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Gonadal status upon spring arrival in long-distance and short-distance migrating stonechats (*Saxicola torquata*)

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Abstract 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 must, therefore, be initiated 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. We studied long-distance migratory Siberian stonechats in northern Kazakhstan and short-distance migratory European stonechats in Slovakia. We hypothesized that migratory distance and gonadal status at the time of arrival are related. We 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 by physiological constraints rather 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.

Keywords Migration · Gonads · Reproductive timing · Breeding · *Saxicola torquata*

Introduction

The timing of reproduction is a crucial factor in determining avian reproductive success (e.g. Baker 1938; Lack 1968; Perrins 1970; Murton and Westwood 1977; Nilsson 1999). Most birds shut down their reproductive system in the nonbreeding season (Murton and 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 and Westwood 1977; Wingfield and 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 (Sillert and 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.

We studied migratory Siberian stonechats (*Saxicola torquata maura*) in northern Kazakhstan and European stonechats (*S. t. rubicola*) in central Slovakia. Both the areas are located in temperate zones; however, the length of the environmental breeding window and the number of clutches the local stonechats produce annually differ markedly. 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 (Raess et al. unpublished).

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Siberian stonechats are long-distance migrants that winter in northern Africa and subtropical India/Pakistan. Thus, spring migration can last for more than 2 months and cover more than 6,000 km in some populations; large ecological barriers such as seas, deserts and high mountain ranges have to be crossed on the way (Dement'ev and Gladkov 1954; Glutz von Blotzheim and Bauer 1988; Urquhart 2002). The stonechats from Slovakia, on the other hand, are short-distance migrants that migrate the ~1,500 km distance from their wintering grounds in Northern Africa to their breeding grounds within 1 month (Cramp 1988; Glutz von Blotzheim and Bauer 1988; Urquhart 2002). 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 study, we 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.

Methods

Study sites and field methods

This study was carried out during the breeding seasons of 1999 and 2000 in Northern Kazakhstan (52°N, 64°E), close to the town of Dokuchaevka (now Karamendy) and the Naurzumskij gosudarstvenij zapovednik (Naurzum National Nature Reserve), and during the breeding seasons of 2001 and 2002 in central Slovakia, close to the city of Zvolen and the Pol'ana Biosphere Reserve (49°N, 19°E). The Kazakh study site is characterised by a strongly continental climate with short, hot summers and long, cold winters. The mean temperature in July is 20.4°C. In January, the mean temperature is -16.9°C. Temperatures below 0°C prevail from the second half of October until the end of March. The climate at the Slovak study site is less extreme, with relatively mild summer and winter conditions. The mean temperature is 18.2°C in July and -3.8°C in January; temperatures below 0°C prevail from the end of November until the beginning of February (data source: IRI website: <http://iri.columbia.edu/>).

During the early breeding season (i.e. from arrival until the onset of egg laying in the populations), stonechat males were caught using mealworm-baited traps or mistnets. The birds were unilaterally laparotomised and the size of the left testis (at the narrow side of the ellipsoid, hence we measured testis *widths*) was determined to an accuracy of 0.1 mm. This study was part of a bigger project on the breeding biology of stonechats in Kazakhstan and Slovakia and therefore the birds were colour-banded and morphometric measures and small blood samples were taken before the birds were released. Males that subsequently left the study area without attempting to breed were recorded as passage migrants (these 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 with or without successful breeding) were recorded as local breeders.

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, USA). All statistical tests were carried out two-tailed.

Results

In both populations, testis widths increased significantly in males caught from the time of arrival to the period of egg production. When the date was taken into account, there was no difference in gonadal widths between males that stayed to breed and 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. 1a). 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 were 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. 1b).

For a comparison of the gonadal development between subspecies, the data were matched for the mean laying date of the first egg in the population (Fig. 2). Relative to the populations' reproductive timing, there were no fundamental differences between the two populations in the way testicular development proceeded during 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 first egg: $F_{1,46}=16.13$, $P<0.001$; population \times days to first egg: $F_{1,46}=0.002$; $P=0.97$; fitted lines: Kazakhstan: $y=4.27+0.032x$; Slovakia: $y=4.45+0.033x$ (Fig. 2).

Figure 3 shows a comparison of the gonadal cycles of captive and free-living male Siberian and European stonechats. Captive birds were held individually under photoperiodic conditions simulating the annual cycle, including breeding, wintering, and migration of the two subspecies (Helm and Gwinner, unpublished; Helm and Gwinner, this issue). Like their free-living conspecifics, captive European stonechats initiate testicular growth earlier in the season than Siberian stonechats. The captive European stonechats keep their gonads longer in the developed state than the Siberian birds. The free-living Siberian stonechats in Kazakhstan seem to initiate gonadal regression later in the season than their captive conspecifics.

