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S40-2　Timing of molt as a buffer in the avian annual cycle

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Abstract　Birds in seasonal environments must time stages in their annual life cycles precisely. While the fitness costs of mistimed reproduction and migration are widely recognized, molt has been viewed as a more flexible element. Birds modify the timing of molt in various ways to keep to overall timetables, but recent studies provide evidence for considerable attendant costs in fitness. Selective pressure, therefore, affects the timing of molt and its flexibility, favoring timing mechanisms that are finely tuned to local conditions. We illustrate such timing mechanisms for post-juvenal molt in stonechats (*Saxicola torquata*). These widely distributed passerines differ in life history traits such as length of breeding season, number of clutches and migratory behavior. To understand adjustments to temporal environments, we compared the temporal plasticity of captive African, European, and Siberian stonechats. The subspecies from these regions differed from each other in their reaction norms to photoperiod, in temporal patterns related to the timing requirements of their native habitats. Their circannual rhythms thus encode characteristic features of seasonal activities in a population-specific manner. High heritability in post-juvenal molt corroborates the interpretation of molt timing as adaptive. We conclude that stonechat populations adapt to temporal environments not by switching between distinct and rigid programs but by adjusting reaction norms to relevant time cues.

Key words　Molt, Annual cycle, Photoperiod, Stonechat

1　Molt as a timing buffer in the annual cycle

In variable habitats, stages in life cycles must be timed precisely to match periodic environmental change. In general, birds attempt to reproduce, change their plumage, and aclimate to unfavorable conditions or migrate within the annual cycle. These activities impose competing demands such that the timing of the activities involves compromises and trade-offs. Timing of migration and reproduction is thought to be closely regulated by selection. Mistimed migration imposes fitness costs if birds encounter severe weather conditions, and the timing of migration thus responds to weather-mediated selection (Brown and Brown, 2000). Timing of reproduction is closely related to maximal food abundance, and mismatching reduces fitness (Visser and Lambrechts, 1999; Thomas et al., 2001). Because of the fitness correlates of reproductive and migratory timing, it has been suggested that molt functions as a buffer in annual cycles (Noskov et al., 1999).

If environmental conditions allow, passerines molt at relaxed rates and either avoid major overlaps with other costly activities or molt so slowly that the costs are small (Jenni and Winkler, 1994; Kjellen, 1994; Berthold, 2001). But often birds run out of time for it, as in populations with long migratory journeys and short breeding seasons. Another source of time stress is late breeding. Although the value of eggs generally declines over the breeding season, late clutches contribute markedly to recruitment in some years (Van Noordwijk et al., 1981). Hence, birds often attempt late breeding. Under such time constraints, birds modify molt to catch up in several mutually nonexclusive ways. Molt is a flexible system that allows birds to keep to their timetable, particularly in northern hemisphere passerines (Hahn et al., 1992; Jenni and Winkler, 1994; Kjellen, 1994; Noskov et al., 1999).

2　Fitness implications of molt as a timing buffer

Evidence is growing that modifications of molt schedules are costly. Late breeding birds often start molt while still tending young (Jenni and Winkler, 1994; Kjellen, 1994) and thereby risk trading off current reproduction against future reproductive opportunities. Experimental simulation of molt by wing clipping reduced the body condition and fitness of feeding parents (Hedenström, 1999). Sexual differences in the overlap of molt and breeding are indicative of trade-offs between the two activities late in the breeding season. Males are more likely than females to initiate molt during chick-rearing, thereby reducing offspring provisioning or abandoning young. Reduced paternal investment often leads to poorer condition and lower recruitment of young. Presumably, the benefits of a timely molt for males outweigh additional fitness gains of breeding late. Females are more likely to delay molt during breeding than males, and sometimes the delay increases with clutch size (Slagsvold, 1999). They may compensate for reduced paternal provisioning at the cost of their own condition and survival chances (Hemborg and Merilä, 1998). Such costs in late-breeding females may be attributable in part to delayed molt.

Offspring from late clutches experience similar time-pressures when undergoing post-juvenal molt. Their molt is advanced compared to that in siblings from early clutches and may overlap with final growth stages and juvenal establishment (Jenni and Winkler, 1994). To our knowledge, there is no direct evidence of the cost of overlapping molt and post-fledging establishment, but disadvantages, such as a low social rank, are likely (König, 1996).

