

TIMING OF POSTJUVENAL MOLT IN AFRICAN (*SAXICOLA TORQUATA AXILLARIS*) AND EUROPEAN (*SAXICOLA TORQUATA RUBICOLA*) STONECHATS: EFFECTS OF GENETIC AND ENVIRONMENTAL FACTORS

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ABSTRACT.—Data on the timing of postjuvénal body molt of 322 Stonechats (*Saxicola torquata*) were examined by multifactorial residual maximum-likelihood analysis for effects of external and genetic factors. The Stonechats, which belonged to the European subspecies (*S. t. rubicola*), the African subspecies (*S. t. axillaris*), and their F₁ and F₂ hybrids, were exposed to different photoperiodic conditions. The birds differed conspicuously in the timing and duration of their postjuvénal molt. These differences were significantly related to photoperiodic conditions, genotypic group, and the interaction of these factors. European birds generally molted earlier and faster than African birds, and hybrids showed intermediate patterns. Both subspecies started molt earlier under shorter photoperiods but took longer to complete it. African Stonechats had a weaker response to photoperiod than the European subspecies. In addition, molt timing was negatively related to hatching date, with chicks hatched late in the season molting at a younger age than those hatched earlier. Finally, the two subspecies differed in their molt timing when exposed to short days at an early age. The earlier a European bird was placed under short days, the earlier it molted; the reverse was true in African Stonechats. From a small data base, we estimated heritabilities (h^2) through full-sib analyses and offspring-parent regressions. In both subspecies, the timing of molt showed high genetic variation, especially at its onset. Within photoperiodic groups, h^2 at molt onset was close to unity but decreased during the course of molt. The two Stonechat subspecies timed their postjuvénal molts in a qualitatively similar manner but showed differences that may reflect differences in the selection pressures of their respective environments. Received 26 March 1998, accepted 6 November 1998.

WE ANALYZED POSTJUVENAL MOLT in Stonechats (*Saxicola torquata*) from two different populations to assess the influence of environmental factors on the timing of molt (see Gwinner et al. 1983, Gwinner and Neußer 1985). Postjuvénal molt is the first molt in Stonechats and corresponds to the first prebasic molt in the terminology of Humphrey and Parkes (1959). Here, we are concerned only with body molt, although Stonechats previously were found to renew at least some of their secondaries during postjuvénal molt (Gwinner et al. 1983). An appropriately timed molt is an important component of the overall seasonal organization (Gwinner 1986, Jenni and Winkler 1994). The deterioration of climatic conditions toward the end of breeding exerts high pressure to accelerate molt, which may be opposed by energetic limitations (Jenni and Winkler 1994). Molt costs that depend on the rate of molt (Lindström et

al. 1993, Klaassen 1995) may favor slower replacement of feathers. Ideally, molt should not overlap with energetically expensive activities, such as somatic growth and migration. Behavioral observations suggest that costs of molt are high in Stonechats, which catch their prey in short, precise flights (König 1996, Flinks and Kolb 1997). To preserve maneuverability and to reduce daily energy expenditure, Stonechats should maximize the time taken for molt within the range allowed by external conditions.

The two subspecies of Stonechats considered here live in very different environments. Central European Stonechats (*S. t. rubicola* L. 1776) are short-distance migrants that winter in the Mediterranean region (Cramp 1988, Glutz von Blotzheim and Bauer 1988). They produce two or three clutches of about five eggs each season. When new young hatch, siblings from previous clutches are driven out of the territory, where they molt in aggregations of juveniles (König 1996). Young from late clutches must prepare for migration much faster than their older sib-

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TABLE 1. Classification of Stonechats used in the present study according to factors relevant to the analyses. Shown are absolute numbers, as well as row and column totals. Origin indicates the number of chicks taken from nests or raised in captivity. For all genotypic groups, the number of families and the average family size are given.

	Origin		Family data		Total
	Field	Captivity	No. of sibgroups	Family size (\bar{x})	
Africa	130	35	52	3.0	165
Central Europe	107	14	31	3.8	121
F ₁ hybrid	—	22	5	4.4	22
F ₂ hybrid	—	14	5	7.0	14
Total	237	85	93	3.5	322

lings. The so-called "calendar effect" relates an earlier and quicker molt to a later hatching date (Berthold 1993, Jenni and Winkler 1994, König 1996). Late-hatched young may reduce the extent of their flight-feather molt, and sometimes they start migration while still molting (H. Flinks pers. comm.). Time pressure to complete molt is high for Central European Stonechats. The seasons of the year are reliably reflected in the photoperiodic cycle, and the birds' molt responds to day length (Gwinner et al. 1983).

The African Stonechats (*S. t. axillaris* Shelley 1884) in our study originated from Kenya, close to the equator, where the photoperiod is nearly constant. The climate undergoes seasonal changes between a dry season and two rainy seasons (Brown and Britton 1980). Birds maintain pair territories year-round (Dittami and Gwinner 1985). African Stonechats initiate breeding quickly with the beginning of the first rainy season. The birds anticipate the approximate timing of rainfall to prepare their reproductive systems, relying on an endogenous circannual rhythm (Gwinner and Dittami 1990). They usually produce only one clutch of three eggs per year, and the young stay within parental territories for several months before dispersing. Hence, they can go through postjuvenile molt without obvious external time pressure. Nevertheless, African Stonechats are also responsive to photoperiodic changes (Gwinner et al. 1983, Gwinner and Dittami 1985). Here, we study differences in molt between the two subspecies, using an analysis of hybrids, environmental manipulation of photoperiod, and exploratory quantitative genetics.

METHODS

Study area and birds.—Most Stonechats in this study were collected between 1982 and 1990 in two loca-

tions: African birds originated from the Lake Nakuru region in Kenya (0°14'S, 36°00'E), and European birds originated from Lower Austria (48°14'N, 16°22'E). We transported nestlings to Andechs, Germany, and hand-reared them as described elsewhere (Gwinner et al. 1987). The remaining birds hatched in captivity (Table 1). Birds of both subspecies and their hybrids of the F₁ generation successfully bred in aviaries, and hatchlings were fed either by their parents or by humans (Gwinner et al. 1987). The variation in rearing conditions caused small differences in molt duration (Helm 1997). After fledging, all birds fed on a standard diet and lived either individually in cages, or in groups of four to eight birds in aviaries (König 1996).

