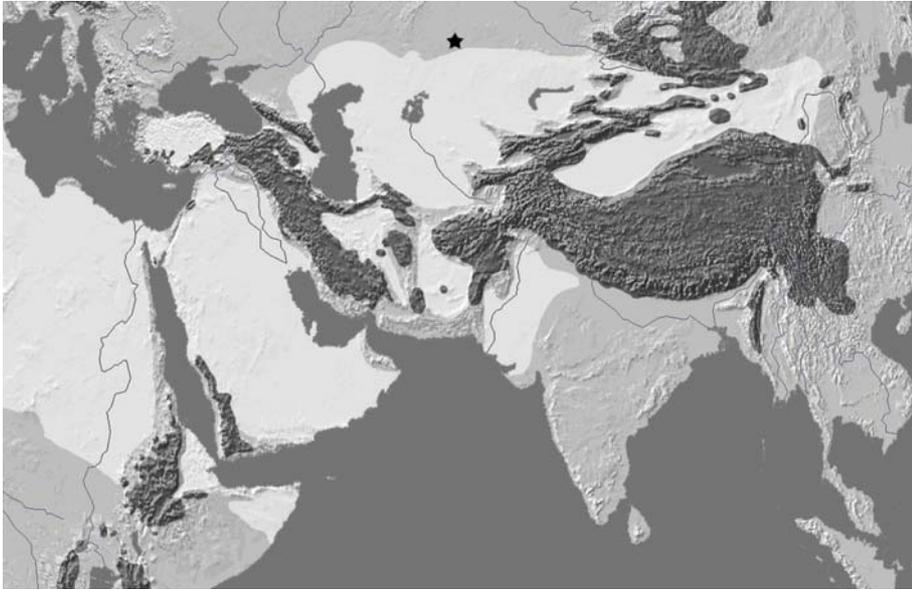
Fig. 3.3. Between the breeding range of Siberian stonechats in Central Asia and Siberia and their wintering range in north-east Africa, the Middle East and India (cf. *Fig. 2.2*) extend high mountain ranges (dark areas show elevations of 2000 m a.s.l. and more) and deserts and semi-deserts (light areas). The location of my Central Asian study area is indicated by the star.

Using data from studies on the timing of stonechat migration in different locations within western Siberia and Central Asia we can trace the spatio-temporal pattern of the migratory movements within that area. In spring, the first birds arrive in the area around Tashkent on the western edge of the Tien-Shan mountains in mid to late March. From there the early arrivals spread into central and eastern Kazakhstan in April and further into western (Pechora area) and central Siberia (Yenissej area) in May. Peak passage takes place in April in the south, and in May to June in more northerly areas. Spring migration ends in the south in late April or early May, but lasts until late May to early June further north (*Fig. 3.4.*). The northward progression is significantly related to the calendar date in all

three temporal segments of spring migration (start, main passage, end; *Table 3.3.*)

In autumn, migration starts in late August, but in most areas the first birds leave September or even October. The main passage takes place in September in the northern parts of the breeding range, and in October in the southern part of the breeding range (Altai Mountains and eastern and southern Kazakhstan) The last birds leave the area in September, however along the Tien-Shan mountains and in the area of Tashkent the last birds do not leave until October (*Fig. 3.5.*). The southward movement is not very concerted in the early birds but gets more and more temporally synchronised during the main passage and during late autumn migration (*Table 3.3.*).

This analysis corroborates the view, that the majority of stonechats, as other small migratory birds, do not pass the high mountain ranges of Central Asia. In spring, the first birds appear in Tashkent, Uzbekistan, which is situated on the western rim of the Tien-Shan Mountains (*Fig. 3.1.B.*) and move from there northwards and north-eastwards. In autumn, the birds are funnelled along the northern rim of the Tien-Shan Mountains south-westward into the area of Tashkent. Birds that breed north-west of the Central Asian mountain ranges may move south and north in a broad front on a way not obstructed by high elevations. Unfortunately, we lack data on stonechat migrations within the area between the Caspian Sea and Tashkent, particularly in autumn.

Table 3.3. The relationship between the migratory latitude or migratory distance (calculated from Tashkent, Uzbekistan) and calendar date in different temporal sections of the spring and autumn migrations of Siberian stonechats.

Season		df	latitude (°N)			distance (km)		
			F	p	R^2	F	p	R^2
Spring	start	1, 36	68.24	< 0.001	0.66	53.77	< 0.001	0.60
	main passage	1, 16	27.54	< 0.001	0.63	57.83	< 0.001	0.78
	end	1, 8	7.88	< 0.05	0.50	6.90	< 0.05	0.46
Autumn	start	1, 14	0.62	0.45	0.04	0.07	0.80	0.01
	main passage	1, 15	7.31	< 0.05	0.33	3.59	0.08	0.19
	end	1, 15	32.87	< 0.001	0.69	17.97	< 0.01	0.55
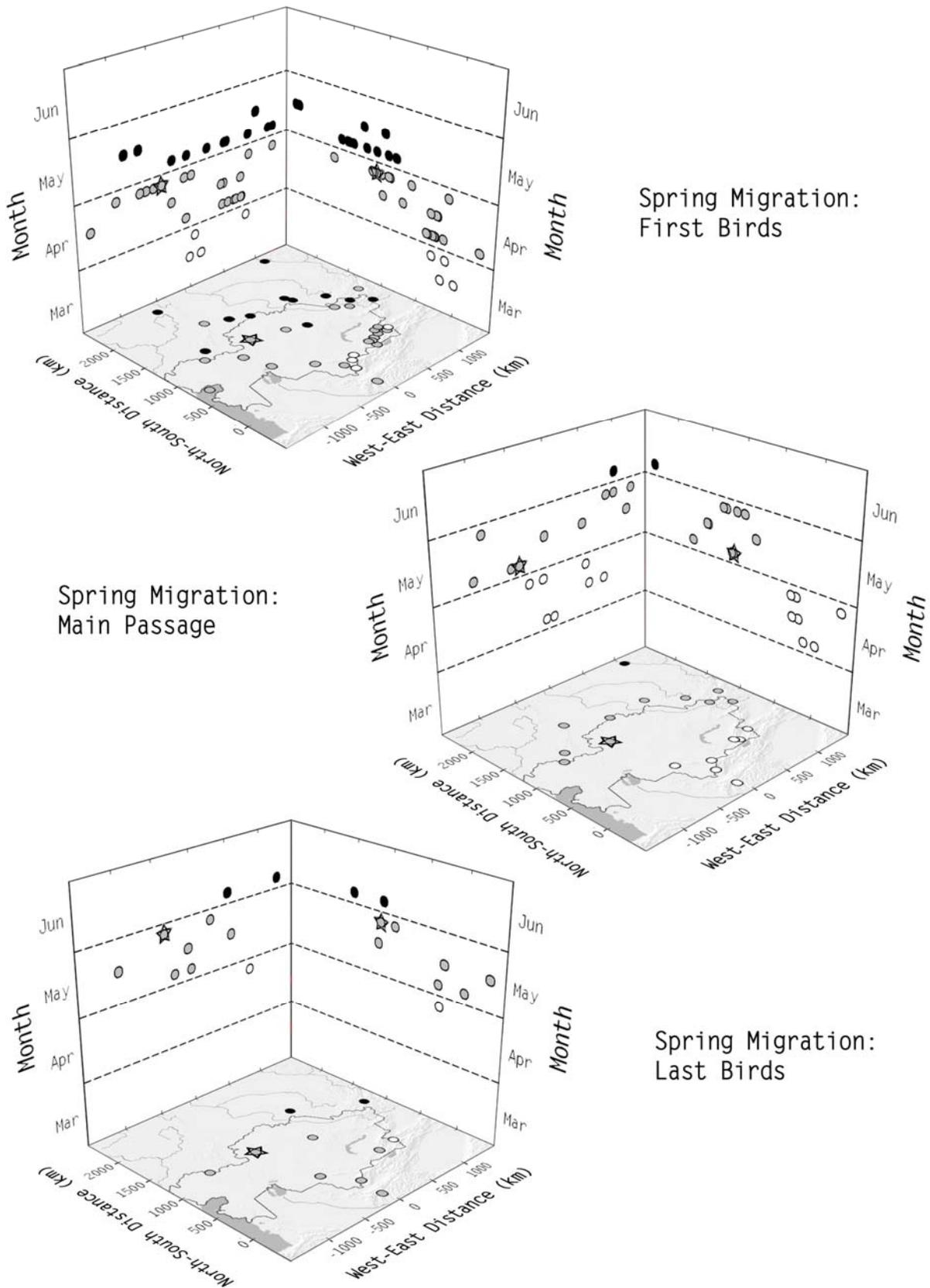
**Fig. 3.4.** The timing of spring migration of Siberian stonechats within Central Asia and western Siberia. Circles of the same colour (white, grey, black) indicate movements within the same month. Distances are given relative to Tashkent in Tadzhikistan. The map is the same as in *Fig. 3.1*.
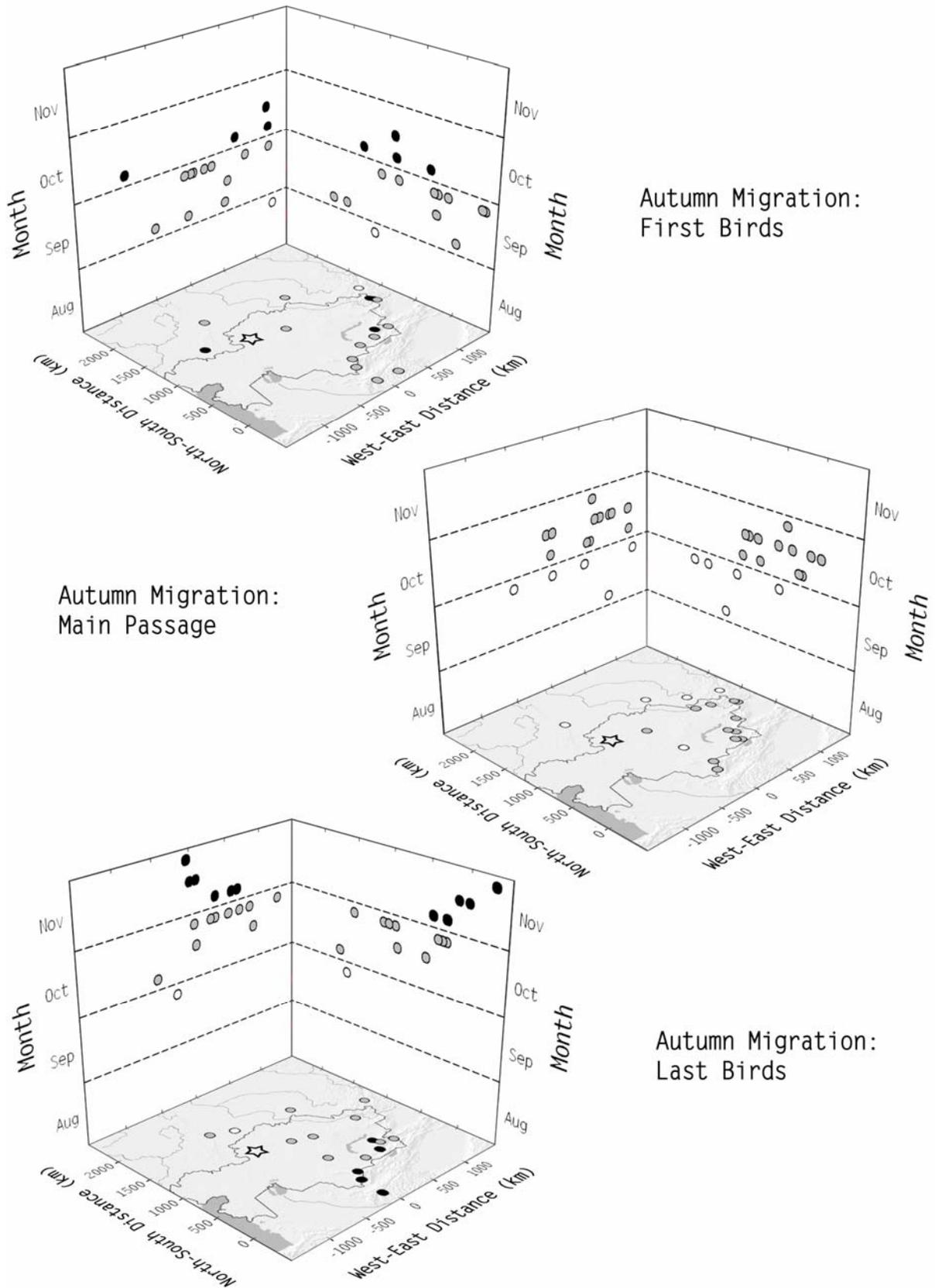
Fig. 3.5. The timing of autumn migration of Siberian stonechats within Central Asia and western Siberia. See *Fig. 3.4.* for explanations.

Data on the movements beyond the area treated above are scarce and often rather vague: The main passage through northern Afghanistan takes place in mid-September, the Arabian Emirates are passed in the same month, the influx into Israel starts mid-September, but is highest between mid and late October. In Sudan, the birds arrive as late as mid-November and stay there until the end of February. The first birds pass through Israel in early February, but the main passage is in mid March to early April. On their way to the breeding areas they pass the southern Caspi in Iran from mid February to early April (with a peak in mid March). For the eastern part of the wintering range it is only stated that the birds stay in India "from October to March" (Urquhart 2002).

3.4.3 The speed of migration in European and Siberian stonechats

Eastern European stonechats

Based on the reported passage dates and the migratory distances from the ringing recoveries (*Table 3.1.*), the stonechats from Eastern Europe travel in spring with an average speed of 61 km/day (range 39 to 82 km/day), including the time spent on stopovers. In autumn they travel with an average speed of 38 km/day (range 22 to 55 km/day) (*Fig. 3.6.A.*). These estimates are in the region of published results of other European passerines (Hilden & Saurola 1982, Ellegren 1990a, Ellegren 1993, Fransson 1995). Yohannes (2003) carried out a detailed analysis of the spring and autumn migrations of passerines that migrate from Europe to Africa on the eastern flyway. Nine out of eleven species for which she had data on both migratory seasons travelled faster in spring than in autumn, as is the case in the European stonechats in our study (*Fig. 3.6.B.*).

A possible explanation for this may be different selective pressures on the migration speed in the two seasons. In spring, there is competition over early arrival in the breeding areas, and early arrivals are usually in better shape and have higher reproductive success than late arrivals (Perrins 1970, Price et al. 1988, Marra et al. 1998, Marra & Holberton

1998, Kokko 1999) In autumn, many migrant species are not as pressed to arrive early, because they do not defend territories in the nonbreeding season, and food availability is usually better in mid-winter than in late autumn and early winter. However, as some authors have pointed out, the selective advantage of a migratory strategy in spring which minimises time rather than energy (Alerstam & Lindström 1990, Hedenström & Alerstam 1998) may be condition-dependent and thus not equal for all birds in the population (Kokko 1999, Drent et al. 2003). European stonechats are territorial during winter and the time of territorial establishment is a period of fierce interspecific competition (Gwinner et al. 1994, Rödl 1995, Raess et al. in prep.). Hence they could apply a time-minimisation strategy in autumn as well, which would ameliorate the difference between spring and autumn migration speeds.
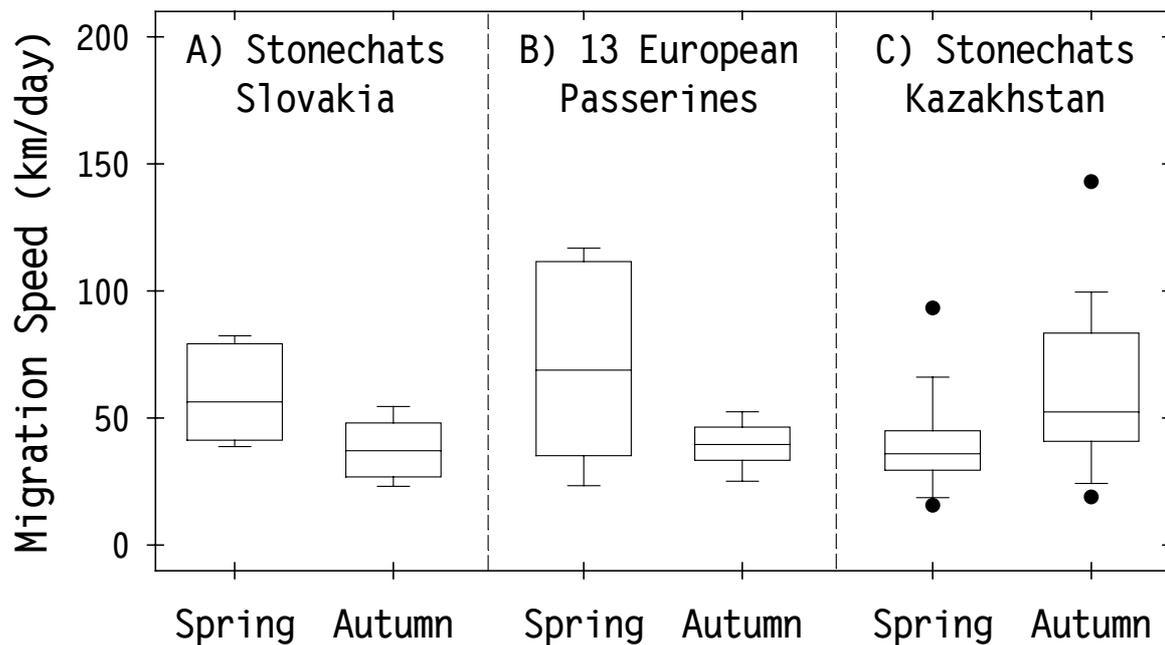
Fig. 3.6. The speed of migration of *A)* eastern European stonechats and *B)* 13 other European passerines migrating between their breeding and winter quarters, and *C)* of Siberian stonechats migrating within Central Asia and Siberia. The data on the European passerines was compiled from Yohannes (2003).

Another factor could contribute to the observed seasonal differences in migratory speed: the individual timing of autumn migration is determined

by the time required for breeding and moulting (Ellegren 1990b). Hence failed and successful breeders may initiate autumn migration at different dates. Furthermore, adults and juveniles often migrate at different times and with different speeds (Ellegren 1990a, Ellegren 1993, Yohannes 2003). While population-level studies on migration speed usually try to single out age-effects (e.g. Yohannes 2003), longer passage periods due to less synchronised autumn migration may still lead to an under-estimation of individual migration speed in these studies (but see below). More data on individual migrations of marked birds is needed to clarify this point.

Siberian stonechats

The migration speed for the whole journey from Siberia or Central Asia to Northern Africa or northern India/Pakistan is difficult to assess, because the data on the southern end of the migrations is scarce and sometimes vague and we lack the knowledge of the exact wintering grounds of different populations. A rough estimate of maximum migration speeds is given in *Table 3.4*. Within Central Asia and western Siberia, however, I can calculate migration speed using the extracted data from the literature (*Table 3.2.*). According to this data, stonechats travel with an average speed of 41 km/day (range 3 to 159 km/day) in spring, and in autumn the average migration speed is 63 km/day (range 18 to 153 km/day)(*Fig. 3.6.C.*).

The estimates between the migration speed for the whole migratory distance and within Siberia and Central Asia differ, particularly for the spring migratory period, less for autumn migration. A bird travelling from Siberia (Sverdlovsk region) to Tashkent in autumn would cover the distance of approx. 1800 km in about 30 days, based on my estimate of the migration speed within Central Asia. Hence it would have to cover the remaining distance to Sudan (~3800 km) within 40 days (i.e. 95 km/day) or to India (~3000 km) within 30 days (100 km/day) (cf. *Table 3.4.*). In spring, however, the distance between Tashkent and Sverdlovsk is covered in about 44 days, if the average speed within Central Asia is considered. Therefore, a bird would have to fly the distance from Sudan or India to Tashkent in

six days (~630 km/day from Sudan, ~500 km/day from India)!. Given that my estimate of the migration speed within Central Asia is based on much more information than my estimate for the whole migration distance, the discrepancy is likely to be caused by an inaccurate estimate of the speed of migration south of Central Asia.

Table 3.4. The approximate migration speed of Stonechats breeding in Siberia and wintering in Africa (**A**) or southern Asia (**B**).

Breeding	Wintering	approximate distance [A]	approximate duration [B]	approximate max. speed
A				
Siberia (57°N, 62°E)	Sudan (9°N, 40°E)	5650 km	spring: 50 days autumn: 70 days	113 km/day 81 km/day
B				
Siberia (57°N, 62°E)	India (15°N, 75°E)	4800 km	spring: 50 days autumn: 60 days	96 km/day 80 km/day

[A] orthodromatic distances, any detours due to ecological barriers are not considered.
[B] based on main passage dates from the literature.

It should be noted, however, that migration speed can change in the course of migration. Several authors report different speeds in different sections of the migratory route (Ellegren 1990a, Fransson 1995, Yohannes 2003). Migration within Central Asia takes place either before (autumn) or after (spring) the crossing of a broad belt of ecological barriers (*Fig. 3.3.*), which may require non-stop flights to overcome them (Dolnik 1990, Bolshakov 2002). Thus, different migratory strategies may contribute to the differences in the estimated migration speeds in the different sections.

Unlike in eastern European stonechats and other European passerines that migrate to Africa, the migration speed in Siberian stonechats is not higher in spring than in autumn (*Fig. 3.6.*). My calculations of migrations speeds are based on the assumption that birds that pass early or late at a given location will also pass early or late at consecutive locations along the migratory route. For the spring migratory period this approach seems justified because the movement along the migratory route is significantly

related to calendar date, In autumn, however, migratory movements are less synchronised. Hence I may actually over-estimate migration speed, if not individual timing but rather distance determines the sequence of the birds passing Tashkent, my referecence point. However, if I use only the late autumn migration period, which is significantly related to the calendar date (cf *Table 3.3.*), I get an estimated migration speed of 52 km/day (range 18 to 90 km/day). This more conservative estimate is still higher than that for the spring migratory period.

Siberian stonechats breed quite synchronously and late breeding bears costs (see Chapters 5 and 9 of this thesis). We can therefore assume that the selective pressure for early arrival on the breeding grounds in spring is at least as high as in the European passerines. A reason for the relatively slow progress of spring migration may be the local climatic conditions. The climate in continental Central Asia and Siberia is much harsher than in Europe, and the north-south temperature gradient in spring is much more pronounced. Thus, stonechats migrating north in continental Asia may have to adjust their rate of progress to the rate of amelioration of spring conditions. And indeed, passage dates within Central Asia and Siberia fall on the 10°C isothermal line (*Fig. 3.7.*), suggesting that their migration speed is determined by the timing of the onset of spring along their migratory route. Two factors may contribute to this dependency on spring ambient temperatures: (*1*) high energetic costs, due to increased demands on thermoregulation, but also due to the overlap of migration and reproductive development (see Chapter 4 of this thesis) may force birds to apply energy- rather than time-minimising migration strategies (Alerstam & Lindström 1990, Hedenström & Alerstam 1997, Wikelski et al. 2003); and (*2*) low food availability may decrease fuelling rates and thus migration speed (Pierce & McWilliams 2004). Spring migration in the European stonechats seems to be rather unconstrained by ambient temperatures (except unpredictable spells of cold weather) (*Fig. 3.7.*).
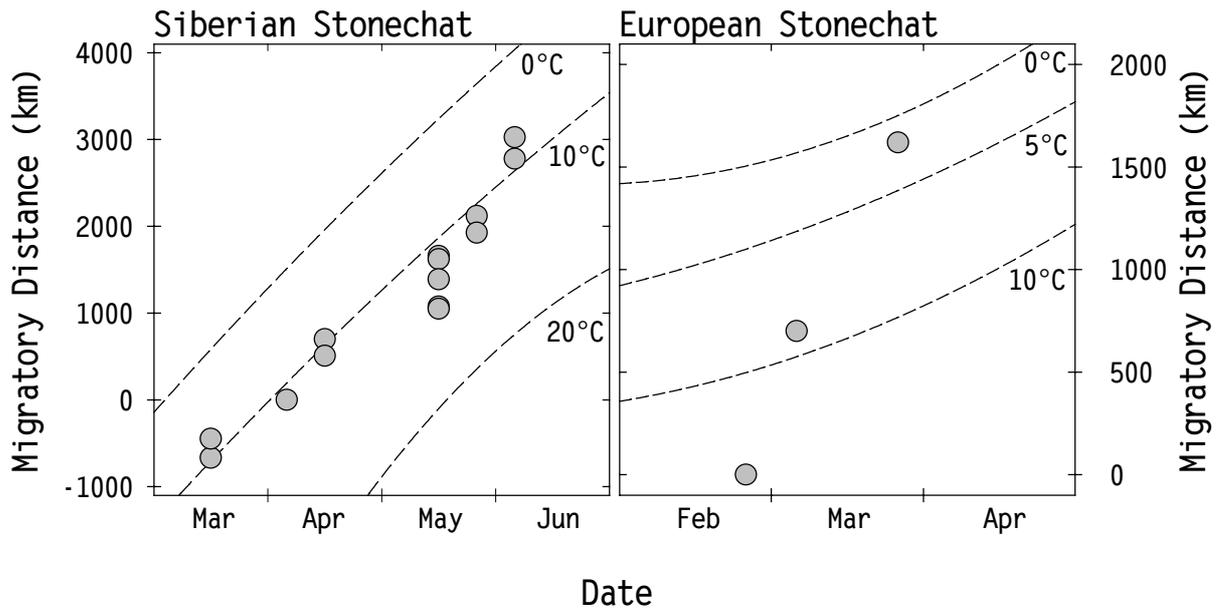
Fig. 3.7. The timing of passage in Siberian and European stonechats in relation to local climatic conditions. The dashed lines show the isothermal lines in relation to migration distance and date. The migratory distances were calculated from Tashkent, Uzbekistan, for the Siberian stonechats and from northern Tunisia (37°N, 6°E) for the European stonechats. Climate data from the IRI website (http//iri.columbia.edu).

In both locations the temperatures at the time of spring arrival increased in recent years, whereas they did not change as much at the time of autumn departure (*Fig. 3.8.*). Given the difference in the dependency of migration to the ambient temperatures between the populations, these current climatic changes may affect the evolution of migratory strategies to a higher degree in the Siberian than in the European stonechats. More knowledge on the migratory phenology within Asia is needed to clarify whether this applies more generally to the central Palearctic-African/South-Asian and western Palearctic-African migration systems.
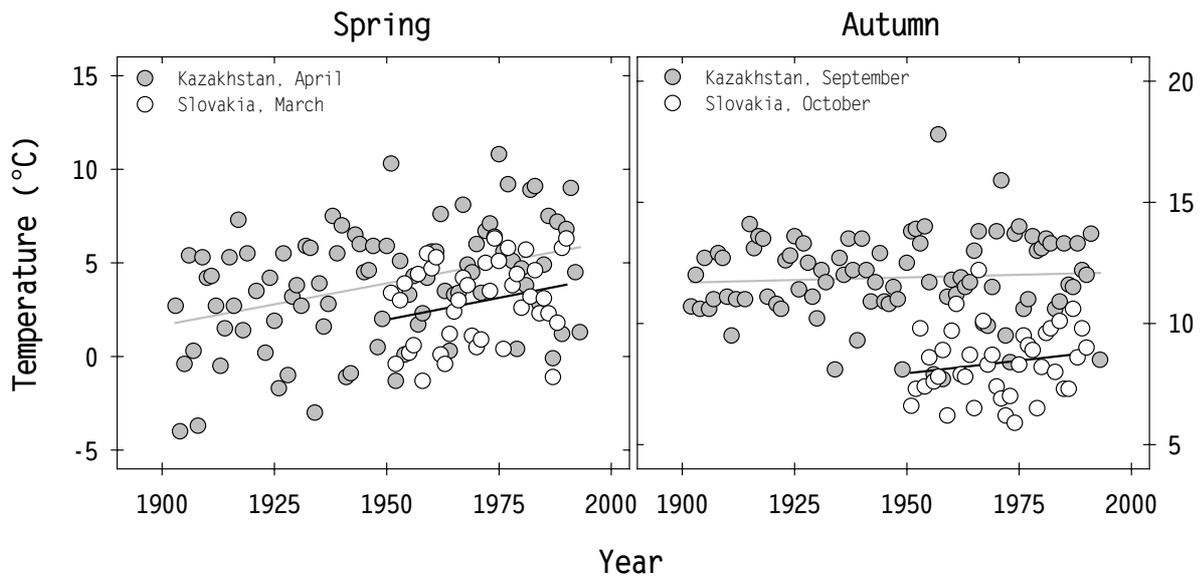
Fig. 3.8. Temperature trends during the periods of spring arrival and autumn departure of Siberian and European stonechats. In both areas temperatures increased during spring, whereas in autumn they stayed equal (Kazakhstan) or increased to a lesser degree (Slovakia).

3.5   References

Alerstam, T. & Lindström, A. (1990). Optimal bird migration: the relative importance of time, energy, and safety. *In* E. Gwinner (Ed.), *Bird Migration: Physiology and Ecophysiology*, pp. 331-351. Springer-Verlag, Berlin.

Bairlein, F. & Gwinner, E. (1994). Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annual Review of Nutrition* 14, 187-214.

Bauchinger, U. & Biebach, H. (1998). The role of protein during migration in passerine birds. *Biologia e Conservazione della Fauna* 102, 299-305.

Bauchinger, U. & Biebach, H. (2001). Differential catabolism of muscle protein in Garden Warblers (Sylvia borin): Flight and leg muscle act as a protein source during long-distance migration. *Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology* 171(4), 293-301.

Berthold, P. (2001). *Bird migration. A general survey*, 2nd ed. Oxford University Press, Oxford.

Berthold, P., Gwinner, E. & Sonnenschein, E. (Eds.). (2003). *Avian migration*. Springer, Berlin.

Berthold, P., Helbig, A., Mohr, G. & Querner, U. (1992). Rapid microevolution of migratory behavior in a wild bird species. *Nature* 360, 668-670.

Berthold, P., Wiltschko, W., Miltenberger, H. & Querner, W. (1990). Genetic transmission of migratory behaviour into a non-migrating population. *Experientia* 46, 107-108.

Biebach, H. (1996). Energetics of Winter and Migratory Fattening. *In* C. Carey (Ed.), *Avian Energetics and Nutritional Ecology*. Chapman & Hall, New York.

Biebach, H. (1998). Phenotypic organ flexibility in Garden Warblers *Sylvia borin* during long-distance migration. *Journal of Avian Biology* 29(4), 529-535.

Bingman, V. P. & Able, K. P. (2002). Maps in birds: representational mechanisms and neural bases. *Current Opinion in Neurobiology* 12, 745-750.

Blinova, T. K. & Blinov, V. N. (1997). *Ptitsy Yushnogo Zauralya: Lesostep i step [The Birds of Southern Trans-Uralia: Forest steppe and steppe]*. Nauka, Novosibirsk.

Bolshakov, C. V. (2002). The Palaearctic-African bird migration system: The role of desert and highland barrier of western Asia. *Ardea* 90(3), 515-523.

Bowlin, M. S., Cochran, W. W. & Wikelski, M. C. (2005). Biotelemetry of New World thrushes during migration: Physiology, energetics and orientation in the wild. *Integrative and Comparative Biology* 45(2), 295-304.

Brown, C. R. & Brown, M. B. (2000). Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behavioral Ecology and Sociobiology* 47, 339-345.

Brown, R. H. J. (1963). Flight of birds. *Biological Reviews of the Cambridge Philosophical Society* 38(4), 460.

Butler, C. J. (2003). The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis* 145(3), 484-495.

Calmaestra, R. G. & Moreno, E. (2001). A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in passeriformes. *Ardea* 89(2), 407-416.

Cantos, F. J. & Telleria, J. L. (1994). Stopover site fidelity of four migrant warblers in the Iberian Peninsula. *Journal of Avian Biology* 25(2), 131-134.

Chernyshov, V. M. (1982). Sravitel'naya ecologiya chernogolovogo chekana i varakushki v Barabinskoi lesostepi [Comparative ecology of the stonechat and bluethroat in the Barabinsk forest steppe], *Razmeshchenie i chislenost' pozvonochnykh Sibiri [Distribution and number of vertebrates in Siberia]*, pp. 84-110. Nauka, Novosibirsk.

Cochran, W. W. (1987). Orientation and other migratory behaviors of a Swainson thrush followed for 1500 km. *Animal Behaviour* 35, 927-929.

Cochran, W. W. & Applegate, R. D. (1986). Speed of flapping flight of merlins *Falco columbarius* and peregrine falcons *Falco peregrinus*. *Condor* 88(3), 397-398.

Cochran, W. W., Mouritsen, H. & Wikelski, M. (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* 304(5669), 405-408.

Cotton, P. A. (2003). Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America* 100(21), 12219-12222.

Cramp, S. (1988). *Handbook of the birds of Europe, the Middle East and North Africa*, Vol. 5. Oxford University Press, Oxford.

Danko, S., Darolová, A. & Krištín, A. (2002). *Bird distribution in Slovakia*. Veda, vydavatel'stvo Slovenskej akadémie vied, Bratislava.

Dement'ev, G. P. & Gladkov, N. A. (1954). *Birds of the Soviet Union*, Vol. Volume VI. Gosudarstvenno Izdatstelstvo Sovetskaya Nauka, Moskow.

Deviche, P. (1995). Androgen regulation of avian premigratory hyperphagia and fattening - from eco-physiology to neuroendocrinology. *American Zoologist* 35(3), 234-245.

Dolnik, V. R. (1990). Bird migration across the arid and mountainous regions of Middle Asia and Kazakhstan. *In* E. Gwinner (Ed.), *Bird Migration*. Springer-Verlag, Berlin, Heidelberg.

Drent, R., Both, C., Green, M., Madsen, J. & Piersma, T. (2003). Pay-offs and penalties of competing migratory schedules. *Oikos* 103(2), 274-292.

Egorov, V. A. (1985). *O gnesdovanii drozdovykh v Kalbe (Vostochno-Kazakhstanskaya oblast) [On the nesting of turdids in Kalba (Region East-Kazakhstan)]*. Leningrad State Pedagogic Institute, Leningrad.

Ellegren, H. (1990a). Autumn migration speed in Scandinavian bluethroats *Luscinia svecica*. *Ringing and Migration* 11(3), 121-131.

Ellegren, H. (1990b). Timing of autumn migration in bluethroats *Luscinia s. svecica* depends on timing of breeding. *Ornis Fennica* 67(1), 13-17.

Ellegren, H. (1993). Speed of migration and migratory flight lengths of passerine birds ringed during autumn migration in Sweden. *Ornis Scandinavica* 24(3), 220-228.

Erokhov, S. N. & Gavrilov, E. I. (1993). Nekotorye demograficheskie parametry sezonny migratsiy chernogolovykh chekanov v predgoryakh Severnogo Tyan-Shana [Some demographical parameters of the seasonal migrations of stonechats in the foothills of the Northern Tian-Shan], *Fauna i biologiya ptits Kazakhstana [Fauna and biology of the birds of Kazakhstan]*, pp. 184-186, Almaty.

Forsman, J. T. & Monkkonen, M. (2003). The role of climate in limiting European resident bird populations. *Journal of Biogeography* 30(1), 55-70.

Fransson, T. (1995). Timing and speed of migration in North and West European populations of Sylvia warblers. *Journal of Avian Biology* 26(1), 39-48.

Glutz von Blotzheim, U. & Bauer, K. M. (1988). *Handbuch der Vögel Mitteleuropas*, Vol. 11. Aula-Verlag, Wiesbaden.

Gwinner, E. (1986). *Circannual rhythms*. Springer Verlag, Heidelberg.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology* 199(1), 39-48.

Gwinner, E. (2001). Bird migration: its control by endogenous clocks. *In* D. Baltimore, R. Dulbecco, F. Jacob & R. Levi-Montalcini (Eds.), *Frontiers of Live*, Vol. 4: The Living World, pp. 193-206. Academic Press, New York.

Gwinner, E. (2003). Circannual rhythms in birds. *Current Opinion in Neurobiology* 13(6), 770-778.

Gwinner, E., Hau, M. & Heigl, S. (1997). Melatonin: Generation and modulation of avian circadian rhythms. *Brain Research Bulletin* 44(4), 439-444.

Gwinner, E., Rödl, T. & Schwabl, H. (1994). Pair territoriality of wintering stonechats: Behaviour, function and hormones. *Behavioral Ecology and Sociobiology* 34(5), 321-327.

Gwinner, E., Schwabl-Benzinger, I., Schwabl, H. & Dittami, J. P. (1993). Twenty-four hour melatonin profiles in a nocturnally migrating bird during and between migratory seasons. *General and Comparative Endocrinology* 90(1), 119-124.

Hake, M., Kjellen, N. & Alerstam, T. (2001). Satellite tracking of Swedish ospreys *Pandion haliaetus*: Autumn migration routes and orientation. *Journal of Avian Biology* 32(1), 47-56.

Hansson, B., Bensch, S., Hasselquist, D. & Nielsen, B. (2002). Restricted dispersal in a long-distance migrant bird with patchy distribution, the great reed warbler. *Oecologia* 130(4), 536-542.

Hedenström, A. & Alerstam, T. (1997). Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189(3), 227-234.

Hedenström, A. & Alerstam, T. (1998). How fast can birds migrate? *Journal of Avian Biology* 29(4), 424-432.

Helm, B. (2002). Seasonal timing in different environments: comparative studies in Stonechats. Ph.D. thesis, Ludwig-Maximilians-Universität München, Germany.

Hilden, O. & Saurola, P. (1982). Speed of autumn migration of birds ringed in Finland. *Ornis Fennica* 59(2-3), 140-143.

Holberton, R. L. (1999). Changes in patterns of corticosterone secretion concurrent with migratory fattening in a neotropical migratory bird. *General and Comparative Endocrinology* 116(1), 49-58.

Hoover, J. P. (2003). Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84(2), 416-430.

Hubalek, Z. (2004). Global weather variability affects avian phenology: a long-term analysis, 1881-2001. *Folia Zoologica* 53(3), 227-236.

Hudec, K. & Cerný, W. (1983). *Fauna CSSR, Ptaci-Aves*. Academia, Praha.

Hüppop, O. & Hüppop, K. (2003). North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270(1512), 233-240.

Imboden, C. & Imboden, D. (1972). Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beringungs- und Wiederfundort. *Vogelwarte* 26, 336-346.

Jenni, L. & Kéry, M. (2003). Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270(1523), 1467-1471.

Karyakin, I. V., Bystrykh, S. V. & Konovalov, L. I. (1999). *Ornitofauna Sverdlovskoi oblasti [Ornithofauna of the Sverdlovsk region]*. Manuscript Press, Novosibirsk.

Kjellen, N., Hake, M. & Alerstam, T. (2001). Timing and speed of migration in male, female and juvenile ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. *Journal of Avian Biology* 32(1), 57-67.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68(5), 940-950.

Kubán, V. & Matoušek, B. (1999). Výsledky krúžkovania vtákov Viliama Kubána na Slovensku v rokoch 1960-1999. *Tichodroma* 12, 136-215.

Kuz'mina, M. A. (1970). Rod Chekan [Genus Saxicola], *Ptitsy Kazakhstana [The birds of Kazakhstan]*, Vol. Volume 3, pp. 557-570, Almaty.

Landys, M. M., Ramenofsky, M., Guglielmo, C. G. & Wingfield, J. C. (2004). The low-affinity glucocorticoid receptor regulates feeding and lipid breakdown in the migratory Gambel's white-crowned sparrow Zonotrichia leucophrys gambelii. *Journal of Experimental Biology* 207(1), 143-154.

Lindström, A. & Alerstam, T. (1992). Optimal fat loads in migrating birds - a test of the time-minimization hypothesis. *American Naturalist* 140(3), 477-491.

Marchetti, K., Price, T. & Richman, A. (1995). Correlates of wing morphology with foraging behavior and migration distance in the genus *Phylloscopus*. *Journal of Avian Biology* 26(3), 177-181.

Marra, P. P., Hobson, K. A. & Holmes, R. T. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282(5395), 1884-1886.

Marra, P. P. & Holberton, R. L. (1998). Corticosterone levels as indicators of habitat quality effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116(1-2), 284-292.

McNamara, J. M., Welham, R. K. & Houston, A. I. (1998). The timing of migration within the context of an annual routine. *Journal of Avian Biology* 29(4), 416-423.

McWilliams, S. R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology* 35(5), 377-393.

Merom, K., Yom-Tov, Y. & McClery, R. (2000). Philopatry to stopover site and body condition of transient reed warblers during autumn migration through Israel. *Condor* 102(2), 441-444.

Mettke-Hofmann, C. & Gwinner, E. (2003). Long-term memory for a life on the move. *Proceedings of the National Academy of Sciences of the United States of America* 100(10), 5863-5866.

Mikkonen, A. V. (1983). Breeding site-tenacity of the chaffinch *Fringilla coelebs* and the brambling *Fringilla montifringilla* in northern Finland. *Ornis Scandinavica* 14(1), 36-47.

Mills, A. M. (2005). Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* 147(2), 259-269.

Monkkonen, M. (1995). Do migrant birds have more pointed wings? A comparative study. *Evolutionary Ecology* 9(5), 520-528.

Moreau, R. E. (1972). *The Palaearctic-African Migration Systems*. Academic Press, London and New York.

Mouritsen, H. & Ritz, T. (2005). Magnetoreception and its use in bird navigation. *Current Opinion in Neurobiology* 15(4), 406-414.

Nolan, V. & Ketterson, E. D. (1991). Experiments on winter-site attachment in young dark-eyed juncos. *Ethology* 87(1-2), 123-133.

Paz, U. (1987). *The birds of Israel*. Billing & Sons, Worcester, UK.

Perrins, C. M. (1970). The timing of birds breeding seasons. *Ibis* 112(2), 242-255.

Pierce, B. J. & McWilliams, S. R. (2004). Diet quality and food limitation affect the dynamics of body composition and digestive organs in a migratory songbird (*Zonotrichia albicollis*). *Physiological and Biochemical Zoology* 77(3), 471-483.

Price, T., Kirkpatrick, M. & Arnold, S. J. (1988). Directional selection and the evolution of breeding date in birds. *Science* 240(4853), 798-799.

Pulido, F. P., Berthold, P., Mohr, G. & Querner, U. (2001). Heritability of the timing of autumn migration in a natural bird populations. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 268, 953-959.

Robertson, I. (1977). Identification and European status of eastern stonechats. *British Birds* 70, 237-245.

Rödl, T. (1995). The wintering of territorial stonechat pairs *Saxicola torquata* in Israel. *Journal fuer Ornithologie* 136, 423-433.

Rödl, T. & Flinks, H. (1996). Nutrition of Stonechats (*Saxicola torquata*) and Mourning Wheatears (*Oenanthe lugens*) wintering sympatrically in Israel. *Ökologie der Vögel* 18, 107-126.

Rogacheva, H. (1992). The birds of central Siberia, pp. 503-507. Husum Druck- und Verlagsgesellschaft, Husum.

Shirihai, H. (1996). *The Birds of Israel*. Academic Press, London.

Shnitnikov, V. N. (1949). *Ptitsy Semirechya [Birds of Semirechie]*. House of the Academy of Science of the USSR, Moscow-Leningrad.

Sol, D., Levebvre, L. & Rodriguez-Teijeiro, J. D. (2005). Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 272, 1433-1441.

Stakheev, V. A. (2000). *Ptitsy Altaiskogo zapovednika [The birds of the Altai Nature Reserve]*, Shushenskoe.

Stervander, M., Lindström, A., Jonzen, N. & Andersson, A. (2005). Timing of spring migration in birds: long-term trends, North Atlantic Oscillation and the significance of different migration routes. *Journal of Avian Biology* 36(3), 210-221.

Sutherland, W. (1998). Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology* 29, 441-446.

Toropova, V. I. & Eremchenko, V. K. (1979). K razmnozheniyu chernogolovogo chekana v Kirgizii [On the breeding of the stonechat in Kirghizia], *Ekologiya gnezdovaniya ptits i metody eyo izucheniyu [Nesting ecology in birds and methods of its study]*, pp. 214, Samarkand.

Tsybulin, S. M. (1999). *Ptitsy Severnogo Altaya [Birds of Northern Altai]*. Nauka, Novosibirsk.

Urquhart, E. (2002). *Stonechats: A guide to the genus Saxicola*. Christopher Helm, London.

Vähätalo, A. V., Rainio, K., Lehikoinen, A. & Lehikoinen, E. (2004). Spring arrival of birds depends on the North Atlantic Oscillation. *Journal of Avian Biology* 35(3), 210-216.

van Hecke, P. (1965). The migration of the west-european Stonechat, *Saxicola torquata* (L.), according to ringing data. *Le Gerfaut* 55, 146-194.

Viscor, G. & Fuster, J. F. (1987). Relationships between morphological parameters in birds with different flying habits. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 87(2), 231-249.

Wallraff, H. G. (2004). Avian olfactory navigation: its empirical foundation and conceptual state. *Animal Behaviour* 67(2), 189-204.

Wikelski, M., Tarlow, E. M., Raim, A., Diehl, R. H., Larkin, R. P. & Visser, G. H. (2003). Costs of migration in free-flying songbirds. *Nature* 423(6941), 704-704.

Wiltschko, R. & Wiltschko, W. (2003). Avian navigation: from historical to modern concepts. *Animal Behaviour* 65, 257-272.

Yohannes, E. (2003). Causal analysis of spatio-temporal patterns of passerine migration along the eastern flyway, Leopold-Frantzens-Universität Innsbruck.

Zink, G. (1973). *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel*, Vol. 1. Vogelwarte Radolfzell, Möggingen.

4   GONADAL STATUS AT SPRING ARRIVAL IN SIBERIAN AND EUROPEAN STONECHATS [§]

4.1   Summary

Long-distance migration is often associated with relatively short breeding seasons and a start of reproductive activities shortly after arrival. The full activation of the reproductive system from the regressed state takes, however, several weeks and has to be initiated therefore in the winter quarters or during spring migration. Hence, long-distance migrants face a potential conflict between the energetic and temporal requirements of migration and the preparation for reproduction. I studied long-distance migrating Siberian stonechats in northern Kazakhstan and short-distance migrating European stonechats in Slovakia. I hypothesised, that migratory distance and gonadal status at the time of arrival are related. I found that males of both populations arrived with gonads that were not fully developed. However, the populations neither differed in gonadal state at the time of arrival, nor in the rate of testicular development to the fully active state at the time of egg laying. The rate of the last stages of gonadal development may be determined rather by physiological constraints than by a trade-off between migration and reproduction. Within populations, passage migrants and local breeders could not be distinguished on the basis of their testicular development. However, passage migrants showed higher variation in gonadal size than local breeders, which could relate to the differences in migratory distance and hence reproductive timing.

4.2 Introduction

The timing of reproduction is a crucial factor in determining avian reproductive success (e.g. Baker 1938, Lack 1968, Perrins 1970, Murton & Westwood 1977, Nilsson 1999). Most birds shut down their reproductive system in the nonbreeding season (Murton & Westwood 1977, Dawson et al. 2001). A decrease of hypothalamic gonadotropin-releasing hormone (GnRH) is associated with a reduced secretion of gonadotropins from the pituitary and gonadal regression (Murton & Westwood 1977, Wingfield & Moore 1987, Dawson et al. 2001). Gonadal re-activation takes several weeks. Therefore, to achieve full reproductive capacity at the beginning of the breeding season, migratory birds have to initiate gonadal recrudescence during spring migration or in their winter quarters (Gwinner 1986, 1987, Dawson et al. 2001, Gwinner 2003). Migration makes substantial energetic demands on birds (Berthold et al. 2003, Wikelski et al. 2003, McWilliams et al. 2004), as indicated by a high differential mortality during that period (Sillett & Holmes 2002). Therefore migratory birds, and in particular long-distance migrants, face a potential conflict between the requirements of spring migration and the activation of the reproductive system.

I studied migratory Siberian stonechats (*Saxicola torquata maura*) in northern Kazakhstan and European stonechats (*S. t. rubicola*) in central Slovakia (see Chapter 2 of this thesis). Both areas are located in the temperate zones, they differ however markedly in the length of the environmental breeding window and the number of clutches the local stonechats produce annually. While the Siberian stonechats breed once during May and June, with replacement clutches occurring also in July, the European stonechats breed from April to the beginning of September and can produce up to three full clutches in that period. As a consequence, breeding is much more synchronised in the Siberian than in the European population (see Chapter 5 of this thesis).

Siberian stonechats are long-distance migrants that winter in Northern Africa and subtropical India / Pakistan. Thus, spring migration can last for more than two months and cover more than 6000 km in some

populations, and large ecological barriers such as seas, deserts and high mountain ranges have to be crossed on the way (see Chapter 3 of this thesis). The stonechats from Slovakia, on the other hand, are short-distance migrants that migrate within one month the approx. 1500 km distance from their wintering grounds in Northern Africa to their breeding grounds (see Chapter 3 of this thesis). The two subspecies may apply different strategies for the activation of the reproductive system in relation to the severity of constraints they meet during the migratory period.

In this Chapter I try to assess the effects of the different migratory regimes on gonadal recrudescence in Siberian and European stonechats, by comparing the developmental state (as indicated by size) of the testes of arriving males and the rate of an eventual further increase towards full gonadal size. Siberian stonechats are potentially more constrained during spring migration and may arrive with smaller gonads than European stonechats. As a consequence they may have to increase their rate of gonadal development to achieve fully functional testes at the time of offspring production. However, gonadal state may also be modified by reproductive timing decisions, and therefore within populations, birds on passage and birds that intend to stay and breed may show differences in gonadal development at the time of arrival at our study sites.

4.3   Methods

4.3.1 Field methods

During the early breeding season (i.e. from arrival until the onset of egg laying in the populations) stonechats males were caught using mealworm-baited traps or mistnets. The birds were unilaterally laparatomised and the size of the left testis (at the narrow side of the ellipsoid, hence we measured testis *widths*) determined to an accuracy of 0.1 mm. Males that subsequently left the study area without attempting to

breed were recorded as *passage migrants* (this group may also include floaters that stayed in the area but failed to establish a territory). Males that stayed in the study area and attempted to breed (i.e. establishment of a territory, successful or failed breeding) were recorded as *local breeders*.

4.3.2 Statistical analysis

The data fulfilled the requirements for parametric testing and was analysed with general linear models (GLMs) using the statistical package SPSS 12.1 (SPSS Inc., USA). All statistical tests were carried out two-tailed.

4.4 Results

In both populations, testis widths increased significantly in males caught from the time arrival to the period of egg production. When date is taken into account, there is no difference in gonadal widths between males that stayed to breed or males that did not attempt to breed in the area, either because they moved on after capture or failed to breed for other reasons (GLM; Kazakhstan: *CAPTURE DATE*: $F_{1,28} = 5.22$, $p < 0.05$; *NESTING STATUS*: $F_{1,28} < 0.001$, $p = 0.99$; $r^2 = 0.19$; Slovakia: *CAPTURE DATE*: $F_{1,16} = 5.26$, $p < 0.05$; *NESTING STATUS*: $F_{1,16} = 0.11$, $p = 0.74$; $r^2 = 0.38$) (*Fig. 4.1.A*). In both populations, the residual testis sizes of the *passage migrant* group showed higher variation than those of the *local breeder* group, however the differences in the variance between passage migrants and local breeders are only significant in the Siberian stonechats (F-test: Kazakhstan: $F_{23.7} = 6.61$, $p < 0.05$; Slovakia: $F_{7, 10} = 3.50$, $p < 0.1$) (*Fig. 4.1.B*).