Discussion

In Kazakhstan as well as in Slovakia, testicular growth was not complete 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 spermatogenic apparatus. Bauchinger (2002) caught garden warblers, *Sylvia borin*, during their final stop-over in Egypt before crossing the Mediterranean Sea and compared their 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

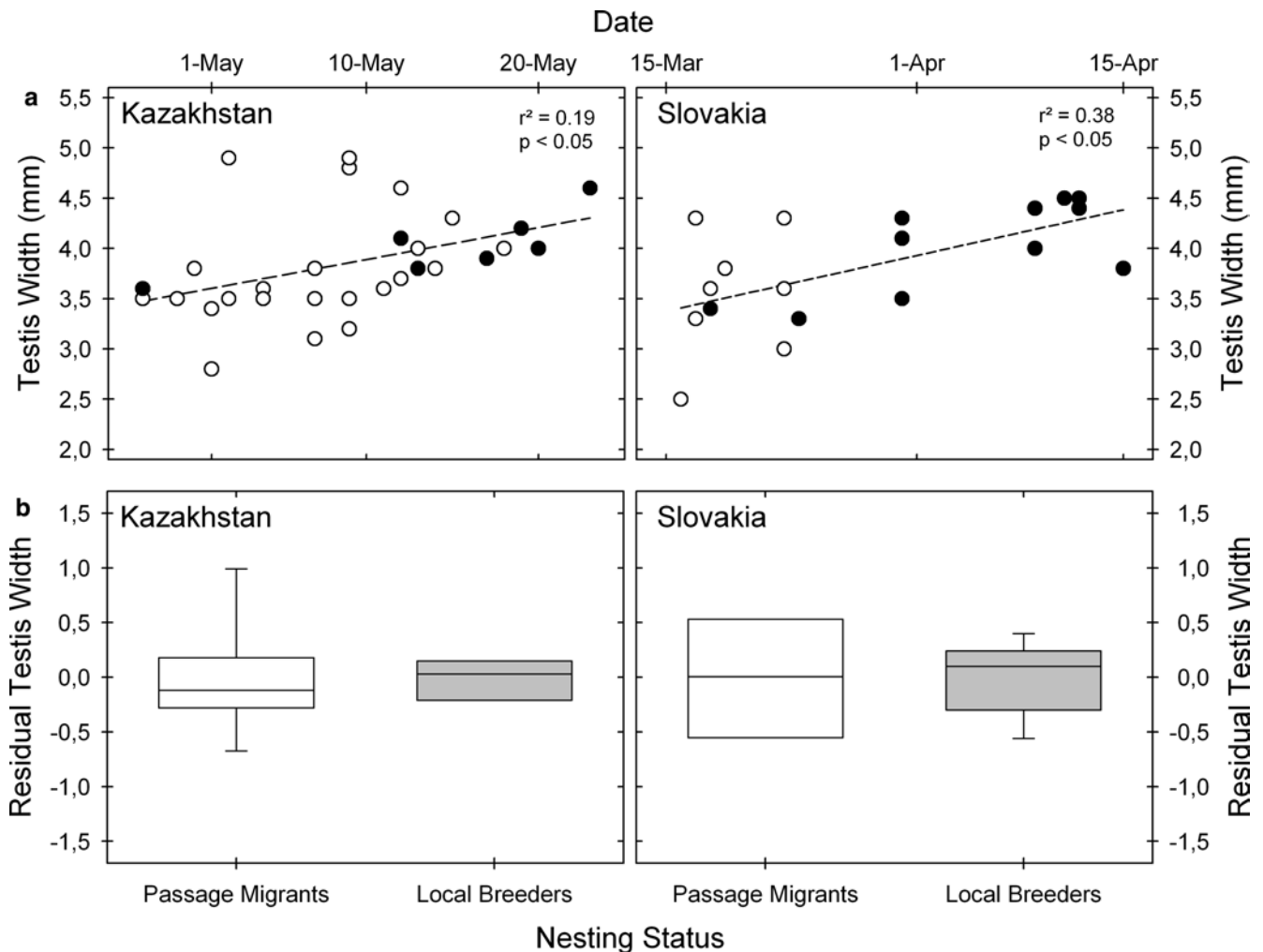


Fig. 1a,b Testis widths in Siberian and European stonechat males in the early breeding season. **a** In both populations testis widths increase from the time of arrival to the time of egg laying. There is no difference in gonadal development of males that breed in the area (black circles) and males that are caught on passage or do not breed for other reasons (white circles). **b** In both populations, the residual testis widths of males that did not breed in the area (passage migrants) show higher variation than those of birds that stayed and bred (local breeders)

