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Running head: Moult and photoperiod in Siskins

Seasonal changes in moult, body mass and reproductive condition in Siskins *Carduelis spinus* exposed to daylength regimes simulating different latitudes

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Birds use change in daylength during the year to time events during their annual cycles. Individual Eurasian siskins *Carduelis spinus* can breed and winter in widely separated areas in different years. Birds at different latitudes will experience different changes in photoperiod. So how does latitude affect photoperiodic control? Our aim in this study was to find whether siskins caught from the wild in Britain and exposed to different photoperiodic regimes, typical of widely separated latitudes, would differ in the subsequent timing and duration of their moults and associated processes. Siskins were caught in late February and early March, and initially kept outside on natural photoperiods. From the spring equinox (21 March), they were divided into three groups kept under photoperiodic regimes that simulated latitudes 40º, 55º and 70º N respectively. All three groups showed highly significant subsequent changes in body mass, fat scores and cloacal protuberance size. Moult of the primary feathers started during June – August (mean 9 July), and lasted 61-99 days (mean 75 days). Birds that started to moult late in the season had shorter moult durations. All individuals showed lower mass and fat levels during moult than before or after moult. Crucially, there were no significant differences in the timing of these events between the three photoperiodic groups. Apparently these birds did not use prevailing absolute photoperiod or the prevailing rate of change in photoperiod to time moult-related seasonal events, but used instead some other feature of the annual photoperiod cycle or some form of interval timer linked to photoperiod.

Keywords: body weight, brood patch, *Carduelis spinus*, cloacal protuberance, fat score, moult, photoperiod, siskin

Many species of birds have breeding ranges which span a wide range of latitudes. Within such species, breeding typically begins later in the year at higher latitudes and in some it extends over a shorter period. In species which moult in their breeding areas, this process is also spread over a shorter period at higher latitudes (Berthold 1993). Since the timing of breeding and moult are controlled by photoperiod (Dawson et al. 2001), either directly or by entraining an endogenous circannual rhythm (Gwinner 1986), it is unclear how the timing of seasonal events relates to the different patterns of change in photoperiod at different latitudes.

At higher latitudes, photoperiod is longer at the summer solstice and shorter at the winter solstice, and consequently the rate of change in photoperiod is greater at all times of year than at lower latitudes (excepting the summer period at high latitudes under continuous daylight). Moreover, the differences in photoperiod per degree of latitude increase as latitude increases. For example, at 10°N the photoperiod at the summer solstice is less than 30 min greater than at 0°N, whereas at 70°N it is 5 hours longer than at 60°N (and see Fig. 1). Birds at the north and south of the breeding range will therefore experience very different changes in photoperiod during those parts of the year when they are in their breeding areas, and this is particularly true for species breeding at high latitudes.

Rowan (1925) first demonstrated that an increase in photoperiod during winter caused gonadal maturation. Later studies showed that when birds were transferred from a short photoperiod to a longer photoperiod, the rate of gonadal maturation was proportional to the length of the longer photoperiod (Farner and Wilson, 1957; Farner et al. 1966), and the time to the onset of gonadal regression and post-nuptial moult was inversely proportional to photoperiod (Dawson and Goldsmith 1983). Given these markedly different responses to

different photoperiods, it is unclear how birds at different latitudes use photoperiod to time seasonal events.

Most bird species show high site fidelity, with young birds breeding in the general region of their birth, and adults returning each year to the same areas (Newton 2008). In this situation, birds could become genetically adapted to respond appropriately to the cycle in photoperiod at their natal latitude. Silverin et al. (1993) exposed great tits *Parus major* caught at different latitudes to the same experimental changes in photoperiod. Birds from Italy responded to a shorter photoperiod than birds from southern Sweden, providing support for this hypothesis. However, there was no difference between the birds from southern Sweden and others from northern Norway, even though they were from equally different latitudes. Helm et al. (2009) exposed two closely related subspecies of stonechats *Saxicola torquata maurus* and *S. t. torquata*, which naturally breed at similar latitudes, to the same annual cycle in photoperiod. Their responses differed, and corresponded to their different natural schedules.