For a comparison of the gonadal development between subspecies the data was matched for the mean laying date of the first egg in the population (*Fig. 4.2.*). Relative to the populations' reproductive timing,

there were no fundamental differences between the two populations in the way testicular development proceeded in the time between arrival and offspring production: the rate of increase in testis width was similar in Siberian and European stonechat males (GLM: *POPULATION: $F_{1,46}$ = 0.38, p = 0.54*; *DAYS TO EGG: $F_{1,46}$ = 16.13, p < 0.001*; *POPULATION * DAYS TO EGG: $F_{1,46}$ = 0.002; p = 0.97*; fitted lines: Kazakhstan: *y = 4.27 + 0.032x*; Slovakia: *y = 4.45 + 0.033x*) (*Fig. 4.2.*).
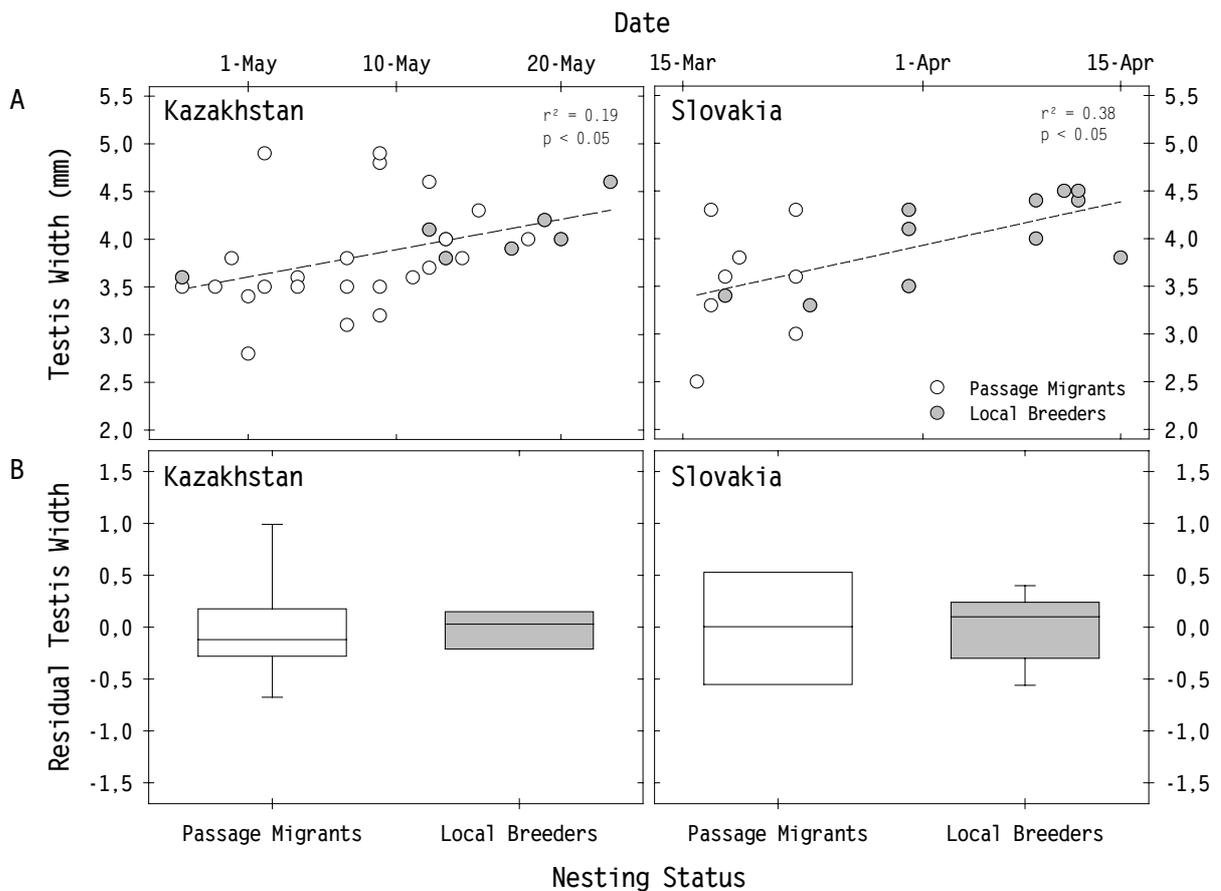
Fig. 4.1. Testis widths in Siberian and European stonechat males in the early breeding season. *A:* In both populations testis widths increase from the time of arrival to the time of egg laying. There is no difference in gonadal development of males that breed in the area and males that are caught on passage or do not breed for other reasons. *B:* In both populations, the residual testis widths of passage migrants show higher variation than those of local breeders.

Fig. 4.3. shows a comparison of the gonadal cycles of captive and free-living male Siberian and European stonechats. Captive birds were either held singly under photoperiodic conditions simulating the annual cycle, including breeding, wintering, and migrations of the two subspecies, or they were paired in spring in outdoor aviaries in Andechs, Germany (48°N, 11°E), (Helm and Gwinner, in prep., Helm & Gwinner 2005). Like their free-living conspecifics, captive European stonechats initiate testicular growth earlier in the season than Siberian stonechats. The timing of gonadal regression seems to be influenced by the social context. Birds with access to partners and breeding opportunities regress their testis later than birds that are held singly. The field data of stonechats in Kazakhstan and Slovakia fits into that scheme (*Fig. 4.3.*).
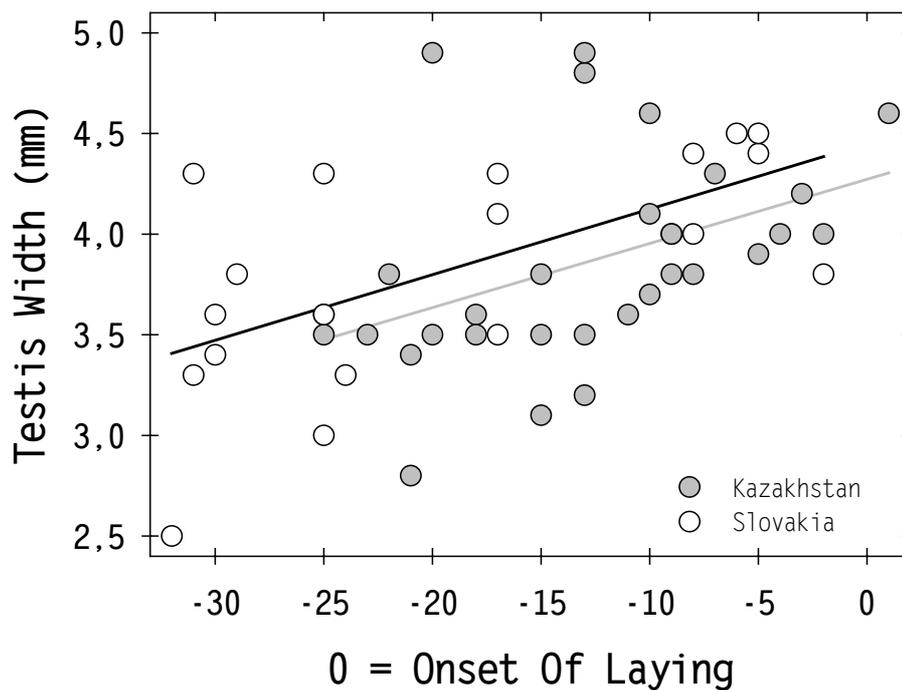
Fig. 4.2. Gonadal development in Siberian and European stonechat males does not differ in respect to reproductive activities in the two populations (data is matched for the mean laying date of the first egg in each population).
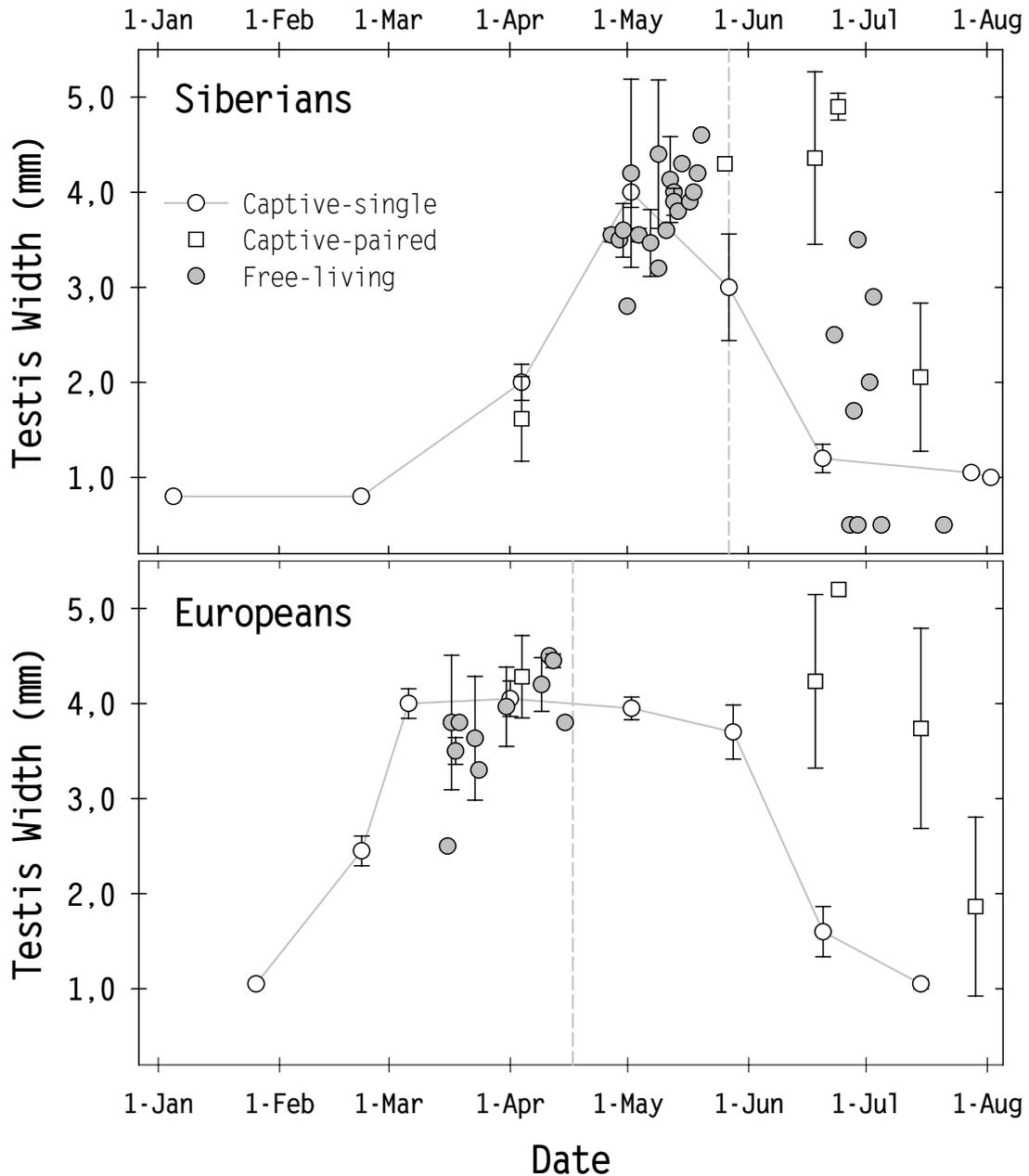
Fig. 4.3. The gonadal cycles of captive and free-living male Siberian and European stonechats (data shown as means ± SD). The captive birds were held singly or in breeding pairs under photoperiodic conditions simulating the complete annual cycle of each population. Superimposed are testis widths of free-living stonechats from our field sites in Kazakhstan and Slovakia. The vertical dashed line shows the average laying date for the first clutch in the two study populations. (Data on captive stonechats from Helm and Gwinner, unpubl. data; Helm and Gwinner 2005).

4.5 Discussion

In Kazakhstan as well as in Slovakia, testicular growth was not completed at the time of arrival. In males of both subspecies the testis width increased on average by about 30% (the volume by about 120%, if we assume globular testes) between arrival and breeding. Testis size correlates with the functional development of the spermatogenetic apparatus. Bauchinger (2002) caught garden warblers *Sylvia borin* during their final stop-over in Egypt before crossing the Mediterranean Sea and compared the testicular morphology to that of birds in the full breeding state. The testes of the migrating birds had less than half of the final mass and contained differentiating spermatids, but no functional sperm. Pied flycatchers *Ficedula hypoleuca* caught during the last stage of migration in Sweden had testes of about 60% of the final size that contained only a few sperm bundles, indicating that ejaculates produced at that time would have been of poor quality (Silverin 1975). Accordingly, we can assume that in arriving stonechats males of both populations the testes had not acquired full spermatogenetic capacity.

There was no difference in the rate of gonadal development in Kazakh and Slovak stonechat males when the two populations were matched for reproductive timing. Siberian stonechats arrived, however, about one to two weeks later in relation to the onset of laying. Despite the potentially more constraining migratory regime of the Siberian stonechats, they did not show delayed gonadal development at the time of arrival, when compared to their European conspecifics. This could indicate that the birds from both populations arrest gonadal growth at a certain stage once they start to migrate. After arrival this inhibition is removed and the birds resume gonadal maturation. The data on the gonadal development in captive stonechats indicates, however, that testicular growth proceeds during the subjective spring migratory periods (i.e. when the birds show nocturnal migratory restlessness, Helm & Gwinner 2005). Whether these patterns correspond to those of free-living stonechats is not known. Several passerines do grow their gonads during migration, most likely during the

stop-over periods (Fry 1972, Silverin 1975, Bauchinger 2002), which comprise about 80 to 90% of the total migratory period (Hedenström & Alerstam 1997). There are indications that the last stages of the spring movements of Siberian stonechats might be restricted by the local conditions, i.e. that they have to wait until the snow has melted and the environment is productive enough to support them (see Chapter 3 of this thesis). It is therefore possible that Siberian stonechat males grow their gonads predominantly during the stopovers in southern Asia, when they have to wait for ameliorating spring conditions.

During the final stages of gonadal development, testis mass in pied flycatchers and garden warblers is mainly determined by the amount of functional sperm it contains (Silverin 1975, Bauchinger 2002). The rate of spermatogenesis is species-specific (Murton & Westwood 1977). Therefore, the similar rates of testicular development from arrival to the initiation of reproduction in Siberian and European stonechats may be a result of similar physiological constraints in both subspecies. This does not preclude, however, that earlier stages of gonadal development proceed differently in the two subspecies. Gonadal development is controlled by endogenous circannual programmes and the photoperiod experienced during wintering and spring migration (Gwinner et al. 1988, Gwinner 1989, 1998, Dawson et al. 2001, Dawson 2002, Gwinner 2003). Helm and Gwinner (2005) show that slight differences in the photoperiodic signal have eminent effects on the gonadal cycle of captive European stonechats. Thus, while the endpoint of testicular development is set to match reproductive timing in both subspecies, the initial stages may differ due to a combined effect of the different photoperiods experienced during wintering and spring migration, and the different energetic requirements of the migratory period. Clearly, more knowledge on the development of the reproductive system along the migratory routes is required (see e.g. Bauchinger 2002).

Testis sizes in greenfinches *Charduelis chloris* (Merilä & Sheldon 1999) and savannah sparrows *Passerculus sandwichensis* (Rising 1987) differ between males of the same reproductive stage but of different geographic

locations. It has been suggested that varying degrees of sperm competition and local variations in mating systems select for different testis sizes. Within populations, individual variation in testis size has been attributed to age, body size, and individual phenotypic quality (Rising 1987, Weatherhead et al. 1993, Merilä & Sheldon 1999). As yet, there is not enough data on free-living stonechat males in the fully reproductive state to assess individual variation in gonadal size. The data on captive birds suggests, however, that Siberian and European stonechats have similar testis sizes when they reproduce (Helm and Gwinner, unpubl. data).

Within the populations, males on passage and males that attempted to breed at our study sites were not distinguishable on the basis of the developmental state of their gonads. Similarly, in a study on stonechats in southern Siberia, passage migrants and local breeders had similar testis sizes in spring (Chernyshov 1982). Our data could indicate that we sampled only from populations with breeding areas close-by. Thus the remaining migratory distance and the resulting shift in the onset of reproduction may have been too small to be reflected in a corresponding shift in the gonadal development. Alternatively, migrating stonechats could have a fixed program of gonadal development that does not account for differences in the timing of reproduction between northerly and southerly populations. This is, however, rather unlikely because phenotypic plasticity in the response to photoperiod has been shown in stonechats and other migratory passerines (Coppack et al. 2003, Helm & Gwinner 2005). The differences in gonadal development between passage migrants and local could, however, be obscured by the higher variation of testis widths in the passage migrant group, which could be a reflection of the different destinations of the birds that do only stop-over.

Contrary to the onset of gonadal recrudescence, which in migrants is mainly controlled by photoperiod and endogenous timing mechanisms, the timing of the regression of the reproductive system integrates photoperiodic information with the prevailing reproductive status (Runfeldt & Wingfield 1985, Wingfield & Moore 1987, Dawson et al. 2001). Hence, in

the captive birds with access to a partner gonadal regression starts later than in the captive birds without breeding opportunities. In the free-living Siberian stonechats gonadal regression shows a similar pattern than those of their captive conspecifics that were allowed to breed. The variation in testis sizes in the Kazakh stonechats is much higher late in the breeding season, when males that have succeeded with their first breeding attempt occur together with males that had to replace a lost first clutch or completely failed to breed.

The control of avian reproductive cycles by endogenous timing programs and their modification by the photoperiod have been the subject of extensive scientific research (Murton & Westwood 1977, Gwinner 1986, Dawson et al. 2001, Dawson 2002, Gwinner 2003) and these studies continue to produce intriguing results (Helm & Gwinner 2005). Supplementary information, such as social cues, can further modify the opening and the closing of the endogenous reproductive window (Runfeldt & Wingfield 1985, Gwinner et al. 1987, Wingfield & Moore 1987, Dawson et al. 2001). Migration, especially over long distances and time periods, has the potential to further affect the pattern of reproductive recrudescence. Our study suggests that differences in gonadal development between closely related long-distance and short-distance migrating birds might be ameliorated at the time of arrival at the breeding grounds and that earlier stages of gonadal maturation and migration should be included in further studies.

4.6   References

Baker, J. R. (1938). The evolution of breeding seasons. *In* G. R. de Beer (Ed.), *Evolution: Assays on Aspects of Evolutionary Biology*, pp. 161-177. Oxford University Press, London.

Bauchinger, U. (2002). Phenotypic flexibility of organs during long-distance migration in garden warblers (*Sylvia borin*): implications for migratory and reproductive periods. PhD thesis, Technische Universität München.

Berthold, P., Gwinner, E. & Sonnenschein, E. (Eds.). (2003). *Avian migration*. Springer, Berlin.

Chernyshov, V. M. (1982). Sravitel'naya ecologiya chernogolovogo chekana i varakushki v Barabinskoi lesostepi [Comparative ecology of the stonechat and bluethroat in the Barabinsk forest steppe], *Razmeshchenie i chislenost' pozvonochnykh Sibiri [Distribution and number of vertebrates in Siberia]*, pp. 84-110. Nauka, Novosibirsk.

Coppack, T., Pulido, F., Czisch, M., Auer, D. P. & Berthold, P. (2003). Photoperiodic response may facilitate adaptation to climatic change in long-distance migratory birds. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: S43-S46 (Suppl. 1).

Dawson, A. (2002). Photoperiodic control of the annual cycle in birds and comparison with mammals. *Ardea* 90: 355-367.

Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. (2001). Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* 16: 365-380.

Fry, C. H. (1972). Flight muscle hypertrophy and ecophysiological variation of yellow wagtail *Motacilla flava* races at Lake Chad. *Journal of Zoology* 167: 293-306.

Gwinner, E. (1986). *Circannual rhythms*. Springer Verlag, Heidelberg.

Gwinner, E. (1987). Annual rhythms of gonadal size, migratory disposition and molt in Garden Warblers (*Sylvia borin*) exposed in winter to an equatorial or a southern hemisphere photoperiod. *Ornis Scandinavica* 18: 251-256.

Gwinner, E. (1989). Effects of photoperiod on the circannual systems of the collared and pied flycatcher, *Ficedula albicollis, F. hypoleuca*. *Journal fuer Ornithologie* 130: 1-14.

Gwinner, E. (1998). Photorefractoriness in equatorial migrants, *Proc. 19 Int. Ornithol. Congr., Ottawa*, pp. 626-633. Ottawa University Press, Ottawa.

Gwinner, E. (2003). Circannual rhythms in birds. *Current Opinion in Neurobiology* 13: 770-778.

Gwinner, E., Dittami, J. P. & Beldhuis, H. J. A. (1988). The seasonal development of photoperiodic responsiveness in an equatorial migrant, the garden warbler *Sylvia borin*. *Journal of Comparative Physiology A Sensory Neural and Behavioral Physiology* 162: 389-396.

Gwinner, H., Gwinner, E. & Dittami, J. P. (1987). Effects of nestboxes on LH, testosterone, testicular size, and the reproductive behavior of male European starlings in spring. *Behaviour* 103: 68-82.

Hedenström, A. & Alerstam, T. (1997). Optimum fuel loads in migratory birds: Distinguishing between time and energy minimization. *Journal of Theoretical Biology* 189: 227-234.

Helm, B. & Gwinner, E. (2005). Carry-over effects of day length during spring migration. *Journal of Ornithology* DOI 10.1007/s10336-005-0009-5.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen, London.

McWilliams, S. R., Guglielmo, C., Pierce, B. & Klaassen, M. (2004). Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology* 35: 377-393.

Merilä, J. & Sheldon, B. C. (1999). Testis size variation in the greenfinch *Carduelis chloris*: relevance for some recent models of sexual selection. *Behavioral Ecology and Sociobiology* 45: 115-123.

Murton, R. K. & Westwood, N. J. (1977). *Avian Breeding Cycles*. Clarendon Press, Oxford.

Nilsson, J.-A. (1999). The fitness consequences of the timing of reproduction. *In* N. J. Adams & R. H. Slotow (Eds.), *Proc. 22 Int. Ornthol. Congr., Durban*, pp. 234-247. BirdLife South Africa, Johannesburg.

Perrins, C. M. (1970). The timing of birds breeding seasons. *Ibis* 112: 242-255.

Rising, J. D. (1987). Geographic variation in testis size in savannah sparrows (*Passerculus sandwichensis*). *Wilson Bulletin* 99: 63-72.

Runfeldt, S. & Wingfield, J. C. (1985). Experimentally prolonged sexual acticity in fermale sparrows delays termination of reproductive activity in their untreated males. *Animal Behaviour* 33: 403-410.

Sillett, T. S. & Holmes, R. T. (2002). Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71: 296-308.

Silverin, B. (1975). Reproductive organs and breeding behavior of the male pied flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica* 6: 15-26.

Weatherhead, P. J., Metz, K. J., Bennett, G. F. & Irwin, R. E. (1993). Parasite Faunas, Testosterone and Secondary Sexual Traits in Male Red-Winged Blackbirds. *Behavioral Ecology and Sociobiology* 33: 13-23.

Wikelski, M., Tarlow, E. M., Raim, A., Diehl, R. H., Larkin, R. P. & Visser, G. H. (2003). Costs of migration in free-flying songbirds. *Nature* 423: 704-704.

Wingfield, J. C. & Moore, M. C. (1987). Hormonal, social and environmental factors in the reproductive biology of free-living male birds. *In* D. Crews (Ed.), *Psychobiology of Reproductive Behaviour: An Evolutionary Perspective*, pp. 149-175. Prentice-Hall, New York.

5 BREEDING PERFORMANCE IN SIBERIAN AND EUROPEAN STONECHATS

5.1 Summary

Siberian stonechats arrive at their breeding areas in Kazakhstan in the beginning of May and begin to lay two to three weeks later. They generally produce only one clutch per season, but lost clutches are often replaced. Most breeding pairs have independent young in early to mid July, those birds that have to replace clutches until mid August. European stonechats arrive in early March in Slovakia and start to breed in mid April. They lay two to three clutches and finish their reproductive activities in about mid August. The breeding activities of the Kazakh stonechats are much more synchronised than those of the Slovak stonechats. Siberian stonechats lay larger clutches than European stonechats. Clutch size decreases with season in the Siberian stonechats, while in the European stonechats clutches first decrease in size, however very late in the season increase again. Siberian stonechats have a higher fledging success, mostly due to lower nest predation rates than European stonechats. The differences in nest predation rates may be affected by the breeding synchrony, however they may be simply an effect of different predators. Fledging success decreases with season in both populations. This is mainly due to a change in clutch sizes in Kazakhstan, and due to a combination of the effects of clutch size and nest predation in Slovakia. On average, a Siberian stonechat pair in Kazakhstan produces about 20% less fledglings than a European stonechat pair in Slovakia. How this translates into reproductive success is not known, because data on post-fledging survival is not available. Increasing spring temperatures in both study areas may lead to a change in the breeding phenology and the underlying reproductive physiology. The chapter ends with a brief description of facultative

polygyny in Siberian stonechats, a phenomenon that has been previously reported in European stonechats.

5.2   Introduction

Reproductive success in birds breeding in the temperate zones decreases in the course of the breeding season (Baker 1938, Lack 1954, Perrins 1970, Daan et al. 1986, Price et al. 1988). This decrease has been mainly attributed to a seasonal decline in the productivity of the environment and hence the resources available for offspring production (Lack 1954, Drent & Daan 1980, Daan et al. 1986). Support for this *timing hypothesis* has been found in several studies (Brinkhof et al. 1993, Verboven & Verhulst 1996, Svensson 1997, Verboven & Visser 1998, Lepage et al. 1999, Sanz 1999). The alternative *quality hypothesis* states that the seasonal decline in reproductive success is caused by variation in the quality of the breeding birds. High-quality birds are able to breed earlier than low-quality birds, therefore breeding success is higher early in the season (Hipfner et al. 1999, Hansson et al. 2000, Christians et al. 2001, De Neve et al. 2004). The two hypotheses are not mutually exclusive, and both factors may explain the observed seasonal patterns of reproductive success (Rowe et al. 1994, Verhulst et al. 1995, Wardrop & Ydenberg 2003).

Reproductive timing in migrants is linked to the arrival date on the breeding grounds (Francis & Cooke 1986, Gustafsson et al. 1994, Lozano et al. 1996, Marra et al. 1998, Smith & Moore 2005). Early arrivals often obtain better territories and better breeding partners (Hasselquist 1998, Marra et al. 1998, Kokko 1999, Forstmeier 2002, Smith & Moore 2005). In many migratory species males arrive earlier than females. This is often related to sexual size differences (Morbey & Ydenberg 2001, Kissner et al. 2003). The larger males are socially dominant, which gives them better access to resources in the winter quarters, which in turn enables them to embark earlier on their spring migrations (Marra et al. 1998, Marra &

Holberton 1998, Marra 2000). Variation in arrival time within sexes is often linked to experience or quality: older birds and individuals of higher phenotypic quality arrive earlier than younger ones or birds of lower quality (Moller 1994, Lozano et al. 1996, Potti 1998, Forstmeier 2002, Ninni et al. 2004). There is, however, counter-selection against too early arrival (Brown & Brown 2000).

The recent changes in global climate have led to advances in both, arrival times of migrants (Sutherland 1998, Cotton 2003, Hüppop & Hüppop 2003, Jenni & Kéry 2003, Hubalek 2004, Vähätalo et al. 2004), and avian breeding schedules (Crick et al. 1997, Forchhammer et al. 1998, McCleery & Perrins 1998, Dunn & Winkler 1999, Cresswell & McCleery 2003, Both et al. 2004). This has led in some cases to an increase in reproductive output (Moller 2002, Cresswell & McCleery 2003), while in other cases the onset of laying and the food peak seem to get de-synchronised, resulting in a decrease in reproductive success (Stevenson & Bryant 2000).

Variability in individual phenotypic quality and the external environment affects reproductive success not only via reproductive timing decisions, but has also a strong effect on reproductive performance *per se*. Individual breeding success is affected by intrinsic factors such as age (Newton 1989, Forslund & Pärt 1995, Lozano et al. 1996, Geslin et al. 2004, Mauck et al. 2004, Sockman et al. 2004), body condition and the state of the immune system (Bonneaud et al. 2003, Bize et al. 2004, Fitze et al. 2004, Marzal et al. 2005, Verhulst et al. 2005), and extrinscic factors such as neighbour density (Sillett et al. 2004, Verboven et al. 2005), or carry-over effects from the winter habitat (Norris et al. 2004).

Besides a high variation in reproductive success within a population (see also Chapter 1 of this thesis), there are also general trends in reproductive phenology and annual fecundity across populations and species. Ecological differences between groups, such as variation in nest predation rates between temperate and tropical breeders, or between open-nesting and hole-nesting species, are thought to affect reproductive parameters such as clutch size and drive the evolution of divergent live-histories (Williams

1966, Skutch 1967, Lack 1968, Ricklefs 1969, Charnov & Krebs 1974, Boehning-Gaese et al. 2000).

In this chapter, I compare the reproductive activities of Siberian stonechats in Kazakhstan and European stonechats in Slovakia. Both breeding areas are located in the northern temperate zones, the photoperiodic conditions are therefore similar. They differ, however, markedly in the prevailing climatic conditions. The harsh continental climate in Kazakhstan with a large annual temperature range and lower annual precipitation limits the time available for breeding when compared to Slovakia (see Chapter 2 of this thesis). Furthermore, different migratory schedules as a consequence of long-distance migration in the Siberian stonechats and short-distance migration in the European stonechats put different temporal strains on reproductions in the two populations (see Chapter 3 of this thesis). I will examine the annual patterns of reproductive timing and reproductive output in the two populations and relate them to the different reproductive schedules. I will also give a brief description of the occurrence of facultative polygyny in the Siberian stonechats, which to my knowledge has not been described previously.

5.3   Methods

5.3.1 Monitoring of breeding activities in the field

I monitored reproductive activities as early as possible in the breeding cycle. To this end, once a bird settled in a territory, I checked regularly for pairing status, sexual behaviours, nest building, and incubation by the females. The location of nests was detected by observing birds carrying nest material, females leaving or entering the nest between incubation bouts, or a parent carrying food items to the nest. Stonechats are ground nesters, and their nests are usually well concealed, even in the seemingly sparse vegetation of the Kazakh steppe. In order to minimise disturbances which could lead to abandonment of the nest, and to prevent

the exposure of the nest site to potential predators, several precautionary measures were taken when searching for or visiting nests: Potential nest sites were only approached when the location of the nest was already known within narrow limits, and only one person approached the nest site. Prolonged searching at the nest site was avoided. When a nest site was visited, a second person carried out sham searching movements at a different location to distract watching predators (especially corvids). After the nest visit the vegetation surrounding the nest was restored to its former condition. Number and duration of nest visits were limited to the absolutely necessary, and care was taken not to create a track to the nest site. After the young had left the nest, the parental status of the breeding pairs was assessed by regular observations of parental activities and by checking for alarm calls elicited by the observers' approach.

5.3.2 Analysis of the temporal patterns of breeding activities

To compare the breeding activities between the two populations, the proportion of active nests relative to the number of breeding pairs was calculated. The analysis is based on 134 nesting attempts in Kazakhstan in the breeding seasons from 1999 to 2001, and on 72 nesting attempts in Slovakia in the breeding seasons 2001 and 2002. Birds that failed to acquire a territory or a partner were not included. Each nest that contained at least one egg or nestling was counted as active. Stonechat females lay one egg per day, thus the date of clutch initiation could be easily determined when a nest was found during laying. For each population, the mean duration of the incubation period was calculated from nests of which information from laying to hatching was available. If full clutches were discovered during the incubation stage, the date of clutch initiation was inferred from the mean interval between the onset of laying and hatching for the given clutch size in the population. If nests were discovered during the nestling stage, the nestlings' body mass was used to age the birds and the date of clutch initiation was inferred from the mean interval between the onset of laying and hatching for the given clutch size

in the population. Mean laying dates were calculated for the different breeding attempts in the two populations. I did not calculate fledging dates because fledging was influenced by our activities at the nest (we colour-banded nestlings at about the time of fledging).

The degree of overlap of breeding activities in the populations was calculated as a 'nesting synchrony index' (*SI*), analogous to the method used by Kempenaers (1993) to describe the synchrony of female fertility in a population. The synchrony index for nest *n* depends on the number of other nests *a* that are active at the same time. Hence, for each day t_n nest *n* is active, the number of other active nests a_i is summed up and divided by the maximum number of other active nests in that period $t_n * a$. The population synchrony index *SI* is the mean synchrony index of all nests ($n_1+n_2+...n_i = A$) in the population:

$$SI = \frac{1}{A} \sum_{n=1}^{A} \left[\frac{\sum_{i=1}^{t_n} a_i}{t_n * a} \right]$$

A synchrony index of 0.0 indicates no overlap of breeding activities, whereas an index of 1.0 indicates full synchrony in the population.

5.3.3 Analysis of fledging success

For the comparison of fledging success between breeding attempts and populations, I calculated the proportions of eggs that fledged, or failed to do so due to infertility, embryonic death and hatching failures, predation, or other reasons. The latter include the desertion of nests due to adverse weather conditions or due to predation attempts on the parents at the nest site, and the destruction of nests by cattle or sheep. Eggs that did not hatch were candled with a torch to check for embryonic development, indicated by the presence of a network of blood vessels or an embryo. Ten eggs that failed to hatch in Kazakhstan could not be checked for embryonic development in that way. These cases were included in the

'other mortality' group. Predation on single eggs was extremely rare (2 occasions), usually the whole clutch was depredated. Hence, eggs that disappeared from the nest at the time of hatching were considered as hatching failures. The small beaks of stonechats do not allow them to remove intact eggs from the nest. However eggs that have been pierced by the hatchling can be handled, and stonechats remove young that died during hatching together with the egg shells of their hatched siblings. The removed eggs are deposited distantly from the nest and are therefore seldom found in the field. In the captive stonechats that breed at our institute, however, the remains of young that died during hatching can be found in the corners of the aviaries.

For a comparison of the breeding performances of Siberian and European stonechats I generated seasonal profiles of fledgling production (*Fig. 5.8.*). This was done by calculating the cumulative mass of the clutches produced by each pair for each day in the breeding cycle (2.0 g for each egg; for each chick the average mass at a given age; data from postnatal growth curves of nestlings of the two populations, see Chapter 8 of this thesis). The offspring mass produced was than averaged for all pairs and - to make the data mass-independent and therefore comparable between populations - divided by the mean chick mass at the age of 20 days (when fledgling mass had reached a stable level).

5.3.4 Statistical analysis

The data on clutch sizes and offspring numbers were not normally distributed and therefore nonparametric statistical tests were applied. I used Mann-Whitney-U tests when comparing two groups, and Kruskal-Wallis tests with Dunn's post-hoc tests when comparing more than two groups. Data relations were explored with Spearman's rank-order correlations. Percentage data were compared with G-tests with William's correction for small sample sizes. The statistical tests were carried out with SPSS 12.1 (SPSS Inc., USA) and SsS 1.1 (Rubisoft Software GmBH, Germany). The synchrony indices were compared with t-tests, p-values were Bonferroni-adjusted for multiple

testing. All data distributions are reported as means ± standard deviations.

5.4   Results

5.4.1   Reproductive timing

The first birds arrived between 24 April and 1 May on the study site in Kazakhstan. The bulk of birds arrived about one to two weeks later. The first eggs were laid between 12 May and 15 May, mean laying date of first clutches was 22 May (± 5 days, n = 107). Thus, the majority of birds initiated a clutch within two to three weeks after arrival. About 80% of the breeding pairs had active nests in early June, when the breeding activity in Kazakhstan peaked (*Fig. 5.1.*). Siberian stonechats in Kazakhstan produced one clutch per season, however lost clutches were often replaced. Replacements were initiated on average 7.6 days (± 3.6 days, n = 9) after a clutch was lost (*Fig. 5.2.*). Initiation dates of replacement clutches ranged from 7 June to 2 July with a mean of 18 June (± 8 days, n = 24).

In Slovakia the first stonechats arrived around 10 March and most birds arrived within the next two to three weeks. European stonechats in Slovakia had active nests from the beginning of April until August (*Fig. 5.1.*). Earliest laying occurred 4 April in 2002 and 10 April in 2001, mean laying date of first clutches was 17 April (± 7 days, n = 47). Most European stonechats in Slovakia initiated their first clutch within three to four weeks after arrival. Subsequently, they relaid after successful attempts or replaced lost clutches up to three times per season. Replacement of lost clutches occurred on average 7.2 days (± 1.5 days, n = 5) after nest loss, relaying after a successful breeding attempt occurred 18.5 days (± 8.4 days, n = 17) after fledging of the previous clutch (*Fig. 5.2.*). Successful breeders therefore initiated a new clutch every 50.9 ± 8.0 days. Egg laying by the females occurred while the fledged

young of the previous clutch were still cared for by their fathers ("telescoping" of clutches). The mean number of breeding attempts per pair in the breeding season 2002 was 2.09 (± 0.51, n = 23). Second clutches were initiated on average on 2 June (± 19 days, n = 21), third clutches on 2 July (± 10 days, n = 4).
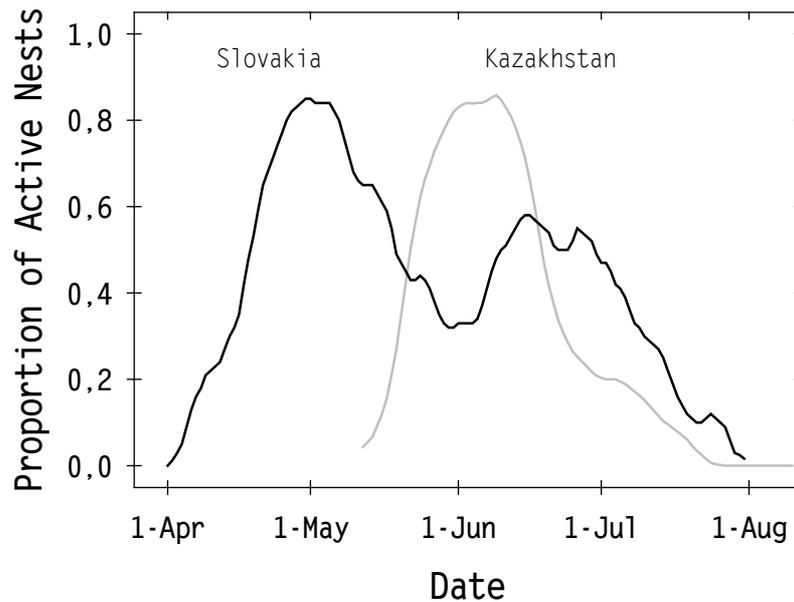

Fig. 5.1. The breeding activities of Siberian and European stonechats in Kazakhstan and Slovakia, plotted as the proportion of nests that contain either eggs or hatched young. Note that parenting behaviours continue after the young have left the nest for about 20 days until the young become fully independent. Shown are 5-day moving averages of 114 Kazakh breeding pairs from 1999 to 2001 and of 23 Slovak breeding pairs in 2002.

Due to the shorter period of reproductive activities, breeding was much more synchronised in Kazakhstan (*Table 5.1.*). Siberian stonechats have higher breeding synchrony indices (*SI*) for the whole reproductive period, but also when only the first breeding attempts in the two populations are compared. Furthermore, while the synchrony of replacement clutches in Kazakhstan is in the order of that of first clutches, the synchrony of second and third broods in Slovakia decreases (*Table 5.1.*).
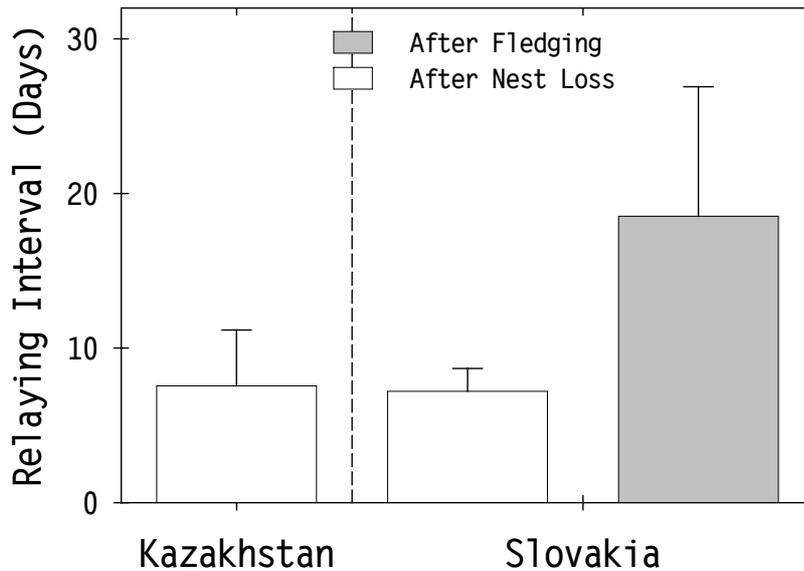
Fig. 5.2. The time interval between nest loss or the fledging of a successful clutch and the initiation of a new clutch in Siberian and European stonechats (means ± SD). Replacements of lost clutches occurs after a similar time period in both populations. Note that in the Slovak Nest Loss group, two outliers of 29 and 51 days were omitted because intermediate unsuccessful breeding attempts cannot be rouled out.

Table 5.1. The synchrony indices (*SI*) for the nesting activities of Siberian and European stonechats. A *SI*-value of 0.00 indicates no, a *SI*-value of 1.00 full overlap. The *SI* of all breeding attempts and first clutches only are compared with Mann-Whitney-U tests.

Synchrony Index (SI)	All Attempts			First Broods			Replacements / Second Broods			Third Broods		
	mean	SD	n	mean	SD	n	mean	SD	n	mean	SD	n
Kazakhstan	0.57	0.17	113	0.76	0.10	102	0.70	0,07	23			
Slovakia	0.33	0.16	72	0.62	0.12	47	0.34	0.13	21	0.49	0.17	4
U	1110.0			655.0								
p	< 0.001			< 0.001								

5.4.2 Clutch size

Taken all breeding attempts together, Siberian stonechats in Kazakhstan laid significantly larger clutches (5.90 ± 0.73 eggs, n = 136) than European stonechats in Slovakia (5.40 ± 0.77 eggs, n = 53)(Mann-Whitney-U test, *U = 2323.0, p < 0.001, Fig. 5.3.*). In both populations clutch sizes differed in consecutive breeding attempts (*Fig. 5.4.*). In

Kazakhstan, first clutches were significantly larger than replacement clutches (*first*: 6.00 ± 0.66, n = 120; *replacement*: 5.21 ± 0.80; Mann-Whitney-U test: *U = 383.0, p < 0.001*). In Slovakia, first clutches were significantly larger than second clutches, and third clutches were larger than first and second clutches, however the sample size of third clutches is low and the difference is not significant (*first*: 5.58 ± 0.55, n = 36; *second*: 4.77 ± 0.93, n = 13; *third*: 5.75 ± 0.96, n = 4; Kruskal-Wallis test: *H = 9.80, p < 0.01*). Accordingly, there is a significant correlation between clutch size and laying date in Kazakhstan (Spearman's rank-correlation; first and replacement clutches: $r_s = -0.33, p < 0.001$), whereas in Slovakia the correlation is only significant when the third clutches are excluded (*first* and *second* only: $r_s = -0.31, p < 0.05$; all clutches: $r_s = -0.23, p = 0.10$)(*Fig. 5.4.*).
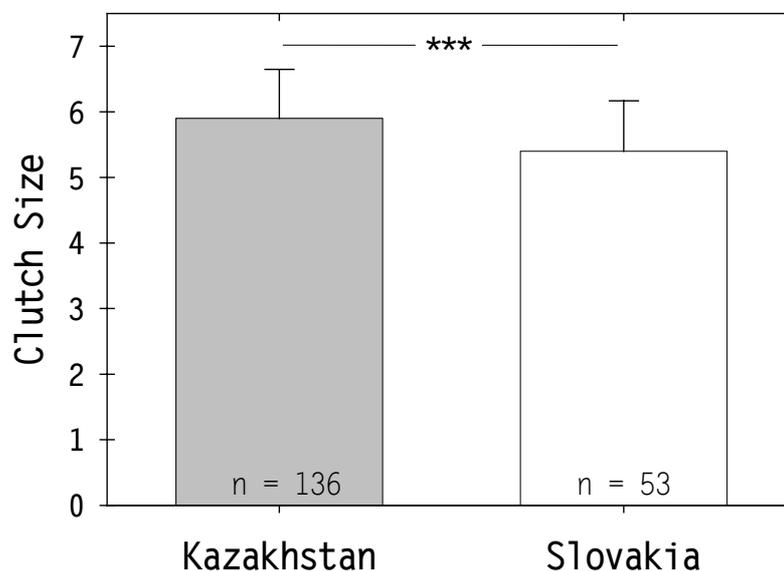
Fig. 5.3. The mean clutch size (+SD) of all breeding attempts in Siberian and European stonechats. Siberian stonechats lay significantly larger clutches.
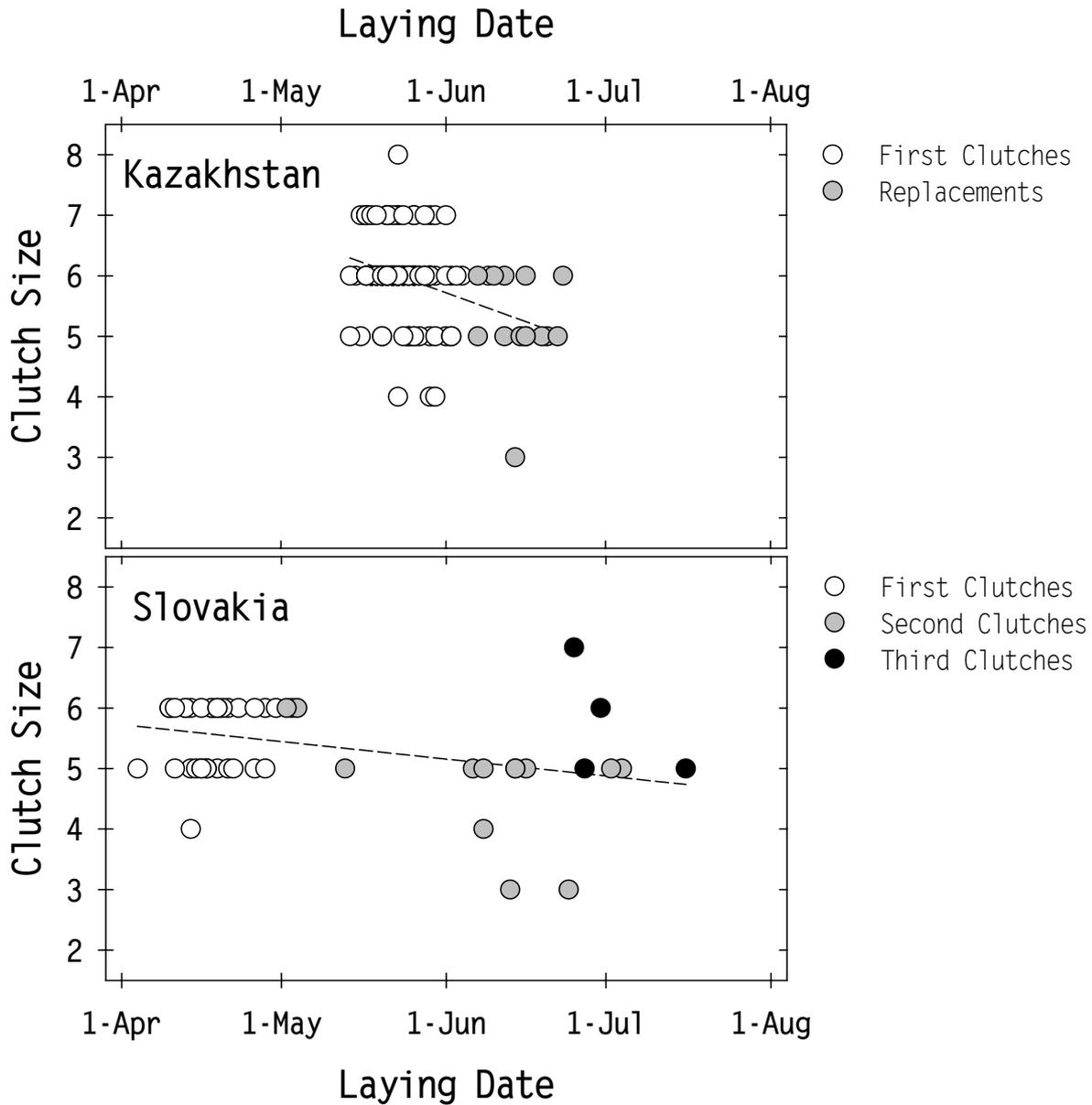
Fig. 5.4. The relationship between clutch size and laying dates in Siberian and European stonechats.