We accumulated the data for this study from different experiments. About 20% of the data have been previously published, as indicated in Table 2. African Stonechats contributed more than one-half of the data, European Stonechats more than one-third, and the two hybrid generations together made up 11.2% of the birds (Table 1). Chicks collected in the field usually came in complete sibling groups. The degree of relatedness of the birds was high. Owing to differences in clutch size (Gwinner et al. 1995), African birds had, on average, fewer siblings than European birds. Because chicks bred in captivity often had siblings from more than one brood, the families of hybrids were relatively large. Chicks from the European population hatched between April and July, and those from East Africa in April. The hatching dates of birds breeding in constant conditions are distributed throughout the year. In this study, we give the date as the serial number of the day in the year (Julian date, from 1 to 365). In comparisons of the two sexes, we found no differences and therefore pooled all birds (Helm 1997).

Photoperiodic conditions.—In all experiments, light intensity was about 400 lux during daytime and 0.01 lux at night. The birds were assigned to 11 photoperiodic groups (Table 2) that experienced one or more of the following three types of light-dark (LD) regimes. The first was constant equatorial photoperiod. In early studies, we used LD 12.8:11.2 hours,

TABLE 2. Photoperiodic treatments of all Stonechats, classified by genotypic group (data are number of individuals). Photoperiod (PP; see Fig. 1) is given as the light : dark (LD) subdivisions of the 24-h day. Day x refers to x days after a bird hatched. Groups are numbered by type of photoperiodic treatment followed by a serial number. Treatment types include unchanged (1), shortened (2), and extended (3) PP. The single birds in groups 1-2 and 2-2 were only considered in comprehensive analyses. In groups 3-3 and 3-4, some data were eliminated after days 160 to 180 because of experimental complications.

Group	African	European	F ₁	F ₂	Description of photoperiodic treatment
1-1	88 ^a	3	17 ^b	14	LD 12.25:11.75 from hatching; control condition for African Stonechats.
1-2	1	23 ^a			Naturally fluctuating European PP from hatching; control condition for European Stonechats.
2-1		57	4		European PP, changed to LD 12.25:11.75 after day 2 to 20.
2-2		6	1		European PP, changed to LD 14.5:9.5, then LD 12.25:11.75 between days 6 to 18.
2-3	16				European PP, changed to LD 12.25:11.75 after day 35 to 50.
2-4	16 ^{b,c}				LD 12.25:11.75, changed to European PP after day 8 to 14, then to LD 12.8:11.2.
2-5		17 ^{b,c}			European PP, changed to LD 12.8:11.2 after day 40 to 50.
3-1	15 ^c				LD 12.25:11.75, changed to European PP after day 1 to 9.
3-2		15 ^c			European PP; after days 15 to 40, PP was set back by 11 weeks; i.e. at identical absolute day length, PP changed from decreasing to increasing (see Fig. 1).
3-3	16				LD 12.25:11.75, changed to LD 12.8:11.2 after day 11 to 30.
3-4	13				LD 12.25:11.75, changed to LD 12.8:11.2 after day 10 to 20, then to LD 16:8 after day 30.

^a Some data on molt completion in König 1996.

^b Some data published in Gwinner and Neußer 1985.

^c Some data published in Gwinner et al. 1983.

corresponding to the interval between onset and end of civil daylight at the equator (i.e. an approximately 0.1-lux threshold in the morning and evening). Subsequently, we changed this to LD 12.25:11.75 (Dittami and Gwinner 1985) to more closely approximate the day length equatorial birds perceive in the field, measured as the time between a 10-lux threshold in the morning and evening (Gwinner and Dittami 1990). Hence, we used LD 12.25:11.75 as the control condition for African Stonechats. The second was naturally fluctuating European photoperiod. Birds exposed to this photoperiodic cycle lived either outdoors in the light conditions of Andechs or under a simulation of the light conditions at 47°30' N (Fig. 1). We changed day length at weekly intervals, and in October and February, adjusted it to simulate migration to and back from a latitude of 40°N (Gwinner et al. 1983). The European natural day length serves as the control condition for European Stonechats. The third regime was constant long photoperiod. Some groups lived in long (LD 14.5:9.5) or very long days (LD 16:8). Figure 1 shows the seasonal changes of the European photoperiod, and the other photoperiods in relation to it. The various experimental sequences of light regime, in which photoperiod either increased, decreased, or remained the same, are summarized in Table 2. Transfer of birds between natural photoperiods and the simulation of photoperiods in the laboratory had no observable effects (Helm 1997). One group of European birds (group 3-

2 in Table 2) kept in the European photoperiod was shifted forward by 11 weeks symmetrical to mid-summer (horizontal arrows in Fig. 1).

Monitoring molt and derivation of variates.—After they fledged, we inspected immature Stonechats for body molt in 19 plumage areas (modified from Berthold et al. 1970). Initially, we examined the birds two to three times per week, and later weekly or biweekly. The number of plumage areas molting provided a molt score (range 0 to 19) for that date. Molt scores were plotted against the age at checking, resulting in roughly bell-shaped individual molt curves for each bird. For statistical analysis, we derived four molt parameters: (1) onset and (2) completion of molt, which were the days on which a minimum or maximum, respectively, of five body parts had growing feathers; (3) duration of molt, or the number of days between onset and completion of molt; and (4) middle of a molt plateau, which was indicated by continuous molt in at least 17 body parts. We defined peak of molt as the bird's age on the day in the middle of this plateau. Some data for molt onset, completion, and, as a consequence, duration, were missing. Sample sizes in the analysis were 286 for onset, 322 for peak, 306 for ending, and 271 for duration. Each of the variables clearly depended on the preceding one. Separately, all four represented specific aspects of molt timing, but their dependency had to be considered when interpreting the data.

Statistical methods.—We faced two major difficul-

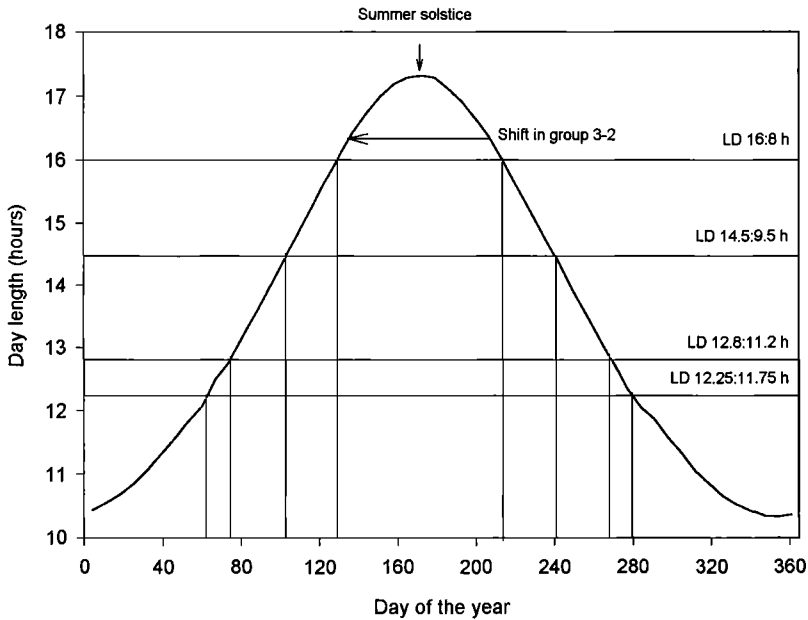


FIG. 1. Photoperiodic conditions (hours) used in the experiments. Bold line denotes simulation of the naturally fluctuating European photoperiod, and thin lines denote constant photoperiods and the days of the year to which they correspond. Arrow pointing to the left is treatment of group 3-2.