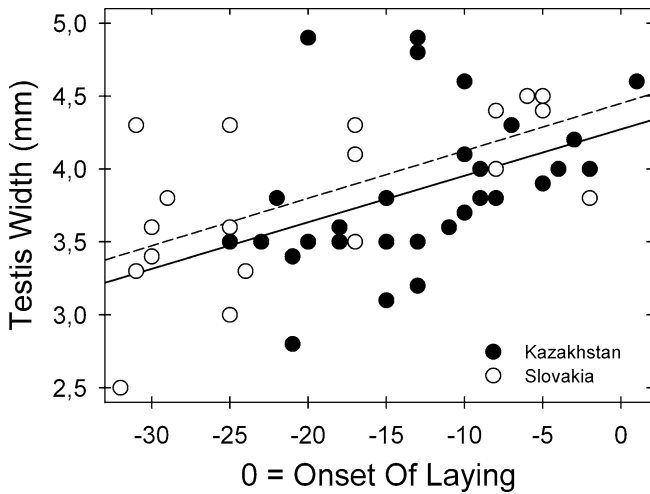
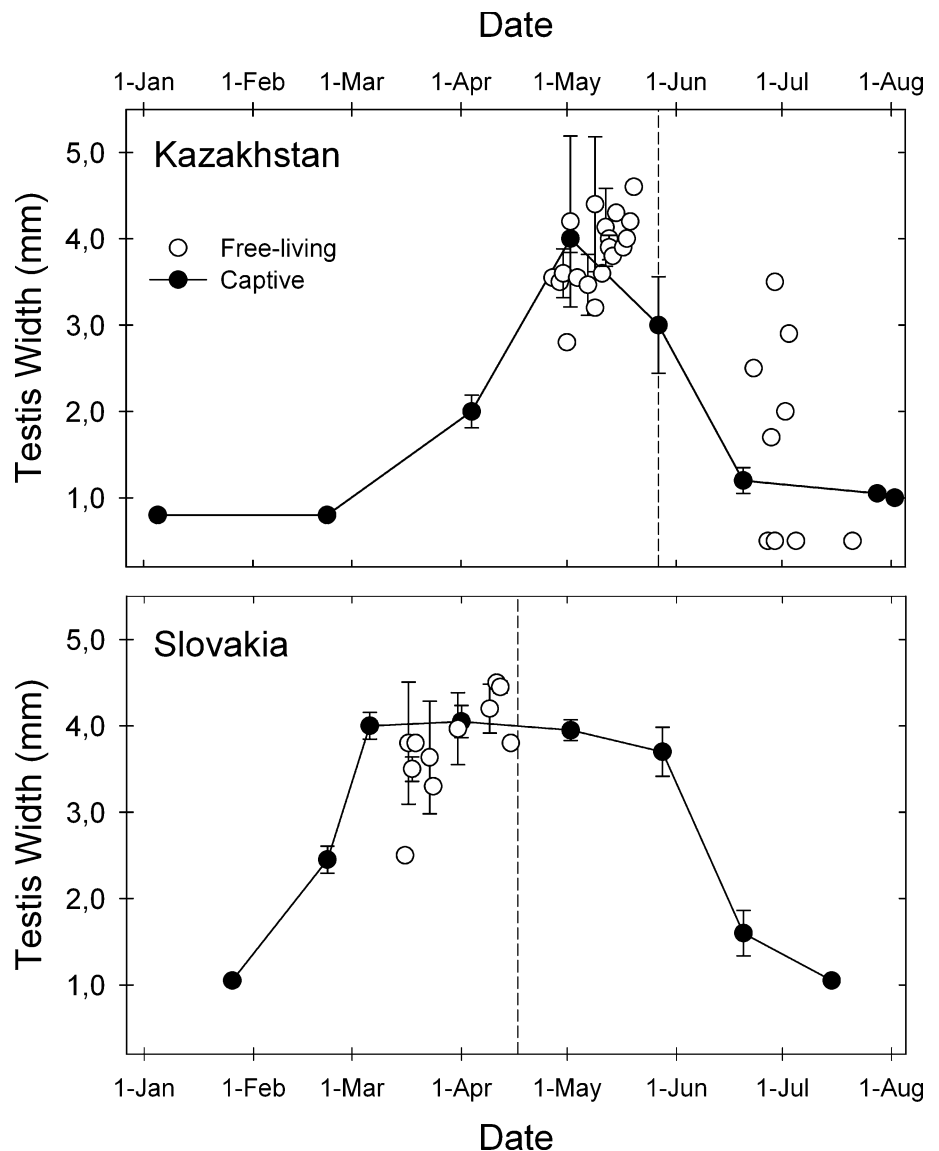