5.4.3 Fledging success

There was a significantly higher probability that an egg of a Siberian stonechat in Kazakhstan survives until fledging than a European stonechat egg in Slovakia (G-test: *df = 1, G = 22.69, p < 0.001*)(*Fig. 5.5.*). Whereas the rates of embryonic development and of hatching failures were similar between the two populations (but note that predation removed eggs of both categories prematurely), the likelihood of mortality through

predation of eggs or nestlings was much higher in Slovakia (*Fig. 5.5.*). In Kazakhstan fledging probability decreased somewhat between first clutches and replacements, however this difference is not significant (G-test: *df = 1, G = 0.27, p = 0.61*)(*Fig. 5.6.*). In Slovakia, first clutches had a much higher likelihood of producing fledglings than second or third clutches (G-test: *df = 1, G = 13.42, p < 0.001*)(*Fig. 5.6.*). Predation was much higher during second and third breeding attempts. A high proportion of eggs of Slovak third clutches failed to hatch, however sample size in this group is low (three nests, containing 0, 2, and 3 hatching failures, one nest depredated during the egg stage). As a result of the seasonal differences in clutch sizes and survival probabilities until fledging, the number of fledglings produced per clutch decreased with laying date in both populations, however these results are not significant (Spearman's rank correlation; Kazakhstan: *rs = -0.14, p = 0.11*; Slovakia: *rs = -0.16, p = 0.21*) (*Fig. 5.7.*).
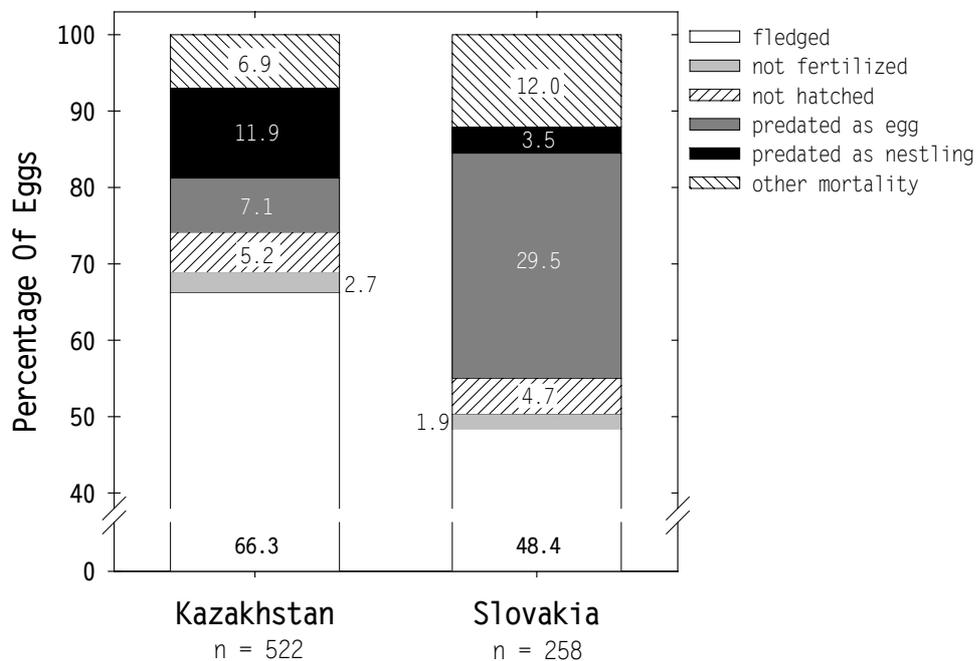

Fig. 5.5. The percentage of eggs of Siberian and European stonechats that either survives to fledging or fails due to sterility, hatching failures, egg and nestling predation, or other reasons.
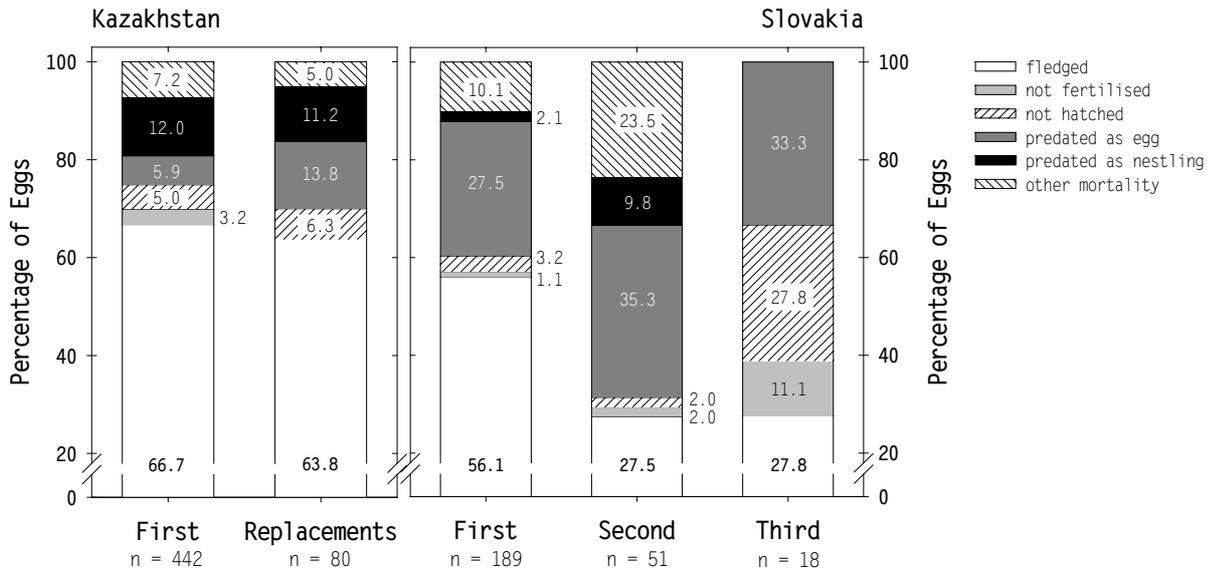
Fig. 5.6. Fledging and mortality rates in consecutive breeding attempts of Siberian and European stonechats.

How do the different measures of clutch size, number of broods, and fledging success combine into annual reproductive output? *Fig. 5.8.* shows cumulative seasonal profiles of the fledgling production in the Kazakh and the Slovak population. The Siberian stonechats produced the majority of their offspring in a relatively short period of time. On average, each breeding pair produced 5.2 fledglings in the year 1999 and 4.3 fledglings in the year 2000. By the beginning of August 2002, a European stonechat pair had produced on average 6.9 fledglings.

5.5   Discussion

5.5.1   Seasonal patterns of reproductive activities

The length of the breeding season decreases with increasing latitude (Baker 1938, Murton & Westwood 1977). However, also at similar latitudes different climatic regimes affect the time available for reproduction. The climate in Kazakhstan is strongly continental, with a long strong winter and a relatively short hot and dry summer, when compared to central European Slovakia. Hence, while stonechats arrive in Slovakia already in

March and may not finish their reproductive activities (post-fledging care for young of the last clutch) before late August, stonechats in northern Kazakhstan arrive in late April or early May and finish breeding in most cases in mid July, while birds that have lost their clutches may proceed until mid August. Accordingly, the Siberian stonechats in northern Kazakhstan raise only one clutch per season, while European stonechats in Slovakia undertake up to three breeding attempts per season.
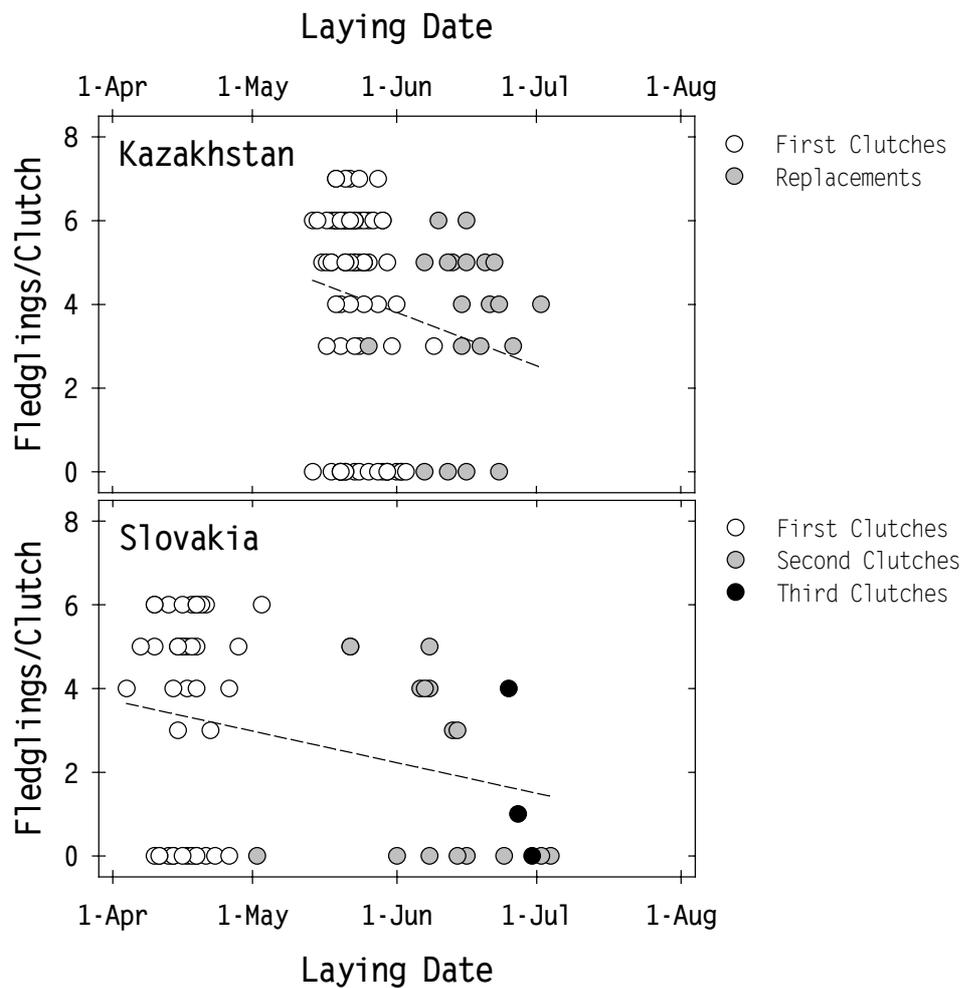
**Fig. 5.7.** The number of fledglings produced per breeding attempt decreases with laying date in Siberian and European stonechats.

Within my Kazakh stonechat population reproduction starts within a shorter interval after arrival and the breeding activities are more synchronised than in the eastern European population. A high breeding synchrony is the result of a narrow time window with optimal breeding

conditions and, if these optimal conditions are missed, high costs in terms of reproductive success. The synchrony of the first breeding attempts is higher in Kazakhstan than in Slovakia, and this suggests that the environmental conditions in Central Asia, besides limiting the number of breeding opportunities, also set a narrower window for the optimal laying date then in eastern Europe. Synchrony remains high in the Kazakh replacement clutches. While this is affected by the temporal pattern of nest loss in the population, it also shows that the time period during which the production of a replacement clutch pays off is short. Some of the costs that prevent breeding too late in Kazakhstan will be discussed in Chapter 7 of this thesis.

In the eastern European stonechats, breeding synchrony is highest for the first breeding attempt. The second and third breeding attempts are more desynchronised because nesting success or failure determine the timing of renesting. The European stonechats initiate a new clutch after nest loss as fast as do the Siberian stonechats, and probably at the fastest rate possible. This can be expected if it is assumed that birds try to maximise their reproductive output in a situation where climatic conditions become steadily less favourable for the raising of offspring.
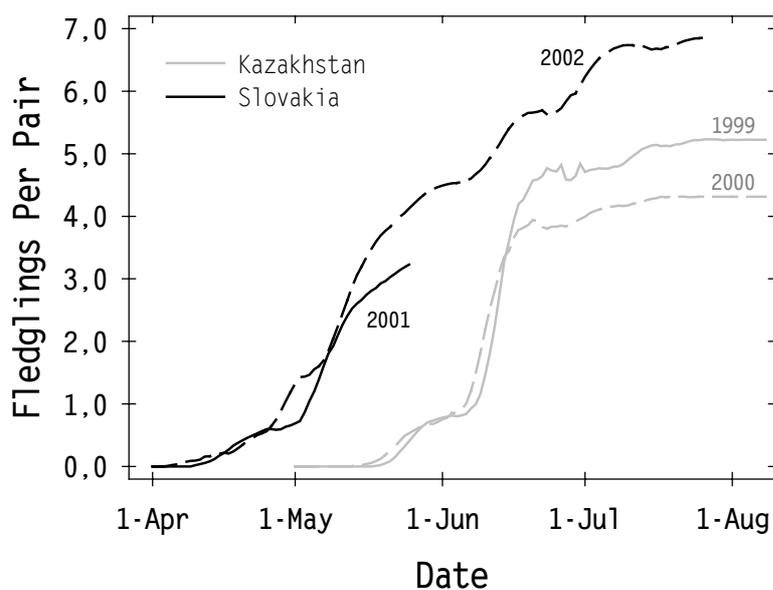

Fig. 5.8. The seasonal profiles of fledgling production in Siberian and European stonechats.

The rigid reproductive time-frame in Kazakhstan, together with a seeming constraint on too early arrival in the Siberian stonechats (see Chapter 3 of this thesis), results in a pre-breeding period - during which territory and mate acquisition have to be achieved - which is effectively about one week shorter in Kazakhstan than in Slowakia. Hence, because the costs of failing are higher, the level of intraspecific competition over territories and mates may be higher in the Siberian than in the European stonechats. On the other hand, because time and energy should be put into reproduction and not wasted in lengthy agonistic encounters, selection may favour optimisation rather than escalation: rapid social stabilisation and the amelioration of territorial conflicts by dear-enemy effects (Fisher 1954) would then lead to decreasing levels of intraspecific competition. Furthermore, a high degree of breeding synchrony may decrease intraspecific competition, because mates have to be less intensely guarded as the time available for seeking out extra-pair copulations is short (Birkhead & Biggins 1987, Saino et al. 1999, Thusius et al. 2001). The causality of the relationship between breeding synchrony and the rate of extra-pair fertilisations is, however, under debate. Some authors advocate the view that high breeding synchrony *increases* the likelihood of extra-pair fertilisations because females can choose between a higher number of extra-pair mates (Stutchbury & Morton 1995, Stutchbury 1998a, b), while other studies do not find any connection between the two phenomena (Dunn et al. 1994, Westneat & Sherman 1997, Weatherhead & Yezerinac 1998, Westneat & Gray 1998, Arlt et al. 2004).

I do not have enough quantitative data to compare the interspecific competitive behaviour in the Kazakh and Slovak stonechat populations. However, my oberservations suggest that the levels of song activity and territorial disputes were lower in the Siberian than in the European stonechats. This view is backed up by endocrinological data: the levels of circulating androgens in males and females, which are related to the levels of intraspecific competition in a reproductive context (Wingfield et al.

1987, Wingfield 1990, Wingfield et al. 1990), are lower in the Kazakh population (see Chapter 6 of this thesis).

5.5.2 Seasonal patterns of reproductive investment and reproductive output

Taken all breeding attempts together, Siberian stonechats lay larger clutches than European stonechats. Siberian stonechats seem to invest more into a given reproductive bout, probably to increase life-time reproductive success in the light of limited breeding opportunities (Williams 1966, Stearns 1992). We can therefore expect higher reproductive investment also in the later parenting stages. Siberian stonechats show indeed a much higher degree of nest defence, when their nest is approached by a human investigator, as was done regularly to measure the postnatal development of the chicks (see Chapter 8 of this thesis). We did not quantify these reactions, because they were probably confounded by systematic differences in the experiences of the birds with humans. The stonechats in Kazakhstan generally had lower flight distances than the Slovak stonechats an this may be due to different exposure to human persecutions. Both in Slovakia and northern Kazakhstan small passerines are not hunted by humans, this practice is however wide-spread in the Mediterranean wintering areas of the European stonechats, while it is probably less common on the wintering grounds of the Siberian stonechats (Urquhart 2002).

The Kazakh stonechats do not only produce larger clutches, they also manage to raise more fledglings per clutch than the Slovak stonechats. This is mainly due to lower predation rates. In Slovakia, more nests were directly predated, and more nests were given up in response to predation attempts on the incubating parent. Nest predation is negatively related to breeding synchrony in red-winged Blackbirds, *Agelaius phoeniceus* (Westneat 1992). A similar effect may explain the differences in nest predation rates between the different breeding attempts in Kazakhstan and Slowakia (*Fig. 5.9.*). This pattern could, however, be explained by other factors and breeding synchrony and nest predation rates may not be causally linked.

Predator activity may increase in the course of the breeding season independently of the synchrony of stonechat nesting. Different predation rates in the two populations could be the result of different principal nest predators in the two populations (see Weatherhead & Sommerer 2001). While in Kazakhstan more nests were lost during the nestling stage, nest predation during the egg stage was predominant in Slovakia, and this may be indicative of different kinds of nest predators.
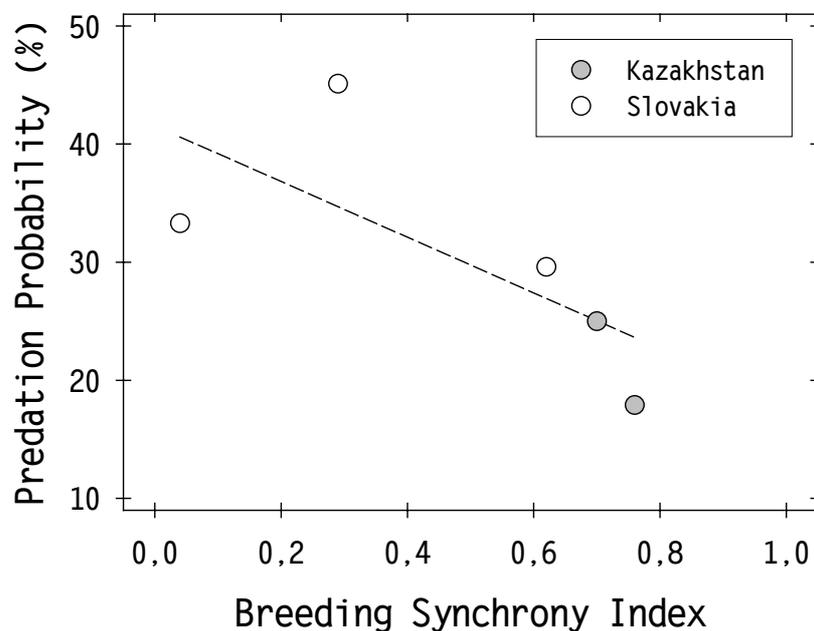
Fig. 5.9. The relationship between the predation probability per egg for the different breeding attempts and the breeding synchrony indices of these breeding attempts (data compiled from *Table 5.1.* and *Fig. 5.6.*).

In Kazakhstan, clutch size decreases in the course of the breeding season. In Slovakia, there is a similar trend, however the clutch sizes of third breeding attempts increases again. While this could simply be the effect of the small sample size in this group, it could also indicate that only high-quality parents can afford to produce three clutches per season. Alternatively, if the previous two breeding attempts failed, clutch sizes could be increased in the last possible attempt as a form of 'terminal investment' (Schaffer 1974, Gustafsson et al. 1994, Cichon 2001).

Clutch size is thought to be ultimately regulated by a trade-off of the survival probabilities of the offspring against the increase of the parents' mortality induced by their reproductive investment (Charnov & Krebs 1974). Therefore decreasing offspring survival should result in decreasing clutch sizes. In both populations, clutch size decreases in the course of the breeding season (with the exception of the third clutches in the European stonechats). And in fact, the percentage of eggs that produce a fledgling decreases as well in both populations in consecutive breeding attempts (although the decrease in Kazakhstan is only small and not significant). I could not acquire data on post-fledging survival in my stonechat populations. Many other studies in passerines, however, find a decrease in post-fledging survival with laying date (e.g. Svensson 1997, Verboven & Visser 1998, Naef-Daenzer et al. 2001), and it is likely that this applies also to the stonechats in Kazakhstan and Slovakia.

In many stonechat populations with three annual clutches located in western Europe or on the British Islands the second brood is the one with the largest average clutch size (compiled in Cramp 1988, Glutz von Blotzheim & Bauer 1988, Urquhart 2002). I have only data on one full breeding season in Slovakia, and it might well be that a more long-term study would reveal a similar annual pattern in clutch size than in the studies of the more westerly populations. It would be interesting to know more about the relationship of seasonal patterns of clutch size and offspring survival in the different locations.

There is no difference in the frequency of unfertilised eggs or eggs that are fertilised but fail to hatch in the two populations. Rogacheva (1992) reports a slightly larger number of 5% of unfertile eggs, however it is not clear if she includes hatching failures in that number. This is interesting, because it has been speculated that the synchrony of the partners may contribute to the hatchability of a clutch. In captive stonechats mixed pairs of European and Siberian stonechats produce less offspring. This has been attributed to a reduced synchrony in the reproductive physiology and behaviour in the mixed subspecies pairs (Helm

2002). Apparently the shorter span between arrival and reproduction in the Kazakh stonechats does not affect the synchrony between the pair partners. This is in line with the result that testis sizes normalised for the onset of reproduction in Siberian and European stonechat males do not differ (see Chapter 4 of this thesis).

As a result of the larger number in broods in Slovakia at the one hand, larger clutches and larger fledging success in Kazakhstan on the other hand, the annual reproductive output (in terms of fledgling numbers), is smaller in the Siberian stonechats, but only by about 20%. How these differences in annual reproductive output translate into differences of annual reproductive success cannot be determined because I do not know the proportions of fledglings that make it into the respective breeding populations. If, however, as in other passerines, reproductive success in both stonechat populations decreases in the course of the season, selection on early arrival on the breeding grounds and an early onset of reproduction would result. Spring temperatures have increased over the last decades in both locations, whereas autumn temperatures have not changed to the same degree (cf. Chapter 3, *Fig. 3.8.*). It has been shown recently that eastern European stonechats respond to large scale climatic changes and advance arrival in warm springs (Hubalek 2003, 2004). The same is probably true for the Siberian stonechats. It is therefore to be expected that, if climatic change goes on as predicted, the reproductive windows will change for both populations. This will affect migratory and reproductive schedules and the expression of the underlying physiological mechanisms.

5.6   A brief note: facultative polygyny in the Siberian stonechat

Johnson (1961) described the occurance of facultative polygyny in European stonechats in Britain. In the year 2000 I witnessed similar pair constellations in my Kazakh population, possibly due to a skew in the breeding sex ratio towards the females in that season. Four of 45 breeding

males (9%) produced an additional clutch with one secondary female each. All secondary nest sites were located on the boundaries of the polygynous males' territories. Males that engaged in polygynous matings may have been of higher quality or may have held better territories than the average monogamous male. Primary nests of polygynous males were initiated earlier, had larger clutches, and produced more fledglings than the nests of monogamous males (*Table 5.2.*). Secondary clutches were initiated 9, 10, 22, and 29 days after the primary clutches. Thus in all cases the periods of male parental care (nestling and fledgling stages) overlapped in primary and secondary clutches. As in the European stonechats (Johnson 1961), the polygynous Siberian stonechat males fed young at both nest locations, and they showed nest defence behaviours in response to the observer's approach at both nest sites. How the males partitioned their parental care between the primary and secondary nests is not known.

Secondary females had to pay a cost in terms of reproductive success: secondary nests were initiated later, had smaller clutch sizes, and produced fewer fledglings than primary and monogamous clutches (*Table 5.2.*). Both, the potentially reduced paternal care and the later reproductive timing may have contributed to this reduction in reproductive success. Secondary females may have paid additional costs, due to a higher degree of overlap of reproduction and postnuptial moult, which potentially reduces survival (see Chapter 9 of this thesis).

Table 5.2. A comparison of laying dates, clutch sizes and number of fledglings of first clutches and polygynous primary and secondary clutches in Kazakhstan in the breeding season 2000.

	Monogynous First Clutches (n = 40)	Polygynous Primary Clutches (n = 4)	Polygynous Secondary Clutches (n = 4)
Laying Date	23 May ± 5 days	19 May ± 3 days	6 June ± 12 days
Clutch Size	5.9 ± 0.6	6.25 ± 0.5	5.0 ± 1.4[A]
Fledglings	3.9 ± 2.7	5.5 ± 1.2	3.7 ± 0.6[B]

(A) clutch size known for two clutches
(B) fledgling number known for three clutches

5.7   References

Arlt, D., Hansson, B., Bensch, S., Von Schantz, T. & Hasselquist, D. (2004). Breeding synchrony does not affect extra-pair paternity in great reed warblers. *Behaviour* 141: 863-880.

Baker, J. R. (1938). The evolution of breeding seasons. *In* G. R. de Beer (Ed.), *Evolution: Assays on Aspects of Evolutionary Biology*, pp. 161-177. Oxford University Press, London.

Birkhead, T. R. & Biggins, J. D. (1987). Reproductive synchrony and extra-pair copulation in birds. *Ethology* 74: 320-334.

Bize, P., Roulin, A., Tella, J. L., Bersier, L.-F. & Richner, H. (2004). Additive effects of ectoparasites over reproductive attempts in the long-lived alpine swift. *Journal of Animal Ecology* 73: 1080-1088.

Boehning-Gaese, K., Halbe, B., Lemoine, N. & Oberrath, R. (2000). Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evolutionary Ecology Research* 2: 823-839.

Bonneaud, C., Mazuc, J., Gonzalez, G., Haussy, C., Chastel, O., Faivre, B. & Sorci, G. (2003). Assessing the cost of mounting an immune response. *American Naturalist* 161: 367-379.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., Enemar, A., Gustafsson, L., Ivankina, E. V., Jarvinen, A., Metcalfe, N. B., Nyholm, N. E. I., Potti, J., Ravussin, P. A., Sanz, J. J., Silverin, B., Slater, F. M., Sokolov, L. V., Torok, J., Winkel, W., Wright, J., Zang, H. & Visser, M. E. (2004). Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 271: 1657-1662.

Brinkhof, M. W. G., Cave, A. J., Hage, F. J. & Verhulst, S. (1993). Timing of reproduction and fledging success in the coot Fulica atra: Evidence for a causal relationship. *Journal of Animal Ecology* 62: 577-587.

Brown, C. R. & Brown, M. B. (2000). Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behavioral Ecology and Sociobiology* 47: 339-345.

Charnov, E. L. & Krebs, J. R. (1974). On clutch size and fitness. *Ibis* 116: 217-219.

Christians, J. K., Evanson, M. & Aiken, J. J. (2001). Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. *Journal of Animal Ecology* 70: 1080-1087.

Cichon, M. (2001). Diversity of age-specific reproductive rates may result from ageing and optimal resource allocation. *Journal of Evolutionary Biology* 14: 180-185.

Cotton, P. A. (2003). Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences of the United States of America* 100: 12219-12222.

Cramp, S. (1988). *Handbook of the birds of Europe, the Middle East and North Africa*, Vol. 5. Oxford University Press, Oxford.

Cresswell, W. & McCleery, R. (2003). How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology* 72: 356-366.

Crick, H. Q. P., Dudley, C., Glue, D. E. & Thompson, D. L. (1997). UK birds are laying eggs earlier. *Nature* 388: 526.

Daan, S., Dijkstra, C., Drent, R. & Meijer, T. (1986). Food supply and the annual timing of avian reproduction. *In* H. Ouellet (Ed.), *Acta XIX Congressus Internationalis Ornithologici*, pp. 391-407. University of Ottawa Press, Ottawa.

De Neve, L., Soler, J. J., Soler, M. & Perez-Contreras, T. (2004). Differential maternal investment counteracts for late breeding in magpies *Pica pica*: an experimental study. *Journal of Avian Biology* 35: 237-245.

Drent, R. H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.

Dunn, P. O., Whittingham, L. A., Lifjeld, J. T., Robertson, R. J. & Boag, P. T. (1994). Effects of breeding density, synchrony, and experience on extrapair paternity in tree swallows. *Behavioral Ecology* 5: 123-129.

Dunn, P. O. & Winkler, D. W. (1999). Climate change has affected the breeding date of tree swallows throughout North America. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 266: 2487-2490.

Fisher, J. (1954). Evolution and bird sociality. *In* J. Huxley, A. C. Hardy & E. B. Ford (Eds.), *Evolution as a process*. Allan & Unwin, London.

Fitze, P. S., Tschirren, B. & Richner, H. (2004). Life history and fitness consequences of ectoparasites. *Journal of Animal Ecology* 73: 216-226.

Forchhammer, M. C., Post, E. & Stenseth, N. C. (1998). Breeding phenology and climate. *Nature* 391: 29-30.

Forslund, P. & Pärt, T. (1995). Age and reproduction in birds: hypothesis and tests. *Trends in Ecology and Evolution* 10: 374-378.

Forstmeier, W. (2002). Benefits of early arrival at breeding grounds vary between males. *Journal of Animal Ecology* 71: 1-9.

Francis, C. M. & Cooke, F. (1986). Differential timing of spring migration in wood warblers, *Parulinae*. *Auk* 103: 548-556.

Geslin, T., Questiau, S. & Eybert, M.-C. (2004). Age-related improvement of reproductive success in bluethroats *Luscinia svecica*. *Bird Study* 51: 178-184.

Glutz von Blotzheim, U. & Bauer, K. M. (1988). *Handbuch der Vögel Mitteleuropas*, Vol. 11. Aula-Verlag, Wiesbaden.

Gustafsson, L., Nordling, D., Andersson, M. S., Sheldon, B. C. & Qvarnstrom, A. (1994). Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philosophical Transactions of the Royal Society of London B - Biological Sciences* 346: 323-331.

Hansson, B., Bensch, S. & Hasselquist, D. (2000). The quality and the timing hypotheses evaluated using data on great reed warblers. *Oikos* 90: 575-581.

Hasselquist, D. (1998). Polygyny in great reed warblers: A long-term study of factors contributing to male fitness. *Ecology* 79: 2376-2390.

Helm, B. (2002). Seasonal timing in different environments: comparative studies in Stonechats. Ph.D. thesis, Ludwig-Maximilians-Universität München, Germany.

Hipfner, J. M., Gaston, A. J., Martin, D. L. & Jones, I. L. (1999). Seasonal declines in replacement egg-layings in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? *Journal of Animal Ecology* 68: 988-998.

Hubalek, Z. (2003). Spring migration of birds in relation to North Atlantic Oscillation. *Folia Zoologica* 52: 287-289.

Hubalek, Z. (2004). Global weather variability affects avian phenology: a long-term analysis, 1881-2001. *Folia Zoologica* 53: 227-236.

Hüppop, O. & Hüppop, K. (2003). North Atlantic Oscillation and timing of spring migration in birds. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 233-240.

Jenni, L. & Kéry, M. (2003). Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 1467-1471.

Johnson, E. D. (1961). The pair relationship and polygyny in the Stonechat. *British Birds* 54: 213-225.

Kempenaers, B. (1993). The use of a breeding synchrony index. *Ornis Scandinavica* 24: 84.

Kissner, K. J., Weatherhead, P. J. & Francis, C. M. (2003). Sexual size dimorphism and timing of spring migration in birds. *Journal of Evolutionary Biology* 16: 154-162.

Kokko, H. (1999). Competition for early arrival in migratory birds. *Journal of Animal Ecology* 68: 940-950.

Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds*. Methuen, London.

Lepage, D., Desrochers, A. & Gauthier, G. (1999). Seasonal decline of growth and fledging success in snow geese Anser caerulescens: an effect of date or parental quality? *Journal of Avian Biology* 30: 72-78.

Lozano, G. A., Perreault, S. & Lemon, R. E. (1996). Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. *Journal of Avian Biology* 27: 164-170.

Marra, P. P. (2000). The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behavioral Ecology* 11: 299-308.

Marra, P. P., Hobson, K. A. & Holmes, R. T. (1998). Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science* 282: 1884-1886.

Marra, P. P. & Holberton, R. L. (1998). Corticosterone levels as indicators of habitat quality effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116: 284-292.

Marzal, A., Lope, F. d., Navarro, C. & Moller, A. P. (2005). Malarial parasites decrease reproductive success: an experimental study in a passerine bird. *Oecologia* 142: 541-545.

Mauck, R. A., Huntington, C. E. & Grubb, T. C. (2004). Age-specific reproductive success: Evidence for the selection hypothesis. *Evolution* 58: 880-885.

McCleery, R. H. & Perrins, C. M. (1998). Temperature and egg laying trends. *Nature* 391: 30-31.

Moller, A. P. (1994). Phenotype-dependent arrival time and its consequences in a migratory bird. *Behavioral Ecology and Sociobiology* 35: 115-122.

Moller, A. P. (2002). North Atlantic Oscillation (NAO) effects of climate on the relative importance of first and second clutches in a migratory passerine bird. *Journal of Animal Ecology* 71: 201-210.

Morbey, Y. E. & Ydenberg, R. C. (2001). Protandrous arrival timing to breeding areas: a review. *Ecology Letters* 4: 663-673.

Murton, R. K. & Westwood, N. J. (1977). *Avian Breeding Cycles*. Clarendon Press, Oxford.

Naef-Daenzer, B., Widmer, F. & Nuber, M. (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70: 730-738.

Newton, I. (1989). *Lifetime reproduction in birds*. Academic Press, London.

Ninni, P., de Lope, F., Saino, N., Haussy, C. & Moller, A. P. (2004). Antioxidants and condition-dependence of arrival date in a migratory passerine. *Oikos* 105: 55-64.

Norris, D. R., Marra, P. P., Kyser, T. K., Sherry, T. W. & Ratcliffe, L. M. (2004). Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proceedings of the Royal Society of London*. *Series B, Biological Sciences* 271: 59-64.

Perrins, C. M. (1970). The timing of birds breeding seasons. *Ibis* 112: 242-255.

Potti, J. (1998). Arrival time from spring migration in male Pied Flycatchers: Individual consistency and familial resemblance. *Condor* 100: 702-708.

Price, T., Kirkpatrick, M. & Arnold, S. J. (1988). Directional selection and the evolution of breeding date in birds. *Science* 240: 798-799.

Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contrib. Zool.* 9: 1-48.

Rogacheva, H. (1992). The birds of central Siberia, pp. 503-507. Husum Druck- und Verlagsgesellschaft, Husum.

Rowe, L., Ludwig, D. & Schluter, D. (1994). Time, condition, and the seasonal decline of avian clutch size. *American Naturalist* 143: 698-772.

Saino, N., Primmer, C. R., Ellegren, H. & Moller, A. P. (1999). Breeding synchrony and paternity in the barn swallow (Hirundo rustica). *Behavioral Ecology and Sociobiology* 45: 211-218.

Sanz, J. J. (1999). Seasonal variation in reproductive success and post-nuptial moult of blue tits in southern Europe: An experimental study. *Oecologia* 121: 377-382.

Schaffer, W. M. (1974). Optimal reproductive effort in fluctuating environments. *American Naturalist* 108: 783-790.

Sillett, T. S., Rodenhouse, N. L. & Holmes, R. T. (2004). Experimentally reducing neighbor density affects reproduction and behavior of a migratory songbird. *Ecology* 85: 2467-2477.

Skutch, A. F. (1967). Adaptive limitation of the reproductive rate of birds. *Ibis* 109: 579-599.

Smith, R. J. & Moore, F. R. (2005). Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. *Behavioral Ecology and Sociobiology* 57: 231-239.

Sockman, K. W., Williams, T. D., Dawson, A. & Ball, G. F. (2004). Prior experience with photostimulation enhances photo-induced reproductive development in female European starlings: A possible basis for the age-related increase in avian reproductive performance. *Biology of Reproduction* 71: 979-986.

Stearns, S. C. (1992). *The Evolution of Life-Histories*. Oxford University Press, Oxford.

Stevenson, I. R. & Bryant, D. M. (2000). Avian phenology: climate change and constraints on breeding. *Nature* 406: 366-367.

Stutchbury, B. J. & Morton, E. S. (1995). The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* 132: 675-690.

Stutchbury, B. J. M. (1998a). Breeding synchrony best explains variation in extra-pair mating system among avian species. *Behavioral Ecology and Sociobiology* 43: 221-222.

Stutchbury, B. J. M. (1998b). Female mate choice of extra-pair males: breeding synchrony is important. *Behavioral Ecology and Sociobiology* 43: 213-215.

Sutherland, W. (1998). Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology* 29: 441-446.

Svensson, E. (1997). Natural selection on avian breeding time: Causality, fecundity-dependent, and fecundity-independent selection. *Evolution* 51: 1276-1283.

Thusius, K. J., Dunn, P. O., Peterson, K. A. & Whittingham, L. A. (2001). Extrapair paternity is influenced by breeding synchrony and density in the common yellowthroat. *Behavioral Ecology* 12: 633-639.

Urquhart, E. (2002). *Stonechats: A guide to the genus Saxicola*. Christopher Helm, London.

Vähätalo, A. V., Rainio, K., Lehikoinen, A. & Lehikoinen, E. (2004). Spring arrival of birds depends on the North Atlantic Oscillation. *Journal of Avian Biology* 35: 210-216.

Verboven, N., Evans, N. P., D'Alba, L., Nager, R. G., Blount, J. D., Surai, P. F. & Monaghan, P. (2005). Intra-specific interactions influence egg composition in the lesser black-backed gull (*Larus fuscus*). *Behavioral Ecology and Sociobiology* 57: 357-365.

Verboven, N. & Verhulst, S. (1996). Seasonal variation in the incidence of double broods: The date hypothesis fits better than the quality hypothesis. *Journal of Animal Ecology* 65: 264-273.

Verboven, N. & Visser, M. E. (1998). Seasonal variation in local recruitment of great tits: The importance of being early. *Oikos* 81: 511-524.

Verhulst, S., Riedstra, B. & Wiersma, P. (2005). Brood size and immunity costs in zebra finches *Taeniopygia guttata*. *Journal of Avian Biology* 36: 22-30.

Verhulst, S., Vanbalen, J. H. & Tinbergen, J. M. (1995). Seasonal decline in reproductive success of the great tit - variation in time or quality. *Ecology* 76: 2392-2403.

Wardrop, S. L. & Ydenberg, R. C. (2003). Date and parental quality effects in the seasonal decline in reproductive performance of the Tree Swallow *Tachycineta bicolor*: interpreting results in light of potential experimental bias. *Ibis* 145: 439-447.

Weatherhead, P. J. & Sommerer, S. J. (2001). Breeding synchrony and nest predation in red-winged blackbirds. *Ecology* 82: 1632-1641.

Weatherhead, P. J. & Yezerinac, S. M. (1998). Breeding synchrony and extra-pair mating in birds. *Behavioral Ecology and Sociobiology* 43: 217-219.

Westneat, D. F. (1992). Nesting synchrony by female red-winged blackbirds: Effects on predation and breeding success. *Ecology* 73: 2284-2294.

Westneat, D. F. & Gray, E. M. (1998). Breeding synchrony and extrapair fertilizations in two populations of red-winged blackbirds. *Behavioral Ecology* 9: 456-464.

Westneat, D. F. & Sherman, P. W. (1997). Density and extra-pair fertilizations in birds: a comparative analysis. *Behavioral Ecology and Sociobiology* 41: 205-215.

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.

Wingfield, J. C. (1990). Interrelationships of Androgens, Aggression and Mating Systems. *In* M. Wada, S. Ishii & C. G. Scanes (Eds.), *Endocrinology of Birds: Molecular to Behavioral*, pp. 187-205. Japan Sci. Soc. Press / Springer-Verlag, Tokyo / Berlin.

Wingfield, J. C., Ball, G. F., Dufty, A. M., Hegner, R. E. & Ramenofsky, M. (1987). Testosterone and aggression in birds. *American Scientist* 75: 602-608.

Wingfield, J. C., Hegner, R. E., Dufty, J. A. M. & Ball, G. F. (1990). The "challenge-hypothesis": theoretical implications for patterns of testosterone secretion, mating systems and breeding strategies. *American Naturalist* 136: 829-846.

6 CIRCULATING GONADAL STEROIDS DURING THE BREEDING SEASON IN SIBERIAN AND EUROPEAN STONECHATS

6.1 Summary

Circulating androgen levels in Siberian and European stonechats show the seasonal patterns that have been found in other temperate breeders, with high levels during the territorial and low levels during the parental stages. Siberian stonechat males have lower T breeding baseline levels and lower T maximum levels than European stonechats. This result is discussed in the light of the *challenge hypothesis* which makes predictions on the effects of male-male competition and parental care on seasonal androgen profiles. The level of aggression in staged intraspecific encounters is high throughout the season in Siberian stonechats and therefore not coupled to circulating androgen profiles. Similar results have been achieved in a recently published study on European stonechats. It is unknown, however, how simulated territorial intrusions affect short-term fluctuations in androgen levels immediately after the encounter. Siberian stonechat males have a higher share of DHT in the total amount of circulating androgens. This may be due to different roles of the two androgens in the regulation of reproductive behaviour, and to different costs associated with high circulating levels of T and DHT. Circulating gonadal steroids in females of both populations are either low or do not vary markedly during the breeding season, the contribution of these hormones to the regulation of female reproductive behaviours remains unresolved.

6.2   Introduction

Male reproductive behaviours in the temperate zones are associated with high plasma levels of gonadal steriods (Murton & Westwood 1977, Wingfield & Farner 1980, Wingfield et al. 1990, Ketterson & Nolan 1992, Rost 1992). The relationship between reproductive behaviours and plasma androgen levels is, however, not as clear-cut as initially perceived. There exists high individual variation in plasma androgen levels in the time when males express the full repertoire of reproductive behaviours. This has led to the formulation of the *challenge hypothesis* which states that the seasonal pattern of androgen secretion is shaped by a trade-off between the beneficial effects of high androgen levels during male-male interactions, and their potential costs, e.g. in terms of reduced parental care (Wingfield 1990, Wingfield et al. 1990, Beletsky et al. 1995). This leads to a 'breeding baseline' of androgen levels (the minimum circulating androgen levels necessary for the expression of reproductive behaviours) which is coupled with temporary surges in response to social interactions. These transient rises in androgen levels facilitate appropriate social behaviours during subsequent encounters (Wingfield et al. 1990, Hirschenhauser et al. 2003, Smith et al. 2005).

The predictions of the *challenge hypothesis* have been tested experimentally. Many behavioral components of male reproduction, e.g. song, male-male aggression, or sexual displaying could be altered by either enhancing or removing the effects of androgens (Wingfield 1984, Wingfield et al. 1987, Beletsky et al. 1989, Schwabl & Kriner 1991, Ketterson & Nolan 1992, Canoine & Gwinner 2002). There were, however, also cases where aspects of male reproductive behaviours were insensitive to hormonal manipulations (Moore & Kranz 1983, Wingfield 1994b, Hunt et al. 1997). Experimentally elevated T levels decreased feeding activity in males of several species (Silverin 1980, Hegner & Wingfield 1987, Beletsky et al. 1995, Hunt et al. 1999, Stoehr & Hill 2000, Peters et al. 2002). In other species, however, T treatment failed to decrease paternal feeding rates (Lynn et al. 2002, Van Duyse et al. 2002, Lynn et al. 2005).

Despite these partially conflicting results some common features emerge from experimental and comparative studies: The *androgen responsiveness*, i.e. the difference between breeding baselines and elevated levels in response to social encounters is related to the intensity of male-male competition and the degree of parental care provided by the males (Wingfield et al. 1990, Hirschenhauser et al. 2003). An uncoupling of reproductive behaviour and circulating androgen levels is more likely in situations where the breeding seasons are very long (e.g. in the tropics: Wikelski et al. 1999a, 1999b, Hau et al. 2000, Goymann et al. 2004) or very short (e.g. in the arctic: Hunt et al. 1995, Hunt et al. 1997, Wingfield & Hunt 2002).

Siberian stonechats in Kazakhstan and European stonechats in Slovakia breed both in the temperate zones under comparable photoperiodic conditions (Chapter 2 of this thesis). However, the length of the environmental breeding window differs markedly between the two locations. While the Siberian stonechats breed only once during May and June, with replacement clutches occurring in July, the European stonechats breed from April to the beginning of September and can produce up to three full clutches during that period. As a consequence, breeding is much more synchronised in the Siberian than in the European population (Chapter 5 of this thesis). The *challenge hypothesis* predicts a longer period of elevated androgen levels in the European stonechats, because the breeding season and hence the period of increased male-male competition is longer in Slovakia. Furthermore, peak androgen levels may be higher in Kazakhstan, reflecting more intense competition in a condensed breeding season. A comparative study in tropical birds revealed a relationship between the length of the breeding season and peak androgen levels (Goymann et al. 2004).

In this chapter, I compare the seasonal patterns of androgen release (testosterone *T* and dihydrotestosterone *DHT*) into the plasma of male Siberian and European stonechats. I assess the intensity of one component of male reproductive behaviour, territorial aggression, in simulated territorial encounters at different phases of the breeding season of

Siberian stonechats. The results are discussed in relation to circulating androgen levels measured during these stages and compared with recently published data on territorial aggression during the breeding of European stonechats (Schwabl et al. 2005). I also report the secretion patterns of circulating estradiol E_2 in males and of all three gonadal steroids in the females of both populations.

6.3   Methods

6.3.1   Blood sampling

Stonechats were caught using mealworm-baited traps or mistnets. After capture (mean handling time 14.5 ± 10.6 minutes SD), a small blood sample (approx. 60 μl of plasma) was taken from the alar vein. Blood samples were collected into heparinised capillaries and centrifuged in the field. Plasma was stored on ice for up to four hours before it was transferred into liquid nitrogen. Before analysis, the samples were kept in liquid nitrogen and then at -70°C until they were assayed. The plasma concentrations of gonadal steroids were unrelated to handling time in both populations.

6.3.2   Simulated territorial intrusions

I tested the reaction of territorial males in Kazakhstan to simulated territorial intrusions by mounting a stuffed male stonechat in the centre of the territory. The response of the birds was subsequently recorded for 20 minutes. The aggressive response was scored as follows: *0* - no approach; *1* - bird approaches not closer than 5 meters; *2* - bird approaches not closer than 2 meters; *3* - bird approaches between 2 m and 0.3 meters; *4* - bird approaches closer than 0.3 meters and shows threat displays or flight attacks without touching the dummy; *5* - bird attacks the dummy with body contact. The same STI procedure was applied in the study on European stonechats that I use for comparison (Schwabl et al. 2005).

6.3.3   Hormone assays

Plasma concentrations of the sex steroids testosterone (T), dihydro-testosterone (DHT), and estradiol (E_2) were determined in radioimmunoassays, following the original protocol of Wingfield & Farner (Wikelski et al. 1999a, Hau et al. 2000, Wingfield & Hunt 2002, Goymann et al. 2004) with modifications from Fusani et al. (2000). In short, after adding tritiated hormone for extraction recoveries, steroids were extracted with dichloromethane and dried at 40°C under nitrogen. The samples were resuspended in ethyl acetate in isooctane and separated on celite columns (diatomaceous earth/ddH_2O for the water trap; diatomaceous earth/ethylene glycol and propylene glycol for the glycol phase). The steroid hormones were separated on the basis of their polarity with increasing concentrations of ethyl acetate in isooctane. The fractions were collected, dried at 40°C under nitrogen and redissolved in 0.1M phosphate buffer pH 7.0. Aliquots of each fraction were measured in a scintillation counter (Beckmann LS 6000) to estimate extraction efficiency. Samples were then measured in separate assays for each hormone. Hormone concentrations were determined against a standard curve of stock standard solutions serially diluted to concentrations ranging from 1.95 to 2000 pg/ml. Samples and standard curves were measured in duplicates. After adding tritium-labelled hormone (NEN PerkinElmer, Boston, USA: NET 553 (T), NET 453 (DHT), NET 517 (E_2)) and antiserum (Endocrine Sciences, Calabasas Hills, USA: T3-125 (T), DT3-351 (DHT), E26-47 (E_2)), samples were incubated over night at 4°C (except for DHT samples which were incubated at 25°C). Bound and free fractions were separated by absorption on dextran-coated charcoal and centrifugation. The supernatants were decanted into scintillation vials and the radioactivity measured in the scintillation counter.

A standard curve was generated and hormone concentration of the samples was calculated using ImmunoFit EIA/RIA Analysis 3.0, (Beckman Instruments Inc., USA). The lower detection limit of the assay was set at the first concentration in the standard curve outside of the 95% confidence interval of the zero standard. They were determined as 15.6 pg/ml for T,

31.3 pg/ml for DHT, and 7.8 pg/ml for E_2. Nondetectable concentrations were set to the concentration of the detection limit. The mean recoveries were 70% for T, 68% for DHT, and 67% for E_2. The mean intrassay coefficients of variation (n = 3) were 12.3% for T, 10.6% for DHT, and 21.3% for E_2. Interassay variation was 10.1% for T, 18.9% for DHT, and 19,9% for E_2.

6.3.4 Statistical analysis

For the analysis of the seasonal patterns of hormone secretion the data were matched for breeding cycle stage (these stages are defined in Chapter 2). The data were analysed using the statistical packages SPSS 12.1 (SPSS Inc., USA). I used Mann-Whitney-U tests when comparing two groups, and Kruskal-Wallis tests for more groups. Dunn's tests were then applied for post-hoc comparisons. All statistical analyses were based on two-tailed tests.

6.4   Results

6.4.1 Seasonal variation of circulating androgen levels in male Siberian and European stonechats

Fig. 6.1. shows the seasonal patterns of androgen (T + DHT) secretion in Kazakh and Slovak stonechat males in relation to the breeding activities at the two locations. In both populations androgen levels peak about two weeks before the breeding activity is maximal. The longer breeding season in Slovakia is mirrored in the longer period of elevated androgen levels in the European stonechats, and in a second peak in the plasma androngens where there is only one in Kazakhstan. Circulating androgen levels are lower in the Siberian than in the European stonechats.
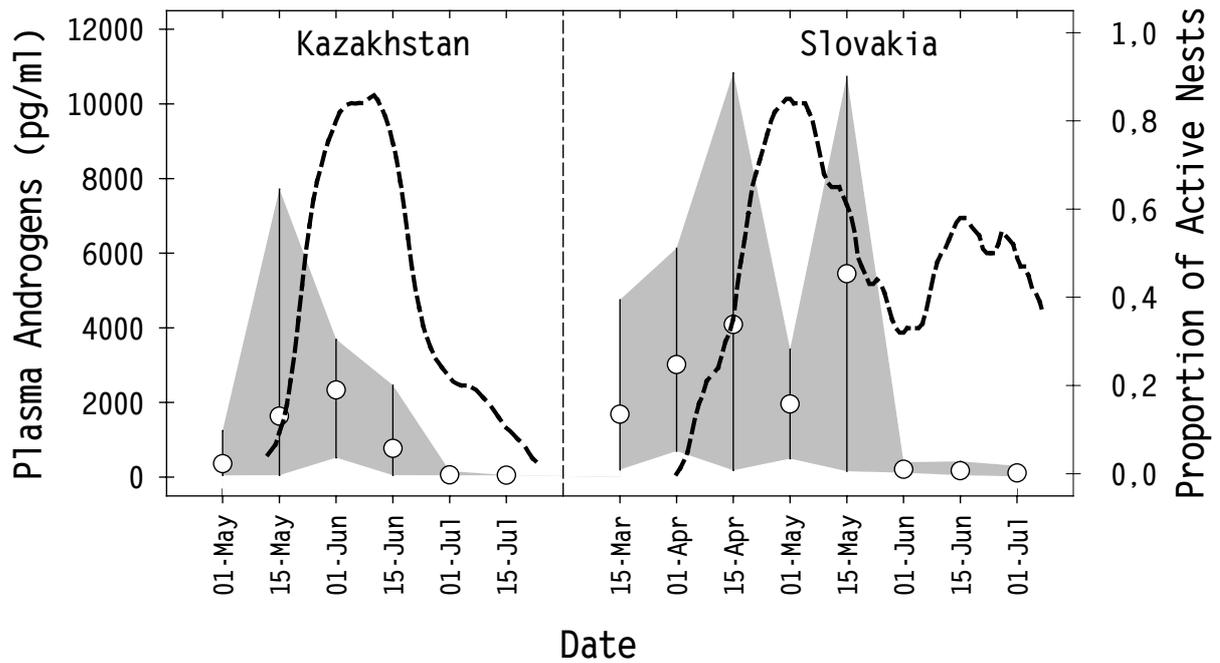
Fig. 6.1. The seasonal patterns of circulating androgens (T + DHT) in Siberian and European stonechats. Shown are mean values (open circles), the ranges are indicated by the vertical lines and the shaded areas. The breeding activities in the population, expressed as the proportion of active nests, are indicated by the dashed lines (cf. Chapter 5).

The levels of circulating T matched for breeding stage varied significantly in the course of the breeding season in males of both populations (Kruskal-Wallis test; Kazakhstan: $H = 15.07, p < 0.001$; Slovakia: $H = 11.31, p < 0.05$). T plasma concentrations were lower in birds arriving on the breeding grounds or on passage to other breeding sites than in birds that established a territory. Later in the season, when males had to care for nestlings and fledged young, T levels decreased significantly. They remained low, even when the birds started an additional breeding attempt (*Fig. 6.2.*). DHT plasma levels showed a similar seasonal pattern in the Siberian stonechats, however the differences were less pronounced in the European stonechats (Kruskal-Wallis test; Kazakhstan: $H = 16.66, p < 0.001$; Slovakia: $H = 2.41, p = 0.31$)(*Fig. 6.2.*).