ties in our analyses. The first was heteroscedasticity, which occurred because under some experimental conditions, birds started to molt extremely early, which led to severe skewness of the data and small variances. Under more relaxed experimental conditions, variances were higher and more evenly distributed. This problem mainly affected the comprehensive analysis of molt onset. Transforming the data to natural logarithms reduced the amount of heteroscedasticity but did not completely remove it. We used significance of Bartlett's test for homoscedasticity as the criterion, because it is also highly sensitive to departures from normality (Sokal and Rohlf 1995). We also used nonparametric methods, including medians, quartiles, and Spearman rank correlations. For mean molt curves, we derived weekly means of molt scores for individual Stonechats and then averaged them across individuals.

The second problem was the imbalance of the data set (Tables 1 and 2), which we addressed by applying residual maximum-likelihood estimation (REML). This method was introduced specifically to recover interblock information that is otherwise lost in unbalanced data sets (Patterson and Thompson 1971). REML estimates effect sizes and calculates Wald statistics as the change in model fit for each factor entered into the model. Wald statistics are asymptotically distributed as Chi-square and are used for significance testing. For details of the algorithms, see Genstat (1993). Robinson (1987) showed that REML

yields the same results as conventional ANOVA in balanced designs, but avoids the bias created by conventional methods in unbalanced designs. The method is becoming increasingly popular, especially in quantitative genetics (Arnold 1994, Boake 1994, Falconer and Mackay 1996, Roff 1997), and was previously applied to compiled Stonechat data in an analysis of clutch size (Gwinner et al. 1995).

We modeled photoperiod primarily as a categorical factor with 11 levels, corresponding to the photoperiodic groups. In addition, we used day length as a continuous measure of photoperiod to obtain response curves for the onset and peak of molt. We analyzed time of hatching, age at photoperiodic shift, and sibling group in data subsets to separate these secondary factors from the overwhelming effects of photoperiod and genotypic group. To reduce the risk of type-I errors, the first time a factor entered the analysis, the probability at which we declared it "significant" was less than 0.05; for post-hoc analyses, we set the critical probability below 0.01. Tables display only significant effects. We carried out all analyses with the software package Genstat 5.4 (Genstat 1993).

Genetic contributions to variation.—We tested for gross genetic effects by crossbreeding and comparing molt timing in the two subspecies and their hybrids. We also used hybrids to check for polygeny by comparison of the two generations (Buckley 1987). Within the two subspecies, we applied quantitative

genetics methods and faced problems common to most quantitative genetics studies of animal behavior concerning the applicability of laboratory-derived methodology (Hailman 1986, Boag and van Noordwijk 1987, Dingle 1990, Stearns 1992, Arnold 1994, Boake 1994). Most important, sample sizes are too small to obtain reliable results, and estimates are therefore tentative. The publication of these results is justified by the novelty of considering genetic parameters in the timing of avian molt. We used two methods to estimate (narrow sense) heritability (h^2) for 185 birds spread over several subsets of each subspecies. First, there was a limited amount of offspring-parent data. We estimated h^2 as the regression slope of midoffspring in relation to midparent and single parent values, weighted for family size (Roff 1997). We doubled single midoffspring-parent slopes to represent h^2 . Second, we estimated h^2 using full-sib analysis (Boag and van Noordwijk 1987, Roff 1997). We calculated separate estimates for all photoperiodic groups of more than 20 birds after correcting for calendar effects; h^2 is estimated as twice the family resemblance, t , given by the ratio of the among-sibship variance component to the sum of the variance components among and within sibships. If most of the variance is among sibships, then t assumes a value close to unity; t -values may be inflated by nongenetic factors that siblings have in common, and also by nonadditive genetic effects (Falconer and Mackay 1995). We assessed the significance of h^2 estimates based on offspring-parent regressions or the probabilities for intraclass correlation coefficients in full-sib analysis (Sokal and Rohlf 1969, 1995; Boag and van Noordwijk 1987; Roff 1997). In a split-brood experiment, siblings from nests in Kenya were divided into two groups and exposed to different photoperiods (Table 2). Group 2-4 was kept in an equatorial photoperiod, whereas group 3-1 lived in the natural European day. From these data, we assessed the relative effects of family versus photoperiod, estimated h^2 under unequal photoperiods, and plotted family reaction norms (Groeters and Dingle 1987, Dingle 1990, Stearns 1992).

RESULTS

Genotypic group.—Statistics for the four molt measures are given in the Appendix. Under their native photoperiods, the timing of molt differed between subspecies (Wald statistics, $df = 1$; onset = 7.9, $P < 0.01$; peak = 13.6, $P < 0.001$; completion = 35.3, $P < 0.001$; duration = 63.1, $P < 0.001$; Fig. 2A). European Stonechats started to molt after African Stonechats, but their molt was intensified more quickly so that they finished it sooner. Figure 2B shows mean molt curves for the subspecies and the two