Other bird species, for example some cardueline finches, can breed in widely separated areas in different years, according to prevailing food-supplies (Newton 2008). In some such species, food supply may play a role in fine-tuning the date of breeding (Hahn et al. 2005). Nevertheless, all such species are thought to be photoperiodic (Hahn 1998). Different species respond differently to the same experimental artificial photoperiods (Hahn et. al., 2004) and have slightly different mechanisms by which photoperiod brings breeding to an end, to suit the unpredictability of their food supplies. When pine siskins *Carduelis pinus*, common redpolls *Carduelis flammea* and white-winged crossbills *Loxia leucoptera* were kept on constant short photoperiods for 4.5 months from the middle of winter, only pine siskins showed significant gonadal development suggesting that siskins may not be highly dependent

on increasing photoperiods to induce sexual maturation. In birds transferred to constant long photoperiods in winter, gonadal maturation occurred in all three species. After 4.5 months on long photoperiods, gonadal regression was complete in redpolls and pine siskins, but only partial in crossbills. Feather moult was most advanced in redpolls, slightly less advanced in pine siskins and least advanced in crossbills. This demonstrates that the reproductive systems of all three species is stimulated by long photoperiods, but that crossbills, which are temporal opportunists, either do not show spontaneous gonadal regression (i.e. absolute photorefractoriness) or developed photorefractoriness more slowly. Body mass and fat depots of pine siskins, unlike the other two species, remained high irrespective of photoperiod. The different photoperiodic responses of these species appear to result from differences in their reproductive neuroendocrinology (Hahn et al. 2008).

Such studies can explain how different species respond differently to the same annual cycles in photoperiod to suit their species-specific ecologies, but how is photoperiod used by individuals of the same species to time seasonal events when the individuals may be at very different latitudes in different years? One possibility is that birds use photoperiod to entrain an endogenous circannual rhythm in reproductive function and moult, but it is unclear how this could operate at different latitudes because such rhythms in reproductive function are usually expressed only under a narrow range of permissive photoperiods (Gwinner and Wozniak 1982, Gwinner 1986, Wikelski et al. 2008). This holds for tropical and for non-tropical species, such as common starling *Sturnus vulgaris* (Gwinner 1996). Another possibility is that birds do not use absolute photoperiod, or even the rate of change in photoperiod. Rather, they may use more subtle information on how photoperiod is changing to indicate calendar date. Evidence for this came from a study in which Starlings were held for three years on a photoperiodic regime simulating either 9°N or 52°N. Gonadal maturation started slightly

earlier at the lower latitude, but regression and moult occurred at exactly the same date (Dawson 2007).

In this paper, we describe an experiment using a cardueline finch ─ the Eurasian siskin *Carduelis spinus*. This species is a seed-eater, specialising on the annually variable seed-crops of certain trees, notably Norway spruce *Picea abies* in the early breeding season. Although migratory, it concentrates in different areas in different years, depending on where good seed-crops are available. Numbers in particular areas fluctuate greatly from year to year, in line with seed abundance, and ringing has confirmed that individual siskins can breed and winter in widely separated areas in different years. Ringed birds have been found in localities up to several hundred kilometres apart in different breeding seasons and at localities up to several thousand kilometres apart in different winters (Newton 2008). Restricted to breeding in coniferous areas, the species has a wide geographical range, extending in some years northward to the tree limit beyond 70ºN and southward into montane forests beyond 40ºN. There is no evidence to suggest that individuals could move to breed successfully over the whole of this wide latitudinal span, but, along with some other tree-seed specialists, siskins clearly show less site fidelity than most other bird species (Newton 2008). Through their migrations, individuals can also winter at localities separated by more than 30º of latitude in different years, so are exposed to different photoperiodic regimes from year to year as they prepare for spring migration and breeding.

In this study, siskins were caught from the wild during spring. There is no information on the timing of gonadal maturation in this species, but in closely related greenfinches, *Carduelis chloris*, testicular maturation starts during winter and by the equinox the testes are nearly fully mature (Dawson unpublished data). Our specific aim in this study was therefore to find

whether siskins caught from the wild and exposed, from the spring equinox, to the different photoperiodic regimes typical of widely separated breeding latitudes differ in the subsequent timing and duration of their moults and other processes associated with the end of breeding and gonadal regression.

Methods

Siskins were caught from the wild during late February and early March 2008 in two localities in Britain, namely Langholm in Dumfriesshire (lat. 55º 10'N) and Kings Lynn in Norfolk (lat. 52º 45'N). The species breeds in both areas, but in winter local numbers are greatly swollen by immigration of winter visitors from further north in Britain and continental Europe, with ring recoveries from as far east as Russia. No subspecific or clinal variation is evident in siskins, and none of our birds had been previously ringed, so their natal areas were unknown. However, each individual was ringed on capture to facilitate future identification, and sexed and aged (as first year or older) using criteria described in Svensson (1992). Only birds in their first year of life (hatched in the previous calendar year) were kept for experiment. They were fed throughout on a commercial seed mixture, which was made continuously available in several dishes to minimise potential competition between individuals. Birds were initially held in an outdoor aviary at 52°N. At the spring equinox (21 March), the birds were separated into three treatment groups and housed as free-flying birds in separate rooms, each with a photoperiod of 12 h light per day. Thereafter, photoperiod was changed each day to simulate changes at 40ºN, 55ºN and 70ºN respectively (Fig. 1), as calculated from the Astronomical Applications Department of the U.S Naval Observatory (http://aa.usno.navy.mil/). Hence, for the 40º group, photoperiod was increased progressively to 15 h on 21 June (the summer solstice) and then decreased appropriately to 9.3 h by 21 December (the winter solstice). For the 55ºN group, photoperiod was increased to 17.4 h on

21 June and then decreased to 7.2 h on 21 December. For the 70º group, photoperiod was increased to 24 h by 16 May, held constant at 24 h until 26 July, and then reduced to 4 h light on 14 November. Photoperiod was not allowed to fall below 4 h (normally the birds would have left such high latitudes by then).