Fig. 2 Gonadal development in Siberian and European stonechat males does not differ in respect to the reproductive activities in the two populations (data are matched for the mean laying date of the first egg in each population)

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 stonechat males of both populations, the testes had not acquired full spermatogenic 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 1 to 2 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 indicate, how-

Fig. 3 The gonadal cycles of captive and free-living male Siberian and European stonechats (data shown as means \pm SD). The captive birds were held individually under photoperiodic conditions simulating the complete annual cycle of each population. Testis widths of free-living stonechats from our field sites in Kazakhstan and Slovakia are superimposed. 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, unpublished data; Helm and Gwinner, this issue)



ever, that testicular growth proceeds during the subjective spring migratory periods (i.e. when the birds show nocturnal migratory restlessness, see Helm and Gwinner, this issue). 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 80–90% of the total migratory period (Hedenström and 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 (M. Raess, unpublished data). It is therefore possible that Siberian stonechat males grow their gonads predominantly during the stopovers in southern Asia, when they have to wait for spring conditions to improve.

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 and 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 (this issue) show that slight differences in the photoperiodic signal have substantial 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 the greenfinch *Charduelis chloris* (Merilä and Sheldon 1999) and the savannah sparrow *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 and Sheldon 1999). As yet, there are 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 suggest, however, that Siberian and

European stonechats have similar testis sizes when they reproduce (Helm and Gwinner, unpublished 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 and Gwinner, this issue). The differences in gonadal development between passage migrants and local breeders could, however, be obscured by the higher variation in testis widths in the passage migrant group, which could be a reflection of the different destinations of the birds that 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 and Wingfield 1985; Wingfield and Moore 1987; Dawson et al. 2001). Hence, in the free-living Siberian stonechats, gonadal regression starts later than in their captive conspecifics which have no breeding opportunities. Furthermore, in the free-living Siberian stonechats, the variation in testis sizes 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 and Westwood 1977; Gwinner 1986; Dawson et al. 2001; Dawson 2002; Gwinner 2003) and these studies continue to produce intriguing results (Helm and Gwinner, this issue). It is known that supplementary information, such as social cues, can further modify the opening and the closing of the endogenous reproductive window (Runfeldt and Wingfield 1985; Gwinner et al. 1987; Wingfield and 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.

Gonadenzustand von lang- und kurzziehenden Schwarzkehlchen (*Saxicola torquata*) bei der Ankunft im Brutgebiet

Zusammenfassung Weitstreckenzug geht oft mit einer relativ kurzen Brutsaison und einen Beginn der Brutaktivität kurz nach der Ankunft im Brutgebiet einher. Da es aber einige Wochen dauert, um das rückgebildete Fortpflanzungssystem wieder in den aktiven Zustand zu versetzen, muss damit schon im Winterquartier oder auf dem Frühjahrszug begonnen werden. Daher besteht für Weitstreckenzieher ein potentieller Konflikt zwischen den zeitlichen und energetischen Anforderungen des Zuges und der Vorbereitung auf die Fortpflanzung. Wir testeten unsere Hypothese, dass die Zugdistanz und der Entwicklungsstand der Hoden zur Ankunftszeit im Brutgebiet miteinander in Beziehung stehen, an weitstreckenziehenden Sibirischen Schwarzkehlchen in Nord-Kasachstan und kurzstreckenziehenden Europäischen Schwarzkehlchen in der Slowakischen Republik. Wir fanden, dass die Männchen aus beiden Populationen mit unvollständig entwickelten Hoden im Brutgebiet ankamen. Weder der Entwicklungsstand des Fortpflanzungssystems, noch die Entwicklungsrate der Hoden zu ihrer vollen Reife zum Zeitpunkt der Eiablage, unterschied sich jedoch zwischen den Populationen. Die Reifungsgeschwindigkeit während der letzten Stadien der Hodenentwicklung könnte daher eher von physiologischen Beschränkungen als von einem Ausgleich zwischen Frühjahrszug und Fortpflanzung bestimmt sein. Innerhalb der Populationen ließen sich Durchzügler und lokale Brutvögel nicht anhand des Standes der Gonadenentwicklung unterscheiden. Die Streubreite der Gonadengrößen war jedoch bei den Durchzüglern größer, was auf Unterschiede in den Zugdistanzen und den daraus resultierenden Fortpflanzungsdaten zurückzuführen sein könnte.

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