The percentage of samples with detectable T or DHT, and the relationship of the two androgens differed markedly between the two populations (*Table 6.1. and Fig. 6.3.*). In the Siberian stonechat males the

proportion of samples containing undetectable amounts of androgens was higher. Furthermore, Siberian stonechat males had relatively higher concentrations of DHT in the plasma (*Table 6.1.*).
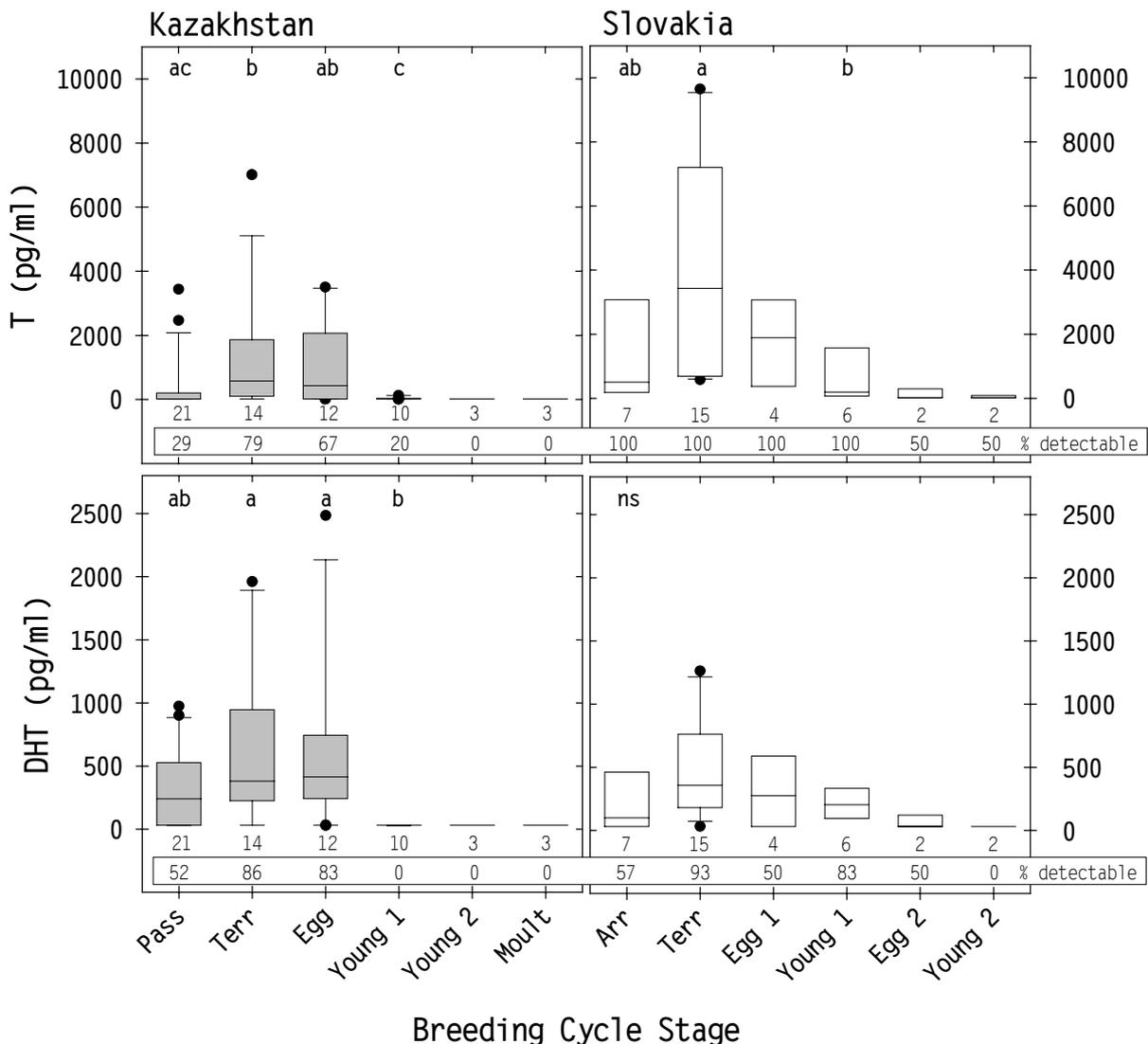

Fig. 6.2. Plasma concentrations of the androgens testosterone (T) and dihydrotestosterone (DHT) in male Siberian and European stonechats. The sample sizes and the percentage of detectable values are indicated below the plots for each breeding cycle stage. The letters above the plots indicate the results of Dunn's post-hoc tests: plots sharing the same letter are not significantly different.

Table 3.1. The percentage of samples containing detectable T and DHT and the relationship between these two androgens in the plasma samples of male Siberian and European stonechats. Differences were tested with a G test (an extension of the Fisher test) with Williams's correction for df = 1.

	Kazakhstan (n = 62)	Slovakia (n = 36)	G test G	p
detectable T	27 (45%)	34 (94%)	25.943	<.001
detectable DHT	33 (53%)	26 (72%)	6.474	.011
detectable T or DHT	38 (61%)	34 (94%)	13.841	<.001
T < DHT	17 (27%)	3 (8%)	4.977	.026

When all male plasma samples were considered, Siberian stonechats had significantly lower plasma T levels, the amount of DHT was equal in the two populations, and the sum of individual androgen levels (T + DHT) was significantly lower in Siberian stonechat males (*Fig. 6.3.A.*). In the subset of samples containing detectable androgens, Siberian stonechats had significantly lower T, but significantly higher DHT levels, thus total androgen (T + DHT) levels were not significantly different from European stonechat males (*Fig. 6.3.B.*). E_2 was undetectable in all samples of European males and in all but one sample of Siberian males, which contained a concentration of 223.1 pg/ml.

6.4.2   Territorial aggression in Siberian and European stonechats in the course of the breeding season

Male Siberian stonechats defended their territories throughout the breeding season, until their young were independent enough to be led away to patches of denser vegetation. Throughout this period they reacted aggressively in simulated territorial intrusions (*Fig. 6.4.*). The degree of escalation (as indicated by the aggression score) did not change from territorial establishment to the period when the young had fledged, but were still bound to the nest area (Kruskal-Wallis-tests: *H = 2.207, p = 0.53*). In each of the four stages tested 80% or more of the birds attacked the simulated intruder (score 4 or 5). In European stonechats studied by Schwabl et al. (2005) in Northern Germany the reactions to STIs were

similar to those of their Asian conspecifics. They varied more across the season, however were not significantly different between the breeding cycle stages (Schwabl et al. 2005) *(Fig. 6.4.)*.

A) all samples

B) samples containing detectable androgen concentrations
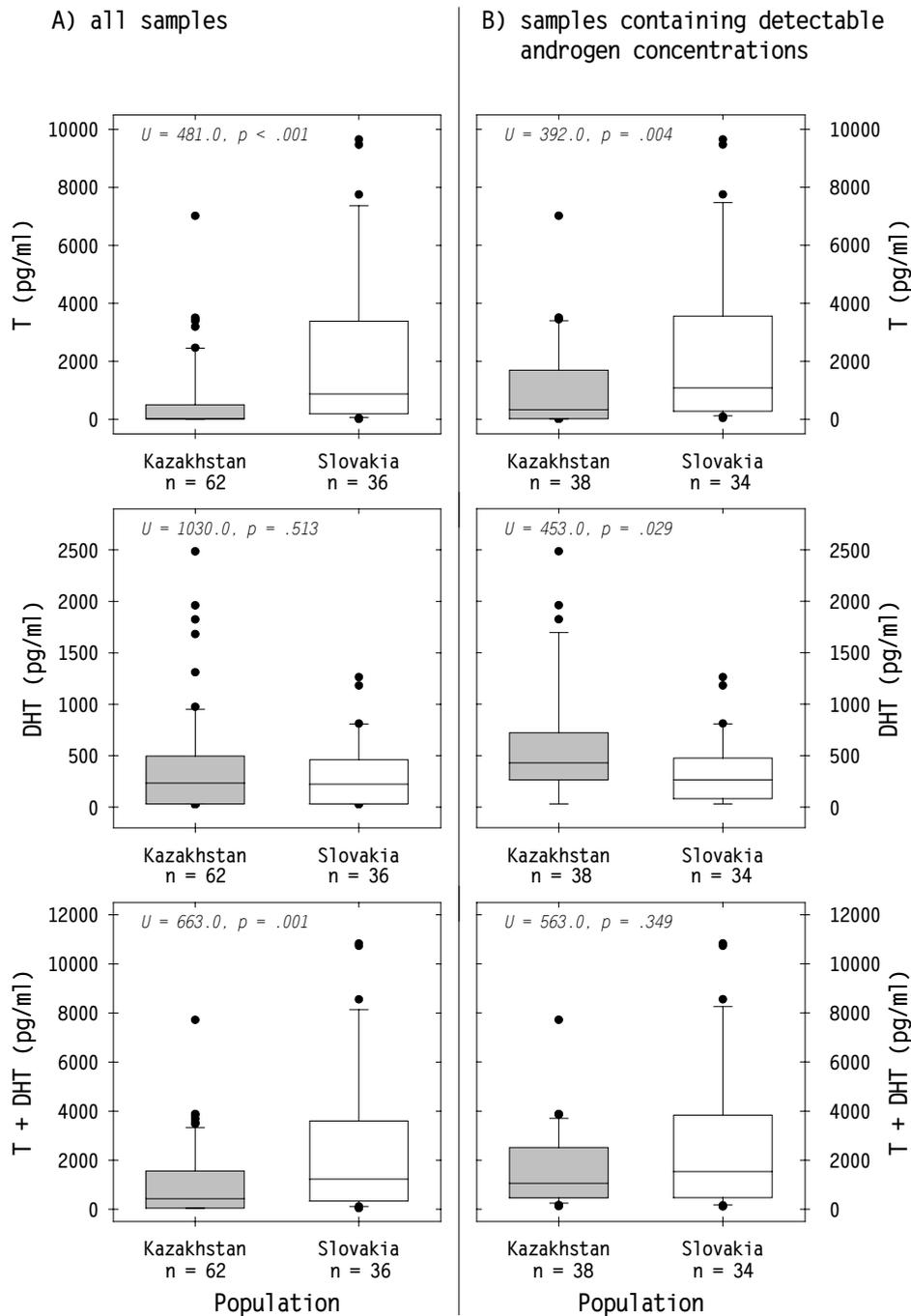
Fig. 6.3. Testosterone (T) and dihydrotestosterone (DHT) in all samples of male Siberian and European stonechats *(A)*, and in only those samples that contain detectable concentrations of either T or DHT *(B)*. The results of Mann-Whitney-U tests comparing androgen levels of the two populations are shown.
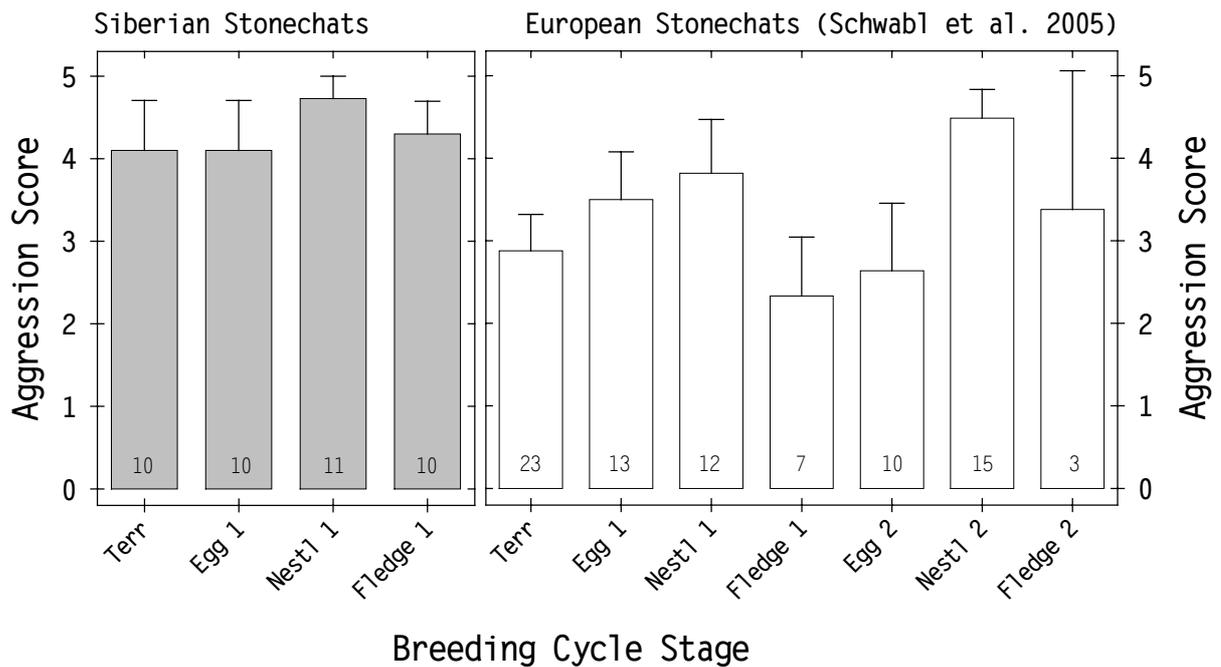
Fig. 6.4. Mean responses (+ SEM) of male Siberian and European stonechats to simulated territorial intrusions. Data for the European stonechats were reproduced from Schwabl et al. 2005, *Fig. 1.A.*

6.4.3   Gonadal steroids in the plasma of female Siberian and European stonechats

T was undetectable in all samples from Siberian stonechats females except one. In contrast, European stonechat females had detectable plasma concentrations of T throughout the breeding season (*Fig. 6.5.*). There was no significant difference in plasma T between the stages of the breeding cycle in European stonechat females (Kruskal-Wallis test: *H = 8.543, p = 0.12*). DHT and E_2 were undetectable in most samples of female Siberian and European stonechats (*Fig. 6.5.*). However, those samples that contained detectable amounts of DHT in the European stonechat females were found exclusively in the early stages of the breeding season (*Fig. 6.5.*).
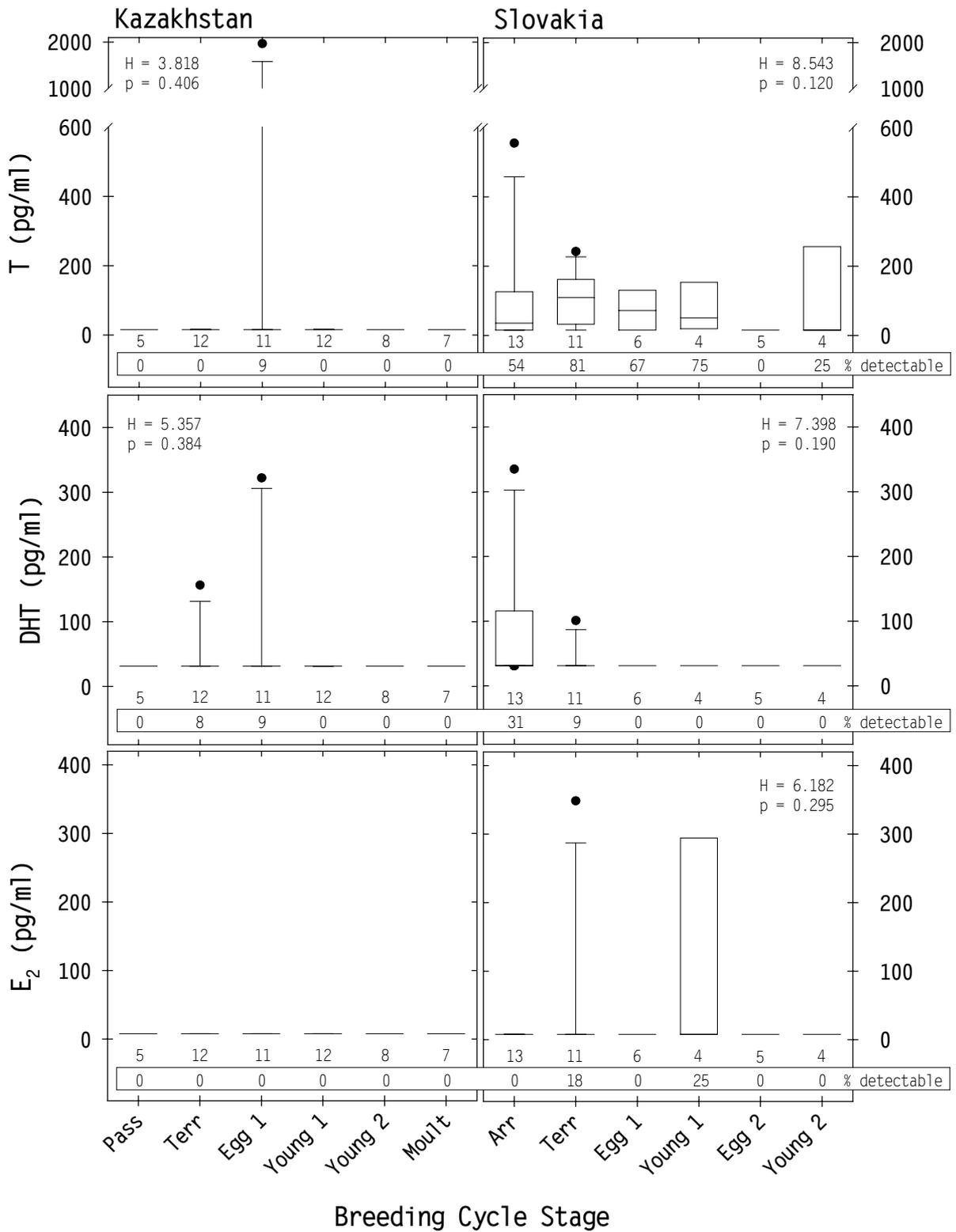
Fig. 6.5. Plasma concentrations of the androgens testosterone (T) and dihydrotestosterone (DHT) and the estrogen estradiol (E_2) in female Siberian and European stonechats. The sample sizes and the percentage of detectable values are indicated below the plots for each breeding cycle stage.

6.5   Discussion

6.5.1   Seasonal patterns of male androgen secretion

Males of both populations show typical seasonal profiles of circulating gonadal steroids of socially monogamous birds that participate in parental care. Circulating androgens are high at the time of territorial establishment and when the females are fertile. Concordant with the hypothesis that high plasma androgen levels interfere with male parental care (e.g. Hegner & Wingfield 1987, Wingfield et al. 1990), circulating T and DHT levels are low in the nestling and fledgling stages. A second peak in the seasonal androgen profile of the European stonechats was caused by a male that had lost its breeding partner, and hence was in the 'territorial' state again. Males caught during the incubation and parenting stages of replacement clutches in Kazakhstan and second clutches in Slovakia did not show an increase of circulating androgen levels, however sample sizes in these groups were low. In European stonechats such an increase may not be expected as the males usually cared for the still dependent fledglings, while the females already initiated the next clutch (the so-called 'telescoping' of clutches).

6.5.2   Factors affecting circulating androgen levels in males

European stonechats had higher mean plasma T and total plasma androgen levels than Siberian stonechats, and this was due to higher maximum as well as minimum levels. Several studies have attempted to explain interspecific variation in maximum androgen levels, or in the differences between breeding baseline and maximum levels. These studies have found increasing androgen levels (or androgen responsiveness) with increasing male-male competition, decreasing androgen levels with increasing paternal brood care and decreasing androgen levels with longer breeding seasons (Wingfield et al. 1990, Hirschenhauser et al. 2003, Goymann et al. 2004). The Siberian stonechats have a shorter breeding season and it is possible that this factor in combination with the single-

broodedness in Kazakhstan leads to an intensified competition for territories and mates. An indication in this direction is the fact that during the territorial stage over 80% of the Siberian stonechats males escalated figths during STI experiments, whereas in European stonechats in Northern Germany (where the breeding season is about as long as in Slovakia) only 20 to 50% of the males reacted in that way (Schwabl et al. 2005). Single-broodedness in Kazakhstan, however, increases also the reproductive value of a given clutch. Furthermore, there exists anecdotic evidence that females in Kazakhstan are less able to compensate when their partner's contribution to parental care is lacking. Hence Kazakh males may invest more into parental care than their European conspecifics. The fact that androgen levels are lower in the Siberian stonechat population may indicate that the degree of parental care has more weight in shaping the circulatory patterns of these gonadal steroids than the degree of male-male competition.

It could, however, also mean that my assessment of the relative competitive situation in the two locations is wrong. It is based on the relative lengths of the breeding seasons and the outcome of the STI experiments. In neither population, however, was the intensity of the response during an STI correlated with circulating androgen levels. This is interesting because total blockage of the effects of T reduces territorial aggression in European stonechats (Canoine & Gwinner 2002). This suggests that territorial aggression in breeding stonechats is affected by androgens or their metabolites, but does not require permanently high levels. In the later breeding stages, when androgen levels are generally low, territorial intrusions may lead to short-lived surges in circulating androgens, as suggested by the *challenge hypothesis*. Unfortunetaly neither in this, nor in the studies on the European stonechat (Canoine & Gwinner 2002, Schwabl et al. 2005), birds were captured immediately after the STI experiment, therefore it remains unresolved whether an increase of plasma androgen levels results from the territorial encounters.

Garamszegi et al. (2005) found a relationship between the degree of sperm competition and the amount of circulating androgens. Unfortunately I do not have data on the relative frequencies of extra-pair fertilisations in my populations. It has been suggested that a higher degree of breeding synchrony, as can be found in the Kazakh stonechats, favours sperm competition (e.g. Stutchbury & Morton 1995), however there are many conflicting results and this issue is as yet unresolved (see also Chapter 5 of this thesis).

None of the studies on the variation of circulating androgen levels has specified the factors that affect breeding baseline levels, and many of them seem to imply that they are the same as for the maximum androgen levels. This has, however, never been put to test. This may be partly due to the difficulty to translate the concept of the breeding baseline (i.e. the minimum circulating androgen concentration in a *socially unchallenged* male that is required to uphold reproductive physiology and behaviour) into a measurable quantity. Hirschenhauser et al. (2003) define the breeding baseline "as the average androgen levels throughout the different breeding phases, including parenting". Applied to my results this would would yield T breeding baselines of about 600 pg/ml plasma for the Kazakh stonechats and about 1400 pg/ml plasma for the Slovak stonechats. One could argue, however, that the breeding baselines are the minimum androgen levels found in males during the reproductive stages, because these are the most likely to represent an unchallenged state. In my study, several males expressed robust reproductive behaviours with low or undetectable T levels, particularly in the Kazakh population. If I assume that the lower 10% of values represents the breeding baseline of socially unchallenged birds, then the T breeding baseline of European stonechats would lie between 40 pg/ml plasma (fledgling stage) and 600 pg/ml plasma (territorial establishment and pair formation). In the Siberian stonechats the T breeding baseline in all stages would be in the non-detectable range of the assay and thus at or below 16 pg/ml plasma.

6.5.3   The relationship between circulating T and DHT in males

Besides lower T levels, Siberian stonechat males showed also a different ratio of the circulating levels of the androgens T and DHT. Unlike most European males (see also Canoine & Gwinner 2002), many Siberian males had higher DHT than T levels in the plasma. 5α-dihydrotestosterone is a reduced metabolite of T that binds to androgen receptors and has been shown to regulate social behaviours differentially from T in some bird species, but usually T is much more potent in eliciting reproductive behaviours (Adkins-Regan 1981, Balthazart 1983, Balthazart & Ball 1993). In contrast to DHT, T can be aromatised to estrogens, a second major pathway by which androgens act on reproductive behaviour (e.g. Balthazart 1983, Schlinger & Callard 1990). It is not known whether social behaviours in the stonechat are differentially regulated by DHT and whether there is a difference between the subspecies. If such a difference exists, one possible explanation might be that some of the costs associated with high T levels, like immunosuppression or increased mortality (Peters 2000, Casto et al. 2001, Wingfield et al. 2001) are mediated by the estrogenic pathway of T action. In song sparrows *Melospiza melodia* exogenous T suppresses cell-mediated immunity, whereas DHT has no such effect (Owen-Ashley et al. 2004). However, a difference in the regulation of social behaviours in the two populations would only come about when there would be not only different costs, but also different benefits associated with high circulating T respective DHT levels. Then differential cost/benefit ratios of the hormones involved in the control of reproduction could drive a divergence in the endocrine control of social behaviours in different ecological situations.

6.5.4   Circulating gonadal steroids in females

Circulating female estrogen levels were generally low in the plasma of both populations. Estrogens play an important role in the development of the female reproductive system and the production of the ovum (Lofts &

Murton 1973, Murton & Westwood 1977), however they apparently do not leak from the gonads into the circulation. Apart from the ovaries, the brain is a major site of estrogen production (Schlinger 1997, Schlinger et al. 1999), and the E_2 that circulates in the plasma might actually come from the brain and not from the gonads (B. Schlinger, pers. comm.). Basal E_2 levels have been found in other studies on stonechats (Gwinner et al., unpublished, Geue & Gwinner, in prep.).

Circulating T levels were undetectable in all but one sample of Siberian stonechat females. In contrast, T was detectable in most samples of European stonechat females. A recent study on a different population of European stonechats also finds detectable T levels in females, with similar concentrations (Schwabl et al. 2005). This study also reports seasonal differences in T levels, with highest values during the territorial stages and lower levels during the parental stages. In the Slovak stonechat females the median levels follow a similar pattern, however the differences between the stages are not significant. Interestingly, both studies find a slight increase in T levels in females during the nestling stage of the second clutch. Plasma DHT levels were low in females of both populations. In European stonechat females all detectable concentrations of DHT were found in the early breeding season. This could indicate a role for DHT at that time or even earlier, during wintering or migration.

Seasonal patterns in female androgen levels have been found in other species (Wingfield & Farner 1978, Hegner & Wingfield 1986, Wingfield 1994a). Some studies addressed the relationship between female androgen levels and female aggression (Kriner & Schwabl 1991, Elekonich & Wingfield 2000, Langmore et al. 2002), however the results are equivocal. Generally, the role of the gonadal steroids in regulating female reproductive behaviours remains poorly understood (Wingfield 1994a). Circulating androgen levels in females have been associated with variation in yolk androgen concentrations, which are thought be an important non-genomic way to manipulate offspring phenotype (Schwabl 1993, Schwabl 1996a, b, Schwabl

et al. 1997). A further clarification of the role of circulating gonadal steroids in the regulation of female behaviour is clearly required.

6.6   References

Adkins-Regan, E. (1981). Hormone specifity, androgen metabolism and social behavior. *American Zoologist* 21: 257-271.

Balthazart, J. (1983). Hormonal correlates of behavior. *In* D. S. Farner, J. R. King & K. C. Parkes (Eds.), *Avian Biology*, Vol. 7, pp. 221-365. Academic Press, New York.

Balthazart, J. & Ball, G. F. (1993). Neurochemical differences in two steroid sensitive areas mediating reproductive behaviors. *In* R. Gilles (Ed.), *Advances in Comparative and Environmental Physiology*, pp. 133-161. Springer-Verlag, New York.

Beletsky, L. D., Gori, D. F., Freeman, S. & Wingfield, J. C. (1995). Testosterone and polygyny in birds. *Current Ornithology* 12: 1-41.

Beletsky, L. D., Orians, G. H. & Wingfield, J. C. (1989). Relationships of steroid hormones and polygyny to territorial status, breeding experience, and reproductive success in male red-winged blackbirds. *Auk* 106: 107-117.

Canoine, V. & Gwinner, E. (2002). Seasonal differences in the hormonal control of territorial aggression in free-living European stonechats. *Hormones and Behavior* 41: 1-8.

Casto, J. M., Nolan, V., Jr. & Ketterson, E. D. (2001). Steroid hormones and immune function: Experimental studies in wild and captive dark-eyed juncos (*Junco hyemalis*). *American Naturalist* 157: 408-420.

Elekonich, M. M. & Wingfield, J. C. (2000). Seasonality and hormonal control of territorial aggression in female song sparrows (Passeriformes: Emberizidae: Melospiza melodia). *Ethology* 106: 493-510.

Fusani, L., Van't Hof, T. J., Hutchison, J. B. & Gahr, M. (2000). Seasonal expression of androgen receptors, estrogen receptors, and aromatase in the canary brain in relation to circulating androgens and estrogens. *Journal of Neurobiology* 43: 254-268.

Garamszegi, L. Z., Eens, M., Hurtrez-Bousses, S. & Moller, A. P. (2005). Testosterone, testes size, and mating success in birds: a comparative study. *Hormones and Behavior* 47: 389-409.

Goymann, W., Moore, I. T., Scheuerlein, A., Hirschenhauser, K., Grafen, A. & Wingfield, J. C. (2004). Testosterone in tropical birds: Effects of environmental and social factors. *American Naturalist* 164: 327-334.

Hau, M., Wikelski, M., Soma, K. K. & Wingfield, J. C. (2000). Testosterone and year-round territorial aggression in a tropical bird. *General and Comparative Endocrinology* 117: 20-33.

Hegner, R. E. & Wingfield, J. C. (1986). Behavioral and endocrine correlates of multiple brooding in the semicolonial house sparrow *Passer domesticus*. II. Females. *Hormones and Behavior* 20: 313-326.

Hegner, R. E. & Wingfield, J. C. (1987). Effects of experimental manipulation of testosterone levels on parental investment and breeding success in male House Sparrows. *Auk* 104: 462-469.

Hirschenhauser, K., Winkler, H. & Oliveira, R. F. (2003). Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. *Hormones and Behavior* 43: 508-519.

Hunt, K. E., Hahn, T. P. & Wingfield, J. C. (1997). Testosterone implants increase song but not aggression in male Lapland longspurs. *Animal Behaviour* 54: 1177-1192.

Hunt, K. E., Hahn, T. P. & Wingfield, J. C. (1999). Endocrine influences on parental care during a short breeding season: testosterone and male parental care in Lapland longspurs (Calcarius lapponicus). *Behavioral Ecology and Sociobiology* 45: 360-369.

Hunt, K. E., Wingfield, J. C., Astheimer, L. B., Buttemer, W. A. & Hahn, T. P. (1995). Temporal patterns of territorial behavior and circulating testosterone in the Lapland longspur and other arctic passerines. *American Zoologist* 35: 274-284.

Ketterson, E. D. & Nolan, V., Jr. (1992). Hormones and life histories: An integrative approach. *American Naturalist* 140: S33-S62.

Kriner, E. & Schwabl, H. (1991). Control of winter song and territorial aggression of female robins (*Erithacus rubecula*) by testosterone. *Ethology* 87: 37-44.

Langmore, N. E., Cockrem, J. F. & Candy, E. J. (2002). Competition for male reproductive investment elevates testosterone levels in female dunnocks, Prunella modularis. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 269: 2473-2478.

Lofts, B. & Murton, R. K. (1973). Reproduction in birds. *In* D. S. Farner & J. R. King (Eds.), *Avian Biology*, Vol. III, pp. 1-107. Academic Press, New York and London.

Lynn, S. E., Hayward, L. S., Benowitz-Fredericks, Z. M. & Wingfield, J. C. (2002). Behavioural insensitivity to supplementary testosterone during the parental phase in the chestnut-collared longspur, - Calcarius ornatus. *Animal Behaviour* 63: 795-803.

Lynn, S. E., Walker, B. G. & Wingfield, J. C. (2005). A phylogenetically controlled test of hypotheses for behavioral insensitivity to testosterone in birds. *Hormones and Behavior* 47: 170-177.

Moore, M. C. & Kranz, R. (1983). Evidence for androgen independence of male mounting behavior in white-crowned sparrows (*Zonotrichia leucophrys gambelii*). *Hormones and Behavior* 17: 414-423.

Murton, R. K. & Westwood, N. J. (1977). *Avian Breeding Cycles*. Clarendon Press, Oxford.

Owen-Ashley, N. T., Hasselquist, D. & Wingfield, J. C. (2004). Androgens and the immunocompetence handicap hypothesis: Unraveling direct and indirect pathways of immunosuppression in song sparrows. *American Naturalist* 164: 490-505.

Peters, A. (2000). Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immunocompetent. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 883-889.

Peters, A., Cockburn, A. & Cunningham, R. (2002). Testosterone treatment suppresses paternal care in superb fairy-wrens, Malurus cyaneus, despite their concurrent investment in courtship. *Behavioral Ecology and Sociobiology* 51: 538-547.

Rost, R. (1992). Hormones and behaviour: a comparison of studies on seasonal changes in song production and testosterone plasma levels in the willow tit, *Parus montanus*. *Ornis Fennica* 69: 1-6.

Schlinger, B. A. (1997). The activity and expression of aromatase in songbirds. *Brain Research Bulletin* 44: 359-364.

Schlinger, B. A. & Callard, G. V. (1990). Aromatization mediates aggressive behavior in quail. *General and Comparative Endocrinology* 79: 39-53.

Schlinger, B. A., Lane, N. I., Grisham, W. & Thompson, L. (1999). Androgen synthesis in a songbird: A study of Cyp17 (17alpha-hydroxylase/C17,20-lyase) activity in the zebra finch. *General and Comparative Endocrinology* 113: 46-58.

Schwabl, H. (1993). Yolk is a source of maternal testosterone for developing birds. *Proceedings of the National Academy of Sciences of the United States of America* 90: 11446-11450.

Schwabl, H. (1996a). Environment modifies the testosterone levels of a female bird and its eggs. *Journal of Experimental Zoology* 276: 157-163.

Schwabl, H. (1996b). Maternal testosterone in the avian egg enhances postnatal growth. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 114: 271-276.

Schwabl, H., Flinks, H. & Gwinner, E. (2005). Testosterone, reproductive stage, and territorial behavior of male and female European stonechats Saxicola torquata. *Hormones and Behavior* 47: 503-512.

Schwabl, H. & Kriner, E. (1991). Territorial aggression and song of male European robins (*Erithacus rubecula*) in autumn and spring: Effects of antiandrogen treatment. *Hormones and Behavior* 25: 180-194.

Schwabl, H., Mock, D. W. & Gieg, J. A. (1997). A hormonal mechanism for parental favouritism. *Nature* 386: 231.

Silverin, B. (1980). Effects of long-lasting testosterone treatment on free-living pied flycatchers, *Ficedula hypoleuca*, during the breeding period. *Animal Behaviour* 28: 906-912.

Smith, L. C., Raouf, S. A., Brown, M. B., Wingfield, J. C. & Brown, C. R. (2005). Testosterone and group size in cliff swallows: testing the "challenge hypothesis" in a colonial bird. *Hormones and Behavior* 47: 76-82.

Stoehr, A. M. & Hill, G. E. (2000). Testosterone and the allocation of reproductive effort in male house finches (Carpodacus mexicanus). *Behavioral Ecology and Sociobiology* 48: 407-411.

Stutchbury, B. J. & Morton, E. S. (1995). The effect of breeding synchrony on extra-pair mating systems in songbirds. *Behaviour* 132: 675-690.

Van Duyse, E., Pinxten, R. & Eens, M. (2002). Effects of testosterone on song, aggression, and nestling feeding behavior in male great tits, Parus major. *Hormones and Behavior* 41: 178-186.

Wikelski, M., Hau, M., Robinson, W. D. & Wingfield, J. C. (1999a). Seasonal endocrinology of tropical passerines: A comparative approach. *In* N. J. Adams & R. H. Slotow (Eds.), *Proc. 22 Int. Ornthol. Congr., Durban*, pp. 1224-1241. BirdLife South Africa, Johannesburg.

Wikelski, M., Hau, M. & Wingfield, J. C. (1999b). Social instability increases plasma testosterone in a year-round territorial neotropical bird. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 266: 551-556.

Wingfield, J. C. (1984). Environmental and endocrine control of reproduction in the song sparrow, *Melospiza melodia:* II. Agonistic interactions as environmental information stimulating secretion of testosterone. *General & Comparative Endocrinology* 56: 417-424.

Wingfield, J. C. (1990). Interrelationships of Androgens, Aggression and Mating Systems. *In* M. Wada, S. Ishii & C. G. Scanes (Eds.), *Endocrinology of Birds: Molecular to Behavioral*, pp. 187-205. Japan Sci. Soc. Press / Springer-Verlag, Tokyo / Berlin.

Wingfield, J. C. (1994a). Hormone-behaviour interactions and mating systems in male and female birds. *In* R. V. Short & E. Balaban (Eds.), *The differences between the sexes*, pp. 303-330. Cambridge University Press, Cambridge.

Wingfield, J. C. (1994b). Regulation of territorial behavior in the sedentary song sparrow, Melospiza melodia morphna. *Hormones and Behavior* 28: 1-15.

Wingfield, J. C., Ball, G. F., Dufty, A. M., Hegner, R. E. & Ramenofsky, M. (1987). Testosterone and aggression in birds. *American Scientist* 75: 602-608.

Wingfield, J. C. & Farner, D. S. (1978). The endocrinology of a natural breeding population of the white-crowned sparrow "(*Zonotrichia leucophrys pugetensis*). *Physiological Zoology* 51: 188-205.

Wingfield, J. C. & Farner, D. S. (1980). Control of seasonal reproduction in temperate-zone birds. *In* R. J. Reiter & B. K. Follett (Eds.), *Progress in Reproductive Biology*, Vol. 5: Seasonal reproduction in higher vertebrates, pp. 62-101. Karger, Basel.

Wingfield, J. C., Hegner, R. E., Dufty, J. A. M. & Ball, G. F. (1990). The "challenge-hypothesis": theoretical implications for patterns of testosterone secretion, mating systems and breeding strategies. *American Naturalist* 136: 829-846.

Wingfield, J. C. & Hunt, K. E. (2002). Arctic spring: hormone-behavior interactions in a severe environment. *Comparative Biochemistry and Physiology Part B: Biochemistry & Molecular Biology* 132: 275-286.

Wingfield, J. C., Lynn, S. E. & Soma, K. K. (2001). Avoiding the 'costs' of testosterone: Ecological bases of hormone-behavior interactions. *Brain, Behavior and Evolution* 57: 239-251.

7   Glucocorticoids in Breeding Siberian and European Stonechats

7.1   Summary

By allostasis, stability through change, organisms facing unpredictable environmental challenges keep up the integrity of their key physiological systems. Glucocorticoids (GCs), which are released as part of the allostatic response, cause the shut down of all energy-demanding processes that do not serve in immediate survival and mobilise the energy that is required to evade or face the environmental threat. Two hypotheses try to explain variation in circulating GC levels. The *reproductive limitation hypothesis* predicts a relationship between the potential number of breeding opportunities and the amount of GC release in response to a stressor. The *energy mobilisation hypothesis* predicts higher GC levels during periods of increased energy demand, such as the avian breeding period. I investigated circulating GC levels during different breeding stages in Siberian and European stonechats. I found overall GC levels in the single-clutched Siberian stonechats to be higher than in the multi-clutched European stonechats. GC levels did not differ between breeding stages, however they decreased in Siberian stonechats when they started to moult. This has been found in other species and may be an indication that high GC levels interfere with the metabolic processes during moult. I did not find a relationship between the costs of loosing a reproductive bout and circulating GC levels; I also did not find circulating GCs to be a simple reflection of energetic need. A broader knowledge of GC secretion patterns in different species will help in refining the current hypothesis on seasonal and individual variation in circulating GC levels.

7.2　Introduction

　　To sustain themselves in a fluctuating environment, organisms have to keep a number of key physiological parameters such as body temperature, blood glucose and oxygen levels and pH within narrow limits. Cannon (1932) coined the term 'homeostasis' for the system of positive and negative feedback mechanisms that adjust the actual values of these parameters once they deviate from a set value. However, homeostatic feedback systems usually only work within a certain range that is determined by the prevailing life-history stage (McEwen & Wingfield 2003). If the departure from the set value exceeds the predictable range, additional regulation systems take over. These trigger physiological and behavioural adjustments that enable an organism to return as quickly as possible to the former equilibrium conditions (McEwen & Wingfield 2003). Often this involves a temporary change of the set values for the key physiological parameters noted above. Hence, in analogy to homeostasis - the maintenance of a steady state -, the concept of 'allostasis' (achieving stability through change) has been introduced by Sterling and Eyer (1988) and extended by McEwen, Wingfield and others (e.g. McEwen & Wingfield 2003, Goymann & Wingfield 2004, Korte et al. 2005) to describe the response mechanisms to unpredictable events.

　　Glucocorticoids (GCs), alongside with the *catecholamines* and the *cytokines* are major allostatic regulators (Axelrod & Reisine 1984, Besedovsky & Del Rey 1996, Sapolsky et al. 2000, Kovacs 2002). GC production and release in the adrenal cortex is stimulated by adrenocorticotropic hormone (ACTH) secreted by the anterior pituitary, which in turn is triggered by corticotropin-releasing hormone (CRH) from the hypothalamus. Based on these secretory tissues involved, this neuroendocrine cascade is termed the hypothalamo-pituitary-gonadal axis (HPA-axis)(Axelrod & Reisine 1984). GCs are continually secreted at low levels during the day, and these basal levels are thought to contribute to the homeostatic control of the energy metabolism (Dallman et al. 1993, Breuner et al. 1999) and prime the organism for potential environmental

challenges (Sapolsky et al. 2000). Basal GC secretion shows a diurnal pattern whith higher levels during the inactive phase than during the active phase and a peak prior to the beginning of the active phase. This is seen as a general preparation of the metabolism for the active phase (Dallman et al. 1993, Breuner et al. 1999, Rich & Romero 2001). Besides these diurnal patterns, there also exist persistent seasonal patterns of the basal GC levels in many species, with for example higher levels during the period of reproductive activities (Romero 2002). It has been hypothesised that elevated GC levels at certain times of the year facilitate energy mobilisation during periods of increased demand or that they generally prepare an organism for periods of increased susceptibility to unpredictable challenges (Romero 2002).

On top of this diurnal and seasonal variation GCs can increase as part of the allostatic response to unforeseen threats to the physical and energetic integrity of an organism. Traditionally, these increases have been termed 'stress-induced' because they are triggered by so-called 'environmental stressors', i.e. unpredictable events that threaten homeostasis. Maximum GC responses in passerine birds are usually reached after 20-40 Minutes of exposure to the challenging situation (e.g. Romero & Romero 2002, Romero & Reed 2005). GCs at stress-induced levels cause the shut down of all energy demanding physiological processes that do not serve immediate survival and they trigger the mobilisation of glucose from the liver, adipose tissue and skeletal muscle while simultaneously preventing the build-up of new energy stores (Axelrod & Reisine 1984, Sapolsky et al. 2000). Stress-induced GC levels often follow the diurnal and seasonal patterns of the basal levels (Breuner et al. 1999, Romero 2002). Furthermore, maximal GC secretion seems to be further modulated according to ecological context: because GCs have the potential to inhibit reproductive activities (Silverin 1986, 1998), species that have only limited possibilities to reproduce, because they are very short-lived or because they breed in extreme environments with short breeding seasons, should either dampen HPA-axis activity altogether or limit the inhibiting

effect of GCs on reproductive physiology and behaviour (Wingfield et al. 1992, Wingfield et al. 1995, Wingfield et al. 1997, Wingfield & Romero 2001, Wingfield & Sapolsky 2003).

In this chapter, I investigate the secretory patterns of corticosterone (CORT, the main GC in passerine birds) during the breeding season in Siberian and European stonechats and relate them to two hypotheses that have been put forward to explain these patterns:

Reproductive limitation hypothesis: the HPA-response to environmental stressors is reduced in species with limited breeding opportunities to avoid interference with reproduction (Wingfield & Sapolsky 2003). Hence, the difference in the length of the breeding season between the single-clutched Siberian and the multi-clutched European stonechats (see Chapter 5 of this thesis) could affect stress-induced CORT levels. Siberian stonechats may decrease HPA-activity to avoid disruptive effects of CORT on reproduction. It has also been suggested that the sex that contributes more to parental care decreases GC secretion (Wingfield et al. 1995). In the stonechats parental investment of both sexes is required to rear a clutch successfully, therefore pronounced sexual differences of CORT secretion during the parenting stages would not be expected.

Energy mobilisation hypothesis: basal GC levels reflect the energy demand during a life-history stage (Romero 2002). Within the two stonechat populations, basal CORT values may therefore vary according to the energetic demand of a breeding stage and may furthermore reflect sexual differences in parental care. In stonechats only the females incubate, hence females could have higher basal CORT levels during the egg stage than males. In males, basal CORT levels should increase after hatching when they participate in provisioning the clutch. In both sexes CORT secretion should decrease after fledging when the young gain independence. Furthermore, in both sexes CORT levels could be inversely related to the amount of body reserves, as has been found in other studies (Wingfield et al. 1997, Marra & Holberton 1998, Breuner & Hahn 2003).

7.3   Methods

7.3.1   Obtaining blood samples and measurements of body condition

During the breeding season Siberian and European stonechats were caught using mealworm-baited traps or mistnets. Within three minutes after capture, a first small blood sample (approx. 60 μl of plasma) was taken from the alar vein. An elevation of circulating CORT levels due to capturing and handling occurs only after approximately three minutes (Romero & Romero 2002, Romero & Reed 2005), hence these samples reflect birds in the state before the capture stressor was applied. Blood samples were collected into heparinised capillaries and centrifuged in the field. Consecutively the birds were either handled to take measurements of body size and body condition (as described in Chapter 2) or kept in opaque cloth bags. 30 minutes after capture, a second blood sample was taken to assess *stress-induced CORT levels*. This sampling protocol was chosen to avoid negative effects on the breeding pairs, while ensuring on the other hand that stress-induced CORT levels are close to the maximal response (Canoine et al. 2002). It is generally assumed that the capture stress protocol yields comparable results between populations and species (Wingfield et al. 1992, Wingfield & Romero 2001). Plasma was stored on ice for up to four hours before it was transferred into liquid nitrogen. Consecutively, the samples were kept either in liquid nitrogen or at -70°C until they were assayed.

Clutch size in Siberian and European stonechats for which CORT samples were available did not differ (Kazakhstan: 5.63 ± 0.76 SD, n = 30; Slovakia: 5.40 ± 0.74, n = 15; t-test: $t_{43} = 0.98, p = 0.33$).

7.3.2   Corticosterone assay

The radioimmunoassay (RIA) used to determine the concentration of basal and stress-induced CORT in the plasma samples followed the basic steps as the RIA for the gonadal steroids described in Chapter 6, After adding tritiated CORT and 6 hours of incubation at 4°C CORT was extracted

with dichloromethane on Extrelut (Merck) columns. The samples were then dried under nitrogen at 40°C and resuspended in 0.1M phosphate buffer pH 7.0. Aliquots of each fraction were measured in a scintillation counter (Beckmann LS 6000) to estimate extraction efficiency. After adding tritium-labelled CORT (NEN PerkinElmer, USA: NET-399) and antiserum (Endocrine Sciences, USA: B3-163) to each sample in duplicate aliquots and incubation at 4°C for 20 hours bound and free fractions were separated by with dextran-coated charcoal and centrifugation, Radioactivity in the supernatant was counted and the CORT concentrations determined with ImmunoFit EIA/RIA Analysis 3.0, (Beckman Instruments Inc., USA). The lower detection limit of the assay was 7.8 pg/ml. Mean recovery was 90%, intrassay variation 18.6% and 10.6%, interassay variation 6.8%.

7.3.3   Statistical analysis

To assess the effect of multiple factors on basal and stress-induced CORT levels, a stepwise general linear model (GLM) procedure was applied. The full model was fitted with *1*. population, *2*. sex, *3*. breeding attempt (first vs. replacements in the Kazakh data set, first vs. second in the Slovak data set), *4*. breeding stage (egg, nestlings, fledglings), and *5*. the fat score as categorical variables and *6*. the time of day of capture as a continuous covariable. In the next step each variable was dropped while the others were kept in the model. If this resulted in a model with a better fit, as indicated by an increase of the adjusted R^2 (which estimates the goodness of fit of the model corrected for the number of variables applied, Grafen & Hails 2002), the next removal step was initiated with the remaining variables. If in one step more than one model with a higher R^2_{adj} was produced, then the model with the best fit was chosen to continue. None of the variables removed had a statistical effect ($p < 0.1$) on CORT. The stepwise GLM procedure was fitted to *(A)* the full data set; *(B)* all data except the 11 values of the fledgling stage in Kazakhstan, which had no counterpart in the Slovak data set, *(C)* all data except the 4 values of the Kazakh replacement clutches (the Kazakh data set contains for the first

clutches 32 basal and 31 stress-induced CORT values from three different breeding stages and for replacement clutches only 4 values from one stage); and (D) all data except the 11 fledging stage values and 4 replacement clutch values from Kazakhstan.

The combined moult score used in this chapter was derived from the moult scores for wing and body feathers (see Chapter 9 of this thesis) in the following way:

$$MS_{combi} = (MS_{wing}/95 + MS_{body}/19) / 2$$

i.e. each of the two moult scores is divided by its maximum value; the two relative scores are then summed up and averaged.

7.4   Results

7.4.1   CORT secretion during the breeding season

In the Siberian stonechats, basal and stress induced CORT secretion varied in a similar way from egg production to moult. CORT levels were higher during the nestling stages of first and replacement clutches than during the other periods (*Fig. 7.1.*). CORT secretion decreased when the birds started to moult. In the European stonechats no clear patterns of CORT secretion during the breeding stages emerged. Neither basal nor stress-induced CORT levels were higher during the nestling stages than during egg production and incubation (*Fig. 7.2.*). During a two-day period of cold weather and snow cover at the time of arrival basal CORT levels were elevated but increased further in response to capture and handling (*Fig. 7.2.*).

The results of the four stepwise GLM procedures for the basal and stress-induced CORT levels reveal that the main improvement of the model fit is achieved by excluding the fledgling stage values from Kazakhstan from the data (*Tables 7.1.B. and 7.2.B*). This yields a far better model fit than the complete data set (*Tables 7.1.A. and 7.2.A.*) or the exclusion of the Kazakh replacement clutch values (*Tables 7.1.C. and 7.2.C.*). Hence,

when both, the Kazakh fledgling stage *and* replacement clutches are removed, the result is similar to the analysis where only the fledgling stage was removed (*Tables 7.1.D. and 7.2.D.*).

Table 7.1. Comparison of stepwise GLM procedures to assess the effect of multiple variables on basal CORT levels. Variables were one by one removed from a full model that contained the time of day of capture (time), the population (pop), the sex, the breeding stage (eggs, nestlings, fledglings), the breeding attempt (first or replacement/second), and the fat score. Only steps resulting in a better fit (a higher R^2_{adj}) are shown. The GLM procedure was applied to four different data sets (A) to (D), see text for details. The results of the final models are shown, significant effects are highlighted with bold characters.

Basal CORT								
Model fit (R^2_{adj})	(A) All data 0.186		(B) Kaz *fledge* excluded 0.430		(C) Kaz *repl* excluded 0.213		(D) Kaz *fledge* + *repl* excluded 0.454	
	↓ *sex dropped* 0.389		↓ *sex dropped* 0.517 ↓ *stage dropped* 0.551 ↓ *time dropped* 0.566		↓ *sex dropped* 0.409 ↓ *attempt dropped* 0.447		↓ *sex dropped* 0.523 ↓ *stage dropped* 0.562 ↓ *time dropped* 0.574	
Final models	(Mean squares, p-values)							
sex	-	-	-	-	-	-	-	-
time	40.0	.305	-	-	65.6	.177	-	-
pop	313.6	**.007**	447.1	**< .001**	408.4	**.002**	566.9	**< .001**
stage	80.2	.132	-	-	84.1	.103	-	-
attempt	81.3	.148	67.0	.122	-	-	50.6	.182
fat	44.4	.331	83.4	**.022***	72.6	.091	138.1	**.002****
error	36.6		26.3		34.2		27.0	

* pop x fat x attempt: p = .027
** pop x fat: p = .027

Table 7.2. Comparison of stepwise GLM procedures to assess the effect of multiple variables on stress-induced CORT levels. See *Table 7.1.* and text for details.