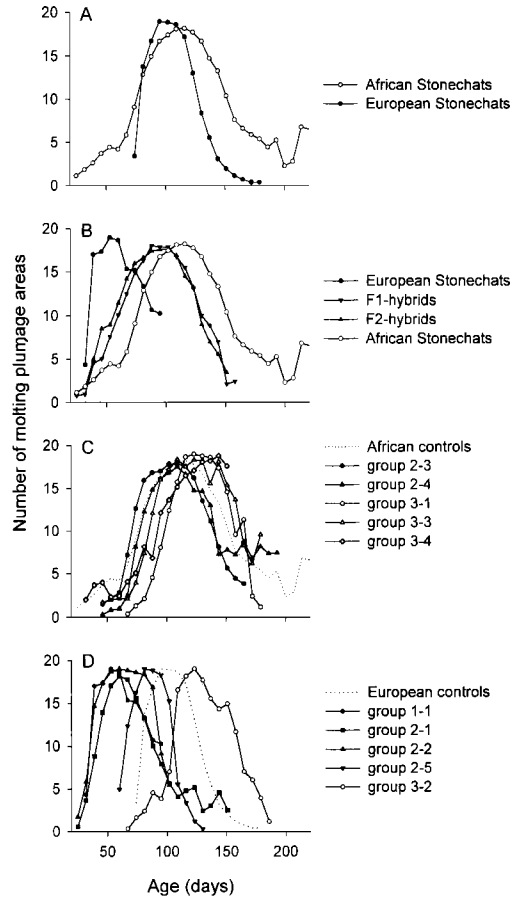


FIG. 2. Molt curves showing changes in weekly means. The ordinate shows how many of a total of 19 plumage areas were molting at a given age. Each point represents the average of at least five birds. Groups are explained in Table 2. (A) Birds of both subspecies under their respective native photoperiods: African Stonechats (open circles) in constant LD 12.25:11.75 (group 1-1), European Stonechats (filled circles) under the changing European photoperiod (group 1-2). (B) Mean molt curves for all four genotypic groups under LD 12.25:11.75 from hatching (groups 1-1). The curve for European Stonechats represents three birds. (C) Molt curves of African experimental groups. (D) Molt curves of European experimental groups.

groups of hybrids kept under the same equatorial photoperiod. Differences between subspecies were pronounced, and molt patterns of hybrids were intermediate. The two hybrid generations were indistinguishable in both their medians and their variation (Appendix); hence, they were subsequently pooled. Differ-

TABLE 3. Comprehensive analysis of effects of genotypic group and photoperiod, and their interaction on postjuvinal molt parameters in Stonechats. Data are Wald statistics.

	df	Molt onset ^a	Molt peak	Molt completion	Molt duration
Genotypic group	3	401.2**	688.0**	483.1**	214.3**
Photoperiod	10	633.5**	551.4**	255.7**	72.8**
Genotypic group × photoperiod	3	38.6**	25.2**	10.8*	3.8
Sample size		286	321	306	271

*, $P < 0.05$; **, $P < 0.001$.

^a Bartlett's test indicated heteroscedasticity between genotypic groups at $P < 0.001$.

ences between the subspecies and the pooled hybrids were significant for all parameters (Wald statistics, $df = 2$; onset = 74.3, $P < 0.001$; peak = 85.4, $P < 0.001$; completion = 88.4, $P < 0.001$; duration = 11.7, $P < 0.01$).

Comprehensive analysis of the whole data set confirmed these differences (Table 3). In general, European Stonechats started postjuvinal molt earliest and molted fastest so that they finished molt long before the other genotypic groups. Figures 2C and D show mean molt curves for the photoperiodic groups of the two subspecies. In European Stonechats, molt intensified rapidly, resulting in steep, pointed molt curves. In African Stonechats, molt increased slowly so that their molt curves tended to be rounded and wide. In all groups, molt onset was correlated with the timing of peak molt (African, $r = 0.66$; European, $r = 0.85$; hybrids, $r = 0.48$; $P < 0.001$ in all cases). The correlation was highest in European birds, reflecting the rather uniform, quick intensification of their molt. In all genotypic groups, molt onset was negatively correlated with duration so that the later a bird started molt, the less time it took (African, $r = -0.17$, $P < 0.05$; European, $r = -0.29$, $P < 0.001$; hybrids, $r = -0.23$, $P > 0.05$).

Photoperiod.—The effect of photoperiod and its interaction with genotypic group were both significant (Table 3). Generally, Stonechats began their postjuvinal molt earlier under shorter photoperiods and finished it later than under longer photoperiods. In greater detail, the subspecies responded differently to photoperiodic manipulations. European birds displayed a wider spectrum of response than African birds (Figs. 2C and D). We calculated mean timing of molt onset and peak in relation to day length. Figure 3 shows linear regressions of the group medians for both subspecies. The slopes for molt peak were steeper than those for molt onset. For both measures, the slopes of the pho-

toperiodic response were more than three times steeper in European than in African Stonechats. The slopes of the two subspecies intersected at a day length of about 14.75 h. At longer day lengths, European Stonechats molted later than African conspecifics. The magnitude of the genotypic effect on the response to photoperiod depended on the day length under which the birds were kept. The data were explained equally well by asymptotic regressions, indicating that there was an asymptotic trend in the response curves.

In addition, molt timing was related to the age at which birds were transferred to short equatorial photoperiods. In both subspecies, molt timing differed between groups transferred to short days at various ages (see European groups 1-1, 2-1, 2-2, 2-5, and African groups 1-1, 2-3, 2-4; Figs. 2C and D). Figure 4 shows for both subspecies the relationship between median age at molt peak and median age at transfer into an equatorial photoperiod. Regression with subspecies as groups accounted for 99.2% of the variance. The earlier a European bird was placed under short days, the earlier it molted. The reverse was true for African Stonechats, although the trend was much weaker. We used peak of molt as an example, but the relationship was similar for the onset ($P < 0.05$) and completion ($P < 0.01$) of molt. For molt duration, the slopes were negative in both subspecies (Helm 1997).

Time of hatching.—We examined molt timing for effects in relation to hatching date (calendar effects) in all photoperiodic groups. Significant results for peak of molt are shown in Table 4. Birds kept under constant equatorial day length showed no calendar effects, not even the African Stonechats that had hatched in Africa and thus had experienced local environmental conditions for several days. In contrast, in most groups that experienced European day lengths