To avoid such costs, birds may delay the onset of molt at the cost of reduced survival. Molt is then either greatly accelerated or overlaps with subsequent life cycle phases. In residents, late molt can impair preparations for overwintering, such as territorial establishment or food hoarding; and thermoregulatory costs rise under inclement conditions (Kjellen, 1994; Jenni and Winkler, 1994). Migratory birds may delay fall departure briefly or extend overlap between molt and migration. Data from captive passerines reveal a close correlation between the completion of molt and the onset of migratory restlessness (Helm and Gwinner, unpubl. data; Pulido and Coppack, pers. comm.), suggesting that migration may be delayed until peak molt has passed. Some studies show that late breeders and young from late clutches migrate while still in molt (Flinks, 1999). Flight theory predicts high costs if wing molt overlaps migration, but experimental evidence is still inconclusive (Hedenström, 1999).

Instead of or in addition to overlaps with other seasonal activities, birds can control the time taken for molt by accelerating it, limiting its extent, or even suspending it temporarily. Costs of molt, such as elevated metabolism, are likely to increase with molt rate (Lindström et al., 1993). Fast molt may also impair flight, increasing wing gaps (Hedenström, 1999). Moreover, it can have long-term consequences due to reduced feather quality, as the following data show. Thermoregulatory costs after rapid molt rose by 15% (Nilson and Svenson, 1996). In a comparison of wader populations, speed of molt correlated with plumage abrasion (Serra, 2001). Captive passerines that molted faster than controls grew less symmetrical and less rigidly built flight feathers that subsequently suffered greater damage and abrasion (Dawson et al., 2000). Feathers grown under time constraints can also be significantly shorter in both adult and young birds (Hall and Fransson, 2000; Albrecht, Helm and Gwinner, unpubl. data). In birds that lack a prenuptial molt, greater feather wear is correlated with reduced fitness during the next breeding season, especially in species subject to sexual selection (Fitzpatrick and Price, 1997).

Many passerines reduce the extent of molt under time constraints. Some renew only part of the plumage and then resume molt under favorable conditions. Suspension of molt ranges from arresting flight feather renewal to completely delaying molt (Jenni and Winkler, 1994; Kjellen, 1994; Berthold, 2002). Hall and Fransson (2001) report that, by suspending molt, passerines which had initiated it late were able to finish it simultaneously with conspecifics. These birds had less symmetrical flight feathers than those that had undergone complete moult, indicating that incompletely molted birds suffer disadvantages from partly worn plumage.

3 Precisely timed post-juvenal molt in captive stonechats

3.1 Cues for the timing of molt

The various strategies by which time-constrained birds modify molt schedules are costly and hence subject to selection. As a consequence, the extent and mechanism of molt-timing can be expected to be adjusted by selection to best match local conditions. The physiological basis of precise timing in birds relies on circannual programs, such as photoperiod (Gwinner, 1986; Wingfield et al., 1992; Gwinner, 1999). In keeping with costs of molt schedules, the timing of responses to environmental cues often differ regionally and can be described by population reaction norms (van Noordwijk, 1990). Timing programs also meet a genetic precondition for evolutionary adjustment: a sufficient amount of additive genetic variance within populations. Evolvable timing has been shown in wild and captive birds for migration, reproduction, and molt (van Noordwijk et al., 1981; Larsson, 1996; Helm and Gwinner, 1999, 2001; Brown and Brown, 2000; Pulido et al., 2002). We illustrate a flexible molt-timing mechanism that is fine-tuned to local conditions by summarizing research on post-juvenal molt in stonechats (*Saxicola torquata*).