Stress CORT								
Model fit (R^2_{adj})	(A) All data 0.232		(B) Kaz *fledge* excluded 0.472		(C) Kaz *repl* excluded 0.264		(D) Kaz *fledge* + *repl* excluded 0.507	
	↓ *sex dropped* 0.253				↓ *attempt dropped* 0.282 ↓ *time dropped* 0.290			
Final models			(Mean squares, p-values)					
sex	-		4.8	.856	7.8	.842	128.3	.359
time	290.7	.231	696.4	**.048**	-	-	696.3	**.048**
pop	1957.9	**.004**	817.5	**.034**	3435.5	**< .001**	932.1	**.026**
stage	666.7	**.047**	83.3	.457	821.9	**.029**	83.3	.457
attempt	93.9	.492	216.7	.240	-	-	62.9	.517
fat	180.7	.474	310.3	.126	174.6	.493	309.4	.127
error	192.8		140.2		191.1		140.2	

Common to all analyses is that sex had no significant effect on basal and stress-induced CORT levels in Siberian and European stonechats. Another robust result is that basal and stress-induced CORT levels differed significantly between the two populations (Tables 7.1. and 7.2.). CORT secretion was generally higher in Kazakhstan than in Slovakia (*Fig. 7.3.*). When the data is analysed without the Kazakh fledgling stage, a significant effect of fat scores on basal CORT levels and a significant effect of the capture time on the stress-induced CORT levels is revealed (*Tables 7.1.B.* and *7.1.D; 7.2.B* and *7.1.D.*). Fat scores are negatively related with basal CORT levels in the Siberian stonechats, but not in the European stonechats (as indicated by significant interactions between fat scores and population). When the data was analysed with the Kazakh fledgling stage, the breeding stage had a significant effect on the stress-induced CORT levels (*Tables 7.1.A.* and *7.1.C; 7.2.A* and *7.1.C.*). This is due to the huge

decrease in the stress-induced CORT levels from the nestling to the fledgling stage in the Kazakh birds (*Fig. 7.1.)*
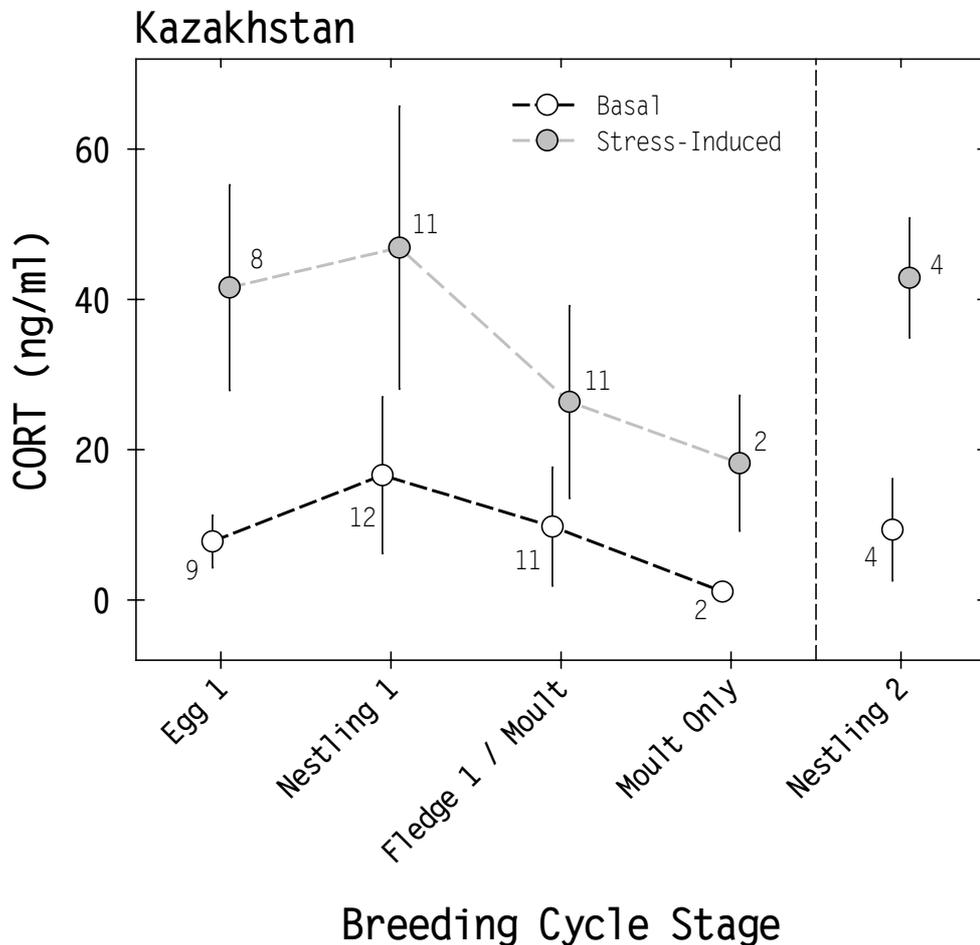

Fig. 7.1. Basal and stress-induced CORT levels in Siberian stonechats. Shown are mean values and standard deviations, the sample sizes are indicated. Both, basal and stress-induced plasma concentrations are highest during the nestling stages of first and replacement clutches. *Egg* stage: egg production and incubation. The suffixes *1* and *2* denominate first and replacement clutches.

7.4.2 CORT secretion in relation to offspring age and moult in Siberian stonechats

Basal CORT levels increased in Siberian stonechats from early incubation to fledging, then they decreased again. This was best described with a quadratic relationship ($F_{2,31} = 4.34$, $p < 0.05$, $R^2 = 0.22$). Stress-

induced CORT levels stayed about equal from early incubation to fledging and decreased subsequently with offspring age. Despite this change in the dynamics between the stages, this was best described by a linear relationship ($F_{1,30}$ = 4.31, p < 0.05, R^2 = 0.13)(Fig. 7.4.). Both basal and stress-induced CORT levels were highest at offspring age 8-9. The young fledge at an age of about 10 to 14 days. Moult scores increased from about offspring age 12 on. The relationship between the offspring age and the moult score was best described with a quadratic relationship ($F_{2,15}$ = 71.31, p < 0.01, R^2 = 0.91)(Fig. 7.4.).
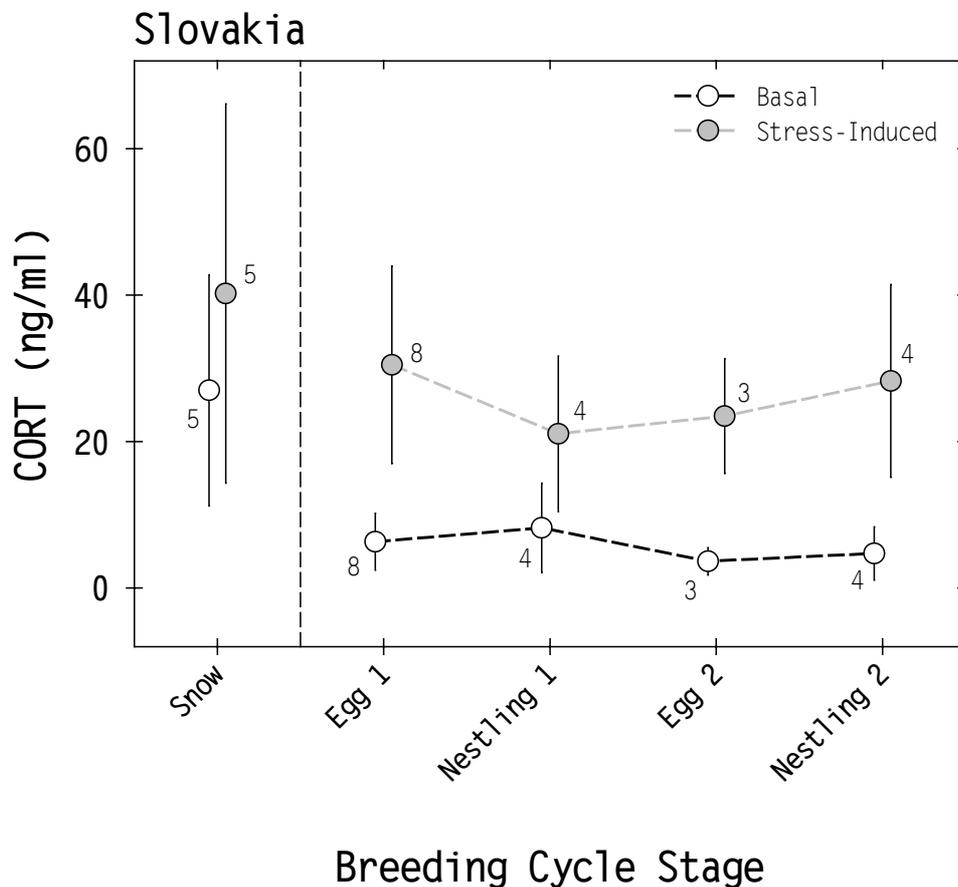
Fig. 7.2. Basal and stress-induced CORT levels in European stonechats. Shown are mean values and standard deviations, the sample sizes are indicated. During the breeding stages there are no clear patterns in the circulating plasma concentrations. Both, basal and stress-induced CORT levels are highest during a spell of inverse weather. *Snow*: A two-day period of low temperatures and snow cover during arrival; *Egg*: egg production and incubation. The suffixes *1* and *2* denominate first and second clutches.
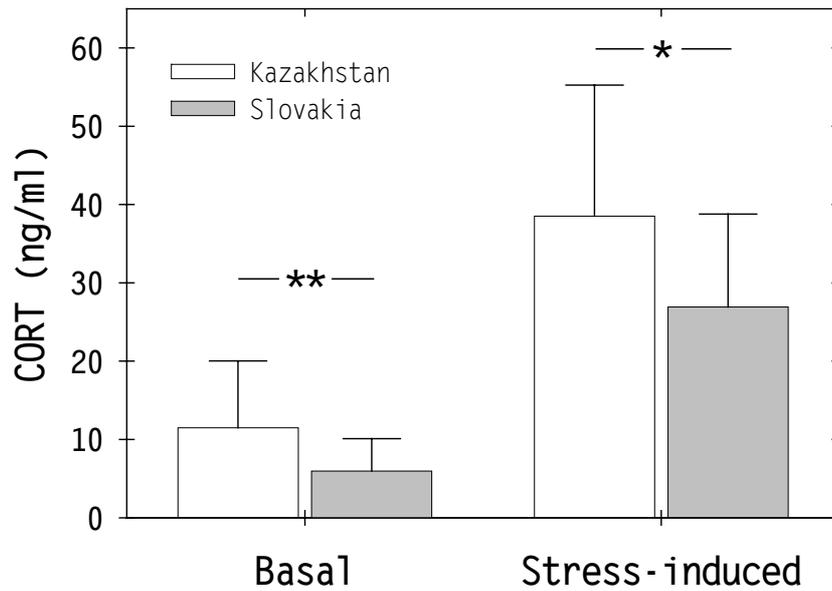
Fig. 7.3. Basal and stress-induced CORT levels during the breeding stages (egg production, nestling and fledgling stages) are significantly higher in Siberian than in European stonechats. The bars show means and standard deviations.
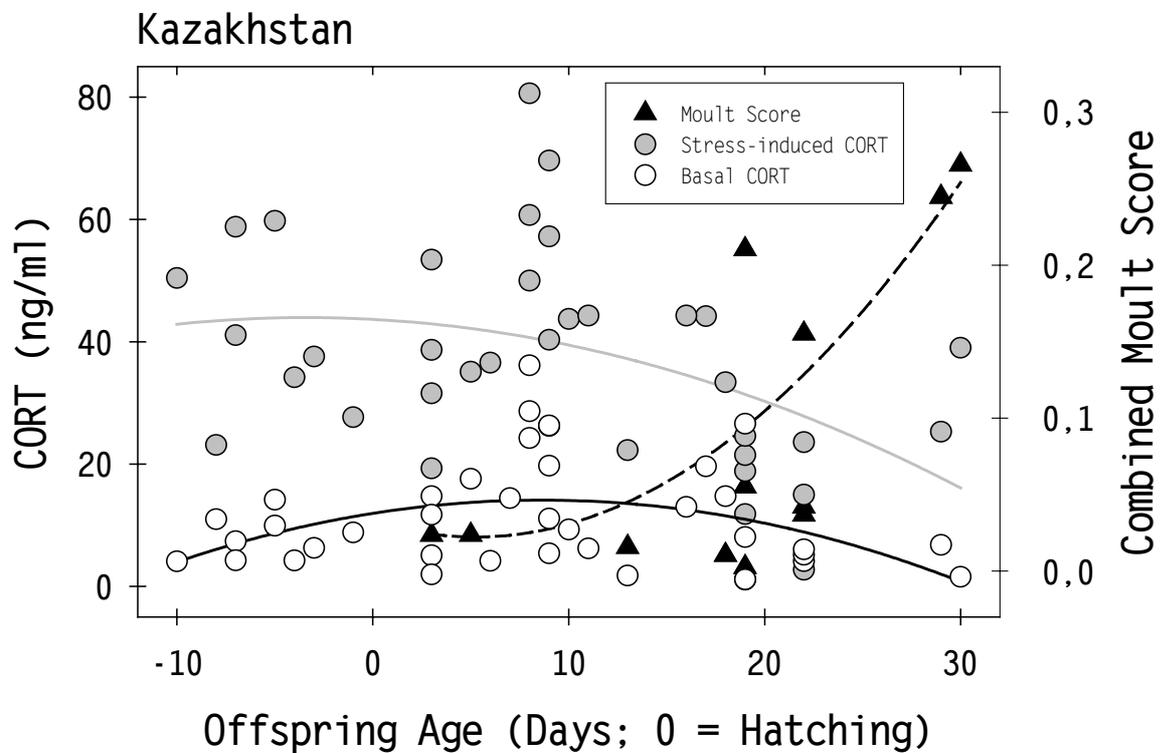

Fig. 7.4. Basal CORT, stress-induced CORT, and moult score in relation to offspring age in Siberian stonechats.

7.5   Discussion

7.5.1   CORT in relation to the length of the breeding season

CORT secretion during the breeding stages was higher in the single-clutched Siberian stonechats with a short breeding season than in the multi-clutched European stonechats with a long breeding season. Thus, the simplest prediction of the *reproductive limitation hypothesis*, a relationship between the potential number of annual clutches and HPA-activity (Wingfield & Romero 2001, Lynn et al. 2003, Wingfield & Sapolsky 2003), was not confirmed in this study. Support for this prediction has however been found in other species, predominantly in high-latitude breeders (Astheimer et al. 1994, Wingfield et al. 1994, Silverin et al. 1997, Romero et al. 1998, Silverin & Wingfield 1998, Meddle et al. 2003) and high-altitude breeders (Bears et al. 2003, Pereyra & Wingfield 2003, Goerlich 2004) with short breeding seasons. All these species down-regulate GC output during breeding relative to other life-history stages or relative to conspecifics with longer breeding season and this has been attributed to the potential disruptive effects of GCs on reproduction (Sapolsky et al. 2000).

Due to the sampling protocol applied it is possible that I missed changes in the stress-induced CORT secretion after more than 30 minutes of exposure. The stress-induced GC levels of dark-eyed juncos *Junco hyemalis* breeding at low and high altitudes did not differ after 30 minutes of handling stress, however after 60 minutes the low-altitude birds had higher GC levels (Bears et al. 2003). In the Siberian stonechats higher CORT levels were consistent in both the basal and the stress-induced levels. Thus, to achieve a change in the direction of the differences, stress-induced CORT secretion would have to increase considerably after 30 minutes. In European stonechats subjected to the capture-stress protocol for 30 minutes CORT reactions are usually close to the maximum (Canoine et al. 2002, Canoine et al., unpubl. results). Thus, higher CORT levels in

European than in Siberian stonechats in late stages of the GC response are unlikely.

Not all of the avian species with short breeding seasons studied so far show a decrease in the GC secretion during reproduction. Arctic-breeding white-crowned sparrows *Zonotrichia leucophrys gambelii* have higher basal and stress-induced CORT levels during breeding than during migration and winter (Astheimer et al. 1994, Romero et al. 1997, Romero & Wingfield 1998). Arctic-breeding Lapland longspurs *Calcarius lapponicus* have similar GC levels during breeding and migration (Astheimer et al. 1995). The white-rumped and the rufous-necked snowfinch *Onychostruthus taczanowskii* and *Pyrgilauda ruficollis* breed both in high altitudes, however they do not show a reduction in GC release during reproduction (Richardson et al. 2003).

Wingfield & Sapolsky (2003) suggest four possible mechanisms to avoid disruptive environmental effects on reproduction: *(1)* the perception of stressors is altered, *(2)* the HPA-activity and thus GC output are reduced, *(3)* the reproductive system is rendered insensitive to the HPA output, and *(4)* the reproductive system is hyper-stimulated to compensate for GC effects. The first two mechanisms do not seem to be effective in this study: stonechats of both populations clearly responded to the capture-stress protocol by increasing CORT secretion and apparently did not modulate GC output. In white crowned sparrows breeding at different latitudes (and hence different lengths of the breeding season) stress-induced GC levels did not differ between the populations (Breuner et al. 2003). There was however, a difference in the levels of corticosterone-binding globulin (CBG), which is thought to regulate the amount of biologically active GCs in the target tissues (Mendel 1989, Hammond 1995, Breuner & Orchinik 2002). As a result, the amount of biologically active (or *free*) GCs was lower in white-crowned sparrows breeding in higher latitudes which produce fewer clutches (Breuner et al. 2003). It is possible that similar mechanisms operate in Siberian and European stonechats. However, preliminary results on the CBG capacities and free

CORT in the two populations do not support this idea (Raess et al., unpublished data). European starling females had higher free GCs during the chick-rearing stage than during the laying and incubation stages, however nest abandonment was higher during laying and incubation than during chick-rearing. Within each stage, those females that gave up breeding had higher free GC levels than those females that did not abandon (Love et al. 2004).

The evaluation of the last two mechanisms, resistance or compensatory stimulation of the reproductive system in the presence of high GC levels, is beyond the possibilities of this study. Birds in both populations reacted to some environmental perturbations (e.g. a predator attack on the incubating female) by giving up a current breeding bout. It is however difficult to assess whether there were any differences in the responsiveness to stress between the populations. Nest desertions were more frequent in the European population, however the two locations presumably differed in predator densities (see Chapter 5 of this thesis).

It is important to note that this study and others with similar results do not rule out a modulation of the allostatic response mechanisms in relation to the length of the breeding season. GCs are elements of a complex neuroendocrine response cascade with several connections to the reproductive system (Wingfield & Sapolsky 2003). And indeed, most suppressive effects of stress on reproduction in birds have been attributed to effectors further upstream in the HPA-axis, e.g. to direct hypothalamic effects of CRH on the reproductive axis (Pottinger 1999).

7.5.2 CORT in relation to energetic demand and general risk of perturbation

The breeding period has been recognised as being particularly energetically costly (e.g. Hails & Bryant 1979, Drent & Daan 1980, Chastel et al. 2003, Schneider 2004). While most studies on the energetics of reproduction have focused on the chick rearing phase, recent studies emphasise the costs of egg formation and incubation (Monaghan & Nager 1997, Chastel et al. 2003, Cresswell et al. 2004). The *energy mobilisation*

hypothesis predicts that basal GC levels should reflect the energetic demand of a live-history stage (Dallman et al. 1993, Breuner et al. 1999, Romero 2002, Love et al. 2004). In the Siberian stonechats CORT levels increased from the stage of egg production and incubation to the nestling stage, and decreased again in the fledgling stage. These differences were more pronounced in the stress-induced than in the basal CORT levels. In the European stonechats, basal and stress-induced CORT levels did not differ between the egg and the nestling stages, data for the fledgling stage was not available. In neither population did sex influence CORT secretion in any of the breeding stages.

Only a few other studies on circulating GCs during breeding have attempted to differentiate between the breeding stages. In captive female European starlings basal and stress-induced CORT levels increased from laying and incubation to chick rearing, however only when the free fraction was considered (Love et al. 2004). In black redstarts *Phoenicurus ochruros* basal CORT levels during chick feeding were equal in both sexes. During incubation, females had lower levels and males higher levels than during feeding (Goerlich 2004). In grey-faced petrels *Pterodroma macroptera*, large long-lived seabirds breeding in New Zealand, basal CORT levels decreased from incubation to chick rearing in females and increased in males (Adams et al. 2005).

Fig. 7.5. summarises the results of the available studies on GC variation between breeding stages. In females, CORT increased from the egg to the nestling stage in three species and decreased or stayed equal in two. In males, CORT increased from the egg to the nestling stage in four and decreased in one species. Note that only the study on the captive starlings produced significant differences, while the studies on free-living birds failed to do so (*Fig. 7.5.*). How are these results to be interpreted in the light of the *energy mobilisation hypothesis*? The largest differences between the egg and the nestling stage in terms of energetic costs and hence basal GC levels would be expected in the non-incubating sex, because incubation itself is costly (Monaghan & Nager 1997, Cresswell

et al. 2004). While CORT levels increase from the egg to the nestling stage in male stonechats, they decrease in male redstarts. Male and female grey-faced petrels take alternating incubation shifts, however CORT levels increase in males but decrease in females. Clearly these patterns cannot be explained by stage-dependent energetic requirements alone.
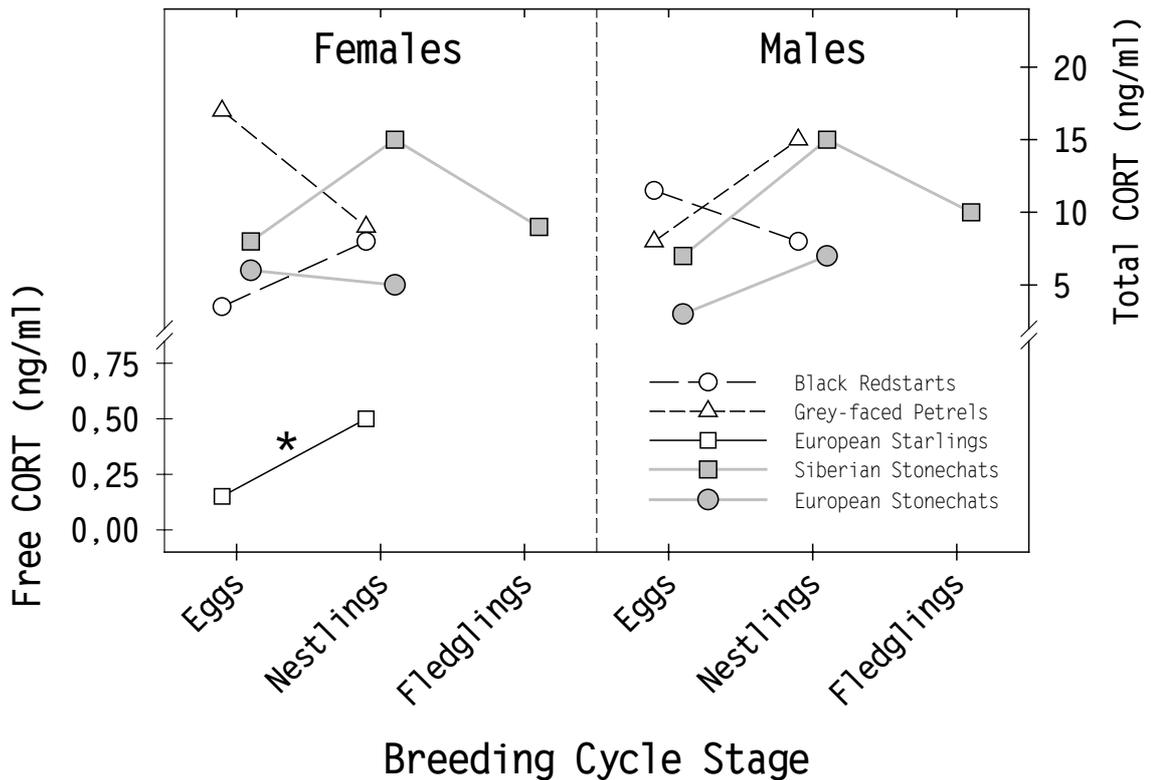

Fig. 7.5. Variation of CORT levels between the breeding stages in different species. Females are plotted on the left, males on the right of the graph. The asterisk marks a significant difference between stages. See text for further explanations.

Basal and stress-induced CORT levels in the European stonechats were highest during a short period of cold weather and snow-cover at the time of arrival. Also in other species inclement weather has the potential to increase GC secretion, however the actual GC response seems to depend on additional factors, such as the energy balance of a bird (Wingfield et al. 1983, Rogers et al. 1993, Astheimer et al. 1995, Wingfield & Ramenofsky

1997, Romero et al. 2000). During breeding, individual body condition, as indicated by the amount of stored body fat, affected basal GC levels in the Siberian, but not in the European stonechats. Again these results do not provide unequivocal support for an effect of energy balance on HPA activity. In his review on seasonal patterns of GC secretion Romero (2002) found that circulating GC levels decreased during moult in most avian species. He considered this as the strongest argument against the *energy mobilisation hypothesis*, because energy requirements during the moult stage are high (e.g. Murphy 1996, 1999). Siberian stonechats initiated moult immediately after their offspring had fledged. Because the birds consecutively overlapped two energetically costly tasks, parental care and moult, the *energy mobilisation hypothesis* would predict particularly high GC levels during that period. The opposite was true, however, basal and stress-induced CORT levels decreased steeply. The fact that in the Siberian stonechats and other species circulating GC levels are particularly low during the moulting stage could indicate that some aspects of the GC action are incompatible with the metabolic requirements during moulting.

Could the difference in the circulating CORT levels between the populations be explained by the different energetic requirements during breeding in Siberian and European stonechats? GC levels have been found to increase with clutch size in some species (Silverin 1982, Love et al. 2004). Generally, Siberian stonechats lay larger clutches than European stonechats (see Chapter 5 of this thesis), however in the sub-sample of birds where both clutch size was known and CORT samples were available clutch size did not differ significantly. Other unknown factors, such as prey availability or individual parental quality and experience further complicate any assessment of a difference in the energetic costs of breeding between the populations. There is however one factor that could potentially contribute to the observed variation between populations: Siberian stonechats had higher metabolic rates than European stonechats in a common garden experiment with captive birds during summer (Wikelski et al. 2003). The authors attributed this to general differences in the life-

histories of the populations. Buttemer and co-workers (1991) did not find a direct effect of CORT on metabolic rates in white-crowned sparrows and pine siskins *Carduelis pinus*. However, little is known about the relationship of circulating GC levels and metabolic rates in birds, and a connection is well conceivable.

Sapolsky et al. (2000) developed a system for characterising GC actions, and among these were *preparative* effects, i.e. GC serve to set up the organism for future environmental challenges. Based on this Romero (2002) developed the *preparative hypothesis* which predicts that seasonal changes in circulating GC levels are related to variation in the propensity to encounter environmental stressors. However, as Romero points out, seasonal differences in the probability of encountering adverse conditions are difficult to quantify. Furthermore, the predictions derived from this hypothesis are in part hard to separate from those of the *energy mobilisation hypothesis*. The breeding stage, for example, is both a period of high energetic demand, and of increased vulnerability to predators and inclement weather.

At the moment neither the *preparative hypothesis* nor any of the other hypothesis brought forward succeeds to satisfactory explain interspecific and seasonal variation in the levels of circulating glucocorticoids. Both is needed, a deeper understanding of the integration of the GCs with other components of the allosteric response such as the catecholamines and the cytokines, and a broader knowledge base of how different species modify these response systems according to their life-histories.

7.6   References

Adams, N. J., Cockrem, J. F., Taylor, G. A., Candy, E. J. & Bridges, J. (2005). Corticosterone responses of grey-faced petrels (*Pterodroma macroptera gouldi*) are higher during incubation than during other breeding stages. *Physiological and Biochemical Zoology* 78: 69-77.

Astheimer, L. B., Buttemer, W. A. & Wingfield, J. C. (1994). Gender and seasonal differences in the adrenocortical response to ACTH challenge in an arctic passerine, *Zonotrichia leucophrys gambelii*. *General and Comparative Endocrinology* 94: 33-43.

Astheimer, L. B., Buttemer, W. A. & Wingfield, J. C. (1995). Seasonal and acute changes in adrenocortical responsiveness in an arctic-breeding bird. *Hormones and Behavior* 29: 442-457.

Axelrod, J. & Reisine, T. D. (1984). Stress hormones: their interaction and regulation. *Science* 224: 452-459.

Bears, H., Smith, J. N. M. & Wingfield, J. C. (2003). Adrenocortical sensitivity to stress in dark-eyed juncos (Junco hyemalis oregonus) breeding in low and high elevation habitat. *Ecoscience* 10: 127-133.

Besedovsky, H. O. & Del Rey, A. (1996). Immune-neuro-endocrine interactions: Facts and hypotheses. *Endocrine Reviews* 17: 64-102.

Breuner, C. W. & Hahn, T. P. (2003). Integrating stress physiology, environmental change, and behavior in free-living sparrows. *Hormones and Behavior* 43: 115-123.

Breuner, C. W. & Orchinik, M. (2002). Plasma binding proteins as mediators of corticosteroid action in vertebrates. *Journal of Endocrinology* 175: 99-112.

Breuner, C. W., Orchinik, M., Hahn, T. P., Meddle, S. L., Moore, I. T., Owen-Ashley, N. T., Sperry, T. S. & Wingfield, J. C. (2003). Differential mechanisms for regulation of the stress response across latitudinal gradients. *American Journal of Physiology* 285: R594-R600.

Breuner, C. W., Wingfield, J. C. & Romero, L. M. (1999). Diel rhythms of basal and stress-induced corticosterone in a wild, seasonal vertebrate, Gambel's white-crowned sparrow. *Journal of Experimental Zoology* 284: 334-342.

Buttemer, W. A., Astheimer, L. B. & Wingfield, J. C. (1991). The effect of corticosterone on standard metabolic rates of small passerine birds. *Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology* 161: 427-432.

Cannon, W. B. (1932). *The Wisdom of the Body*. W. W. Norton, New York.

Canoine, V., Hayden, T. J., Rowe, K. & Goymann, W. (2002). The stress response of the European stonechat depends on the kind of stressor. *Behaviour* 139: 1303-1311.

Chastel, O., Lacroix, A. & Kersten, M. (2003). Pre-breeding energy requirements: thyroid hormone, metabolism and the timing of reproduction in house sparrows *Passer domesticus*. *Journal of Avian Biology* 34: 298-306.

Cresswell, W., Holt, S., Reid, J. M., Whitfield, D. P., Mellanby, R. J., Norton, D. & Waldron, S. (2004). The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behavioral Ecology* 15: 498-507.

Dallman, M. F., Strack, A. M., Akana, S. F., Bradbury, M. J., Hanson, E. S., Scribner, K. A. & Smith, M. (1993). Feast and famine - critical role of glucocorticoids with insulin in daily energy-flow. *Frontiers in Neuroendocrinology* 14: 303-347.

Drent, R. H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.

Goerlich, V. (2004). Altitudinal modulation of the stress response in black redstarts (Phoenicurus ochruros). Masters thesis, Ludwig-Maximilians-Universität Munich.

Goymann, W. & Wingfield, J. C. (2004). Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour* 67: 591-602.

Grafen, A. & Hails, R. (2002). *Modern Statistics for the Life Sciences*. Oxford University Press, Oxford.

Hails, C. J. & Bryant, D. M. (1979). Reproductive energetics of a free-living bird. *Journal of Animal Ecology* 48: 471-482.

Hammond, G. L. (1995). Potential functions of plasma steroid-binding proteins. *Trends in Endocrinology and Metabolism* 6: 298-304.

Korte, S. M., Koolhaas, J. M., Wingfield, J. C. & McEwen, B. S. (2005). The Darwinian concept of stress: benefits of allostasis and costs of allostatic load and the trade-offs in health and disease. *Neuroscience & Biobehavioral Reviews* 29: 3-38.

Kovacs, K. J. (2002). Neurohypophyseal hormones in the integration of physiological responses to immune challenges. *In* D. Poulain, S. Oliet & D. Theodosis (Eds.), *Progress in Brain Research*, Vol. 139, pp. 127-146. Elsevier.

Love, O. P., Breuner, C. W., Vezina, F. & Williams, T. D. (2004). Mediation of a corticosterone-induced reproductive conflict. *Hormones and Behavior* 46: 59-65.

Lynn, S. E., Hunt, K. E. & Wingfield, J. C. (2003). Ecological factors affecting the adrenocortical response to stress in chestnut-collared and McCown's longspurs (*Calcarius ornatus*, *Calcarius mccownii*). *Physiological and Biochemical Zoology* 76: 566-576.

Marra, P. P. & Holberton, R. L. (1998). Corticosterone levels as indicators of habitat quality effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia* 116: 284-292.

McEwen, B. S. & Wingfield, J. C. (2003). The concept of allostasis in biology and biomedicine. *Hormones and Behavior* 43: 2-15.

Meddle, S. L., Owen-Ashley, N. T., Richardson, M. I. & Wingfield, J. C. (2003). Modulation of the hypothalamic-pituitary-adrenal axis of an arctic-breeding polygynandrous songbird, the

Smith's longspur, *Calcarius pictus*. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 1849-1856.

Mendel, C. (1989). The free hormone hypothesis: a physiologically based mathematical model. *Endocrine Reviews* 10: 232-274.

Monaghan, P. & Nager, R. G. (1997). Why don´t birds lay more eggs? *Trends in Ecology and Evolution* 12: 270-274.

Murphy, M. E. (1996). Energetics and nutrition of molt. *In* C. Carey (Ed.), *Avian Energetics and Nutritional Ecology*, pp. 158-198. Chapman & Hall, New York.

Murphy, M. E. (1999). Energetics and nutrition of moulting. *In* N. J. Adams & R. H. Slotow (Eds.), *Proc. 22 Int. Ornithol. Congr., Durban*, pp. 527-535. BirdLife South Africa, Johannesburg.

Pereyra, M. E. & Wingfield, J. C. (2003). Changes in plasma corticosterone and adrenocortical response to stress during the breeding cycle in high altitude flycatchers. *General and Comparative Endocrinology* 130: 222-231.

Pottinger, T. G. (1999). The impact of stress on animal reproductive activities. *In* P. H. M. Balm (Ed.), *Stress Physiology in Animals*, pp. 130-177. Sheffield Academic Press, Sheffield.

Rich, E. L. & Romero, L. M. (2001). Daily and photoperiod variations of basal and stress-induced corticosterone concentrations in house sparrows (Passer domesticus). *Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology* 171: 543-547.

Richardson, M., Moore, I. T., Soma, K. K. & Wingfield, J. C. (2003). How similar are high latitude and high altitude habitats? A review and a preliminary study of the adrenocortical response to stress in birds of the Qinghai-Tibetan Plateau. *Acta Zoologica Sinica* 49: 1-19.

Rogers, C. M., Ramenofsky, M., Ketterson, E. D., Nolan, V., Jr. & Wingfield, J. C. (1993). Plasma corticosterone, adrenal mass, winter weather, and season in nonbreeding populations of dark-eyed juncos (*Junco hyemalis hyemalis*). *Auk* 110: 279-285.

Romero, L. M. (2002). Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology* 128: 1-24.

Romero, L. M., Ramenofsky, M. & Wingfield, J. C. (1997). Season and migration alters the corticosterone response to capture and handling in an Arctic migrant, the white-crowned sparrow (Zonotrichia leucophrys gambelii). *Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology* 116: 171-177.

Romero, L. M. & Reed, J. M. (2005). Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 140: 73-79.

Romero, L. M., Reed, J. M. & Wingfield, J. C. (2000). Effects of weather on corticosterone responses in wild free-living passerine birds. *General and Comparative Endocrinology* 118: 113-122.

Romero, L. M. & Romero, R. C. (2002). Corticosterone responses in wild birds: The importance of rapid initial sampling. *Condor* 104: 129-135.

Romero, L. M., Soma Kiran, K. & Wingfield, J. C. (1998). The hypothalamus and adrenal regulate modulation of corticosterone release in redpolls (*Carduelis flammea*-an arctic-breeding song bird). *General and Comparative Endocrinology* 109: 347-355.

Romero, L. M. & Wingfield, J. C. (1998). Seasonal changes in adrenal sensitivity alter corticosterone levels in Gambel's white-crowned sparrows (Zonotrichia leucophrys gambelii). *Comparative Biochemistry and Physiology Part C: Pharmacology, Toxicology and Endocrinology* 119: 31-36.

Sapolsky, R. M., Romero, L. M. & Munck, A. U. (2000). How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine Reviews* 21: 55-89.

Schneider, J. E. (2004). Energy balance and reproduction. *Physiology and Behavior* 81: 289-317.

Silverin, B. (1982). Endocrine correlates of brood size in adult pied flycatchers, *Ficedula hypoleuca*. *General and Comparative Endocrinology* 47: 18-23.

Silverin, B. (1986). Corticosterone-binding proteins and behavioral effects of high plasma levels of corticosterone during the breeding period in the pied flycatcher *Ficedula hypoleuca*. *General and Comparative Endocrinology* 64: 67-74.

Silverin, B. (1998). Behavioural and hormonal responses of the pied flycatcher to environmental stressors. *Animal Behaviour* 55: 1411-1420.

Silverin, B., Arvidsson, B. & Wingfield, J. C. (1997). The adrenocortical responses to stress in breeding Willow Warblers Phylloscopus trochilus in Sweden: Effects of latitude and gender. *Functional Ecology* 11: 376-384.

Silverin, B. & Wingfield, J. C. (1998). Adrenocortical responses to stress in breeding pied flycatchers Ficedula hypoleuca: Relation to latitude, sex and mating status. *Journal of Avian Biology* 29: 228-234.

Sterling, P. & Eyer, J. (1988). Allostasis: a new paradigm to explain arousal pathology. *In* S. Fisher & J. Reason (Eds.), *Handbook of Life Stress, Cognition and Health*, pp. 629-649. Wiley, New York.

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A. & Gwinner, E. (2003). Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 2383-2388.

Wingfield, J. C., Breuner, C. W. & Jakobs, J. (1997). Corticosterone and behavioral responses to unpredictable events. *In* S. Harvey & R. J. Etches (Eds.), *Perspectives in Avian Endocrinology*, pp. 267-278. Journal of Endocrinology Ltd., Bristol.

Wingfield, J. C., Deviche, P., Sharbaugh, S., Astheimer, L. B., Holberton, R., Suydam, R. & Hunt, K. (1994). Seasonal changes of the adrenocortical responses to stress in redpolls, *Acanthis flammea*, in Alaska. *Journal of Experimental Zoology* 270: 372-380.

Wingfield, J. C., Moore, M. C. & Farner, D. S. (1983). Endocrine responses to inclement weather in naturally breeding populations of white-crowned sparrows (*Zonotrichia leucophrys pugetensis*). *Auk* 100: 56-62.

Wingfield, J. C., O´Reilly, K. M. & Astheimer, L. B. (1995). Modulation of the adrenocortical responses to acute stress in arctic birds: a possible ecological basis. *American Zoologist* 35: 285-294.

Wingfield, J. C. & Ramenofsky, M. (1997). Corticosterone and facultative dispersal in responses to unpredictable events. *Ardea* 85: 155-166.

Wingfield, J. C. & Romero, L. M. (2001). Adrenocortical responses to stress and their modulation in free-living vertebrates. *In* B. S. McEwen (Ed.), *Handbook of Physiology. Section 7: The Endocrine System*, Vol. 4: Coping with the Environment: Neural and Endocrine Mechanisms, pp. 211-234. Oxford University Press, Oxford.

Wingfield, J. C. & Sapolsky, R. M. (2003). Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology* 15: 711-724.

Wingfield, J. C., Vleck, C. M. & Moore, M. C. (1992). Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. *Journal of Experimental Zoology* 264: 419-428.

8 DEVELOPMENTAL RATES IN SIBERIAN AND EUROPEAN STONECHATS

8.1 Summary

Developmental rates are shaped by a trade-off between factors favouring fast growth, such as time-dependent mortality, factors promoting slow development, such as the investment into complex tissues like the nervous and immune systems, and physiological constraints on growth. Differences in the life-histories of Siberian and European stonechats may also affect their early development. Siberian stonechats have slightly shorter incubation periods, which may be an indication for a faster embryonic development in this population. After hatching, the increase in body size is slower in the European stonechats, whereas wing growth (but not the growth of the 8th primary) proceeds faster. In neither population calendar date seems to have a profound effect on the growth rates of body size and wing length. Runts, nestlings that have hatched later than their nestmates, start out heavier and larger in both populations, but soon loose this headstart, due to their relative competitive disadvantage and resulting slower growth. As in the captive birds, free-living Siberian stonechat juveniles initiate postjuvenile moult at an earlier age than their European conspecifics. The onset of moult is affected by calendar date, late-hatched Siberian stonechats may initiate moult at the earliest age that is physiologically possible.

8.2   Introduction

8.2.1 The significance of the developmental period

During the developmental phase the phenotype is shaped by the interaction of the genotype with the environment. Therefore, the conditions experienced during early life have profound and long-lasting consequences (reviewed in Lindström 1999, see also Karten et al. 2005 for a recent result). Often, these early conditions are strongly influenced by the parents, e.g. by the body condition of the pregnant mother (Kaiser & Sachser 2005). Because the abilities of the developing organism to control its environment are very restricted or lacking, parental effects have strong implications for the formation of the adult function (Mousseau & Fox 1998, Lindström 1999).

The avian embryo develops in an enclosed environment which has been fitted by the mother with all the nutrients and other agents that are conducive to the embryo's development (Williams 1994, Perrins 1996, Apanius 1998, Müller et al. 2004, Groothuis et al. 2005). After hatching, altricial chicks continue to depend on their parents for the provisioning of food and warmth, until they attain the full capacity to thermoregulate and gather food autonomously. Several studies show that nestling condition affects the probability of short-term survival and recruitment into the breeding population (Garnett 1981, Tinbergen & Boerlijst 1990, Magrath 1991 and citations therein, Merilä & Svensson 1997, Both et al. 1999). Other studies describe long-lasting effect of early conditions on features of the adult phenotype such as immune function and longevity, song performance, and clutch size (Haywood & Perrins 1992, Schluter & Gustafsson 1993, Birkhead et al. 1999, Buchanan et al. 2003, Spencer et al. 2003, Buchanan et al. 2004, Spencer et al. 2004). Hence, parental strategies of reproductive investment, and the ability of the offspring to solicit parental care contribute considerably to the shaping of the adult phenotype.

8.2.2   Selection on embryonic and postnatal growth rates

Phenotypic quality may not only vary according to the resources that are placed at the disposal of the developing organism, but also depend on the rate at which adult function is attained. Extremely slow growth is energetically inefficient (Ricklefs & Starck 1998, Ricklefs et al. 1998). There are, however, theoretical considerations, backed up by empirical evidence, that the adult capacities of complex tissues such as the immune and the nervous systems are negatively related to their rate of formation (Ricklefs 1992, Starck 1993, Apanius 1998, Ricklefs et al. 1998, Tella et al. 2002, Ricklefs 2004). Hence, selection may favour slow growth at least in those species that invest more into the adult function, e.g. long-lived species (Williams 1966, Roff 1992, Stearns 1992). Moreover, faster growth requires more energy (Klaassen & Drent 1991) and may thus lead to increased mortality when resources are scarce (Clutton-Brock et al. 1985).

On the other hand, if the full ability to avoid predation and to withstand adverse environmental conditions depends on the adult function, then there is high selective potential for fast development (Case 1978, Ricklefs 1993, Arendt 1997). High mortality rates characterise the developmental period of many avian species (Newton 1989, Sullivan 1989, Magrath 1991, Naef-Daenzer et al. 2001). Other factors selecting for fast growth are sibling competition (Werschkul & Jackson 1979, Ricklefs 1993) and the energetic costs of parental care (Drent & Daan 1980, Tinbergen & Dietz 1994, Monaghan & Nager 1997, Visser & Lessells 2001, Cresswell et al. 2004).

These mechanisms have led to a diversification of avian growth rates very early in the phylogenetic process (Starck & Ricklefs 1998a). Most of the intraspecific variation in developmental rates resides at high taxonomic levels, and there are strong scaling relationships of growth rates with final body mass (and egg mass), two measures with themselves relate strongly to phylogeny (Ricklefs & Starck 1998, Starck & Ricklefs 1998a). Ontogenetic category (the position within the altricial-precocial spectrum), explains some additional interspecific variation of postnatal

growth rates, but seems to be unrelated to rate of embryonic development (Ricklefs & Starck 1998, Ricklefs et al. 1998).

The length of the breeding season may be another potential factor affecting perinatal growth rates, particularly in migratory species, where the birds relatively early in their lives have to cope with the demands of autumn migration. Ricklefs (1993) found no relationship between the length of the breeding season and the length of the incubation periods. His analysis may, however, been confounded by phylogenetic and latitudinal trends in his data set, and was restricted to the prenatal period. The relationship between postnatal growth rates and the length of the breeding season has as yet not been investigated.

8.2.3   Postjuvenile moult

The end of structural growth usually does not mark the completion of avian development. If we define the *juvenile* stage of development as the period during which the young obtain 'energetic' independence from the parents, i.e. they gain the ability to satisfy their caloric and nutritional needs autonomously, then the *postjuvenile* stage is the period during which full adulthood is attained. This includes the achievement of full reproductive maturity (but note that also the adults of most avian species cycle physiologically through annual states of sexual maturity and 'pre-puberty', see Chapter 4 of this thesis), of adult-like vocalisations, and an adult-like plumage. Passerine fledglings possess a juvenile plumage which consists of fewer, less elaborate feathers than the adult plumage (Jenni & Winkler 1994). It is obtained during the nestling period to serve for insulation once parental brooding ceases. The young carry out a postjuvenile moult during which the body feathers and sometimes also parts of the flight feathers are shed and replaced (Jenni & Winkler 1994). The first purpose of this postjuvenile moult is to obtain adult-like feathers. These feathers have a tighter texture and improved thermoregulatory capacities. Moreover, they usually show the adult colouration, which may however only become apparent after the outer rims have been worn off. The

second purpose of postjuvenile moult is to bring the juveniles moult cycle into phase with that of the adults. Postjuvenile moult and adult postnuptial moult are usually carried out at about the same time (Jenni & Winkler 1994, Winkler 1999).

Avian moult strategies in general are very variable and adapted to the annual cycle and life-history of the species. Postjuvenile moult schedules are strongly influenced by the length of the 'moult window', i.e. the period of conditions favourable for moult. A strong determinant of the length of this moult window is the migratory behaviour of the species, and long-distance migrants usually show the earliest and fastest postjuvenile moult (Berthold et al. 1970, Jenni & Winkler 1994, Helm & Gwinner 1999, Winkler 1999, Helm & Gwinner 2001). There is also a strong effect of hatching date on individual variation in the onset and duration of postjuvenile moult (Helm et al. 2005).

8.2.4   Developmental rates in free-living stonechats

The postnatal development and postjuvenile moult of Siberian, European, and African stonechats (*S.t. axillaris*) has been examined under controlled laboratory conditions (Starck et al. 1995, Helm & Gwinner 1999, 2001, Helm et al. 2005). Common garden experiments revealed the relative contributions of genetic background and of phenotypic plasticity to the diversification of developmental patterns between these subspecies. In the present study, I investigated developmental rates of Siberian and European stonechats under field conditions. This allows assessing the potential effects of the subspecies' life-history and environment on the patterning of juvenile development against the background from what is known about stonechat juvenile development from captive studies.

In this chapter, I compare the duration of the incubation periods between Siberian and European stonechats as an indication of rate of prenatal development. Then, I compare postnatal growth rates between Siberian and European stonechats, using linear and nonlinear (curve-fitting) methods. I explore the effects of calendar date and of hatching

category (core nestlings vs. runts) within populations and clutches. Finally, I examine the schedule of postjuvenile moult in Siberian stonechats. The results of these analyses are discussed on the basis of our current knowledge of life-history parameters and the genetic background and phenotypic flexibility of postnatal development in these populations.

8.3   Methods

8.3.1   Prenatal development

The length of the incubation period reflects the duration of embryonic development (Ricklefs 1993, Ricklefs & Starck 1998). To determine incubation periods, I recorded the number of days from the onset of incubation until hatching of the first chick. This was done only for nests that had been detected before the onset of incubation, i.e. during the egg laying stage, and survived until hatching. This was the case in 12 out of 183 nests in Kazakhstan and in 9 out of 72 nests in Slovakia. The mean incubation periods of the Siberian and the European stonechat populations were compared with a t-test.

8.3.2   Postnatal growth

I determined postnatal growth during the nestling period and in fledged birds that were banded as nestlings and hence their age was known. I measured body mass, wing length, the length of the 8th primary, and tarsus length (See Chapter 2, section 2.4.1. for a detailed description of how the measurements were taken in adult birds, similar methods were applied here). The measurements on nestlings were done *(1)* in focal nests (Kazakhstan: n = 6, Slovakia: n = 10) every day from hatching (= day 0) to the age of day 7 or day 8, these measurements were taken at the same time each day; *(2)* in the remaining nests around day 5 to determine nestling age using the data from the focal nests, or at any time when the age of a newly found nest with older nestlings had to be determined. Whenever a nest was

approached, the precautionary measures were taken as described in Chapter 6 of this thesis. The measurements were carried out in a distance of at least 50 m from the nest. The empty nest cup was meanwhile covered with a cloth bag. Thus the parents experienced an ongoing disturbance at the nest rather than nest loss. The measurements usually took between 3 and 20 minutes, depending on the age of the nestlings. None of the breeding pairs in Kazakhstan or Slovakia gave up a breeding attempt as a response to the measurements. Around day 10 in Kazakhstan and day 11 in Slovakia the nestlings were banded with aluminium and plastic rings for individual recognition. This sometimes induced fledging in the nestlings (particularly if nestlings were banded later than day 11 in Kazakhstan and day 12 in Slovakia). Hence I did not obtain an independent measure of the period between hatching and fledging in our birds.

Incubation of the clutches before the last egg is laid can lead to asynchronous hatching, where one or more nestlings (the *runts*) or younger than their siblings (the *core nestlings*). Runts were identified as nestlings that had consistently lower measurements of body mass and body size.

Statistical analysis

For the analysis of postnatal growth I calculated means for all the nestlings in the clutch, because analysis of individual measures could be biased by kinship. To obtain averages of nestlings of the same age, these means were calculated for core nestlings and runts separately. The analysis of growth rates in the different populations and of the effect of season on growth was then carried out using only data fromt the core nestlings. The difference in growth of core nestlings and runts was compared using only core nestlings of nests that contained also runts.

The rate of body mass gain in Siberian and European stonechats was compared by fitting theoretical nonlinear three-parametric growth curves to the data:

Logistic function: $\quad Y = \dfrac{A}{1 + e^{-K(x-x_0)}}$

Gompertz function: $\quad Y = A * e^{-K(x-x_0)}$ $\quad$ (Starck & Ricklefs 1998b)

where *A* is the asymptotic value of the size variable, *K* is the growth rate constant, and x_0 is the inflection point of the curve (Starck & Ricklefs 1998b). The curve with the better fit (as indicated by a higher R^2-value) was chosen to compare the K-values. The curve-fitting was carried out with GraphPadPrism 3.0, GraphPad Sofware Inc.