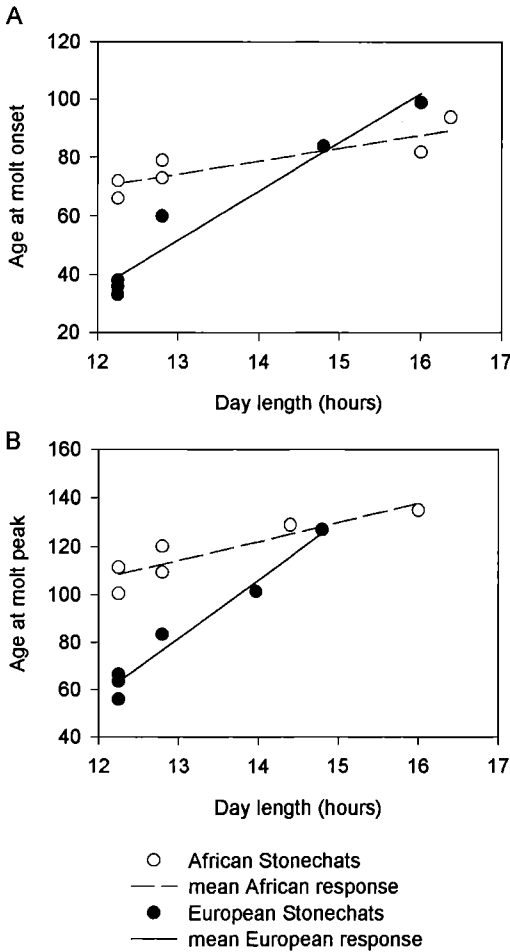


FIG. 3. Molt timing in relation to photoperiod in the two Stonechat subspecies, given by linear regressions. For each group, the median age at molt onset (A) and molt peak (B) is plotted against the median day length on the respective day. Slopes for molt onset were $16.8 \pm \text{SE of } 1.9 \text{ days/h}$ in European Stonechats, and $4.5 \pm 1.2 \text{ days/h}$ in African Stonechats ($r^2 = 0.92$, $df = 11$, $P < 0.001$). For peak of molt, slopes were $24.5 \pm 2.3 \text{ days/h}$ in European Stonechats, and $7.8 \pm 1.9 \text{ days/h}$ in African Stonechats ($r^2 = 0.95$, $df = 11$, $P < 0.001$).

at early ages, molt depended on hatching date. Chicks hatched early in the season were older at the peak of molt than those hatched late. European controls, which lived permanently under the European photoperiod, showed the strongest calendar effects (group 1-2). The effect was less pronounced in birds that were transferred to constant conditions after hatching in the European photoperiod. However, we

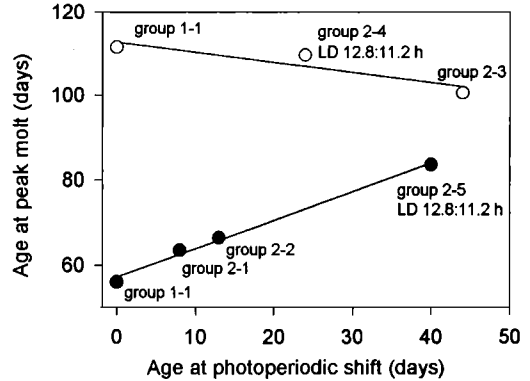


FIG. 4. Effect of age at photoperiodic shift for African (open circles) and European (filled circles) Stonechats. For each group, the regressions of median age at peak molt against the median age of birds at first exposure to short days are shown (slopes are -0.25 ± 0.1 for African Stonechat and 0.67 ± 0.04 for European Stonechat; $P < 0.001$, $df = 6$). Short days refer to LD 12.25:11.75, except for the groups 2-4 and 3-1, which were kept at LD 12.8:11.2.

found an influence of hatching date even in European birds that had been transferred to constant conditions within three days after hatching in the European photoperiod (groups 2-1, 2-2). In group 2-1, the calendar effect even increased after the peak of molt (slope for molt completion = $-0.32 \pm \text{SE of } 0.07$; for duration = -0.27 ± 0.07 ; $P < 0.001$ for both measures). In African Stonechats, we observed a calendar effect in birds that hatched in the European photoperiod (group 2-3) but not in those transferred to the European photoperiod after hatching under constant conditions. In all groups, the timing of molt varied more for birds hatched early in the season than for those hatched later. For European controls, we can

TABLE 4. Significant calendar effects on molt in Stonechats. Estimates are derived from linear regressions of untransformed data on postjuvinal molt peak against day of hatching. Groups 2-1, 2-2, and 2-3 were corrected for effects of age at photoperiodic shift.

Experimental group	r^2	Peak slope \pm SE	n
European 1-2	0.33**	-0.62 ± 0.18	23
European 2-1	0.08*	-0.12 ± 0.05	57
European 2-2	0.96**	-0.57 ± 0.08	6
African 2-3	0.30*	-0.27 ± 0.14	16

*, $P < 0.05$; **, $P < 0.01$.

TABLE 5. Estimates of heritability ($h^2 \pm SE$) from full-sib analysis and parent-offspring regression for onset, peak, completion, and duration of postjuvinal molt in Stonechats. Outlier due to almost identical maternal values is in parentheses.

	No. of birds	No. of families	Molt onset	Molt peak	Molt completion	Molt duration
h^2 from offspring-parent regressions of African group 1-1						
Offspring vs. mid-parent	10	4	1.15 \pm 0.5 ^a	0.41 \pm 0.39		0.06 \pm 0.20
Offspring vs. mother	10	4	(6.88 \pm 1.92)	0.67 \pm 0.47	0.17 \pm 0.35	0.09 \pm 0.26
Offspring vs. father	10	4	1.23 \pm 0.04 ^a	0.94 \pm 0.28		0.17 \pm 0.62
h^2 from full-sib analysis						
African group 1-1 from field	70	25	1.02 \pm 0.24 ^a	0.32 \pm 0.28		
African group 1-1 by year	70	25	0.90 \pm 0.26 ^a	0.28 \pm 0.28		
European group 1-2 ^b	23	6		1.16 \pm 0.45 ^a	0.24 \pm 0.46	
European group 2-1 ^b	51	14	1.11 \pm 0.27 ^a	1.02 \pm 0.28 ^a	1.01 \pm 0.28 ^a	0.87 \pm 0.30 ^a
African groups 2-4 and 3-1 ^c	31	11	0.56 \pm 0.45	0.32 \pm 0.46	0.26 \pm 0.46	0.06 \pm 0.45

^a $P < 0.05$ based on t -values for full-sib correlations and F -values for parent-offspring regressions.

^b Values corrected for hatching date.

^c Values corrected for photoperiodic effects.

compare the calendar effect with the slope of the photoperiod effect. For molt peak, it corresponded to -0.94 (assuming a day length change of 2.3 min/day), which was close to the range of slopes for the calendar effect.

Genetic effects.—We calculated offspring-parent regressions for only a few birds (Table 5). One value was an outlier (midoffspring-mother for molt onset), and the others suggested that molt was completely determined by family at its onset, but that genetic factors quickly lost their influence. Heritability estimates from full-sib analyses agreed with those from offspring-parent regressions. When siblings were treated identically (groups 1-1, 1-2, and 2-1), heritability estimates were high at molt onset but declined quickly in African Stonechats. Heritability estimates remained high until peak molt in European controls, and throughout molt in European birds transferred to LD 12.25:11.75. The longer persistence of a high genetic variation in European Stonechats was the only difference between the subspecies.