During the study all the birds were examined individually at frequent intervals (weekly intervals from the end of June) for body mass and fat score, condition of cloaca (males) or brood patch (females), and state of moult. Body masses were taken to the nearest 0.1 g, fat scores in the tracheal pit were recorded as 0 - 4 (0 - no fat, 1- slight fat, 2 - some fat, 3 - level with edges, or 4 - extending out from the tracheal pit over the pectoral muscles). Reproductive condition was assessed from the size (height (mm) x width (mm) = size) of the cloacal protuberance in males, or from the presence or absence of a brood patch in females (brood patches became de-feathered even though the birds had no opportunity to build a nest). Moult was recorded from the lengths (mm) of the growing primary and secondary feathers in the right wing (for the most part both wings moulted in step with one another). As is usual in most passerines, the primaries were shed in sequence from 1-9 (innermost to outermost), and the secondaries from 1-6 (outermost to innermost). Following the usual convention, the duration of moult was calculated as the period between the shedding of the first (innermost) primary feather and the completion of growth of the last (outermost) primary. Most other feathers were replaced within this period, but at the end of primary moult some birds were still growing one or two secondary feathers in each wing. Successive measurements from the same feathers enabled their growth rates to be calculated, from which the start and end dates of primary moult could be estimated precisely, even though the birds were examined at approximate weekly intervals. Growth rates of equivalent feathers were effectively the same in all individuals: the first (innermost) primary grew at 2.4 mm per day, the ninth (outermost)

primary at 2.7 mm per day, and the sixth secondary at 2.5 mm per day. These rates were used for calculating the start and end dates of primary moult, and the end date of secondary moult (for those birds in which secondary moult ended after primary moult).

Statistical analyses

The number of males present in the three groups, 70ºN, 55ºN and 40ºN, at the start of the study and the start of moult was 10, 11 and 10 respectively. An additional 5 females were included with the 55ºN group. The study ended on 21 December, when, due to mortality, sample sizes for males had decreased to 8, 9 and 8 respectively. Body mass, fat score, and cloacal size were analysed using two-way ANOVA with repeated measures (latitude and date) using GraphPad Prism (2007). Moult data were analysed with single factor ANOVA (latitude). Due to arrested moult in some individuals, moult end dates and duration were calculated from 5, 6 and 8 birds respectively.

Results

Body mass and fat score

All three groups, kept on photoperiodic regimes of 40º, 55º and 70ºN, showed significant but parallel changes in body mass and fat scores with date (Table 1, Fig. 2). In general, mass and fat scores were high on 6 May, having increased substantially from their levels at capture. This may have reflected pre-migratory fat deposition (normally preceding spring migration) but was possibly a consequence of captivity and the availability of excess food. In the absence of migration, mass and fat scores of our birds remained high through the breeding season, but started to decline in advance of the start of moult and reached lowest values towards the end of moult. Thereafter values increased again. These increases could again be attributed to pre-

migratory fat deposition (normally preceding autumn migration). Body mass and fat scores changed in parallel in the three groups, with similar trends through the season. Latitude had no significant effect on either body mass or fat scores (Table 1). No interaction between date and latitude was evident for body mass, but it was for fat scores which decreased somewhat less during moult and increased to greater values in the 70º group during autumn.

Cloacal size

All three groups showed significant changes in cloacal protuberance with date (Table 1, Fig. 2). No males showed any sign of a cloacal protuberance when they were caught in February/March, but all had well developed protuberances when they were next handled on 6 May. Sizes varied from 4x1 mm to 5x2 mm. By 6 June, cloacal protuberances had enlarged further in some birds, reaching up to 6x3 mm. During the rest of the breeding season, cloacal sizes fluctuated within this range in the same individuals. Scores remained high through the breeding season, and declined during moult. Individuals showed considerable variation in the stage of moult at which the cloacal region appeared flat again, but all had low scores before the end of moult. There was no effect of latitude on cloacal size, and no interaction between date and latitude (Table 1). The five females examined followed similar patterns to males in their body mass and fat levels: their brood patches became de-feathered during May, and re-feathered during the course of moult, as new feathers grew.