The growth rate constant is very sensitive to the asymptotic value the curve is fitted to. The body mass in juvenile stonechats is often highest just prior to fledging (what I term *pre-fledging peak mass*), and decreases after fledging steadily towards adult levels (see *Fig. 8.2.*). To take account for this phenomenon, and to investigate two potential growth trajectories, the asymptotic values *A* were fixed first to the population mean pre-fledging peak mass (Kazakhtsan: m_{d10} = 14.16 g; Slovakia: m_{d11} = 15.13 g), and then to the mean adult mass in the population (Kazakhtsan: m_{adult} = 12.86 g; Slovakia: m_{adult} = 15.44 g). The measurements of tarsus length, wing length and length of the 8th primary were treated the same way; however the curves were fitted only to the average adult values as asymptotic values.

For a subsample of the body mass data, repeated measurements of individual nestlings were available from posthatch days 2 to 7, the linear part of the sigmoid growth curve (see *Fig. 8.2.*). As in the other analyses, these measurements of all core nestlings in a nest were averaged for each day. I then performed three repeated-measures GLMs to compare the subspecies: the first with the absolute mass data, the second with mass expressed as the proportion of the pre-fledging peak mass in the population, and the third with mass expressed as the proportion of the average adult mass of the population. Thus, as in the fitted growth curves, different possible growth trajectories were explored.

There was not enough data of the later breeding attempts in both populations to allow a direct exploration of the effect of calendar date on growth using fitted growth curves or repeated-measures GLMs. Therefore I carried out GLMs of the nest mean values of body mass, length of the 8th primary, and tarsus length at a given age plotted against date.

To compare postnatal growth between core nestlings and runts in Siberian and European stonechats, the nest means of core nestlings and runts of those clutches that contained asynchronously hatched young were matched for age. I then fitted theoretical growth curves to the data, as described above. Al curves were fitted to the mean adult values. In a second step, I assessed a possible effect of nestling age on the difference in growth between core nestlings and runts. To achieve this, I calculated the difference in the growth variables between core nestlings and runts $\Delta R(unt)/C(ore)$ expressed in core nestling units:

$$\Delta R/C \; x_i = \frac{\overline{x}_{i,runt} - \overline{x}_{i,core}}{\overline{x}_{i,core}} \; ,$$

where $\overline{x}_i$ is the mean value of a growth variable at age i. A positive value indicates larger growth values in the runts, a negative value faster growth values in the core nestlings. The effect of nestling age on $\Delta R/C$ was analysed using GLMs.

8.3.3   Postjuvenile moult

Fledged juveniles that had been banded as nestlings were recaptured at various ages with mist nets. The birds were checked for body moult in 19 distinct body parts (adapted from Berthold et al. 1970, see Flinks 1999, Fig. 4). The number of simultaneously moulting body parts gave a moult score which ranged from 1 to 19. When more birds from the same nest were caught at the same day, the scores were averaged. The resulting moult scores were plotted against the age of the birds. I fitted a logistic growth curve analague to the previous section, however not for analytical reasons but to show a possible mean progress of moult. As in studies on captive stonechats (Helm & Gwinner 1999, 2001, Helm et al. 2005), the onset

of moult was defined as the age when five body parts moulted simultaneously. And as in these studies, postjuvenile moult in other areas such as the wing and the tail (Flinks 1999) was not considered.

8.4   Results

8.4.1   Incubation periods

The mean durations of the incubation period were 13.17 days (n = 12, range 12 to 14 days) in Kazakhstan, and 13.67 days (n = 9, range 13 to 15 days) in Slovakia (*Fig. 8.1.*). This difference was not significant (t-test: t_{19} = -1.79, p = 0.09), but power for detection was low.
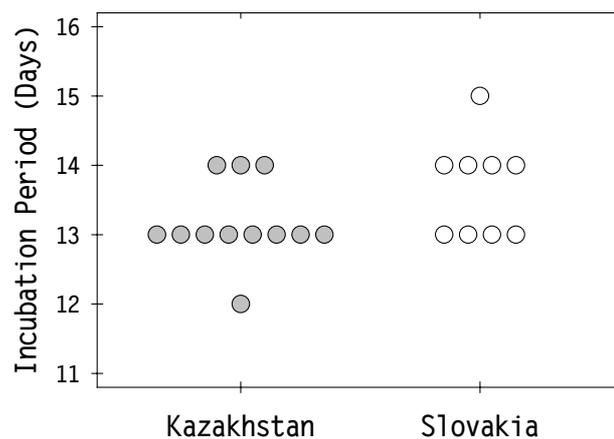
Fig. 8.1. The durations of the incubation periods in Siberian and European stonechats for those clutches for which information for the full incubation period was available.

8.4.2   Postnatal growth

Comparisons between populations

Adult Siberian and European stonechats differ in body mass and body size (see Chapter 2 of this thesis). Accordingly, the absolute gain in body mass and body size per day differs between nestlings of the two populations (*Figs. 8.2. to 8.5.*). The rate of increase towards these absolute values (described by the growth rate constants *K* of the logistic and Gompertz

curves) also differs between Kazakh and Slovak stonechat nestlings. This is indicated by the non-overlapping convidence intervals of the *K*-values (*Table 8.1.*). Growth rates towards pre-fledging peak body mass, adult body mass, adult tarsus length, and adult length of the 8th primary are higher in the Siberian stonechats, whereas the growth rate towards adult wing length is higher in the European stonechats (note, however, that in the European birds the wing measurements stopped before asymptotic size was reached). The differences in the rates of body mass gain are greater when the growth towards the adult mass is compared, than when growth towards the pre-fledging peak mass is compared (*Table 8.1.*).

The analysis of the linear growth curve between day 1 and day 7 reveals no difference in the absolute mass increase between the two populations (repeated-measures GLM; POPULATION: $F_{1,14} = 0.03$, $p = 0.86$; POPULATION x AGE: $F_{5,70} = 0.19$, $p = 0.69$)(*Fig. 8.6.A.*). The two populations also do not differ in the rate the nestlings approach their pre-fledging peak mass (POPULATION: $F_{1,14} = 0.36$, $p = 0.56$; POPULATION x AGE: $F_{5,70} = 0.78$, $p = 0.60$)(*Fig. 8.6.B.*). However, when growth towards the mean adult mass is considered, then there is a clear difference between the two populations. During the linear portion of the growth curve, Siberian stonechat nestlings approach adult mass at a higher rate than European stonechats (POPULATION: $F_{1,14} = 23.67$, $p < 0.001$; POPULATION x AGE: $F_{5,70} = 15.35$, $p < 0.001$)(*Fig. 8.6.C.*).

Table 8.1. The growth rate constants *K* and their 95% confidence intervals of measures of body mass and body size growth in Siberian and European stonechats. The asterisks indicate non-overlaping confidence intervals of the measures of the two populations.

	Kazakhstan K	Slovakia K	
Body mass (growth towards pre-fledging peak mass)[A]	.617	.570	
Body mass (growth towards adult mass)[A]	.726	.545	*
Tarsus length[A]	.687	.562	*
Wing length[A]	.248	.269	*
Length of 8th primary[B]	.236	.219	

[A] best fit with the logistic growth function
[B] best fit with the Gompertz function
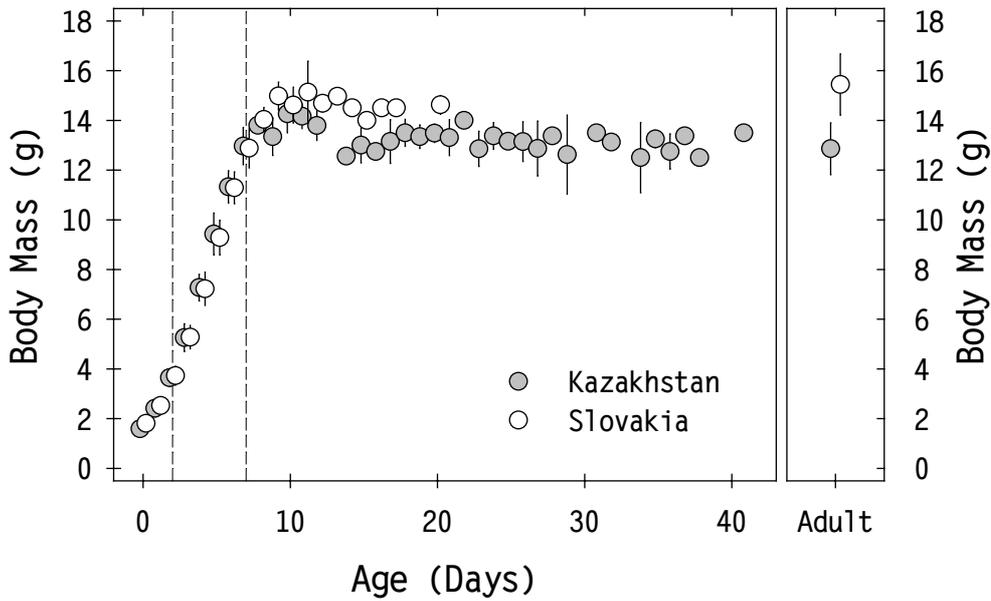
Fig. 8.2. The posthatching increase in body mass in Siberian and European stonechats. Note that the data points of the two populations are offset along the x-axis to allow a better distinction. The two dashed lines indicate the linear portion of the growth curve between day 1 and day 7.
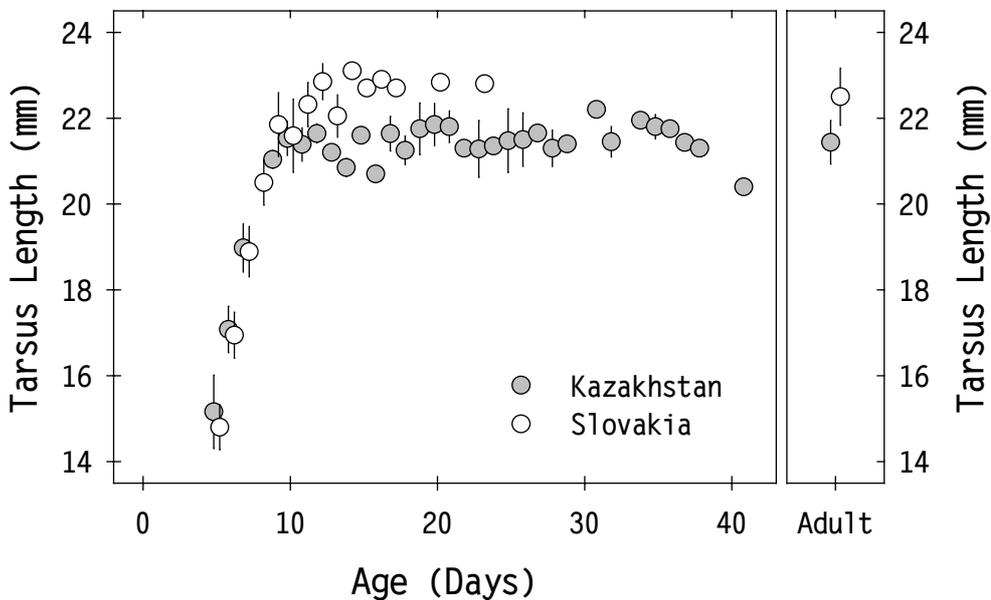
Fig. 8.3. The posthatching increase in tarsus length in Siberian and European stonechats. Note that the data points of the two populations are offset along the x-axis to allow a better distinction.
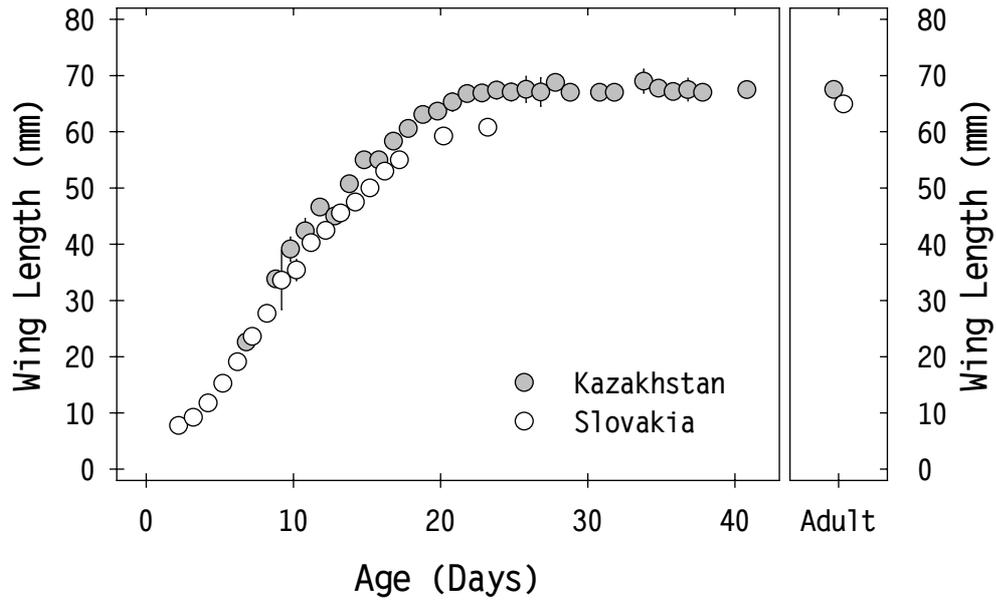
Fig. 8.4. The posthatching increase in wing length in Siberian and European stonechats. Note that the data points of the two populations are offset along the x-axis to allow a better distinction.
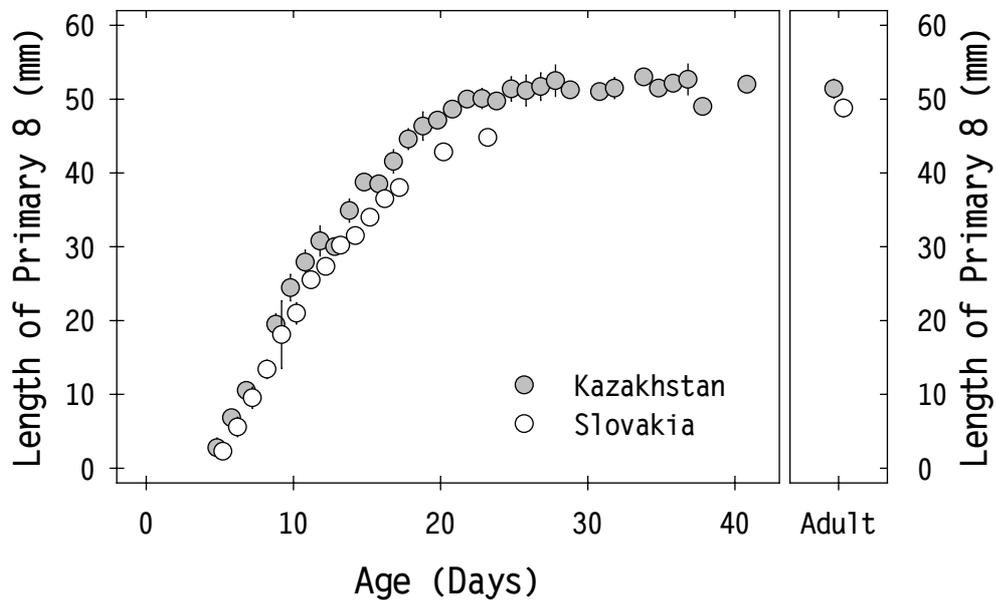
Fig. 8.5. The posthatching increase in the length of the 8th primary in Siberian and European stonechats. Note that the data points of the two populations are offset along the x-axis to allow a better distinction.
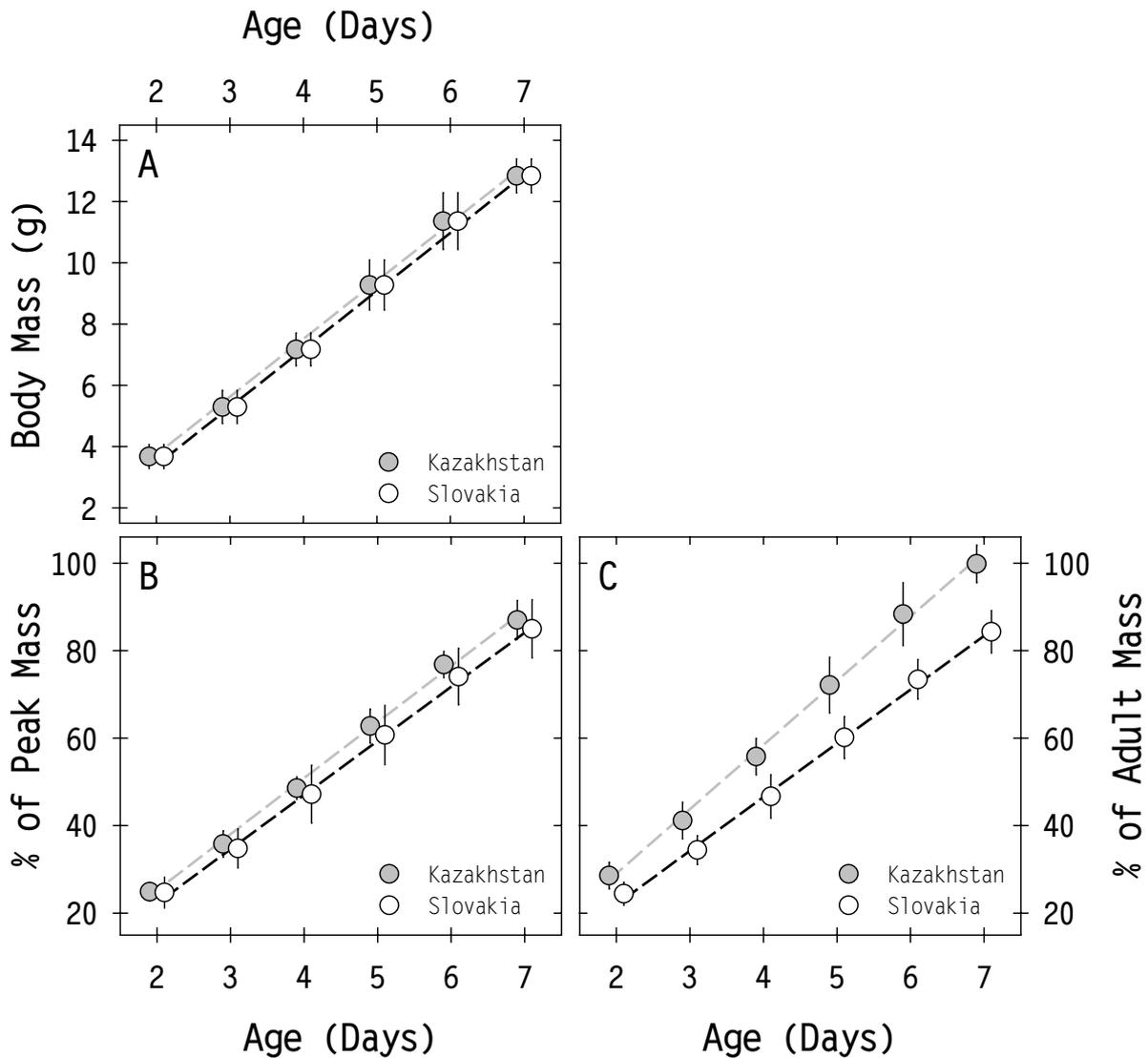
Fig. 8.6. Postnatal body mass increases during the linear phase of the growth curve in Siberian and European stonchats. *A*: the absolute mass gain per day; *B*: the mass gain expressed as the percentage of the mena pre-fledging peak mass; *C*: the mass gain expressed as the percentage of the mean adult mass. Note that the data points of the two populations are offset along the x-axis to allow a better distinction.

Siberian stonechats reached adult-like dimensions of body mass and body size earlier than European stonechats; furthermore they fledged earlier (*Table 8.2.*). Wing growth continued after fledging, adult-like dimensions were reached about 12 days after fledging in the Siberian stonechats. In the European stonechats all caught juveniles had not reached asymptotic wing size.

Table 8.2. Siberian stonechats reach adult-like dimension earlier and fledge earlier than European stonechats.

	Siberian stonechats Post-hatch day	European stonechats Post-hatch day
Adult body size	7	11
Adult tarsus length	10	12
Adult wing length	24	- (29[A])
Adult 8th primary length	25	-
Fledging[B]	11 - 13	13 - 15

[A] data taken from Helm & Gwinner 2001, Fig. 1
[B] estimated from unbanded juveniles

Comparisons within populations

The overall patterns of postnatal mass and size increase are similar in first and replacement clutches of Siberian stonechats and first and second clutches of European stonechats (*Fig. 8.7.*). Moreover, I could not find a consistent effect of calendar date on postnatal body mass and body size gain in the two populations (*Table 8.3., Figs. 8.8. and 8.9.*). Slopes significantly different from zero appear only singly and never clustered and no particular pattern emerges.

Of the 110 nests of Siberian stonechats that went into the analysis of nestling growth, 56 nests (51%) contained one or more later-hatched runt nestlings. While the overall mean nestling number in these clutches was 5.23 nestlings, the mean number of directly competing core nestlings was 4.56. Of the 41 European stonechat nests 24 (58%) contained runts, the mean nestling number was 4.63, whereas the number of core nestligs was 4.00. *Fig. 8.10.* shows the growth curves of runts and the corresponding core nestings in Siberian and European stonechats. A comparison of the growth rate constants of core nestlings and runts reveals that runts are not able to catch up with their older nestmates, the rather grow more slowly (*Table. 8.4.*). Growth rates are higher in core nestlings for body mass and tarsus, and similar for the wing and the 8th primary. Initially, runts started out with higher body masses, when compared to their core nestmates matched for age, but the difference decreased and even changed sign with increasing age

(GLM with age as covariate; Kazakhstan: $F_{1,11}$ = *10.85, p < 0.01, R² = 0.50;* Slovakia: $F_{1,10}$ = *60.28, p < 0.001, R² = 0.86*) (*Fig. 8.11.A.*). Wing length showed the same pattern, however the slope of the relationship of ΔR/C against age was only significant in the European population (Kazakhstan: $F_{1,3}$ = *6.38, p = 0.09, R² = 0.68;* Slovakia: $F_{1,8}$ = *152.07, p < 0.01, R² = 0.65*) (*Fig. 8.11.B.*). The same was true for the length of the 8th primary (Kazakhstan: $F_{1,3}$ = *0.99, p = 0.39, R² = 0.14;* Slovakia: $F_{1,8}$ = *10.74, p < 0.05, R² = 0.64*) (*Fig. 8.11.C.*). There was no significant effect of age on ΔR/C of tarsus length (Kazakhstan: $F_{1,6}$ = *0.27, p = 0.63, R² = 0.04;* Slovakia: $F_{1,6}$ = *2.71, p = 0.15, R² = 0.31*) (*Fig. 8.11.D.*).

8.4.3   Postjuvenile moult in Siberian stonechats

The first bird showed signs of postjuvenile moult (= moult score 1 at an age of 20 days. On average, fledglings of first clutches reached the moult criterion of five simultaneously moulting body areas around the age of 26 days (*Fig. 8.12.*). Although I have very little data (7 nestlings at 4 different ages), there is an indication that juveniles of replacement clutches initiate moult at an earlier age than juveniles of first clutches. On the basis of the scarce data at hand, juveniles of replacement clutches reach the moult criterion at an age of 21 days (*Fig. 8.12.*).
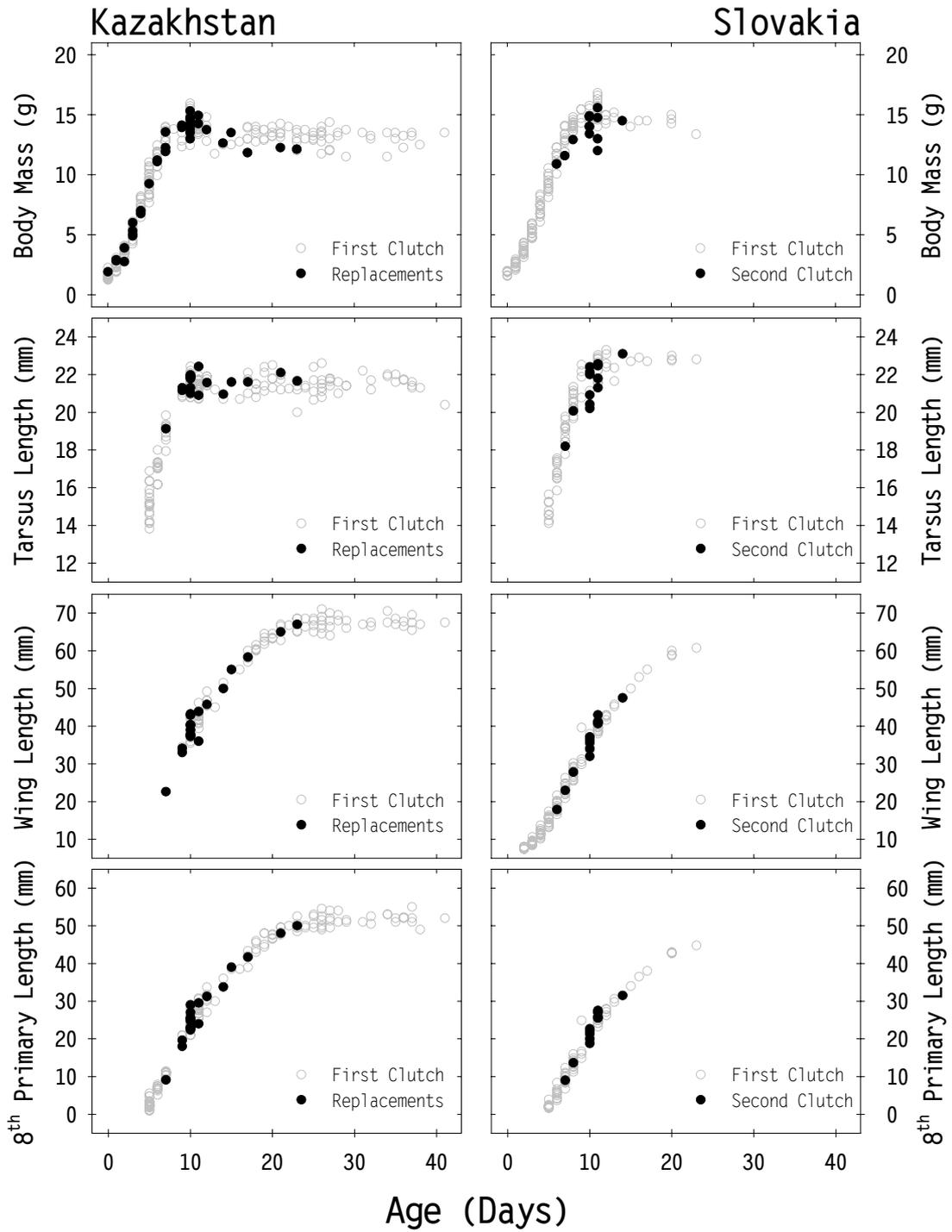
Fig. 8.7. The postnatal increase of body mass and size in first and replacement clutches of Siberian stonechats and first and second clutches of European stonechats.
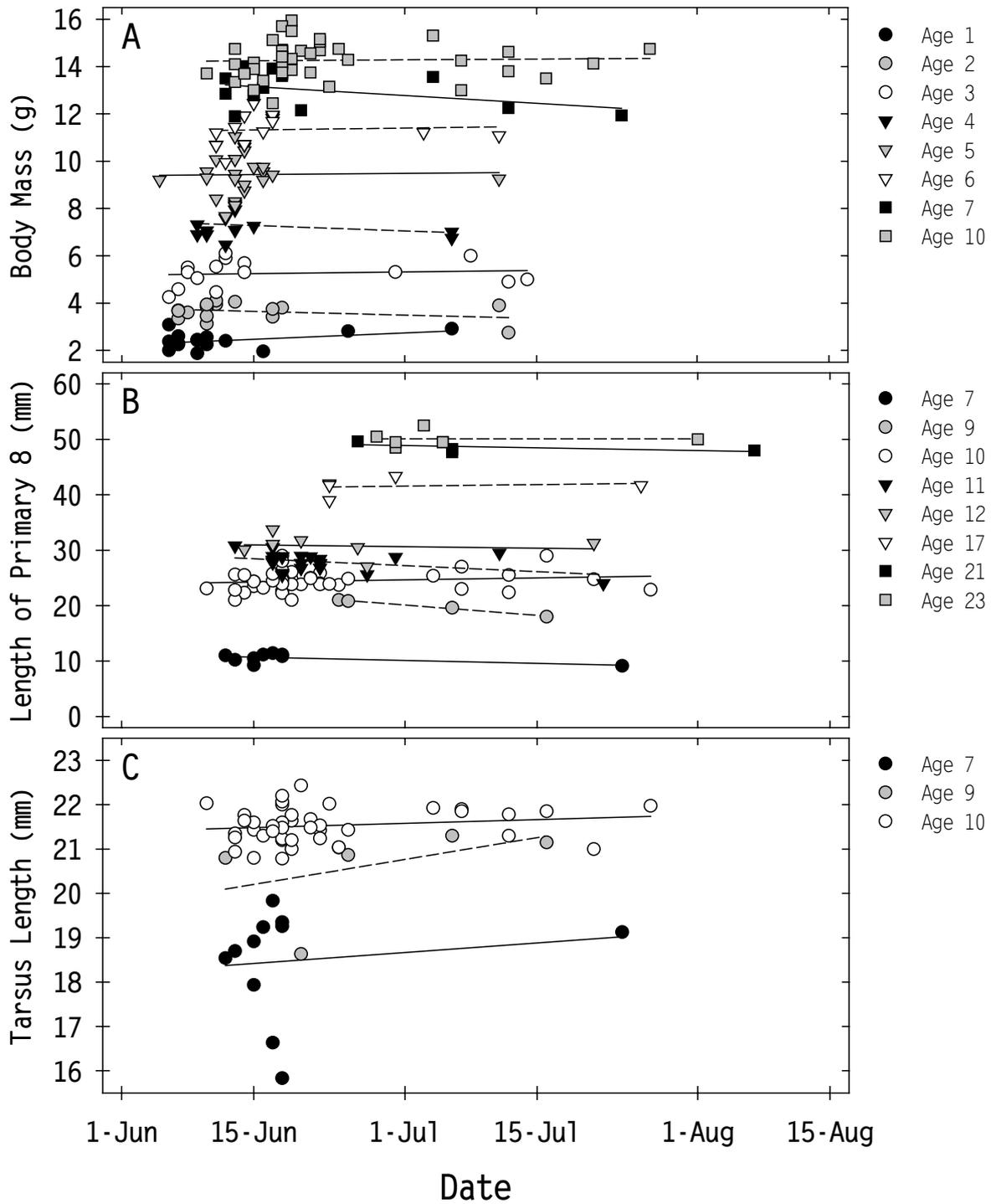
Fig. 8.8. The effect of date on measures of mass and size at different ages in Siberian stonechats. Note that in some cases (e.g. 8th primary length and tarsus length at age 7) there is only one measurement late in the season.
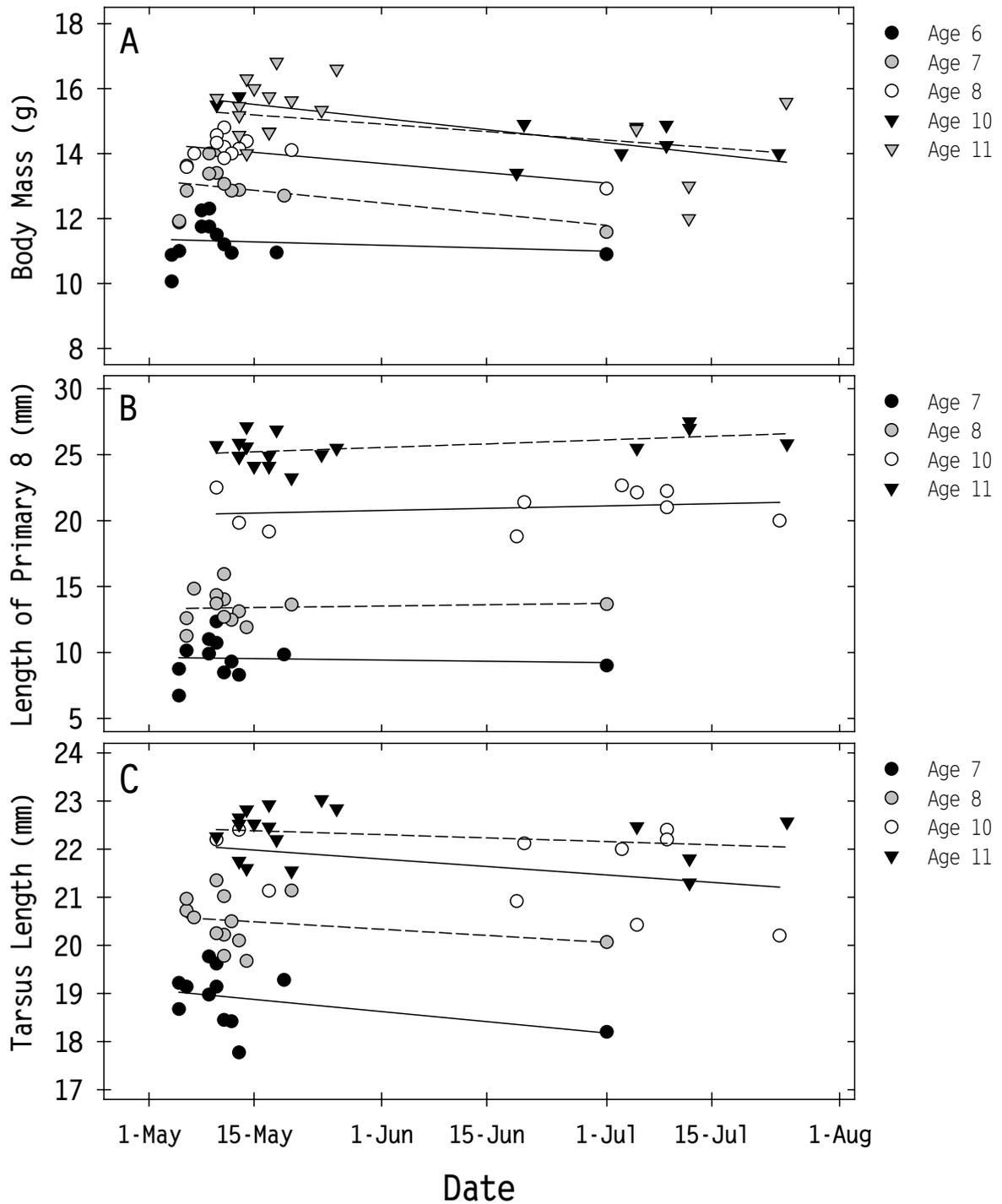
Fig. 8.9. The effect of date on measures of mass and size at different ages in European stonechats. Note that in some cases (e.g. 8th primary length and tarsus length at age 7 and 8) there is only one measurement late in the season.

8.5 Discussion

8.5.1 Embryonic growth

I found variation of the lengths of the incubation periods of Siberian and European stonechats, both between and within populations. Within populations, differences in incubation durations can be caused by variation in incubation temperatures, incubation behaviour (Monaghan & Nager 1997), and by individual differences in the timing of hatching (Ricklefs & Starck 1998). The mean incubation period was shorter in the Siberian stonechats, however this difference was not significant. Shorter incubation periods in Kazakhstan would indicate faster prenatal development in the Siberian stonechats, which could be attributed to the temporal restrictions on breeding in this population. A possible effect of the length of the reproductive window on the length of the incubation period has been discussed, however Ricklefs (Ricklefs 1993) found no convincing evidence for this relationship in a comparative study. A possible alternative factor causing the small differences in the mean length of the incubation periods between the populations could be differences in ambient temperatures between Kazakhstan and Siberia (see Chapter 2 of this thesis).

8.5.2 Postnatal growth rates

Comparisons between populations

The rate of postnatal gain in body mass and body size differs between the populations. Siberian stonechat juveniles have higher rate constants for the growth of body mass, the 8th primary, and tarsus, whereas the growth of the wing approaches asymptotic size faster in European stonechats. The difference between the populations in the growth towards the pre-fledging peak mass is smaller than the difference in the growth towards adult mass. When only the linear portion of the growth curve is analysed, then growth towards pre-fledging peak mass proceeds slightly, however non-

significantly, faster in Siberian stonechats, whereas growth towards the adult mass is significantly faster in Kazakh juveniles.

Are the results of the nonlinear curve-fitting procedures and the linear analysis consistent? Both methods show that the effect of the subspecies is larger when the growth towards adult mass is considered, than when the growth towards the pre-fledging peak mass is considered. This reflects the fact that difference between the pre-fledging peak mass and the adult mass is larger in the Siberian stonechats. Hence, the interpretation of the difference in body mass growth between the populations depends on the growth trajectory that is considered. That the nonlinear method finds a difference between the populations in the growth rate towards the pre-fledging peak mass (as indicated by the non-overlapping confidence intervalls), and the linear method does not, may be attributed to the fact that the curve fit covers a larger portion of the growth curve and a larger set was used in the analysis.

Table 8.3. The effect of date on body mass and body size measures of Siberian and European stonechats at different ages. Shown are F- and p-values of GLMs with date as covariate. Significant effects are highlighted.

Kazakhstan

	Body mass				Length of 8th primary				Tarsus length		
Age	n	F	p	Age	n	F	p	Age	n	f	p
1	14	2.53	0.14	10	41	1.01	0.32	7	8	0.25	0.63
2	15	1.40	0.26	*11*	*21*	*4.19*	*0.05*	*9*	*5*	*9.86*	*0.05*
3	14	0.16	0.70	12	7	0.07	0.80	10	42	1.46	0.23
4	12	0.71	0.42	23	5	0.00	0.99				
5	22	0.01	0.91								
6	14	0.06	0.81								
7	12	1.89	0.20								
10	42	0.05	0.83								

Slovakia

	Body mass				Length of 8th primary				Tarsus length		
Age	n	F	p	Age	n	F	p	Age	n	f	p
10	9	5.01	0.06	10	9	0.40	0.54	10	9	1.08	0.33
11	*16*	*5.66*	*0.03*	11	16	3.43	0.08	*11*	*16*	*17.91*	*0.05*
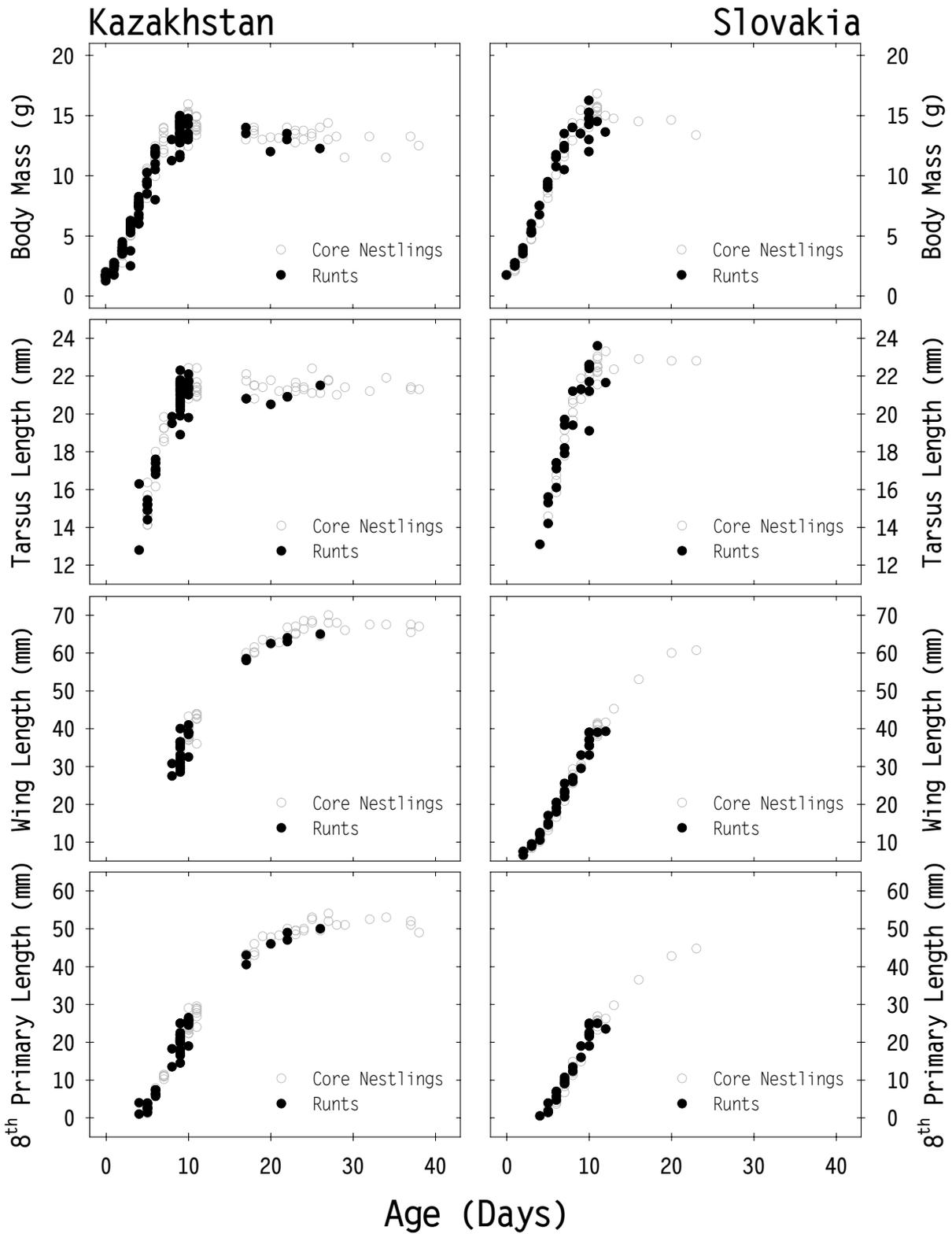
Fig. 8.10. The postnatal increase in body mass and body size in core nestlings and runts of Siberian and European stonechats.

Table 8.4. The growth rate constants K of body mass and body size in core nestlings and runts matched for age in Siberian and European stonechats. K-values with non-overlapping 95% confidence intervals are indicated by asterisks.

	Kazakhstan			Slovakia		
	Core	Runt		Core	Runt	
Body mass[A]	.726	.667		**.548**	**.493**	*
Tarsus length[A]	**.699**	**.580**	*	.529	.493	
Wing length[A]	.249	.227		.276	.276	
8th primary length[B]	.246	.244		.224	.231	

[A] best fit with the logistic growth function
[B] best fit with the Gompertz function

The growth rate constants of captive Siberian stonechats are 0.60 for body mass and 0.26 for wing length in hand-reared birds (Helm & Gwinner 2001). Captive European stonechat juveniles grow faster when reared by their own parents (0.56 for body mass, 0.26 for wing length) than when hand-reared (0.46 for body mass, 0.24 for wing length) (Starck et al. 1995, Helm & Gwinner 2001). Hence, the present study on free-living stonechats confirms the population differences found in captive birds for body mass growth, but not for wing growth, which is the only measure in my study which shows a higher growth rate constant in the European population.

Time-dependent mortality is an important factor selecting for high growth rates (Case 1978, Ricklefs 1993, Arendt 1997). As Arendt (1997) points out, if mortality is not dependent on body size but on the level of immaturity, then selection should not be on growth rate but on developmental rate. Stonechats leave the nest when they have reached adult-like dimensions of body size (as indicated by body mass and tarsus length), however the growth of wing and flight feathers is not completed at the time of fledging. Hence, the development of body size may be more closely related to the thermoregulatory and gross locomotory (development of leg and breast muscles) abilities (Hohtola & Visser 1998, Visser 1998), whereas the development of the wings affects the manouvrability after fledging (Perez-Tris & Telleria 2001). Thus, the evolution of the rates body size growth and wing growth could be affected by different aspects of time-

dependent mortality, the former by the predation on nestlings and the inability to thermoregulate independently, the latter by the predation on fledglings. Both, the fledgling and the nestling stages are periods of high differential mortality (Newton 1989, Sullivan 1989, Magrath 1991, Naef-Daenzer et al. 2001). I do not have enough data on post-fledging survival in my populations, but I can assess predation on nestlings during my study period (see Chapter 6 of this thesis). While overall nest predation is higher in the European population, the contribution of predation on nestlings to overall pre-fledging mortality is higher in Kazakhstan (about 21%) than in Slovakia (about 4%). However, whether this difference in the predation rates on nestlings is consistent enough to drive the diversification of growth rates between the populations is beyond the scope of this PhD project.

The effect of hatching date on postnatal growth

The seasonal variation in clutch size in many species has been attributed to the variation in rescources available for chick rearing (see Chapter 6 of this thesis). However, the reduction in clutch size may not completely buffer the effect of deteriorating conditions in the course of the season, particularly in Kazakhstan, where the reproductive window is short. I couldn't find an effect of hatching date on juvenile development in Kazakhstan and Slovakia. Nestlings that hatched late in the season had about the same body mass, primary length, and tarsus length than conspecifics of the same age hatched early in the season. This suggests that the smaller clutches produced later in the season may enable the parents to provision sufficient food to ensure normal growth of their offspring. Additionally, the parents may invest more into their later clutches, particularly if the preceding breeding attempts failed, as is the case in all the late clutches in Kazakhstan.
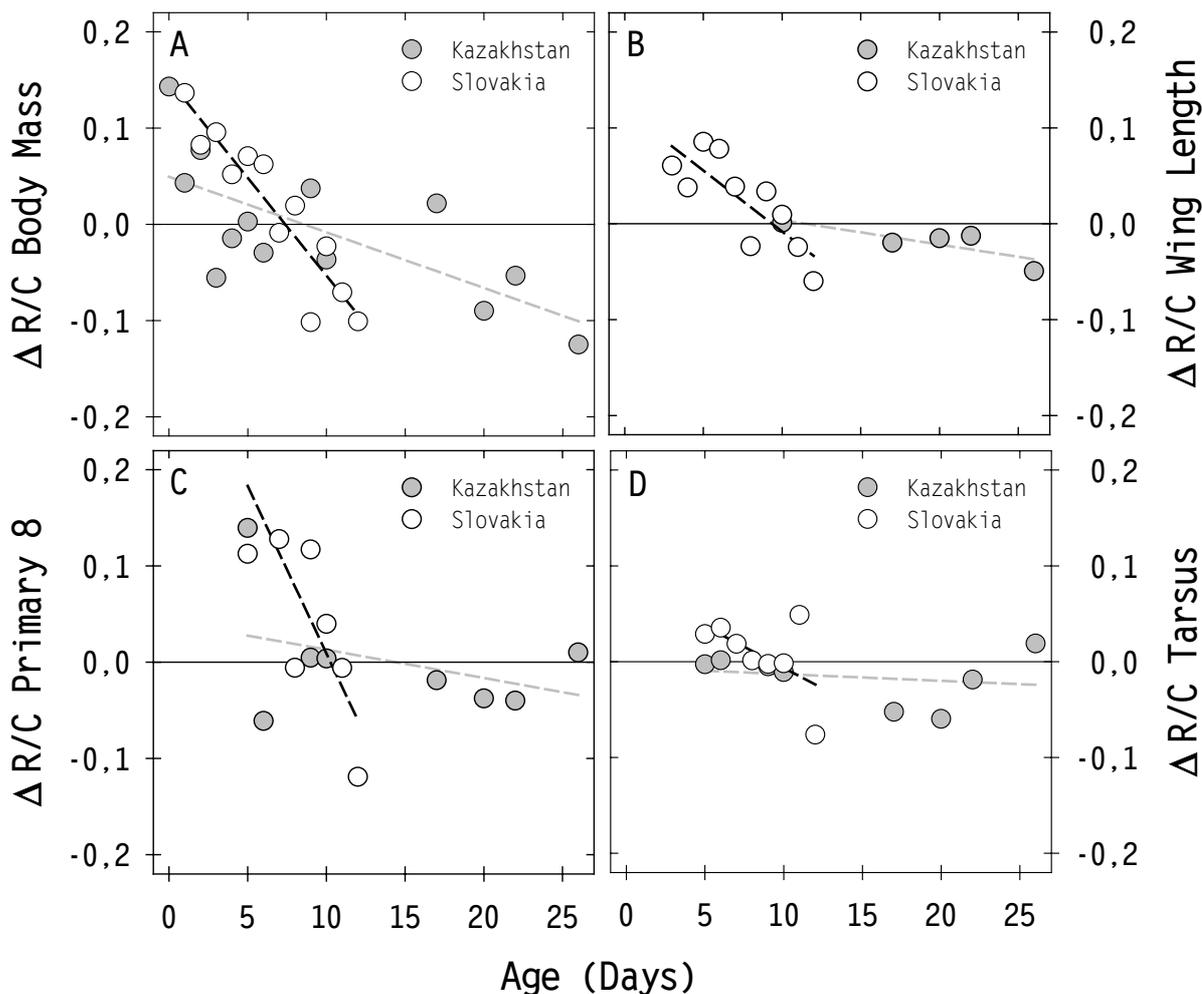
Fig. 8.11. The difference between measures of body mass and body size in core nestlings and runts of Siberian and European stonechats. Each dot represents the difference between the core nestlings and runts of the same nest expressed in core nestling units. A positive ΔR/C indicates larger mass or size of runts, a negative value larger mass or size of core nestlings.

The effect of hatching category on postnatal growth

Ricklefs (1993) considers sibling competition to te the main factor driving the evolution of growth rates. Siberian stonechats produce bigger clutches than European stonechats (see Chapter 6 of this thesis), therefore the potential of sibling competition is higher in Kazakhstan. However, as Ricklefs (1993) also points out, asynchronous hatching is a way of ameliorating sibling competition, because it reduces the number of evenly sized competitors in the nest. (Note that there have been put forward numerous other explanations for the occurance of hatching asynchrony, see

Magrath 1990, Stoleson & Beissinger 1995). Asynchronous hatching reduced the number of matched competitors in both populations; hence it may be a potential way for the parents to control offspring growth rates. A likely alternative explanation is, however, that starting to incubate before the clutch is complete is a timesaving method in temporally constrained birds.