In a split-nest experiment, African siblings were divided and kept either under equatorial (group 2-4), or natural European photoperiods (group 3-1; Table 5). Family effects persisted under different light conditions and were significant for completion and duration of postjuvinal molt (Wald statistics, $df = 10$; completion = 41.3, $P < 0.001$; duration = 29.9, $P < 0.01$) but not for onset and peak, where influences of photoperiod predominated. During molt completion and duration, the interaction between family and photoperiod was equally important

(Wald statistics, $df = 10$; completion = 37.5, $P < 0.001$; duration = 39.9, $P < 0.001$). Heritability estimates were smaller and nonsignificant (Table 5). Figure 5 shows family reaction norms for the split broods. For group 3-1, day length in the natural European day declined from about 17 to 12 h during the experiment, whereas for group 2-4, it remained at constant LD 12.8:11.2. Obviously, the shape of the bundle changed as molt proceeded. For molt onset, the reaction norms were nearly parallel, representing only slight interaction between family and environment. The width of the bundle indicates high variation among families. During the course of molt, variation increased in birds kept under constant conditions, whereas it decreased in birds exposed to the naturally declining photoperiod. This led to increasingly funneled reaction norms toward the European natural day. Slopes were clearly non-parallel, statistically expressed by the significant interaction term. The two groups did not differ statistically in means after peak molt. The main difference was in the amount of variation among families expressed under the two photoperiods.

DISCUSSION

Stonechats from Africa and Central Europe renew their plumage in accordance with patterns described for many other birds of tropical and temperate latitudes (Jenni and Winkler 1994). Over all the photoperiodic groups, European Stonechats molted earlier than African

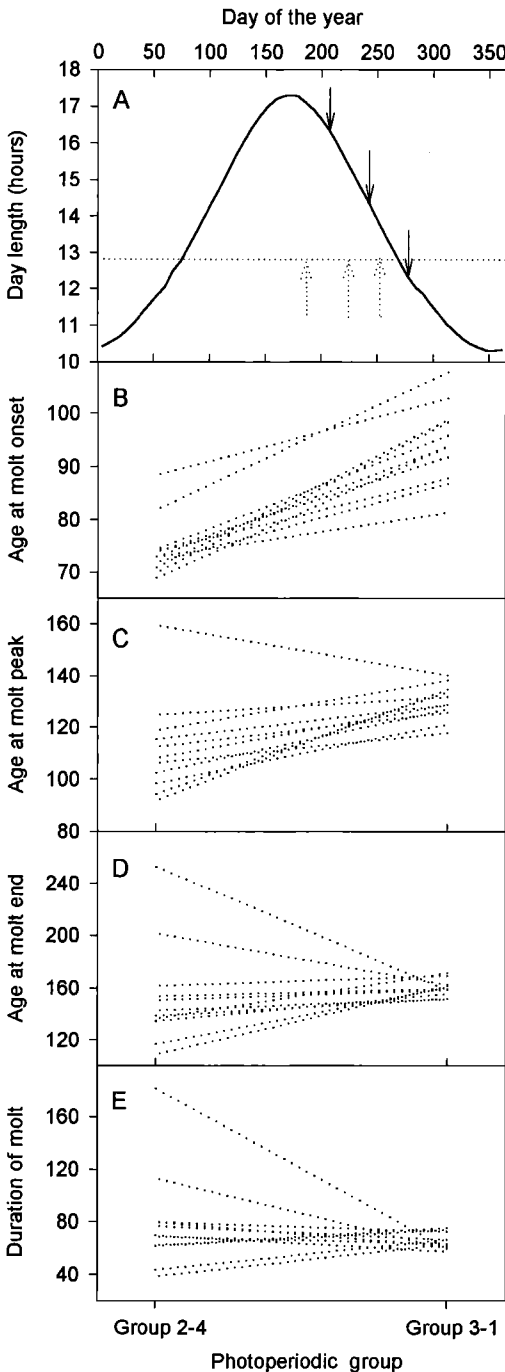


FIG. 5. Family reaction norms in the split-brood experiment. (A) The photoperiod for group 2-4 (dotted line) remained constant at LD 12.8:11.2; dotted arrows indicate, from left to right, median dates of molt onset, molt peak, and molt completion. The photoperiod for group 3-1 (solid line) changed ac-

Stonechats. The genetic basis for differences in the timing of molt was confirmed by intermediate molt patterns for hybrids (Fig. 2B). Molt timing in the two hybrid generations was almost identical. This could indicate that molt timing is controlled by polygenic inheritance, as is typical of a complex performance (Boag and van Noordwijk 1987, Buckley 1987), or, alternatively, that it resulted from a high degree of relatedness. Within subspecies, the timing of molt depended on photoperiod (Figs. 2C and D). Generally, molt started earlier but ended later under short than under long photoperiods. The longer duration of molt can be interpreted as a deceleration of its rate in response to no further reduction in day length (e.g. Noskov and Rymkevich 1985). A deceleration of molt under constant conditions would make sense energetically. If seasonal pressure does not increase, no reason exists to continue intensive molt at a potentially high cost.

In both subspecies, the magnitude of the photoperiodic response also depended on the age at which birds were first exposed to short days (Fig. 4). An effect of photoperiod very early in life has barely been appreciated, which may influence conclusions drawn from studies in which photoperiod was not controlled during the days following hatching (e.g. Jenni and Winkler 1994). Although our present analysis confirms some previous results qualitatively (Gwinner et al. 1983, Gwinner and Neuffer 1985), some of the quantitative differences essentially can be accounted for by photoperiodic effects early in life (Helm 1997). Molt timing was also related to hatching date (calendar effect). In European controls, the timing of molt peak was related to hatching date by a regression slope of -0.62 (Table 4), which agrees with earlier estimates of the calendar effect in European Stonechats (i.e. slopes from -0.42 to -0.9 ; König 1996, H. Flinks pers. comm.) and other European passerines (-0.33 and -0.81 ;

←
 cording to the changing photoperiodic conditions in Europe; solid arrows indicate, from left to right, median dates of molt onset, molt peak, and molt completion. Bundle of reaction norms for each of the four molt parameters: (B) molt onset; (C) molt peak; (D) molt completion; (E) molt duration. Each line connects the molting ages of split siblings kept at the two different photoperiods.

Jenni and Winkler 1994). In European Stonechats that hatched and lived in the European photoperiod for 3 to 19 days, the calendar effect persisted under constant conditions throughout molt. This suggests that environmental factors experienced during early posthatching development are involved in its implementation. African Stonechats that hatched and lived in the European photoperiod for 30 to 50 days also showed a calendar effect. There was no indication of a calendar effect in Stonechats from nests in Kenya. This fact, together with the observation that short photoperiods accelerate molt, suggest that the calendar effect is at least partly a photoperiodic phenomenon.