3.2 The stonechat case study

To study adaptations to conditions in their native areas, we compared timing of molt in several subspecies of the stonechat, a passerine with a wide north-south breeding range (Helm and Gwinner, 1999, 2001). Concordant with the seasonal cycles in their native regions, African stonechats (*S. t. axillaris*), Siberian stonechats (*S. t. maura*) and European stonechats (*S. t. rubicola*) differ in migratory behavior and the time-pressures encountered during post-juvenal molt. African stonechats are single-brooded residents that tolerate young for several months in their year-round territories. Siberian stonechats are long-distance migrants that leave their breeding grounds shortly after raising a single brood. European stonechats are multi-clutched, and the young from the last brood have to prepare rapidly for migration. Because of these different schedules, we expected overall differences not only in the timing and duration of molt, but also in the mechanisms by which the populations respond to seasonal information conveyed by photoperiod.

We studied post-juvenal timing of molt in each population under a range of day-lengths. Short day-lengths simulated molting late in the year and long day-lengths the situation in summer. Fig. 1A plots the age at which young birds under different day-lengths reached peak molt intensity (Helm and Gwinner, 1999). Each data point represents a group of birds, and regression lines estimate population reaction norms. African stonechats molted relatively late, European stonechats at intermediate ages, and Siberian stonechats at the youngest. This sequence of mean molting ages was expected on the basis of the different time-pressures in their life-cycles.

All subspecies tended to molt earlier under short day-length but only in European stonechats was the response to photoperiod pronounced. Fig. 1B shows the times of laying and molting against day length in the three populations. For African stonechats, day-length is continuously short, and a strong photoperiodic response is unlikely to have been selected for. Siberian stonechats breed and molt over a short time interval during midsummer. Day-length changes at the peak intensity of molt are small but later increase quickly. European stonechats, in contrast, are multi-clutched, and the young hatch and molt under very different day-lengths. A strong photoperiodic response allows young from early clutches to delay molt, in contrast to young from late clutches which molt early to prepare for migration. Here the range of correlations between molt peak and photoperiodic pattern highlight the importance of photoperiod as a timing cue for the European population in particular.

Duration of molt was longest in African, intermediate in European, and shortest in Siberian stonechats, as expected from relative time constraints. Under such constraints, adjustments of molt duration were very different from those of molt peak. Molt duration was most flexible in Siberian stonechats. Whereas neither African nor European stonechats shortened their molting under pressure of time, Siberian stonechats reduced its duration to less than half the time taken under long day-length. These birds evidently start to molt early at a fixed time, and then adjust its rate under time constraints (Helm and Gwinner, 2001).

Stonechats from all three populations thus had different strategies for buffering time stress by molt schedules. Siberian stonechats accelerated molt while the other two subspecies shifted the timing of molt onset and peak. Circannual rhythms of stonechats thus encode characteristic features of seasonal activities in a population-specific manner. The differences in plasticity were paralleled by differences in heritabilities (Helm and Gwinner, 2001). In Siberian stonechats, additive genetic variance was high for molt duration, implying a facility for quick adjustments, but onset of molt did not differ between families. In European and African stonechats, heritabilities of molt onset were high, indicating that selection could lead to fast adjustments in the timing of molt; yet families did not differ in duration of molt. The high heritability of these conditions suggests that fitness consequences of molt schedules, as summarized above, can lead quickly to adjustments in the timing of molt to local conditions.

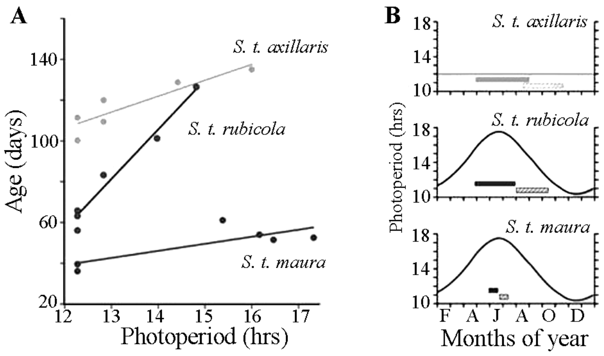

Fig. 1 Timing of post-juvenal molt in stonechats
A: mean population reaction norms for African (*Saxicola torquata axillaris*), European (*S. t. rubicola*), and Siberian stonechats (*S. t. maura*); the x-axis shows the day-length under which the birds were kept, and the y-axis shows the age at which the birds underwent peak molt. B: native photoperiodic conditions (curves), laying dates (solid bars), and dates of peak molt (hatched bars) for the three populations of stonechats.

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