Greigh-Smith (1985) showed that sibling competition affects weight hierarchies and survival of stonechat nestlings from the British Isles (*S. t. hibernans*), without however particularly relating his results to the effects of hatching asynchrony. In the Siberian and European stonechats of the present study runt nestlings that had hatched one or two days later than their nestmates increased body mass and tarsus length at lower rates than the core nestlings. The growth rates of wing length and length of the 8th primary was similar or slightly lower in runt nestlings. This could indicate that the competitively disadvantaged runts invested relatively more into the growth of the wing than into the gain of weight and structural size. In marsh tits *Parus palustris*, the heaviest and the lightest chick differ in the rate of posthatching mass increase, whereas the rate of wing growth is similar (Nilsson & Svensson 1996, Nilsson & Gardmark 2001). This is interpreted as a strategy of runts to fledge with their nestmates to avoid to be left behind by their parents. Stonechats are ground-nesters and the young do not move far from the nest location in the first one or two days after fledging. Parents feed nestlings inside and outside the nest during this time (personal observations), and nestlings may return to the nest after 'fledging' (de Garnica 1986). Hence, the pressure on stonechat nestlings to fledge at the same time than their nestmates may not be as high as in the hole-nesting marsh tits. Therefore the relative increase in wing growth in runt nestlings could be related to other factors such as the ability to avoid predation after fledging. There are indications that the rate of wing growth is much less flexible than the growth of other structures. Even in nestlings that starve to death, wing and feather growth proceeds at rates close to non-starving chicks (A. Scheuerlein, pers. comm., personal observations).
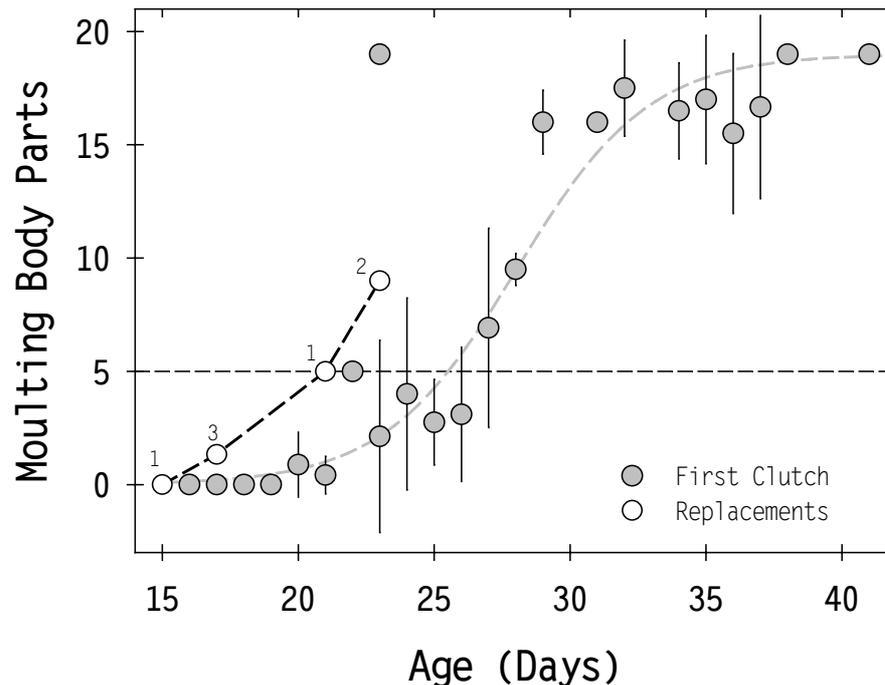
Fig. 8.11. The course of postjuvenile moult in Siberian stonechats. Shown are mean values (± SD) of first clutches and replacement clutches. The moult criterion of five moulting body areas is indicated by the horizontal dashed line. The numerals indicate the number of nestmates that contributed to the nest mean values.

The differences in body mass and size between runt nestlings and their nest mates are not the same over the whole growing period. Runts start out relatively heavier than their core siblings at the same age. However, this headstart is lost in the course of the developmental period, and at later ages core nestlings are relatively larger and heavier than their runt siblings. This pattern is relatively robust over all four measures considered in this study. It could be an indication of maternal effects, such as egg size or the amount of steroid hormones in the egg that initially favour the runts (Williams 1994, Schwabl 1997). However, this boost does not last for the whole developmental period, and due to their competitive disadvantage runt nestlings grow slower and end up lighter and smaller than their core siblings. The possible maternal effects involved are not known. Egg size is a likely candidate, because chicks of larger

eggs have an initial but not a lasting advantage (Williams 1994). If maternal effects are involved, then they do not increase growth rate as has been found in some studies (Schwabl 1996, Eising & Groothuis 2003).

8.5.3   Postjuvenile moult

Free-living Siberian stonechats initiate moult at an age of about 26 days (first broods). The scarce data on young from replacement clutches suggests that these nestlings initiate moult even earlier, at an age of about 21 days. These results corroborate and complement data on postjuvenile moult in captive and free-living stonechats (Flinks 1999, Helm & Gwinner 1999, 2001, Helm 2002, Helm et al. 2005). Common to all these studies are two points: First, Siberian stonechats initiate postjuvenile moult at an earlier age than European stonechats. Captive Siberian stonechats reach the moult criterion at an age of about 30 days, captive and free-living European stonechats at an age of about 80 days (first broods) (Flinks 1999, Helm et al. 2005). Second, there is an effect of hatching date on the onset of postjuvenile moult in Siberian and European stonechats. This effect is very pronounced in the European subspecies, where late-hatched chicks may initiate postjuvenile moult 60 days earlier relative to their age than early-hatched chicks. In the Siberian stonechats the advance of the onset of postjuvenile moult in the course of the season is only about 15 days (Flinks 1999, Helm & Gwinner 2001, Helm et al. 2005). This suggests that in the Siberian stonechats the onset of postjuvenile moult is already shifted to the earliest onset that is physiologically feasible. Siberian stonechats moult also faster; moult duration is approx. 30 to 45 days, compared to approx. 50 to 65 in the European stonechats (moult duration is also affected by hatching date) (Helm et al. 2005).

8.5.4   Juvenile development and the length of the breeding season

Siberian stonechats have slightly shorter incubation periods, the nestlings reach adult-like dimensions earlier and fledge earlier, and they initiate and finish postjuvenile moult earlier than European stonechats.

The whole period from the onset of incubation until the end of fledging lasts about 80 days and thus about half as long as in the European stonechats (median duration for chicks from first clutches). Most of this difference is due to postjuvenile moult, perinatal growth contributes rather little. Onset and rate of post-juvenile feather replacement are also much more plastic than postnatal growth, as indicated by the large effect of hatching date on moult, but not on growth. This suggests that growth rates are much more constrained (by physiology and/or selective pressures on growth) than moult patterns to react to differences in seasonal timing.

8.6   References

Apanius, V. (1998). Ontogeny of immune function. *In* J. M. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development*, pp. 203-222. Oxford University Press, New York.

Arendt, J. D. (1997). Adaptive intrinsic growth rates: An integration across taxa. *Quarterly Review of Biology* 72: 149-177.

Berthold, P., Gwinner, E. & Klein, P. (1970). Vergleichende Untersuchung der Jugendentwicklung eines ausgeprägten Zugvogels, *Silvia borin*, und eines weniger ausgeprägten Zugvogels, *S. atricapilla*. *Vogelwarte* 25: 298-329.

Birkhead, T. R., Fletcher, F. & Pellatt, E. J. (1999). Nestling diet, secondary sexual traits and fitness in the zebra finch. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 266: 385-390.

Both, C., Visser, M. E. & Verboven, N. (1999). Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 266: 465-469.

Buchanan, K. L., Leitner, S., Spencer, K. A., Goldsmith, A. R. & Catchpole, C. K. (2004). Developmental stress selectively affects the song control nucleus HVC in the zebra finch. *Proceedings of the Royal Society of London - Series B: Biological Sciences* 271: 2381-2386.

Buchanan, K. L., Spencer, K. A., Goldsmith, A. R. & Catchpole, C. K. (2003). Song as an honest signal of past developmental stress in the European starling (Sturnus vulgaris). *Proceedings of the Royal Society of London. Series B, Biological Sciences* 270: 1149-1156.

Case, T. J. (1978). Evolution and adaptive significance of postnatal growth rates in terrestrial vertebrates. *Quarterly Review of Biology* 53: 243-282.

Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1985). Parental investment and sex differences in juvenile mortality in birds and mammals. 313: 131-133.

Cresswell, W., Holt, S., Reid, J. M., Whitfield, D. P., Mellanby, R. J., Norton, D. & Waldron, S. (2004). The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behavioral Ecology* 15: 498-507.

de Garnica, R. (1986). Young stonechats, *Saxicola torquata*, returning to the nest after ringing. *Ringing and Migration* 7: 50.

Drent, R. H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.

Eising, C. M. & Groothuis, T. G. G. (2003). Yolk androgens and begging behaviour in black-headed gull chicks: an experimental field study. *Animal Behaviour* 66: 1027-1034.

Flinks, H. (1999). Muster, Intensität und zeitliche Aspekte der postjuvenilen Mauser beim Schwarzkehlchen (*Saxicola torquata*). [Pattern, extent, and time aspects of the postjuvenile moult in stonechats (*Saxicola torquata*)]. *Die Vogelwarte* 40: 11-27.

Garnett, M. C. (1981). Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. *Ibis* 123: 31-41.

Greigh-Smith, P. W. (1985). Weight differences, brood reduction and sibling competition among nestling Stonechats *Saxicola torquata* (Aves: Turdidae). *Journal of Zoology (London)* 205: 453-465.

Groothuis, T. G. G., Muller, W., von Engelhardt, N., Carere, C. & Eising, C. (2005). Maternal hormones as a tool to adjust offspring phenotype in avian species. *Neuroscience & Biobehavioral Reviews* 29: 329-352.

Haywood, S. & Perrins, C. M. (1992). Is clutch size in birds affected by environmental conditions during growth? *Proceedings of the Royal Society of London. Series B, Biological Sciences* 249: 195-197.

Helm, B. (2002). Seasonal timing in different environments: comparative studies in Stonechats. Ph.D. thesis, Ludwig-Maximilians-Universität München, Germany.

Helm, B. & Gwinner, E. (1999). Timing of postjuvenal molt in African (Saxicola torquata axillaris) and European (Saxicola torquata rubicola) stonechats: Effects of genetic and environmental factors. *Auk* 116: 589-603.

Helm, B. & Gwinner, E. (2001). Nestling growth and post-juvenile moult under a tight seasonal schedule in stonechats *Saxicola torquata maura* from Kazakhstan. *Avian Science* 1: 31-42.

Helm, B., Gwinner, E. & Trost, L. (2005). Flexible seasonal timing and migratory behavior. *Annals of the New York Acadamy of Sciences* in press.

Hohtola, E. & Visser, G. H. (1998). Development of locomotion and endothermy in altricial and precocial birds. *In* J. M. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development*. Oxford University Press, New York.

Jenni, L. & Winkler, R. (1994). *Moult and Ageing of European Passerines*. Academic Press, London.

Kaiser, S. & Sachser, N. (2005). The effects of prenatal social stress on behaviour: mechanisms and function. *Neuroscience & Biobehavioral Reviews* 29: 283-294.

Karten, Y. J. G., Olariu, A. & Cameron, H. A. (2005). Stress in early life inhibits neurogenesis in adulthood. *Trends in Neurosciences* 28: 171-172.

Klaassen, M. & Drent, R. (1991). An analysis of hatchling resting metabolism - in search of ecological correlates that explain deviations from allometric relations. *Condor* 93: 612-629.

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology and Evolution* 14: 343-348.

Magrath, R. D. (1990). Hatching asynchrony in altricial birds. *Biological Reviews* 65: 587-622.

Magrath, R. D. (1991). Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology* 60: 335-351.

Merilä, J. & Svensson, E. (1997). Are fat reserves in migratory birds affected by condition in early life? *Journal of Avian Biology* 28: 279-286.

Monaghan, P. & Nager, R. G. (1997). Why don´t birds lay more eggs? *Trends in Ecology and Evolution* 12: 270-274.

Mousseau, T. A. & Fox, C. W. (1998). The adaptive significance of maternal effects. *Trends in Ecology and Evolution* 13: 403-407.

Müller, W., Groothuis, T. G. G., Dijkstra, C., Siitari, H. & Alatalo, R. V. (2004). Maternal antibody transmission and breeding densities in the Black-headed Gull *Larus ridibundus*. *Functional Ecology* 18: 719-724.

Naef-Daenzer, B., Widmer, F. & Nuber, M. (2001). Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *Journal of Animal Ecology* 70: 730-738.

Newton, I. (1989). *Lifetime reproduction in birds*. Academic Press, London.

Nilsson, J.-A. & Gardmark, A. (2001). Sibling competition affects individual growth strategies in marsh tit, *Parus palustris*, nestlings. *Animal Behaviour* 61: 357-365.

Nilsson, J.-A. & Svensson, M. (1996). Sibling competition affects nestling growth strategies in marsh tits. *Journal of Animal Ecology* 65: 825-836.

Perez-Tris, J. & Telleria, J. L. (2001). Age-related variation in wing shape of migratory and sedentary Blackcaps *Sylvia atricapilla*. *Journal of Avian Biology* 32: 207-213.

Perrins, C. M. (1996). Eggs, egg formation and the timing of breeding. *Ibis* 138: 2-15.

Ricklefs, R. E. (1992). Embryonic development period and the prevalence of avian blood parasites. *Proceedings of the National Academy of Sciences of the United States of America* 89: 4722-4725.

Ricklefs, R. E. (1993). Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. *Current Ornithology* 11: 199-276.

Ricklefs, R. E. (2004). The cognitive face of avian life histories. *Wilson Bulletin* 116: 119-133.

Ricklefs, R. E. & Starck, J. M. (1998). Embryonic growth and development. *In* J. M. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development*, pp. 31-58. Oxford University Press, New York.

Ricklefs, R. E., Starck, J. M. & Konarzewski, M. (1998). Internal constraints on growth in birds. *In* J. M. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development*, pp. 266-287. Oxford University Press, New York.

Roff, D. A. (1992). *The Evolution of Life Histories: Theory and analysis*. Chapman & Hall, New York.

Schluter, D. & Gustafsson, L. (1993). Maternal inheritance of condition and clutch size in the collared flycatcher. *Evolution* 47: 658-667.

Schwabl, H. (1996). Maternal testosterone in the avian egg enhances postnatal growth. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 114: 271-276.

Schwabl, H. (1997). Maternal steroid hormones in the egg. *In* S. Harvey & R. J. Etches (Eds.), *Perspectives in Avian Endocrinology*, pp. 3-13. Journal of Endocrinology Ltd, Bristol.

Spencer, K. A., Buchanan, K. L., Goldsmith, A. R. & Catchpole, C. K. (2003). Song as an honest signal of developmental stress in the zebra finch (Taeniopygia guttata). *Hormones and Behavior* 44: 132-139.

Spencer, K. A., Buchanan, K. L., Goldsmith, A. R. & Catchpole, C. K. (2004). Developmental stress, social rank and song complexity in the European starling (Stumus vulgaris). *Proceedings of the Royal Society of London - Series B: Biological Sciences* 271: S121-S123.

Starck, J. M. (1993). Evolution of avian ontogenies. *Current Ornithology* 10: 275-366.

Starck, J. M., Koenig, S. & Gwinner, E. (1995). Growth of stonechats *Saxicola torquata* from Africa and Europe - an analysis of genetic and environmental components. *Ibis* 137: 519-531.

Starck, J. M. & Ricklefs, R. E. (1998a). Variation, constraint, and phylogeny: comparative analysis of variation in growth. *In* J. M. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development*, pp. 247-264. Oxford University Press, New York.

Starck, M. & Ricklefs, R. E. (1998b). Avian growth rate data set. *In* M. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development*., pp. 381-423. Oxford University Press, New York.

Stearns, S. C. (1992). *The Evolution of Life-Histories*. Oxford University Press, Oxford.

Stoleson, S. H. & Beissinger, S. R. (1995). Hatching asynchrony and the onset of incubation in birds, revisited. *Current Ornithology* 12: 191-271.

Sullivan, K. A. (1989). Predation and starvation - age-specific mortality in juvenile juncos (*Junco phaenotus*). *Journal of Animal Ecology* 58: 275-286.

Tella, J. L., Scheuerlein, A. & Ricklefs, R. E. (2002). Is cell-mediated immunity related to the evolution of life-history strategies in birds? *Proceedings of the Royal Society of London. Series B, Biological Sciences* 269: 1059-1066.

Tinbergen, J. M. & Boerlijst, M. C. (1990). Nestling weight and survival in individual great tits (*Parus major*). *Journal of Animal Ecology* 59: 1113-1127.

Tinbergen, J. M. & Dietz, M. W. (1994). Parental energy expenditure during brood rearing in the great tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Functional Ecology* 8: 563-572.

Visser, G. H. (1998). Development of temperature regulation. *In* J. M. Starck & R. E. Ricklefs (Eds.), *Avian Growth and Development*. Oxford University Press, New York.

Visser, M. E. & Lessells, C. M. (2001). The costs of egg production and incubation in great tits (Parus major). *Proceedings of the Royal Society of London - Series B: Biological Sciences* 268: 1271-1277.

Werschkul, D. F. & Jackson, J. A. (1979). Sibling competition and avian growth rates. *Ibis* 121: 97-102.

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.

Williams, T. D. (1994). Intraspecific variation in egg size and egg composition in birds: Effects on offspring fitness. *Biological Reviews* 68: 35-59.

Winkler, R. (1999). Moult strategies of European passerines. *In* N. J. Adams & R. H. Slotow (Eds.), *Proc. 22 Int. Ornithol. Congr., Durban*, pp. 564-567. BirdLife South Africa, Johannesburg.

9 THE TRADE-OFF BETWEEN REPRODUCTION AND MOULT IN SIBERIAN STONECHATS

9.1 Summary

Stonechats replace their body and flight feathers on their breeding grounds before they set out on their autumn migrations. Siberian stonechats lay one clutch per season, but lost clutches are often replaced. Late breeders (birds that replace a lost clutch) may face a conflict between the temporal and energetic requirements of reproduction and moult. Normal breeders (those birds that raised their first clutch successfully) initiate postnuptial moult shortly after their young have left the nest. Late breeders initiate moult later than normal breeders, however at a younger age of their offspring. As a result, they overlap breeding and moult more than normal breeders, and may initiate feather replacement while they still have nestlings, or even eggs in their nests. Such a moult-breeding overlap is thought to be costly and therefore generally avoided. The degree overlap increases with laying date. There are indications that late breeding males initiate moult at an earlier date than their female partners. This may affect the amount of parental care, as has been found in other species. Late breeding birds initiate wing moult relatively earlier in relation to body moult than do normal breeders. Postponing the replacement of body feathers, which serve mainly in insulation, may be associated with different costs than postponing the moult of flight feathers, particularly in a long-distance migrant. Late breeding birds seem to alter their overall moult patterns, giving primacy to the moult of flight feathers.

9.2   Introduction

A trade-off between current and future reproduction is one of the central tenets of life-history theory (Williams 1966, Roff 1992, Stearns 1992). The level of investment into a given breeding bout has to be adjusted to the probability that further breeding bouts are available, and how the current investment will affect this probability (Williams 1966). Reproductive decisions in this context encompass not only adjustments of the *amount of resources* that are invested into the offspring, but also of the *amount of time* that is attributed to the breeding bout. Many palearctic migratory passerines, while present on the breeding grounds, have to accomplish the feats of reproduction, but also to replace parts or the whole of its plumage (Jenni & Winkler 1994, Winkler 1999) and to get into shape for migration (Bairlein & Gwinner 1994, Biebach 1996). Therefore, the amount of time allocated to reproduction comes at the expense of these other seasonal tasks. Furthermore, reproduction, moult, and pre-migratory preparations, are all energetically costly (e.g. Drent & Daan 1980, Lindström et al. 1993, Bairlein & Gwinner 1994, Klaassen 1995, Murphy 1999), and hence most species avoid a temporal overlap of these activities (Jenni & Winkler 1994, Lindström et al. 1994, Dawson et al. 2001, Rubolini et al. 2002). This has led to a complete temporal segregation of reproduction and feather-replacement in some species, particularly in long-distance migrants (Jenni & Winkler 1994, Winkler 1999), this moult strategy is, however, not further discussed in this chapter.

There are strong functional and mechanistic links between the life-history stages of reproduction and moult. Both stages are controlled by endogenous timing programs that respond to photoperiod as a *zeitgeber* (Gwinner 1986, Gwinner & Dittami 1990, Gwinner 1996, Dawson et al. 2001, Gwinner 2003). However, the timing of the onset of moult is also affected by the current state of reproduction (Runfeldt & Wingfield 1985, Siikamäki et al. 1994, Klemp 2000), as indicated by a strong regulatory effect of the hormones testosterone and prolactin on the timing of moult (Schleussner et al. 1985, Hahn et al. 1992, Nolan et al. 1992, Dawson 1994, Dawson & Sharp

1998, Duettmann et al. 1999, Dawson et al. 2001, Clotfelter et al. 2004). In contrast to this temporal flexibility in the onset of feather replacement, the termination of moult seems to be more rigidly controlled, particularly in species which interrupt or cease moult when it is not completed before their autumn movements begin (Schleussner et al. 1985, Duettmann et al. 1999, Hall & Fransson 2001).

Hence, migrants that attribute a lot of time to reproduction, e.g. because they have to re-nest after a failed breeding attempt, may have to speed up moult or sometimes even initiate feather replacement during breeding, in order to avoid an overlap of moult and migration. Both, increasing the rate of moult, or attributing less energy to moult (due to simultaneous parental care), can negatively affect feather quality, affecting thermoregulation, flight performance, and ultimately survival (Nilsson & Svensson 1996, Hemborg & Lundberg 1998, Dawson et al. 2000, Hall & Fransson 2000, Dawson 2004). Furthermore, because plumage serves as secondary sexual trait and in signalling social status and body condition (Jenni & Winkler 1994, McGraw et al. 2002, McGraw & Ardia 2003, McGraw et al. 2003), also sexual attractiveness and hence future reproductive success may be affected (Siefferman & Hill 2003, Norris et al. 2004, Siefferman & Hill 2005). Finally, overlapping reproduction and moult endanger current reproductive success by reducing offspring condition and survival prospects (Hemborg & Lundberg 1998, Moreno et al. 2005).

In many long-distance migrating passerines, an overlap of breeding and postnuptial moult to a certain degree seems to be unavoidable, due to the tight temporal schedule during the breeding season (Ellegren 1990, Hahn et al. 1992, Jenni & Winkler 1994, Hemborg & Lundberg 1998, Hemborg et al. 1998, Eeva et al. 2000, Morton 2002, Artem 2004). Siberian stonechats are long-distance migrants that usually raise one brood during their presence on the breeding grounds (see Chapters 3 and 6 of this thesis), then they initiate full replacement of the body and flight feathers before they embark on their autumn migrations. I investigated the course of postnuptial moult in my study population in Kazakhstan, and its relationship to the

breeding activities of the birds. The stonechats in Kazakhstan often replace lost clutches, and I hypothesised that delayed reproduction results in a considerable overlap of breeding and moulting. Furthermore, the sexes may follow different strategies, when adjusting their moult schedules to their current reproductive status (Hemborg & Merilä 1998, Hemborg 1999b).

In this chapter, I present the moult schedules of normal and late-breeding Siberian stonechats, and investigate how reproductive timing affects a potential overlap of breeding and moult. Potential sexual differences in the relationship between moulting and offspring production will be considered.

9.3   Methods

I captured stonechats during the breeding season in Kazakhstan and inspected them for signs of moult. Those birds that either successfully raised offspring from their first breeding attempt or lost their first clutch but did not engage into another breeding attempt were considered as *normal breeders*. Those birds that were raising replacement clutches were considered as *late breeders*. This group includes birds for which a first breeding attempt could not be documented, but which raised offspring at the same time as other birds with replacement clutches.

The state of moult was coded by separate moult scores, one for the moult of the wing feathers (the primaries, secondaries, and tertials, Jenni & Winkler 1994) and one for the body feathers. The moult score used for the wing feathers is an adaptation from Newton (1966). It ranges from 0 to 95 and is obtained by adding up the scores (0 = old feather; *1* = shedding of the old feather; *2-4* = intermediate moulting stages; 5 = completed feather) for each individual flight feather (in the stonechat: ten primaries, including the *alula*, six secondaries, and three tertials) for each wing separately, and then averaging the scores of the two wings. The moult score of the body feathers ranges from 0 to 19. It is obtained by adding up the

number of body areas that are moulting simultaneously. The considered body areas are derived from Berthold et al. (1970), as shown in Flinks (1999, Fig. 4.). A given body area is considered as moulting, when at least three feathers are found shed or in the state of growing. Note that, unlike the wing score, this moult score increases to a maximum at peak moult, but then decreases again to zero, when all body feathers are moulted. However, this difference did not concern my study, because none of the birds I caught had exceeded the moult peak.

To assess moult patterns of normal and late breeding birds, the moult scores were plotted against the date the birds were captured, and against the age of their offspring at the date of capture. To analyse the effect of the timing of reproduction on the overlap of breeding and moult, I calculated the date when the birds initiated feather replacement. I do not know the rate of moult in my birds, because to obtain this measure, a considerable number of individual recaptures in varying moult stages would have been necessary. This was not feasible in this study. Hence, I estimated the rate of moult from the slopes of the linear regressions of the moult scores of the normal breeders (which breed very synchronously, see Chapter 6 of this thesis) against date. This method makes three major assumptions: *(1)* The rate of moult is linear over the largest part of the moult score. (When calculating the regressions, I excluded the zero and maximum values, because they didn't contain unambiguous information about the timing of moult); *(2)* All birds moult at the same rate, irrespective of their individual status; and *(3)* there is no calendar effect on the rate of postnuptial moult.

9.4   Results

The first birds began feather replacement in the end of June. By beginning of August, the first birds had fully moulted their flight feathers. The first birds at peak body moult (feather replacement in all

body areas) were found already in the beginning of July. However, none of the birds captured had fully completed moult in any of the body areas (*Fig. 9.1.*). In those birds that had replaced a lost clutch the moult patterns lagged behind for about two to three weeks, however males and females seemed to follow different strategies: While in the normal breeders there was no difference between the sexes in their annual timing of moult, in the late breeders the males delayed wing moult less than females. No such difference was observed for body moult (*Fig. 9.1.*).

The initiation of moult in the normal breeders coincided with the time when their offspring were about to leave the nest or had already fledged. Because Siberian stonechat nestlings remain dependent on their parents for about 15 to 20 days after fledging (pers. observation), there was a certain overlap of the period of parental care and wing and body moult, even in normal breeders. This overlap increased in late breeders, which initiated moult at an earlier age of their offspring than normal breeders (*Fig. 9.2.*). Again there are indications that late breeding males and females followed different strategies: males initiated moult at an earlier age of their offspring than females. In the two late breeding pairs, two males initiated wing moult earlier, and one male body moult earlier than their female partners (*Fig. 9.2.*).

The length of the time period between the onset of offspring production and the onset of feather replacement, and hence the overlap between reproduction and moult, was dependent on laying date (*Fig. 9.3.*). While most of the early breeding birds initiated moult after their young fledged, most later breeding birds began feather replacement at earlier breeding stages, and more so the later they initiated breeding. Again, late breeding males seemed to overlap reproduction and moult more than late breeding females (*Fig. 9.3.*).
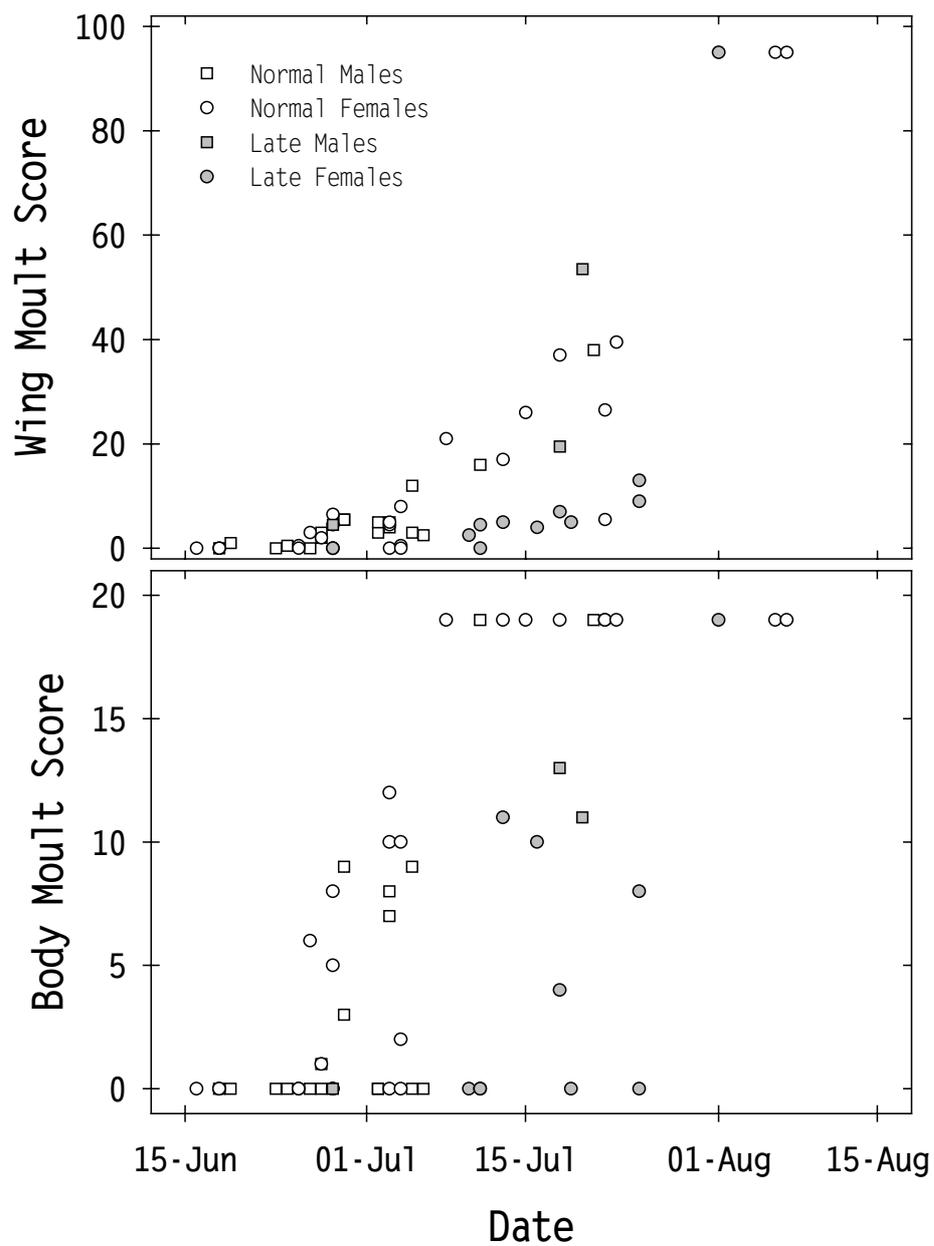
Fig. 9.1. Moult patterns in Siberian stonechats that either produced a successful first clutch (normal breeders) or that had to replace a lost clutch (late breeders). Late breeders postpone the onset of moult.
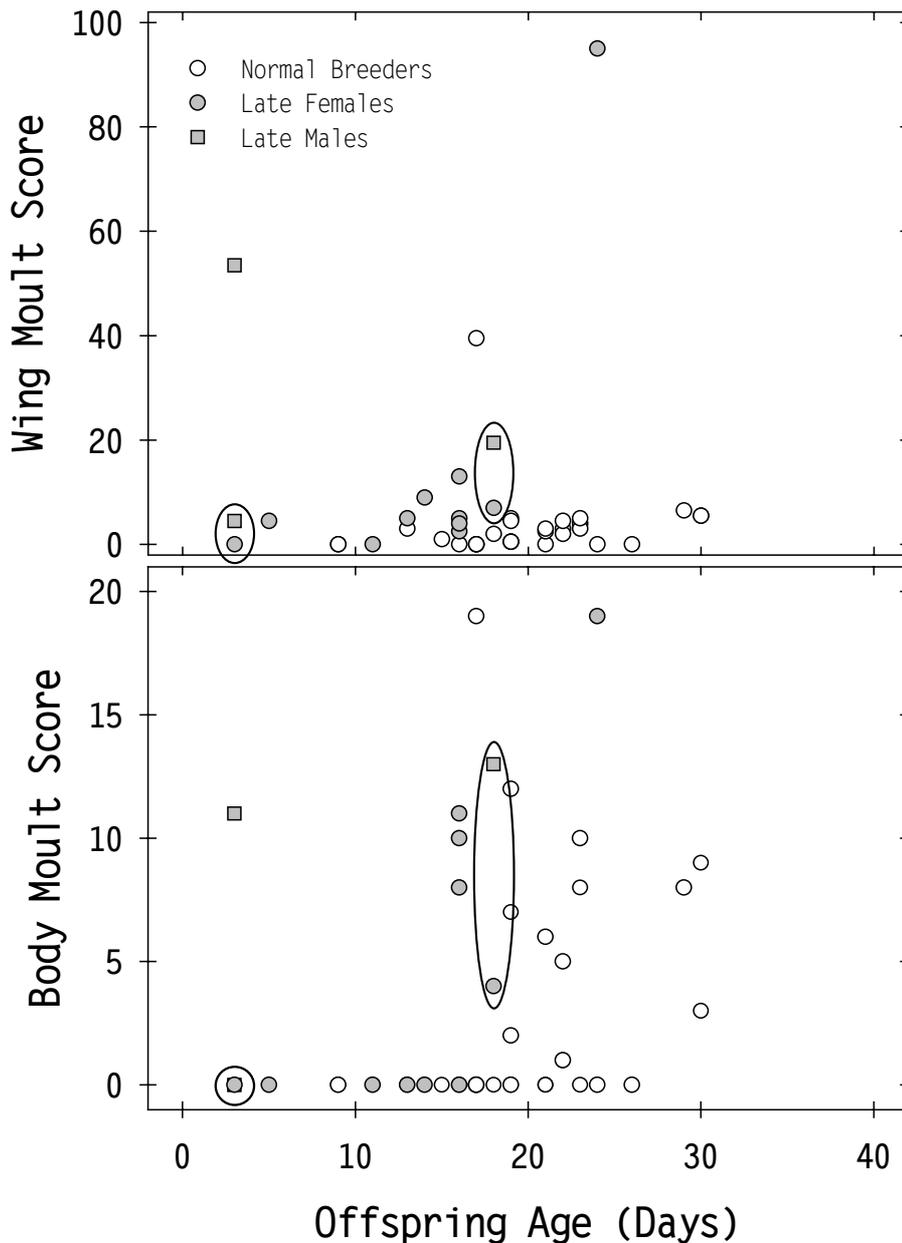
Fig. 9.2. Moult scores of Siberian stonechats in relation to the age of their offspring. The nestlings fledge at an age of 11 to 15 days. The ellipsoids connect the members of late breeding pairs.

After fledging, the young stonechats stayed in the vicinity of the nest locations. In the consecutive days they were led by their parents to patches of higher and denser vegetation than found in the nest habitats. Therefore, normal and late breeding stonechats began to moult at or close to the nest location, but carried out the intense phases of feather replacement in the cover of denser vegetation. I caught birds that had

completed flight feather moult, but no bird that had completed body moult (see above). Furthermore, most adult birds seemed to leave the study area before they had time to complete the replacement of body feathers. By mid-August only late breeders and young stonechats were left on my study sites. I do not know whether the other birds completed their moult in areas located close-by, or whether they embarked on their autumn migrations without having finished their body moult.
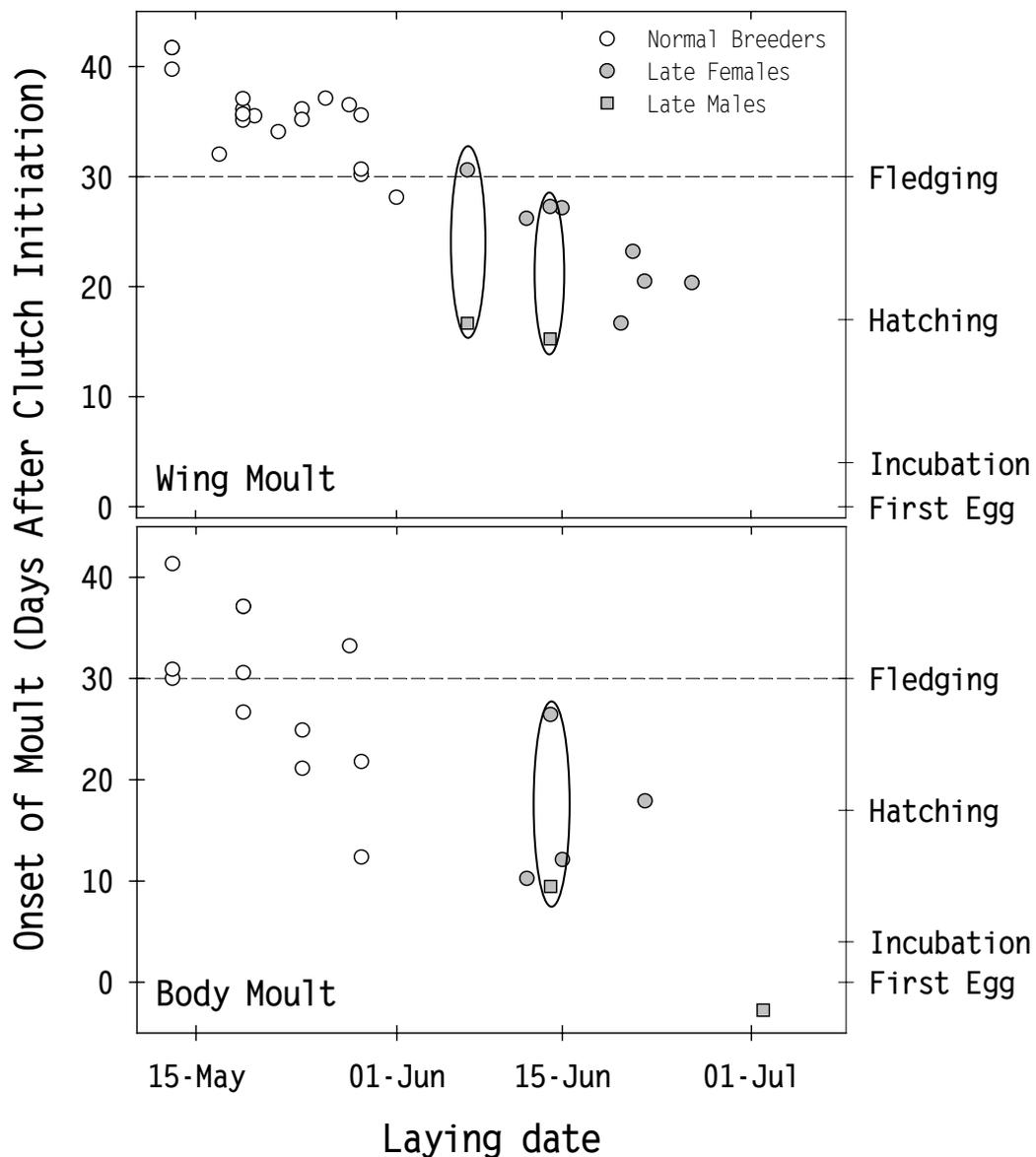
Fig. 9.3. The overlap between breeding and moult in Siberian stonechats. Shown is the time spread between the laying of the first egg and the estimated onset of wing and body moult, which decreases in the course of the season. The ellipsoids connect members of late breeding pairs.

There are indications that the relationship between flight feather moult and body moult differed between normal and late-breeding stonechats. The residuals of the regression of wing moult score against body moult score decrease with laying date, suggesting that birds that bred late in the season initiated wing moult earlier in relation to body moult than did birds that started reproducing early in the season. Alternatively, late breeding birds could have been moulting their wings at a higher rate than early breeders (*Fig. 9.4.*).

Fig. 9.4. The residual wing moult score of Siberian stonechats against the laying date. Birds with negative residuals have initiated wing moult earlier in relation to body moult than the average.

9.5   Discussion

Siberian stonechats, as other long-distance migrants, have only limited time available for breeding and moulting. This may explain why virtually all birds showed an overlap of reproductive activities and feather replacement. Birds that raised their first clutch successfully, initiated body and flight feather moult within a few days after fledging of their offspring, that is during a time when the young were still dependent on the provisioning of food by their parents. Although reproduction and moult are usually separated in birds (Jenni & Winkler 1994, Dawson et al. 2001), a certain overlap is often found in other long-distance migrants (Ginn & Melville 1983, Jenni & Winkler 1994, Hemborg et al. 1998, Hemborg & Merilä 1998).

It may be of significance in this context that feather replacement in normal breeding Siberian stonechats is timed to limit the moult-breeding overlap to the post-fledging period. This is observed also in other passerine species that regularly overlap reproduction and moult (Hemborg 1999a, Hemborg & Merilä 1999). After fledging the energy demand of the offspring is decreasing, because they have finished structural growth and gradually learn to catch their own prey. Furthermore, if the energetic costs during the initial stages of moult are lower than during full moult, the overlap would be restricted to periods of relatively low energy demand both of reproduction and moult. It should be noted, however, that not feather replacement itself, but building and maintaining the machinery necessary for it may be the energetically costly part (Klaassen 1995, Schieltz & Murphy 1997, Murphy 1999). In captive European and African stonechats, resting metabolic rates increased from pre-moulting to moulting, and then decreased in the course of moult (Klaassen 1995). Thus, the energetic costs of moult in free-living Siberian stonechats that care for dependent fledglings may be as high as during later moult stages, when reproduction is finished.

Siberian stonechats that laid a replacement clutch delayed the onset of feather replacement. They did not, however, simply shift the onset of

moult to initiate moult at the same breeding stage as the normal breeders. Late breeders clearly began to moult at an earlier offspring age than normal breeders. This may entail costs in terms of current reproductive success, because breeding and moulting simultaneously may affect parent and/or offspring condition and survival negatively (Svensson & Nilsson 1997, Hemborg & Lundberg 1998, Siikamäki 1998, Moreno et al. 2005). However, in the course of the season the costs of having a plumage that is not suited for migration may exceed the potential reproductive costs of a moult-breeding overlap.

I calculated the individual degree of moult-breeding overlap by estimating the onset of feather replacement from the state of moult at the time of capture. There was a clear relationship with reproductive timing: The later the birds initiated their clutches, the shorter was the interval to the initiation of moult and hence the higher the degree of overlap between reproduction and moult. Because I didn't know the individual speeds of feather replacement, I had to estimate a population level average moult rate. To do this I had to assume that moult rate is constant. Individual feather growth rates are rather constant (Murphy & King 1986, Bensch & Grahn 1993), and during the moulting process the increase in feather mass is linear (Dawson & Newton 2004). However, because the moult scores sum up feather growth over the whole considered plumage area, a curvilinear relationship of moult score with time results (Dawson & Newton 2004). Hence, I induced some error by using a linear approximation of moult rate, especially for birds with very low or very high moult scores. The second assumption of my method for calculating moult speed was that growth rate is equal in all birds irrespective of individual stage or calendar date, which may be more problematic. Numerous studies on captive and free-living birds have shown that the nutritional state of the individual (Murphy et al. 1988, Murphy 1996, Swaddle & Witter 1997b, Murphy 1999) and the calendar date (Dawson 1994, Flinks 1999, Helm & Gwinner 1999, Dawson et al. 2000, Dawson 2004, Hahn et al. 2004, Helm et al. 2005) affect the timing but also rate of moult. While individual differences in body condition will increase

the scatter in the data, an acceleration of moult with date would change the slope of the relationship between timing of reproduction and timing of moult. It is however questionable whether later breeding birds can increase their rate of moult as much as to keep moult-breeding overlap at the level of early breeders. Faster moult does not imply faster growth of the individual feather, but a higher number of feathers being replaced at the same time. The number of wing feathers that can be moulted simultaneously is limited when the ability to fly has to be upheld, as during chick provisioning. Similarly, there is an energetic and thermoregulatory ceiling for the number of body feathers that can be replaced at the same time. Hence, even in the light of the method's weaknesses, the general result that the degree of moult-breeding overlap is related to the reproductive timing is reasonable. In the course of the season the requirements of migration become increasingly important when trading off reproduction and moult.

It is interesting that the stonechats seem to be able to adjust the schedules of flight feather moult and body moult separately to the current state of reproduction and the calendar date. Some of the late breeders delayed body moult, while they initiated wing moult almost at the same time as the normal breeders, or alternatively they may have delayed wing moult to the same degree as body moult but increased the rate of flight feather replacement. Along with the replacement of the wing feathers comes a reduction in flight performance (Swaddle & Witter 1997a, Hedenström & Sunada 1999, Hedenström 2003, Williams & Swaddle 2003). Body moult, on the other hand, affects the insulatory and thermoregulatory properties of the plumage (Hahn et al. 1992, Jenni & Winkler 1994, Nilsson & Svensson 1996, Dawson et al. 2000). Body feathers comprise about 70% of total plumage mass and hence require more energy and nutrients to replace than the flight feathers (Newton 1966, Jenni & Winkler 1994). Hence, the overlap of parental care with wing moult and body moult may lead to different cost-benefit ratios in the Siberian stonechats. Flight performance may be more important than thermoregulation, and furthermore wing moult may be

energetically cheaper then body moult. The mechanisms of the regulation of moult schedules is still largely unknown (e.g. Hahn et al. 1992), however these results suggest that the regulation of wing and body moult are at least partially uncoupled in the Siberian stonechats.

In pied flycatchers and collared flycatchers *Ficedula hypoleuca* and *F. albicollis* moult-breeding overlap is common, however its degree varies in males and females (Hemborg 1998, Hemborg & Merilä 1998, Hemborg 1999a, Hemborg & Merilä 1999). Males initiate moult at an earlier breeding stage than females, particularly when breeding is delayed. At the same time these males reduce their parental investment, which leads to a sexual conflict and a reduction in reproductive success and survival in the females (Hemborg & Merilä 1998, Hemborg 1999b). In this study, male and female Siberian stonechats which raised their original clutch successfully, initiated moult at about the same time and showed therefore the same degree of moult-breeding overlap. Late breeding males initiated moult at earlier offspring ages and therefore had a larger overlap of reproduction and feather replacement. I do not know whether, as a consequence, late males reduced their parental investment. However, the number of fledglings produced per egg was about the same in first and replacement clutches (see Chapter 6 of this thesis). Thus, either the males maintained the level of parental care at the level of the normal breeders, or the females were able to compensate a reduced parental investment of their partners.

9.6   References

Artem, A. V. (2004). Molt and nest overlapping in long-distant migrants: main regularities of plumage replacement in the pied flycatcher, Ficedula hypoleuca (Passeriformes, Muscicapidae), from Karelia. *Russian Journal of Zoology [Zoologicheskii Zhurnal]* 83: 1127-1137.

Bairlein, F. & Gwinner, E. (1994). Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annual Review of Nutrition* 14: 187-214.

Bensch, S. & Grahn, M. (1993). A new method forestimating individual speed of molt. *Condor* 95: 305-315.

Berthold, P., Gwinner, E. & Klein, P. (1970). Vergleichende Untersuchung der Jugendentwicklung eines ausgeprägten Zugvogels, *Silvia borin*, und eines weniger ausgeprägten Zugvogels, *S. atricapilla*. *Vogelwarte* 25: 298-329.

Biebach, H. (1996). Energetics of Winter and Migratory Fattening. *In* C. Carey (Ed.), *Avian Energetics and Nutritional Ecology*. Chapman & Hall, New York.

Clotfelter, E. D., O'Neal, D. M., Gaudioso, J. M., Casto, J. M., Parker-Renga, I. M., Snajdr, E. A., Duffy, D. L., Nolan, J., Val & Ketterson, E. D. (2004). Consequences of elevating plasma testosterone in females of a socially monogamous songbird: evidence of constraints on male evolution? *Hormones and Behavior* 46: 171-178.

Dawson, A. (1994). The effects of daylength and testosterone on the initiation and progress of moult in Starlings *Sturnus vulgaris*. *Ibis* 136: 335-340.

Dawson, A. (2004). The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. *Ibis* 146: 493-500.

Dawson, A., Hinsley, S. A., Ferns, P. N., Bonser, R. H. C. & Eccleston, L. (2000). Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 267: 2093-2098.

Dawson, A., King, V. M., Bentley, G. E. & Ball, G. F. (2001). Photoperiodic control of seasonality in birds. *Journal of Biological Rhythms* 16: 365-380.

Dawson, A. & Newton, I. (2004). Use and validation of a molt score index corrected for primary feather mass. *Auk* 121: 372-379.

Dawson, A. & Sharp, P. J. (1998). The role of prolactin in the development of reproductive photorefractoriness and postnuptial molt in the European starling (*Sturnus vulgaris*). *Endocrinology* 139: 485-490.

Drent, R. H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea* 68: 225-252.

Duettmann, H., Dieleman, S. & Groothuis, T. G. G. (1999). Timing of moult in male and female shelducks Tadorna tadorna: Effects of androgens and mates. *Ardea* 87: 33-39.

Eeva, T., Veistola, S. & Lehikoinen, E. (2000). Timing of breeding in subarctic passerines in relation to food availability. *Canadian Journal of Zoology* 78: 67-78.

Ellegren, H. (1990). Timing of autumn migration in bluethroats *Luscinia s. svecica* depends on timing of breeding. *Ornis Fennica* 67: 13-17.

Flinks, H. (1999). Muster, Intensität und zeitliche Aspekte der postjuvenilen Mauser beim Schwarzkehlchen (*Saxicola torquata*). [Pattern, extent, and time aspects of the postjuvenile moult in stonechats (*Saxicola torquata*)]. *Die Vogelwarte* 40: 11-27.

Ginn, H. B. & Melville, D. S. (1983). *Moult in birds*. British Trust for Ornithology, Tring.

Gwinner, E. (1986). *Circannual rhythms*. Springer Verlag, Heidelberg.

Gwinner, E. (1996). Circadian and circannual programmes in avian migration. *Journal of Experimental Biology* 199: 39-48.

Gwinner, E. (2003). Circannual rhythms in birds. *Current Opinion in Neurobiology* 13: 770-778.

Gwinner, E. & Dittami, J. P. (1990). Endogenous reproductive rhythms in a tropical bird. *Science* 249: 906-908.

Hahn, T. P., Pereyra, M. E., Sharbaugh, S. M. & Bentley, G. E. (2004). Physiological responses to photoperiod in three cardueline finch species. *General and Comparative Endocrinology* 137: 99-108.

Hahn, T. P., Swingle, J., Wingfield, J. C. & Ramenofsky, M. (1992). Adjustments of the prebasic molt schedule in birds. *Ornis Scandinavica* 23: 314-321.

Hall, K. S. S. & Fransson, T. (2000). Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. *Journal of Avian Biology* 31: 583-587.

Hall, K. S. S. & Fransson, T. (2001). Wing moult in relation to autumn migration in adult common whitethroats *Sylvia communis communis*. *Ibis* 143: 580-586.

Hedenström, A. (2003). Flying with holey wings. *Journal of Avian Biology* 34: 324-327.

Hedenström, A. & Sunada, S. (1999). On the aerodynamics of moult gaps in birds. *Journal of Experimental Biology* 202: 67-76.

Helm, B. & Gwinner, E. (1999). Timing of postjuvenal molt in African (Saxicola torquata axillaris) and European (Saxicola torquata rubicola) stonechats: Effects of genetic and environmental factors. *Auk* 116: 589-603.

Helm, B., Gwinner, E. & Trost, L. (2005). Flexible seasonal timing and migratory behavior. *Annals of the New York Acadamy of Sciences* in press.

Hemborg, C. (1998). Sexual differences in the control of postnuptial moult in the pied flycatcher. *Animal Behaviour* 56: 1221-1227.

Hemborg, C. (1999a). Annual variation in the timing of breeding and moulting in male and female Pied Flycatchers Ficedula hypoleuca. *Ibis* 141: 226-232.

Hemborg, C. (1999b). Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers, Ficedula hypoleuca. *Journal of Animal Ecology* 68: 429-436.

Hemborg, C. & Lundberg, A. (1998). Costs of overlapping reproduction and moult in passerine birds: An experiment with the pied flycatcher. *Behavioral Ecology and Sociobiology* 43: 19-23.