The two subspecies had a similar response to photoperiod in the timing of postjuvinal molt. However, their responses appeared to be tailored to their respective local circumstances. The subspecies differed in the quantitative relationship between day length and timing of molt (Fig. 3). European Stonechats responded more strongly to differences in day length than their African conspecifics. We interpret the mean response curves as approximate mean reaction norms of the populations from which our experimental Stonechats were taken (van Noordwijk 1990, Stearns 1992). The different slopes of their reaction norms may be related to differences in the biology of the two subspecies. For Central European Stonechats, a late completion of molt presumably would put birds at high mortality risk during migration or unfavorable seasonal climatic changes. Selection may thus favor a strong response to changes in photoperiod. Conversely, lower slopes of the reaction norms in African Stonechats may reflect lower seasonal pressures. The response curves crossed at a photoperiod of just below 15 h, implying that when comparing the subspecies, results depended on day length. At the day length of the intersection, the subspecies would time their molt identically. At longer day lengths, European Stonechats started molt even later than African conspecifics. However, under their respective native photoperiods (Fig. 2A), European Stonechats molted significantly earlier and faster than African Stonechats.

The only qualitative difference between the subspecies was their molt timing when exposed at a very early age to equatorial days (Fig. 4). In this situation, European Stonechats molted earlier the earlier they were exposed to

short photoperiods, whereas the reverse was true in African Stonechats. This difference may be interpreted in relation to the native latitudes of the subspecies. European Stonechats would encounter an equatorial day length in the field only if they hatched two weeks after the latest recorded hatching date (1 September; Cramp 1988, Glutz von Blotzheim and Bauer 1988). Under these conditions, European Stonechats immediately initiated molt. Conversely, hatching in LD 12.25:11.75 is normal for African Stonechats. These birds molted at intermediate ages, later than birds transferred from the European to the equatorial photoperiod, but earlier than those kept under long days. An extremely late molt can interfere with social demands on young adults. König (1996) kept African Stonechats in small groups and found that birds that finished molt early were high in the rank order and had elevated body masses. An early completion of postjuvinal molt could yield considerable fitness gains, because pair formation and occupation of pair territories can occur soon after the breeding season (Dittami and Gwinner 1985, König 1996). Social benefits would thus counteract energetic pressures to extend molt. The relaxed molt timing when hatching under short days is a modification of the general responsiveness to photoperiod and may be an adaptation to constant life at the equator.

The qualitatively similar responses of the European and African Stonechats to photoperiod are surprising in view of the large photoperiodic differences between their respective native areas. Particularly unexpected is the rather pronounced photoperiodic responsiveness of the equatorial birds originating from an area in which seasonal day length changes are very small. Several explanations have been suggested (Gwinner et al. 1983, Dittami and Gwinner 1985, Gwinner and Dittami 1985). First, African Stonechats might be able to respond to the small changes in photoperiod. Another equatorial species, the Spotted Antbird (*Hylophylax naevioides*), recently has been shown to distinguish between photoperiods only 17 min different from each other (Hau et al. 1998). Corresponding studies have not been carried out with Stonechats. Second, a photoperiodic response in African Stonechats could also be a plesiomorphic character derived from an ancestral population breeding at higher latitudes.

The current study documents modifications of molt timing in accordance with local conditions, and high genetic variation, both of which speak against this explanation. Third, the photoperiodic response could result from immigration of conspecifics from higher latitudes. African Stonechats differ genetically from Eurasian subspecies (Wittman et al. 1995). A common gene pool of African and European Stonechats is therefore unlikely, but African Stonechats may receive genetic input from southern populations breeding at latitudes as high as 34°S (Keith et al. 1992). A common gene pool of African Stonechats at the equator with conspecifics breeding at higher latitudes would explain the simultaneous presence of both photoperiodic reactions and specific adaptations to life at the equator. In contrast to the results of Rohwer and Manning (1990), problems for hybrids of the African populations are unlikely. The continuous distribution of Stonechats in Africa suggests a cline of photoperiodic responses.

In the genetic analysis, we present exploratory heritability estimates within several experimental groups of both subspecies (Table 5). Quantitative genetics methods were only approximated (Boag and van Noordwijk 1987, van Noordwijk 1990, Stearns 1992, Arnold 1994, Boake 1994). Within photoperiodic groups, all estimates of h^2 at molt onset were significant and close to unity, independent of subspecies, photoperiod, or method of calculation. Values close to unity are not exceptional (Hailman 1986, Boag and van Noordwijk 1987, Mousseau and Roff 1987). In our analysis, estimates for h^2 from full-sib analyses were at risk of being inflated by nest effects and nonadditive genetic effects. However, the close resemblance between t -values and h^2 estimates from offspring-parent regressions indicated that such effects were not pervasive. Nest effects generally may be low in our study because most birds were taken from their nests shortly after hatching and then hand-reared. That environmental effects were small is also suggested by the negligible amount of additional variance when African controls were compared according to the year of collection (Table 5). In contrast, h^2 estimates may be inflated by maternal effects, which may even be related to the photoperiod in which mothers were reared (Groeters and Dingle 1987).

Except for possible maternal effects, we believe that the high h^2 values we present are realistic. Within photoperiodic groups, the estimates are in excellent agreement (van Noordwijk 1990). Given the axiom that h^2 estimates are only valid for precisely the population and environmental conditions under which they were measured (van Noordwijk 1990), their consistency in Stonechats is remarkable. Our data suggest that variation in molt onset was almost completely determined by family; thus, they support earlier claims that the timing of molt is genetically based (e.g. Gwinner and Biebach 1977, Berthold and Querner 1982). Heritable effects may not be exclusive to postjuvinal molt. In their analysis of Stonechat growth, Starck et al. (1995) also presented family effects. In their plots, growth curves of siblings appeared to be closely bundled, especially in European Stonechats. This might indicate that developmental patterns are typical of families, and that genetic differences in postjuvinal molt onsets may be a late consequence of family differences in development (van Noordwijk and Marks 1998). There are two exceptions to the consistency of heritability estimates. First, after molt onset, variation arose from other sources. The proportion of variance explained by family declined faster in African than in European birds. Second, heritability was also reduced when photoperiod differed within African Stonechat families in the split-brood experiment. Family patterns persisted to some extent between the two groups, and they were significant for molt completion and duration. During molt, slopes of family reaction norms changed from almost parallel to intersecting (Fig. 5). African Stonechats kept under the European day perceived the continuous decrease of day length as a reliable seasonal cue. Subsequently, they synchronized their molt timing such that variation among families was sharply reduced. The difference in variation under the two photoperiods confirms that the expression of genetic variation depends on the environment (Stearns 1992).