Hemborg, C., Lundberg, A. & Siikamaki, P. (1998). Trade-off between reproduction and moult: A comparison of three Fennoscandian pied flycatcher populations. *Oecologia* 117: 374-380.

Hemborg, C. & Merilä, J. (1998). A sexual conflict in collared flycatchers, Ficedula albicollis: Early male moult reduces female fitness. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 26: 2003-2007.

Hemborg, C. & Merilä, J. (1999). Reproductive investment and moult-breeding overlap in the collared flycatcher Ficedula albicollis: An experimental approach. *Annales Zoologici Fennici* 36: 1-9.

Jenni, L. & Winkler, R. (1994). *Moult and Ageing of European Passerines*. Academic Press, London.

Klaassen, M. (1995). Moult and basal metabolic costs in males of two subspecies of stonechats: The European Saxicola torquata rubicula and the East African S. t. axillaris. *Oecologia* 104: 424-432.

Klemp, S. (2000). Effects of parental effort on second brood, moult and survival in the Grey Wagtail Motacilla cinerea. *Ardea* 88: 91-98.

Lindström, A., Daan, S. & Visser, G. H. (1994). The conflict between moult and migratory fat deposition: A photoperiodic experiment with bluethroats. *Animal Behaviour* 48: 1173-1181.

Lindström, A., Visser, G. H. & Daan, S. (1993). The energetic cost of feather synthesis is proportional to basal metabolic-rate. *Physiological Zoology* 66: 490-510.

McGraw, K. J. & Ardia, D. R. (2003). Carotenoids, immunocompetence, and the information content of sexual colors: An experimental test. *American Naturalist* 162: 704-712.

McGraw, K. J., Dale, J. & Mackillop, E. A. (2003). Social environment during molt and the expression of melanin-based plumage pigmentation in male house sparrows (Passer domesticus). *Behavioral Ecology and Sociobiology* 53: 116-122.

McGraw, K. J., Mackillop, E. A., Dale, J. & Hauber, M. E. (2002). Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology* 205: 3747-3755.

Moreno, J., Merino, S., Sanz, J. J., Arriero, E., Morales, J. & Tomas, G. (2005). Nestling cell-mediated immune response, body mass and hatching date as predictors of local recruitment in the pied flycatcher Ficedula hypoleuca. *Journal of Avian Biology* 36: 251-260.

Morton, M. L. (2002). The mountain white-crowned sparrow: Migration and reproduction in high altitude. *Studies in Avian Biology* 24: 1-236.

Murphy, M. E. (1996). Energetics and nutrition of molt. *In* C. Carey (Ed.), *Avian Energetics and Nutritional Ecology*, pp. 158-198. Chapman & Hall, New York.

Murphy, M. E. (1999). Energetics and nutrition of moulting. *In* N. J. Adams & R. H. Slotow (Eds.), *Proc. 22 Int. Ornithol. Congr., Durban*, pp. 527-535. BirdLife South Africa, Johannesburg.

Murphy, M. E. & King, J. R. (1986). Diurnal constancy of feather growth rates in white-crowned sparrows *Zonotrichia leucophrys gambelii* exposed to various photoperiods and feeding schedules during the postnuptial molt. *Canadian Journal of Zoology* 64: 1292-1294.

Murphy, M. E., King, J. R. & Lu, J. (1988). Malnutrition during the postnuptial molt of white-crowned sparrows: feather growth and quality. *Canadian Journal of Zoology* 66: 1403-1413.

Newton, I. (1966). The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* 108: 41-87.

Nilsson, J.-A. & Svensson, E. (1996). The cost of reproduction: a new link between current reproductive effort and future reproductive output. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 263: 711-714.

Nolan, V. J., Ketterson, E. D., Ziegenfus, C., Cullen, D. P. & Chandler, C. R. (1992). Testosterone and avian live histories: Effects of experimentally elevated testosterone on prebasic molt and survival in male Dark-eyed Juncos. *Condor* 94: 364-370.

Norris, D. R., Marra, P. P., Montgomerie, R., Kyser, T. K. & Ratcliffe, L. M. (2004). Reproductive effort, molting latitude, and feather color in a migratory songbird. *Science* 306: 2249-2250.

Roff, D. A. (1992). *The Evolution of Life Histories: Theory and analysis*. Chapman & Hall, New York.

Rubolini, D., Massi, A. & Spina, F. (2002). Replacement of body feathers is associated with low pre-migratory energy stores in a long-distance migratory bird, the barn swallow (Hirundo rustica). *Journal of Zoology* 258: 441-447.

Runfeldt, S. & Wingfield, J. C. (1985). Experimentally prolonged sexual acticity in fermale sparrows delays termination of reproductive activity in their untreated males. *Animal Behaviour* 33: 403-410.

Schieltz, P. C. & Murphy, M. E. (1997). The contribution of insulation changes to the energy cost of avian molt. *Canadian Journal of Zoology* 75: 396-400.

Schleussner, G., Dittami, J. P. & Gwinner, E. (1985). Testosterone implants affect molt in male European starlings *Sturnus vulgaris*. *Physiological Zoology* 58: 597-604.

Siefferman, L. & Hill, G. E. (2003). Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behavioral Ecology* 14: 855-861.

Siefferman, L. & Hill, G. E. (2005). Male eastern bluebirds trade future ornamentation for current reproductive investment. *Biology Letters* 1: 208-211.

Siikamäki, P. (1998). Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology* 79: 1789-1796.

Siikamäki, P., Hovi, M. & Rätti, O. (1994). A trade-off between current reproduction and moult in the pied flycatcher: An experiment. *Functional Ecology* 8: 587-593.

Stearns, S. C. (1992). *The Evolution of Life-Histories*. Oxford University Press, Oxford.

Svensson, E. & Nilsson, J.-A. (1997). The trade-off between molt and parental care: A sexual conflict in the blue tit? *Behavioral Ecology* 8: 92-98.

Swaddle, J. P. & Witter, M. S. (1997a). The effects of molt on the flight performance, body mass, and behavior of European starlings (Sturnus vulgaris): An experimental approach. *Canadian Journal of Zoology* 75: 1135-1146.

Swaddle, J. P. & Witter, M. S. (1997b). Food availability and primary feather molt in European starlings, *Sturnus vulgaris*. *Canadian Journal of Zoology* 75: 948-953.

Williams, E. V. & Swaddle, J. P. (2003). Moult, flight performance and wingbeat kinematics during take-off in European starlings *Sturnus vulgaris*. *Journal of Avian Biology* 34: 371-378.

Williams, G. C. (1966). Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.

Winkler, R. (1999). Moult strategies of European passerines. *In* N. J. Adams & R. H. Slotow (Eds.), *Proc. 22 Int. Ornithol. Congr., Durban*, pp. 564-567. BirdLife South Africa, Johannesburg.

Summary

The stonechat has one of the widest breeding distributions among the Old World passerines. It breeds under tropical, subtropical, north- and south-temperate, and sub-arctic conditions. Also its migratory strategies vary, ranging from year-round residency in areas such different as the British Isles and equatorial Africa, to long-distance migration in northern Asia. These characteristics and the fact that it can be successfully bred in captivity make the stonechat an ideal model species for studying life-history variation under varying seasonal regimes, both in the field and in the lab. In *Chapter 1* I develop the conceptual framework for the study of annual timing and life-history variation in stonechats.

My studies focus on free-living stonechats from two different populations, *Siberian stonechats* breeding in northern Kazakhstan and *European stonechats* breeding in central Slovakia. The taxonomic status and the basic biology of the stonechat and the characteristics of the two study sites are outlined in *Chapter 2*. Both sites are situated in the temperate zones and hence the local photoperiodic conditions are similar. However, due to the continental climate in Kazakhstan the summer is shorter and hotter and the precipitation lower than in Slovakia, and as a result the breeding season is about two months longer at the European site.

The two populations differ in their migratory strategies (*Chapter 3*). The Siberian stonechats are long-distance migrants that travel up to 6500 km from their breeding to their wintering grounds and pass major ecological barriers like deserts and high mountain ranges on their way. The stonechats from eastern Europe are short-distance migrants that travel about 1500 km. Ringing recovery data suggest that a large proportion of them pass the Mediterranean Sea on their way. There are no ringing recoveries for Siberian stonechats, and information on their migratory routes is sparse and dispersed in different sources. I tried to fill this gap by

reconstructing the spatio-temporal pattern of the stonechat migrations within Central Asia and southern Siberia from published passage data. Stonechats enter Central Asia in spring from the south-west, which suggests that they largely avoid the high inner-Asian mountain ranges. From there they spread northwards into their Central Asian and Siberian breeding areas. In autumn they retrace this pattern backwards, however the movement is less concerted than in spring. The passage data can be used to calculate the average speed of migration within the area and compare it to migration speed in the European stonechats. The European stonechats move at higher speeds during spring than during autumn. This is consistent with data on other European passerines. Within Central Asia, however, the stonechats seem to be constrained in their spring movements because they have to stop and wait for ameliorating local conditions. Increasing spring temperatures due to global warming may therefore have a high potential to change migratory phenology in the Siberian stonechats.

Birds shut down their reproductive system during the nonbreeding seasons. Migratory birds face a potential conflict between the preparation for breeding and migration, because gonadal maturation takes several weeks. I investigated whether the migratory strategy affects the gonadal state at the time of arrival in the breeding areas (*Chapter 4*). Males of both populations arrive at the breeding sites with gonads that are not fully developed. Neither the gonadal state in relation to the onset of reproduction, nor the rate of development to the mature state differ in the two populations. This could indicate that the late stages of reproductive development are mainly affected by the targeted date of reproduction and/or by physiological determinants of gonadal maturation rates, whereas the migratory period has less effect. More knowledge about reproductive development along the migratory route, particularly in long-distance migrants, is required. In my study populations local breeders and passage migrants are not distinguishable on the basis of their gonadal development. However, the data in the passage migrants is more variable, which could

reflect differences in reproductive timing due to different migratory destinations.

Due to the local conditions at the breeding site and the temporal requirements of migration the stonechats in Kazakhstan have a shorter breeding season than their conspecifics in Slovakia (*Chapter 5*). The Siberian stonechats produce generally one clutch per season, but lost clutches are often replaced. European stonechats lay up to three clutches per season. The interval between clutch loss and relaying does not differ between the two populations. Breeding synchrony is significantly higher in Kazakhstan, both over the whole breeding period and when only the first clutches are considered. Overall clutch size is higher in the Siberian stonechats. Clutch size decreases from first to replacement clutches in Kazakhstan, and from first to second clutches in Slovakia. The clutch size of the third clutches in the European stonechats increases again, which may indicate that only high-quality parents initiate a third seasonal breeding attempt, or that a strategy of terminal investment is involved. Fledging success per egg is higher in Kazakhstan and does not differ between breeding attempts. In Slovakia fledging success drops markedly from the first to the later breeding attempts. Predation during the egg stage plays a greater role in the European stonechats, whereas in the Siberian stonechats predation on nestlings is more important. As a result of smaller clutch sizes later in the season, and of higher failure rates in later clutches, particularly in Slovakia, fledgling output per clutch decreases in both populations. A Kazakh breeding pair produces on average about five fledglings per season, a Slovak breeding pair about seven fledglings per season. In one study season 9% of the Kazakh males mated simultaneously with two females. Facultative polygyny has previously been reported in European, but not in Siberian stonechats. The primary clutches of polygynous males were initiated earlier, contained more eggs and produced more fledglings than the comparable first clutches of monogamous males. This may indicate that polygynous males were of superior parental quality. The secondary polygynous clutches were initiated later, contained less eggs

and produced less fledglings, indicating costs in terms of reproductive success for secondary females.

According to the *challenge hypothesis* the length of the breeding period, the degree of inter-male competition, and the degree of parental care affect the seasonal profiles of circulating androgens (*Chapter 6*). Male Siberian stonechats have elevated circulating androgen levels during May and June with a peak in mid-May. In the European stonechats androgens are elevated from March until the end of May, they peak in mid-April and mid-May. In both populations androgen levels are highest in males during the territorial stages and when the females are fertile, and decrease during the parenting stages. Overall androgen levels are higher in the European stonechat males, which could be explained by higher male-male competition and/or a lower degree of paternal care in this population. Male aggression during simulated territorial intrusions is high throughout the season in both populations and therefore apparently unrelated to the circulating androgen levels. In the Siberian stonechat males dihydrotestosterone (DHT) contributes relatively more to the total circulating androgens. This could be related to different roles of DHT and testosterone (T) in regulating male reproductive behaviours, or to different costs associated with high circulating levels of these androgens. Estradiol (E_2) is basal throughout the season in Siberian and European stonechat males. In female stonechats the levels of circulating gonadal steroids (E_2, T, DHT) are basal throughout the season. T is higher in the European stonechat females than in the Kazakh females, however there is no apparent seasonal pattern.

The adrenal glucocorticoids (GCs) are steroid hormones that act in general energy metabolism and as part of the response of an organism to unpredictable threats to its physiological homeostasis (*Chapter 7*). Two hypotheses try to explain seasonal and individual variation in circulating GCs. The *reproductive limitation hypothesis* predicts that, because high GCs may cause nest desertion, GC response to stress is reduced when breeding opportunities are limited, as in the Siberian stonechats. Contrary to this

predictions, overall GC levels are higher in the Siberian than in the European stonechats. Hence there seems to be no simple relationship between the potential number of breeding attempts and GC levels in stonechats. The *energy mobilisation hypothesis* predicts higher GC levels during periods of increased energy demand, such as breeding. The energetic costs may differ between breeding stages, at least in males. However, GC levels do not vary with breeding stage in the stonechats. GC levels decrease in Kazakhstan when the birds start to moult. Feather replacement is an energetically costly task; therefore a simple relationship between energy demand and circulating GCs is not supported. It is possible that GCs interfere with the physiology of feather replacement and are therefore reduced during this period.

Time-dependent mortality, the degree of sibling competition, and internal constraints on growth have been discussed as the major factors affecting the evolution of developmental rates (*Chapter 8*). The length of the breeding season may also affect juvenile development, particularly in migrants, where the juveniles have to gain a certain level of maturity to meet the demands of the autumn movements. Incubation periods are slightly shorter in Kazakhstan than in Slovakia, indicating that embryonic development may proceed at a higher rate in the Siberian stonechats. Postnatal increase rate in body size, but not in wing length, is also higher in the Siberian stonechats. These measures of postnatal growth are not affected by the hatching date. Runt nestlings, which are at a competitive disadvantage because they have hatched later than their nestmates, are initially heavier and bigger but loose this head start during the growth period due to lower growth rates. Postjuvenile moult is initiated very early in the life of Siberian stonechats. as in their captive conspecifics. It is shifted forward by a few days in the late-hatched chicks of replacement clutches, however the effect of hatch date on the onset of moult is much lower than in captive European stonechats. The period from the start of incubation until the end of postjuvenile moult lasts about half as long in the Siberian stonechats than in the European

stonechats, mainly due to differences in the onset and duration of moult between the populations.

Siberian stonechats lay only one clutch per season, but lost clutches are often replaced (*Chapter 9*). Normal breeders (those birds that raised their first clutch successfully) initiate postnuptial moult shortly after their young have left the nest. Late breeders (birds with replacement clutches) moult later than normal breeders. However, they initiate moult earlier in relation to the age of their offspring than normal breeders. As a result, they overlap breeding and moult more than normal breeders. Simultaneous reproduction and feather replacement is thought to be costly and therefore generally avoided. This is not always possible in time-constrained breeders. In the Siberian stonechats the degree of moult-breeding overlap increases the later the offspring hatches in the season. Scarce data suggests that late breeding males initiate moult earlier than their female partners. This may imply that they reduce their share in parental care, as has been found in other species. Postponing moult of body feathers, which serves mainly in insulation, may have less severe consequences in a migratory species, than postponing wing moult. Late breeders postpone body moult more than wing moult.

Siberian stonechats in Kazakhstan and European stonechats in Slowakia are closely related and breed both in the north-temperate zones in the same latitude and under similar photoperiodic conditions. However, due to the different local climatic conditions, the migratory distance and the length of the breeding season differ. This brings about consistent differences between the two populations in the migratory behaviour, the breeding performance, the hormonal regulation of reproduction, the hormonal response to environmental challenges, and the juvenile development. Because the Siberian and Slovak stonechat populations are closely related, a divergent genetic background and/or species-specific physiological constraints probably play a minor role in creating these differences. They rather reflect differences in annual timing, which affect the trade-off between current and future reproductive success in different life-history stages.

The climatic changes that are observed in recent years have been associated with changing migratory and reproductive schedules and shifts in species' distribution ranges. The example of the stonechats shows that a multitude of systemic changes is required to change the annual cycle. The success of an organism in a changing environment will depend on its ability to successfully integrate all these physiological and behavioural alterations.

ZUSAMMENFASSUNG

Annuale Zeiteinteilung und lebensgeschichtliche Variation bei freilebenden Schwarzkehlchen

Das Schwarzkehlchen hat eines der größten Brutareale aller altweltlichen Singvögel. Es brütet in den Tropen, den Subtropen, den gemäßigten nordlichen und südlichen Zonen und unter sub-arktischen Bedingungen. Das Zugverhalten in den verschiedenen Populationen variiert stark. Reine Standvogelpopulation gibt es z.B. im äquatorialen Afrika, teilziehende Populationen (gemeinsames Auftreten von Standvögeln und Zugvögeln) auf den Britischen Inseln, obligate Kurzstreckenzieher in Zentral- und Osteuropa und obligate Weitstreckenzieher im nördlichen Asien. Diese Merkmale und die Tatsache, dass es erfolgreich gezüchtet werden kann, machen das Schwarzkehlchen zu einer idealen Modellart, um den Einfluss unterschiedlicher Jahreszyklen auf die Gestaltung des Lebenszyklus sowohl im Labor als auch im Freiland zu untersuchen. In *Kapitel 1 (Allgemeine Einleitung - Themen und Konzepte)* entwickle ich den konzeptuellen Rahmen für meine Studien der annualen Zeiteinteilung und lebensgeschichtlichen Variation bei Schwarzkehlchen.

Meine Untersuchungen konzentrieren sich auf freilebende Schwarzkehlchen aus zwei verschiedenen Populationen: *Sibirische Schwarzkehlchen*, die in Nord-Kasachstan brüten, und *Europäische Schwarzkehlchen*, die in der Zentral-Slowakei brüten. Der taxonomische Status und die grundlegende Biologie des Schwarzkehlchens, sowie die geographischen und klimatischen Merkmale der beiden Studiengebiete werden in *Kapitel 2 (Charakterisierung der Studiengebiete und der Studienart)* umrissen. Beide Studiengebiete befinden sich in den gemäßigten Breiten und weisen daher ähnliche Tageslängen auf. Weil aber in dem stark vom kontinentalen Klima geprägten Kasachstan die Sommer kürzer, heißer und

trocken sind als in der Slowakei, ist die Brutsaison in dem europäischen Studiengebiet etwa zwei Monate länger.

Die beiden Populationen unterscheiden sich in ihren Zugstrategien (*Kapitel 3, Der Zug von Sibirischen und Europäischen Schwarzkehlchen*). Sibirische Schwarzkehlchen sind Langstreckenzieher. Zwischen ihren Brut- und Überwinterungsgebieten liegen bis zu 6500 km. Auf dem Zugweg liegen ausgedehnte Wüstengebiete und hohe Gebirgszüge. Die Schwarzkehlchen aus Osteuropa sind Kurzstreckenzieher, die etwa 1500 km weit wandern. Ringfunde deuten darauf hin, daß ein Großteil der Vögel auf ihrem Zug das Mittelmeer überquert. Es gibt leider keinerlei Ringfunde für die Sibirischen Schwarzkehlchen, und Informationen über ihre Zugrouten sind knapp und auf unterschiedliche Quellen verteilt. In diesem Kapitel versuche ich diese Lücke zu schließen und das zeitliche und räumliche Muster der Wanderungen des Schwarzkehlchens innerhalb Zentralasiens und des südlichen Sibiriens anhand von veröffentlichten Durchzugsdaten zu rekonstruieren. Die Schwarzkehlchen erreichen Zentralasien von Südwesten her, was darauf schließen läßt, daß sie die hohen innerasiatischen Gebirgszüge großteils meiden. Von dort breiten sie sich nördlich in ihre zentralasiatischen und südsibirischen Brutgebiete aus. Der Herbstzug erfolgt nach ähnlichem Muster in umgekehrter Richtung, jedoch sind die Zugbewegungen zeitlich weniger koordiniert als im Frühjahr. Die Durchzugsdaten können auch genutzt werden, um die durchschnittlichen Zuggeschwindigkeiten in diesem Gebiet zu errechnen und diese Resulte mit den Zuggeschwindigkeiten von Europäischen Schwarzkehlchen zu vergleichen. Diese ziehen im Frühjahr mit höheren Geschwindigkeiten als im Herbst. Ein ähnliches jahreszeitliches Muster der Zuggeschwindigkeiten wurde auch bei dreizehn anderen europäischen Singvogelarten ermittelt. Bei den Sibirischen Schwarzkehlchen jedoch geht innerhalb Zentralasiens der Zug im Frühjahr langsamer vonstatten als im Herbst. Ihr Frühjahrszug ist verlangsamt, weil die Vögel immer wieder auf eine Verbesserung der lokalen Witterungsbedingungen warten müssen, bevor sie weiter nach Norden ziehen können. Der Anstieg der Frühjahrstemperaturen

der derzeit zu beobachten ist, könnte bei den Sibirischen Schwarzkehlchen zu Veränderungen in der Zugphänologie führen.

Vögel bilden ihr Fortpflanzungssystem außerhalb der Brutsaison zurück. Da das Gonadenwachstum mehrere Wochen in Anspruch nimmt, sehen sich Zugvögel einem potentiellen Konflikt zwischen der physiologischen Vorbereitung auf die Brutsaison und den Erfordernissen des Zuges gegenüber. Ich untersuchte, ob die Zugstrategie Einfluß auf den Gonadenzustand zur Zeit der Frühjahrs-Ankunft in den Brutgebieten hat (*Kapitel 4, Der Gonadenzustand zur Frühjahrsankunft bei Sibirischen und Europäischen Schwarzkehlchen*). Die Männchen aus beiden Populationen erreichen das Brutgebiet mit unvollständig entwickelten Gonaden. Sie unterscheiden sich weder im Stand der Hodenentwicklung relativ zum Fortpflanzungs-Beginn gesehen, noch in der Entwicklungsrate der Gonaden zur vollen Reife. Dies könnte bedeuten, daß die späten Stadien der reproduktiven Reifung hautsächlich vom angestrebten Brutdatum oder physiologischen Beschränkungen abhängen, und nur wenig von der Zugphase beeinflusst werden. Ein genaueres Wissen um die reproduktive Entwicklung entlang der Zugwege ist daher vonnöten, insbesondere bei Langstreckenziehern. In meinen Studienpopulationen können Brütvögel und Durchzügler nicht anhand ihres Gonadenzustandes unterschieden werden. Die Gonadengrößen der Durchzügler variieren allerdings stärker, was auf unterschiedliche Brutgebiete und Brutdaten in dieser Gruppe zurückzuführen sein könnte.

Aufgrund der lokalen Bedingungen im Brutgebiet und der zeitlichen Erfordernisse der Zugzeit ist die Brutsaison in Kasachstan kürzer als in der Slowakei (*Kapitel 5, Das Brutgeschehen von Sibirischen und Europäischen Schwarzkehlchen*). Die Sibirischen Schwarzkehlchen produzieren im Allgemeinen ein Gelege pro Saison. Gelegeverlust führt aber oft zu Ersatzbruten. Die Europäischen Schwarzkehlchen legen bis zu drei Gelege in einer Brutsaison. Das zeitliche Intervall zwischen Gelegeverlust und Nachlegen unterscheidet sich zwischen den beiden Populationen nicht. Die Synchronität des Brutgeschehens ist signifikant höher in Kasachstan, sowohl wenn die gesamte Brutperiode, als auch wenn nur die Erstbruten in Betracht

gezogen werden. Die durchschnittliche Gelegegröße ist bei den Sibirischen Schwarzkehlchen höher als bei den Europäischen. Die Gelegegröße sinkt bei den Ersatzbruten in Kasachstan und den Zweitbruten in der Slowakei. Bei den Drittbruten in der Slowakei steigt die Gelegegröße wieder an, und dies könnte anzeigen, daß nur Eltern von guter Qualität ein drittes Gelege anstreben. Am Saisonende könnte auch eine Art „Alles-Oder-Nichts"-Strategie (Terminales Investment) zur Anwendung kommen. In Kasachstan überlebt ein größerer Prozentsatz der Nachkommen bis zum Ausfliegen als in der Slowakei. Erst- und Ersatzgelege sind in Kasachstan etwa gleich erfolgreich, während der Bruterfolg in der Slowakei von den Erstgelegen zu den weiteren Brutversuchen hin stark abfällt. Bei den Europäischen Schwarzkehlchen spielt Prädation während des Ei-Stadiums eine große Rolle. Bei den Sibirischen Schwarzkehlchen hat die Prädation von Nestlingen ein größeres Gewicht. Als Folge von kleineren Gelege später im Jahr und, besonders in der Slowakei, von höheren Verlustraten bei späteren Gelegen, sinkt die Anzahl der flüggen Jungen pro Gelege in beiden Populationen. Im Durchschnitt produziert ein Brutpaar in Kasachstan etwa fünf flügge Junge pro Saison, ein Brutpaar in der Slowakei ungefähr sieben. In einem Studienjahr verpaarten sich 9% der brütenden Sibirischen Schwarzkehlchen-Männchen gleichzeitig mit zwei Weibchen. Fakultative Polygynie wurde schon bei Europäischen Schwarzkehlchen beschrieben, aber noch nicht bei ihren Sibirischen Verwandten. Die Primärgelege von polygynen Männchen wurden früher begonnen, enthielten mehr Eier und brachten mehr flügge Junge hervor, als die vergleichbaren Erstgelege von monogamen Männchen. Dies könnte bedeuten, dass polygynen Männchen im Hinblick auf die Jungenaufzucht eine besondere Qualität innewohnte. Die sekundären polygynen Gelege wurden hingegen später initiiert, enthielten weniger Eier und brachten weniger flügge Junge hervor, was auf einen reduzierten Fortpflanzungserfolg bei den Sekundär-Weibchen hindeutet.

Gemäß der *Challenge-Hypothese* beeinflussen die Länge der Brutsaison, der Grad der innerartlichen Konkurrenz und der Grad der Brutpflege die Muster der saisonalen Androgenausschüttung (*Kapitel 6, Zirkulierende*

Gonaden-Steroide während der Brutsaison bei Sibirischen und Europäischen Schwarzkehlchen). Sibirische Schwarzkehlchen-Männchen haben von Mai bis Juni erhöhte Androgenwerte, die Höchstwerte werden Mitte Mai erreicht. Bei den Europäischen Schwarzkehlchen sind die Androgene von März bis Ende Mai erhöht, die Höchstwerte werden Mitte April und Mitte Mai erreicht. In beiden Populationen sind die Androgenwerte der Männchen am höchsten während der territorialen Etablierung und wenn die Weibchen fertil sind, und sie sinken zur Zeit der Brutpflege. Im Durchschnitt sind die Androgenwerte der Europäischen Schwarzkehlchen-Männchen höher als die der Sibirischen. Dies könnte durch höhere innergeschlechtliche Konkurrenz oder niedrigere väterliche Brutpflege in der Europäischen Populationen erklärt werden. Die Aggressivität der Männchen während simulierter territorialer Konflikte ist in beiden Populationen die gesamte Saison über hoch und steht daher anscheinend nicht mit den zirkulierenden Androgenwerten in Beziehung. Bei den Sibirischen Schwarzkehlchen trägt Dihydrotestosteron (DHT) relativ mehr zur gesamten Androgenmenge in der Zirkulation bei. Dies könnte durch unterschiedliche Aufgaben von DHT und Testosteron (T) bei der Steuerung des männlichen Fortpflanzungsverhaltens bedingt sein. Die potentiellen Nachteile hoher zirkulierender Androgenkonzentrationen (z.B. Immunosuppression, Reduzierung der Brutpflege), könnten sich bei den Populationen unterschiedlich auswirken und so ebenfalls zu divergierenden Ausschüttungsmustern führen. Oestradiol (E$_2$) ist bei den Männchen beider Populationen das gesamte Jahr über sehr niedrig. Bei den Schwarzkehlchen-Weibchen sind die Werte aller gonadalen Steroide (T, DHT, E$_2$) sehr niedrig. Die T-Werte der Europäischen Schwarzkehlchen-Weibchen sind höher als die der Sibirischen, allerdings ist kein saisonales Muster ersichtlich.

Die Glukokortikoide (GC), Steroidhormone der Nebenniere, haben eine Funktion beim Energiestoffwechsel und sind Teil der Reaktion eines Organismus auf unvorhersehbare Gefährdungen seines physiologischen Gleichgewichtes (*Kapitel 7, Glukokortikoide bei brütenden Sibirischen und Europäischen Schwarzkehlchen*). Zwei Hypothesen versuchen saisonale und individuelle Unterschiede von zirkulierenden GC zu erklären. Die *Theorie*

der Reproduktiven Beschränkung sagt voraus, dass die GC-Reaktion auf Stress reduziert ist, wenn die Brutmöglichkeiten stark eingeschränkt sind, da hohe GC-Werte zum Abbruch eines Brutversuchs führen können. Entgegen dieser Theorie sind die GC-Werte bei den Sibirischen Schwarzkehlchen höher als bei den Europäischen Schwarzkehlchen. Es besteht anscheinend kein einfacher Zusammenhang zwischen den potentiellen Brutmöglichkeiten und den GC-Werten bei Schwarzkehlchen. Die *Theorie der Energie-Mobilisierung* sagt höhere GC-Werte während Perioden hohen Energiebedarfs, z.B. während dem Brüten, voraus. Daher könnten sich, zumindest bei den Männchen, die GC-Werte zwischen den verschiedenen Brutstadien (Inkubation, Versorgen von Nestlingen, Versorgen von flüggen Jungen) unterscheiden. Bei den Schwarzkehlchen sind jedoch keine Unterschiede der zirkulierenden GC zwischen den Brutstadien feststellbar. Die GC-Werte sinken bei den Sibirischen Schwarzkehlchen wenn die Vögel mit der Mauser beginnen. Da die Erneuerung des Federkleides mit hohen energetischen Kosten einher geht, werden die Vorrausagen der *Theorie der Energie-Mobilisierung* bei den Schwarzkehlchen nicht bestätigt. Es ist möglich, dass hohe GC-Werte störend auf die physiologischen Vorgänge der Mauser einwirken und daher während dieser Zeit herabgesetzt werden.

Nach derzeitigem Diskussionsstand wird die Evolution von Entwicklungsraten hauptsächlich von Mortalitätsraten während des Wachstums, dem Grad der Konkurrenz zwischen den Geschwistern im Gelege und von physiologischen Beschränkungen des Wachstums beeinflusst (*Kapitel 8, Entwicklungsraten von Sibirischen und Europäischen Schwarzkehlchen*). Darüber hinaus könnte auch die Länge der Brutsaison die Juvenilentwicklung beeinflussen. Dies könnte besonders bei Zugvögeln eine Rolle spielen, da deren Jungvögel rechtzeitig einen bestimmten Entwicklungsstand erreichen müssen, um den Anforderungen des Herbstzuges gewachsen zu sein. Die Bebrütungsdauern sind in Kasachstan ein wenig kürzer als in der Slowakei, was darauf hindeuten könnte, dass die Embryonalentwicklung bei den Sibirischen Schwarzkehlchen schneller verläuft. Der postnatale Zuwachs der Körpergröße, aber nicht der Flügellänge, verläuft ebenfalls höher bei den

Sibirischen Schwarzkehlchen. Der sogenannte Kalender-Effekt, d.h. die Beschleunigung von Entwicklungsmerkmalen im Laufe der Saison, hat auf das Körperwachstum der Schwarzkehlchen keinen messbaren Einfluss. Nesthäkchen schlüpfen einen Tag später als ihre Geschwister. Sie sind anfangs größer und schwerer als ihre Geschwister vergleichbaren Alters. Da sie aber gegen ihre älteren Geschwister im Nachteil sind, haben sie niedrigere Wachstumsraten als diese und büßen daher ihren relativen Vorsprung im Laufe der Juvenilentwicklung ein. Die Postjuvenilmauser beginnt bei den Sibirischen Schwarzkehlchen, wie bei ihren in Gefangenschaft gehaltenen Artgenossen, in einem sehr frühem Alter. Ein später Schlüpftermin, etwa bei Ersatzgelegen, bewirkt ein Vorverlegen des Mauserbeginnes. Dieser Kalender-Effekt fällt jedoch viel geringer aus als bei in Gefangenschaft gehaltenen Europäischen Schwarzkehlchen. Die Zeitspanne vom Bebrütungsbeginn bis zum Ende der Postjuvenilmauser dauert bei den Sibirischen Schwarzkehlchen etwa halb so lang wie bei den Europäischen Schwarzkehlchen. Allerdings wird dieser Unterschied hauptsächlich durch den frühen Mauserbeginn und die kurze Mauserdauer der Sibirischen Schwarzkehlchen bewirkt.

Die Sibirischen Schwarzkehlchen legen nur ein Gelege pro Saison, verlorengegangene Gelege werden aber oft ersetzt (*Kapitel 9, Der Ausgleich zwischen Fortpflanzung und Mauser bei Sibirischen Schwarzkehlchen*). Vögel die ihr erstes Gelege erfolgreich großgezogen haben (Normale Brüter) beginnen mit der postnuptialen Mauser kurz nachdem die Jungen das Nest verlassen haben. Späte Brüter (Vögel mit Ersatzbruten) mausern später im Jahr als normale Brüter. Allerdings beginnen sie mit der Mauser in einem früherem Alter ihrer Jungen als normale Brüter. Deshalb überlappen sich bei ihnen Fortpflanzung und Mauser mehr als bei den normalen Brütern. Es wird angenommen, dass gleichzeitiges Brüten und Mausern mit hohen Kosten verbunden ist und daher im Allgemeinen vermieden wird. Bei zeitlich sehr eingeschränkten Arten ist dies nicht immer möglich. Der Grad der Überlappung zwischen Fortpflanzung und Mauser ist bei den Sibirischen Schwarzkehlchen um so größer, je später ein Gelege begonnen wurde. Es gibt Hinweise, dass spät brütende Männchen eher mit der Mauser beginnen als spät

brütende Weibchen, die Datenlage hierzu ist allerdings nicht sehr umfangreich. Sollte dieser Befund jedoch wirklich zutreffen, dann könnten spät brütende Männchen ihren Anteil an der Brutpflege zurücknehmen, wie bei anderen Arten gefunden wurde. Ein Aufschieben der Mauser des Körpergefieders, das hauptsächlich der Wärmeisolierung dient, könnte bei einem Zugvogel weniger schwerwiegende Auswirkungen haben als das Aufschieben der Mauser des Fluggefieders. Spätbrütende Schwarzkehlchen scheinen daher die Mauser des Körpergefieders weiter hinauszuzögern als die Mauser der Hand- und Armschwingen.

Die Sibirischen Schwarzkehlchen in Kasachstan und die Europäischen Schwarzkehlchen in der Slowakei sind nahe verwandt und brüten beide in den nördlichen gemäßigten Breiten unter ähnlichen photoperiodischen Bedingungen. Aufgrund der lokalen klimatischen Unterschiede differieren allerdings die Zugdistanzen und die Länge der Brutsaison zwischen den beiden Populationen. Dies bewirkt konsistente Unterschiede beim Zugverhalten, dem Brutgeschehen, der hormonellen Steuerung des Reproduktionsverhaltens, der hormonellen Stress-Reaktion und der Juvenilentwicklung. Gemäß dem hohen Verwandtschaftsgrad der Sibirischen und Europäischen Schwarzkehlchen spielen genetische Divergenzen und artspezifische physiologische Beschränkungen wahrscheinlich eine untergeordnete Rolle. Eher spielt die unterschiedliche annuale Zeiteinteilung der beiden Populationen eine Rolle: in jedem Stadium des Lebenszyklus kommt es zu einem evolutiven Kompromiss zwischen dem gegenwärtigen und dem zukünftigen Fortpflanzungserfolg. Dieser Abgleich wird stark vom Jahreszyklus beeinflusst. Die klimatischen Veränderungen der jüngsten Zeit werden - nicht nur bei Vögeln - mit zeitlichen Verschiebungen beim Zug und bei der Fortpflanzung, sowie der Veränderung von Artarealen in Zusammenhang gebracht. Das Beispiel der Schwarzkehlchen zeigt, dass zur Veränderung des Jahreszyklus eine Vielzahl von systemischen Änderungen nötig sind. Nur wenn ein Organismus in der Lage ist, all diese Veränderungen in Einklang zu bringen, wird er sich erfolgreich an eine sich rasch wandelnde Umwelt anpassen können.

Russian Summary

Годовая регуляция событий жизненного цикла и их вариация у свободноживущих черноголовых чеканов (Saxicola torquata).

Черноголовый чекан – один из наиболее широко распространенных видов воробьиных в Старом Свете. Его область размножения включает как тропики, субтропические и умеренные районы, так и Субарктику. Так же широко варьируют и миграционные стратегии этого вида – от оседлости на Британских островах и в экваториальной Африке до дальней миграции в северной Азии. Эти особенности, а также тот факт, что черноголовый чекан легко размножается в неволе, определили этот вид как идеальный для изучения вариации годового цикла в различных сезонных условиях, как в полевых, так и лабораторных условиях. В разделе 1 я представляю концептуальную систему взглядов на изучение регуляции событий годового цикла и их вариаций у черноголового чекана.

В свом исследовании, я фокусирую внимание на чеканах из двух популяций: сибирском черноголовом чекане, который гнездится в северном Казахстане и европейском черноголовом чекане, гнездящемся в центральной Словакии. Таксономический статус и биология двух групп, а также особенности двух районов изучения рассматриваются в разделе 2. Оба изучаемых района расположены в умеренных широтах и их фотопериодические условия совпадают. Однако из-за континентального климата в Казахстане, лето там короче, жарче и количество выпадающих осадков ниже, чем в Словакии. В результате, сезон гнездования в Восточной Европе длится почти на 2 месяца дольше.

Две популяции отличаются своими миграционными стратегиями (Раздел 3). Сибирские чеканы – дальние мигранты, которые в сезон миграции покрывают до 6,5 тыс. км от мест размножения до мест зимовки и пересекают на своем пути такие экологические барьеры, как пустыни и горы. Черноголовые чеканы из Восточной Европы - мигранты на средние дистанции, чей миграционный путь составляет порядка 1,5 тыс. км. Данные повторных отловов показывают, что значительная их доля пересекает Средиземное море. К сожалению, данные повторных отловов сибирских

черноголовых чеканов отсутствуют, поэтому информация об их миграционном маршруте спорадическая и исходит из различных источников. В своей работе я попытался заполнить этот пробел, реконструируя пространственно-временной характер миграции черноголовых чеканов в Центральной Азии и южной Сибири, основываясь на данных по миграции этого вида, доступных из опубликованных источников. Весной черноголовые чеканы прилетают в этот район с юго-запада, что предполагает, что в значительной степени они избегают горных хребтов Центральной Азии. Оттуда они разлетаются в северном направлении в Центральную Азию и Сибирь. Осенью они повторяют этот маршрут в обратном направлении, однако их перемещения в меньшей степени согласованы, чем весной. Данные по пролету могут быть использованы для расчета средней скорости миграции внутри данного района и сравнения со скоростью миграции европейских чеканов. Весенняя скорость миграции европейских черноголовых чеканов превышает осеннюю, что согласуется с данными по другим европейским воробьиным. В Центральной Азии, однако, похоже, что чеканы испытывают ограничения на весенней миграции, поскольку они вынуждены останавливаться и дожидаться улучшения условий. В последние годы весенние температуры увеличиваются в обеих исследуемых точках. Мои результаты показывают высокий потенциал для изменения миграционной фенологии в результате глобального потепления в центральноазиатской миграционной системе.

Птицы редуцируют репродуктивную систему в негнездовой сезон. Мигрирующие птицы сталкиваются с потенциальным конфликтом между подготовкой к размножению и миграцией, так как созревание гонад занимает не меньше нескольких недель. Одной из исследуемой мной проблем было влияние миграционной стратегии на состояние гонад во время прибытия на места гнездования (Раздел 4). Самцы обеих популяций прибывают на гнездование с не полностью развитыми гонадами. Ни состояние гонад в связи с началом гнездования, ни скорость созревания гонад не отличались между изучаемыми популяциями. Это может объясняться тем, что поздние стадии репродуктивного развития в большей степени подвергаются влиянию желаемой даты размножения и/или физиологическими детерминантами степени скорости созревания гонад, в то время как сам миграционный период имеет гораздо меньшее влияние. Однако данных о репродуктивном развитии на миграционном маршруте, особенно у дальних мигрантов, явно недостаточно, так как пролетные и местные размножающиеся особи были неразличимы на основе развития гонад. Несмотря на это,

данные по пролетным особям варьировали гораздо шире, что может отражать различия в репродуктивных сроках из-за различий в удаленности их мест размножения.

Из-за местных условий на местах размножения и временных условий миграции, у черноголовых чеканов в Казахстане более короткий сезон размножения, чем у их сородичей в Словакии (Раздел 5). Сибирские чеканы делают одну кладку за сезон, но повторное гнездование при утере кладки – обычное явление. Европейские чеканы делают до 3 кладок за сезон. Интервал между повторными кладками не отличается в двух популяциях. Синхронизация размножения достоверно выше в Казахстане, как в течение всего гнездового периода, так и в сроках первых кладок. Полный размер кладки выше у сибирских чеканов. Размер кладки уменьшается от первых к повторным кладкам в Казахстане и от первых к вторым кладкам в Словакии. Размер третьих кладок у европейских чеканов возрастает снова, что может объясняться тем, что только родители высокого качества пытаются размножаться в третий раз или т.н. стратегией »последней попытки«. Отношение числа вылетевших молодых к количеству отложенных яиц выше в Казахстане и не отличается между первыми и повторными кладками. В Словакии успешность размножения заметно падает от первых к последующим кладкам. Хищничество в инкубации играет значительную роль у европейских чеканов, в то время как сибирские в большей степени страдают от гибели птенцов. В результате меньшего размера кладок в конце сезона и высокого процента гибели, особенно в Словакии, кол-во успешно вылетевших птенцов на кладку убывает в обеих популяциях по ходу сезона. В среднем, одна пара чеканов из Казахстана выращивает около 5 птенцов за сезон, в то время как на пару из Словакии приходится около 7 удачно вылетевших птенцов. В одном из сезонов работы 9% размножавшихся самцов из Казахстана имели пары одновременно с двумя самками. Факультативная полигамия уже была отмечена для европейских, но не для сибирских черноголовых чеканов. Первые кладки полигамных самцов были отложены раньше, содержали больше яиц и вылетевших птенцов, чем первые кладки моногамных самцов. Это может объясняться тем, что полигамные самцы были особями более высокого качества Вторые кладки самцов-полигамов откладывались позже, содержали меньше яиц, из них вылетало меньше птенцов, что говорит невыгодности полигамии в терминах репродуктивного успеха для вторых самок.

Согласно «гипотезе вызова», продолжительность гнездового периода и уровень родительской заботы влияет на сезонный профиль содержания андрогенов (Раздел 6). У самцов сибирских чеканов повышенный уровень андрогенов отмечен в мае и июне с

пиком, приходящимся на середину мая. У европейских чеканов уровень андрогенов повышен с марта до конца мая, достигая пика между серединой апреля и серединой мая. В обеих популяциях уровни андрогенов на пике в территориальный период, а также в период, когда самки готовы к размножению, и снижаются в период родительской заботы о птенцах. Общий уровень андрогенов выше у европейских черноголовых чеканов, что может объясняться более высокой конкуренцией между самцами и/или более низким уровнем родительской заботы в данной популяции. Самцовая агрессия во время симулированных территориальных вторжений довольно высока в течение всего сезона размножения в обеих популяциях и, очевидно, не связана с уровнем циркулирующих андрогенов. У сибирских чеканов самцовый дигидротестостерон (dihydrotestosterone (DHT)) вносит относительно больший вклад в суммарное кол-во циркулирующих андрогенов. Это может быть связано с различной ролью DHT и тестостерона (T) в регуляции репродуктивного поведения у самцов или различными затратами, связанными с высоким уровнем циркуляции этих андрогенов. Уровень эстрадиола (E_2) не отличается от базального в течение всего сезона как у сибирских, так и у европейских чеканов. У самок черноголового чекана уровни циркулирующих гонадных стероидов (E_2, T, DHT) весь сезон остаются на базальном уровне. T. выше у самок европейских чеканов, чем у самок в Казахстане, однако сезонные изменения явно не выражены.

Адреналные глюкокортикоиды (GCs) – это стероидные гормоны, которые влияют на общий энергетический метаболизм и как часть аллостатического ответа организма на непредсказуемые угрозы физиологическому гомеостазу (Раздел 7). Существуют две гипотезы, объясняющие сезонные и индивидуальные вариации в циркуляции GCs. Гипотеза репродуктивного ограничения предсказывает, что из-за того, что высокий уровень GCs может приводить к оставлению гнезда, GC ответ на стрессовые ситуации редуцируется в ситуации, когда благоприятные возможности для размножения ограничены, как, к примеру, у сибирских чеканов. Абсолютный уровень GC выше у сибирских, чем у европейских птиц. следовательно, нет прямой зависимости между потенциальным числом гнездовых попыток и уровнем GC у чеканов. Гипотеза энергетической мобилизации предсказывает высокий уровень GC в период увеличения энергетического потребления, к примеру, в период размножения. Энергетические затраты могут различаться на разных стадиях размножения, по крайней мере, у самцов. Однако уровень GC не варьирует на разных стадиях размножения у чеканов. Уровень GC падает у казахских чеканов, когда птицы начинают линьку.

Замена перьев энергетически затратное событие, следовательно простые взаимодействия между энергетическими требованиями и циркуляцией GCs не подтверждаются. Возможно, что GCs могут вступать в конфликт с физиологическими изменениями, наблюдаемыми при замене перьев, что приводит к их редукции в этот период.

Зависимая от времени смертность, уровень конкуренции внутри выводка и внутренние ограничения роста обсуждаются как главные факторы, влияющие на эволюцию скорости развития (раздел 8). Длительность сезона размножения также может влиять на ювенальное развитие, особенно у мигрантов, у которых птенцы должны достигнуть определенного уровня зрелости, чтобы преодолеть трудности осенней миграции. Инкубационный период несколько короче в Казахстане, чем в Словакии, что показывает, что эмбриональное развитие может быть более быстрым у сибирских чеканов. Также у сибирских птиц выше скорость постнатального роста размеров тела, но не длины крыла. Однако дата вылупления не оказывает влияния на постнатальный рост. Младшие птенцы в выводке, которые изначально находятся в невыгодном положении по сравнению со старшими собратьями, рождаются более крупными и весят тяжелее, однако быстро теряют это преимущество из-за более медленного роста. Как и у клеточных чеканов, постювенальная линька у особей из сибирской популяции начинается раньше и менее зависит от даты рождения, чем у европейских. Период между началом инкубации и до конца постювенальной линьки у сибирских чеканов примерно в полтора раза длиннее, чем у европейских, однако данное различие образуется в основном из-за различий в начале и длительности линьки.

Сибирские чеканы откладывают одну кладку за сезон, но при потере кладки часто предпринимают повторную попытку размножения (раздел 9). Те, кто успешно вывел птенцов из первой кладки, начинают послегнездовую линьку вскоре после того, как птенцы покидают гнездо. Те же, кто предпринимал повторное размножение, линяют позже, чем птицы из первой категории. Однако они начинают линьку раньше относительно возраста своих птенцов. В результате у них происходит перекрывание размножения и линьки в гораздо большей степени, чем у птиц из первой категории. Замена перьев и размножение считаются энергетически дорогими процессами, и, следовательно, их перекрывания следует избегать. Это не всегда возможно у видов, находящихся в условиях дефицита времени. У сибирских черноголовых чеканов уровень перекрытия линьки и размножения возрастает при более поздних кладках.

Немногочисленные данные подтверждают, что поздногнездящиеся самцы начинают линьку раньше, чем их партнерши. Возможно, это может приводить к уменьшению их участия в родительской заботе о птенцах, как было показано для других видов. Отложенная линька контурного оперения, служащего скорее для теплоизоляции, может иметь менее серьезные последствия для мигрирующих видов, чем отложенная линька маховых. Поздногнездящиеся особи начинают линьку маховых раньше относительно контурной линьки по сравнению с теми, кто гнездится в нормальные сроки.

Сибирские черноголовые чеканы в Казахстане и европейские в Словакии – две близкородственные группы, гнездящиеся в умеренных зонах на той же широте и в условиях одинакового фотопериода. Однако из-за локальных различий в климатических условиях, дистанция миграционного пути и продолжительность сезона размножения у них значительно отличаются. Это приводит к значительным различиям между особями двух популяций в миграционном поведении, особенностях размножения, гормональной регуляции репродукции, аллостатических ответов на изменения в окружающей среде и в постювенальном развитии. Так как сибирские и словацкие популяции чеканов близкородственны, различия в генофонде и/или видоспецифичные физиологические препятствия, вероятно, не являются основными причинами этих различий. Скорее они отражают специфические последствия выбора между текущим и возможным будущим успехом размножения для зависящих от циркадного ритма стадий годового цикла. Климатические изменения, наблюдаемые в последние годы, нашли отражение в изменении сроков миграции и размножения и изменении видового ареала не только у птиц. Пример чеканов показывает, что ответ организма на изменение внешних условий будет зависеть от способности успешно интегрировать множественные систематические изменения необходимые для изменения годового цикла.

ACKNOWLEDGEMENTS

Curriculum Vitae

Persönliche Angaben:

Name: Michael Räß

Geburtsdatum: 07.02.1969

Geburtsort: Vilshofen

Familienstand: verheiratet mit Silke Verena Räß, geb. Steckhan
                 Sohn Janis Sebastian, geb. 2005

Schulausbildung:

1975 bis 1980   Grundschule in München

1980 bis 1990   Gymnasium in München

Zivildienst:

1990 bis 1992   AIDS-Hilfe München e.V.

Studium:

1992 bis 1999   Ludwig-Maximilians-Universität, München
                 Fachbereich Biologie, Hauptfach: Zoologie, Nebenfächer:
                 Neurobiologie, Ökologie, Biochemie
                 Diplomarbeit durchgeführt am Max-Planck-Institut für
                 Verhaltensphysiologie, Andechs: "Funktion und Steuerung
                 des Gesangsverhaltens überwinternder Schwarzkehlchen,
                 Saxicola torquata rubicola"

Dissertation:

1999 bis 2005   Ludwig-Maximilians-Universität, München; durchgeführt am
                 Max-Planck-Institut für Ornithologie, Andechs: "Annual
                 timing and life-history variation in free-living
                 stonechats"
                 Gutachter: Dr. Bart Kempenaers, Prof. Dr. Sebastian Diehl

Publikationen:

Raess, M. & Gwinner, E. (2005). Gonadal status upon spring arrival in long-distance and short-distance migrating stonechats (*Saxicola torquata*). Journal of Ornithology. 146: 325-331.