It has been widely accepted that molt timing is adaptive (Stresemann and Stresemann 1966, Jenni and Winkler 1994). The high h^2 values for molt onset question and support this tenet. On the one hand, strong selection would favor clearcut adaptive values with little genetic variation and low h^2 . On the other hand, h^2 is pro-

portional to the rate at which selection can produce genetic change and thus is a condition for the adaptiveness of a trait (Falconer and Mackay 1996). One interpretation allowing for both aspects would be that high h^2 values are maintained through temporal and spatial fluctuations in optimal molt timing, favoring various genotypes at different times and locations (Ewing 1979, Stearns 1992). The biology of both subspecies suggests that this is entirely possible. Climatic conditions, which bear on optimal molt timing, vary among years and between locations. Assuming that some gene flow occurs, a high degree of genetic variation in molt timing could be maintained (Stearns 1992), and local adaptations could develop quickly. The adaptiveness of reaction norms is still debated (Dingle 1990, Travis 1994, Via et al. 1995) and depends on favorable circumstances. The biology of the Stonechat subspecies suggests that their different responses to day length evolved through selection for particular reaction norms. In relation to their respective environments, the responses of the Stonechat subspecies to photoperiod suggest an adaptive value (van Noordwijk 1990).

In conclusion, we propose that the timing of postjuvencal molt in Stonechats evolves in the following way. The general timing in each subspecies, and possibly their mean responses to photoperiod, are determined polygenically. Within subspecies, selection presumably works on the high genetic variation in molt onset, and probably on the variation in reaction norms. Selection may thus result in a fine tuning of molt timing relative to local environmental conditions. One such adaptation may be the molt timing of equatorial Stonechats after hatching in short days. In equatorial Stonechats, molt timing may be a tradeoff between energetic demands and social benefits. In European Stonechats, energetic benefits probably are counteracted by seasonal pressures. However, direct evidence for the adaptive value of molt timing is lacking. Specifically, assumptions about energetic requirements need further assessment (Jenni and Winkler 1994). Knowledge of the relationship between molt rate and energetic demands in the two Stonechat subspecies would be a first step toward an explicit model on the evolution of molt timing.

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APPENDIX. Detailed nonparametric description of the analyzed molt parameters for all photoperiodic groups, separated by genotypic group. Single birds are excluded. Onset, peak, and completion of postjuvinal molt are given as the age of birds, and duration as the number of days spent for plumage renewal (see text). For the African groups 3-3 and 3-4, no values are presented because for some birds, data were eliminated between days 160 and 180 because of experimental complications. Q = quartile, IQ = inter-quartile.

Group	n	Minimum	Maximum	25% Q	Median	75% Q	IQ range
African: Molt onset							
1-1	73	36	100	62	72	78	16
2-3	15	52	81	64	66	70.75	6.75
2-4	16	67	103	71	73	74.50	3.5
3-1	15	76	108	87.25	94	98.25	11
3-3	16	63	96	77	79.50	84	7
3-4	13	62	119	73.50	82	90.75	17.25
African: Molt peak							
1-1	88	86.5	144	99.2	111.5	123.2	24
2-3	15	83	140	98.1	100.5	119.1	21
2-4	16	92	179	98.7	109.5	117.2	18.5
3-1	15	118	140.5	126.2	129	133.5	7.3
3-3	16	106.5	156	112.5	120.2	139	26.5
3-4	13	119.5	179.5	128.6	135	144.3	15.7
African: Molt completion							
1-1	86	114	289	145	159	169	24
2-3	16	116	243	134	136	147	13
2-4	16	109	253	134.5	138	166	31.5
3-1	15	150	172	153.8	161	162	8.2
African: Molt duration							
1-1	71	54	227	77.25	91	104.50	27.25
2-3	15	57	169	65.50	70	83.75	18.25
2-4	16	39	182	62	68	89	27
3-1	15	58	85	60.50	64	67	6.5

APPENDIX. Continued.

Group	<i>n</i>	Minimum	Maximum	25% Q	Median	75% Q	IQ range
European: Molt onset							
1-1	3	27	36	29.25	36	36	6.75
1-2	9	82	89	82	84	86	4
2-1	53	28	49	34	38	42	8
2-2	6	30	34	31	33	33	2
2-5	17	60	73	60	60	71.25	11.25
3-2	15	70	110	88.50	99	107.25	18.75
European: Molt peak							
1-1	3	48	94.50	50	56	84.87	34.87
1-2	23	90	113	98.50	101.50	131.50	33
2-1	57	41.50	88	56.50	63.50	70	13.5
2-2	6	56	70	63	66.50	69	6
2-5	17	75.50	94.50	78.50	83.50	86.25	7.75
3-2	15	116	135	119.75	127	131.50	11.75
European: Molt completion							
1-1	3	82	116	83.2	87	108.7	25.5
1-2	22	120	147	130	134	141	11
2-1	57	69	149	83	91	103	20
2-2	6	91	105	91	98.5	99	8
2-5	17	101	114	101	101	108.2	7.2
3-2	15	35	206	156	165	167	7
European: Molt duration							
1-1	3	46	80	49.50	60	75	25.5
1-2	9	38	59	48	48	50.75	2.75
2-1	53	39	113	48.75	55	70	21.25
2-2	6	58	72	60	65	69	9
2-5	17	32	44	39	41	41	2
3-2	15	42	126	50	62	69	19
F₁ hybrids: Molt onset							
1-1	17	35	77	44	49	59.25	15.25
2-1	4	59	60	59	59.50	60	1
F₁ hybrids: Molt peak							
1-1	17	74	115	88.87	93.50	101.62	12.75
2-1	4	96	107.50	96.75	101.50	106.50	9.75
F₁ hybrids: Molt completion							
1-1	17	112	162	122.7	136	144.3	21.6
2-1	4	124	169	130	142	158.5	28.5
F₁ hybrids: Molt duration							
1-1	17	66	113	73	78	87	14
2-1	4	65	109	71	82.50	98.50	27.5
F₂ hybrids (group 1-1 only)							
Molt onset	12	36	70	41.50	42.50	55.50	14
Molt peak	14	78	113	85	87.50	107	22
Molt completion	14	111	194	124	130.5	142	18
Molt duration	12	52	151	76	84	92	16