Moult in the three treatment groups

No significant differences in either start dates, end dates or durations of moult emerged between the three treatment groups (Table 1, Fig. 3). The overall mean values for all treatment groups combined were 8.7 July (SE 3.9 days, n = 31) for start dates, 10.9 September (SE 3.3 days, n = 20) for end dates, and 74.9 (SE 2.1 days, n = 19) for moult durations. The

figure for duration (74.9 days) is based only on 19 birds followed to the end of moult, whereas the difference between mean start and mean end dates (with sample sizes of 36 and 19) was 64.2 days. No birds in the 40ºN group showed arrested moult but 3 in each of the other groups did.

In the overall sample, starting dates varied between 6 June and 26 August, end dates between 22 August and 16 October, and durations between 61 and 99 days. The greater spread in start dates (81 days) than in end dates (55 days) resulted at least in part from late-starting birds moulting more rapidly than early-starting birds. This tendency was reflected in the negative relationship between start date and moult duration in the 19 individuals that were followed through a complete moult (Fig. 4).

The above analyses were based on data from males only (some females were included in one group) and compared treatments ignoring possible confounding effects of location of capture. The initial analysis was therefore extended to test for effects of each of these factors after allowing for effects of the other factors (sex and site of capture). No differences in treatments were apparent in either start dates ($p=0.13$), end dates ($p=0.25$) or durations ($p=0.48$). Males showed an earlier start ($p=0.057$) and end ($p=0.003$) than females, but no obvious difference in duration ($p=0.21$). No effects of capture site were evident on any of the moult parameters.

On each bird, most of the feathers were replaced within the period of primary moult, except that some individuals were still growing one or two secondaries at the time the last primary reached full length. The whole moult period of these individuals was thereby extended by up to fourteen further days. The remaining individuals that finished primary moult failed to replace all their secondaries, and retained the last one or two (presumably for another year

until the next moult). Some adult birds when caught from the wild had also retained one or two secondaries through their previous moult, so retention of these feathers may not be unusual among siskins. In addition, some of the captive birds also retained their outer primary feathers, usually one or two, but up to four in some individuals. For these individuals, moult end dates and durations were not calculated.

Discussion

Birds are highly photoperiodic (at least those species that breed outside the tropics) and use the annual cycle in photoperiod in some way to time key stages of the annual cycle: gonadal maturation and regression, moult and migration. In this study we kept siskins under three different photoperiodic regimes, equivalent to those at 40º, 55º and 70ºN. Absolute photoperiod would have been different at all times (apart from the equinoxes) between the three groups, as would the rate of change in photoperiod. Body mass, fat scores, and cloacal protuberance sizes all changed significantly over time, but there were no differences between the groups. All three groups started to moult at the same time, and moult duration did not differ significantly between them. This suggests that the birds did not use prevailing absolute photoperiod or prevailing rate of change in photoperiod to time events during at least this part of the annual cycle. This finding is compatible with the earlier study on starlings held for three years on a photoperiodic regime simulating either 9°N or 52°N in which gonadal maturation started slightly earlier at the lower latitude, but regression and moult occurred at exactly the same dates (Dawson 2007). Some other signal derived from the annual cycle in photoperiod must have been important as an event timer in these birds.

There are several potential explanations for these findings. Firstly, birds may have an innate circannual rhythm driven rather than entrained by photoperiod. One problem with this

hypothesis is that circannual rhythms in reproductive function (but not moult or migratory fattening) are only fully expressed under a narrow range of permissive photoperiods (Wikelski et al. 2008). For example, in the common starling, the 'circannual clock' stops on photoperiods exceeding 13h of light per day (Gwinner and Wozniak 1982); the annual cycle in photoperiod over-rides a circannual clock. Secondly, birds may utilise an interval timer. Photoperiod at one or more times of year (possibly the spring equinox) may be used to programme the timing of subsequent events. In some other seed-eating species, photoperiod before gonadal maturation can affect the timing of autumnal events (King 1963, Farner et al. 1980, Moore et al. 1982, Berthold 2002). In the present study, all three groups of siskins were held on the same photoperiodic changes until the spring equinox, so photoperiod prior to the equinox may have determined the timing of subsequent changes in physiology. However, in the study on starlings (Dawson 2007), birds were held continuously for three years on the different simulated latitudes, and the timing of gonadal regression and moult was exactly the same in all three years. An interval timer, set at some earlier date, is highly unlikely to have operated over such a long time period. However, an interval timer operating specifically from the equinox alone could control subsequent timings. Finally, birds may be taking information from the sinusoidal pattern of change in photoperiod: in other words, not absolute photoperiod or even the rate of change in photoperiod, but how the rate of change in photoperiod is changing – a second order function. Also, although absolute photoperiod and rate of change in photoperiod vary at different latitudes, some features of the annual cycle remain the same at all latitudes. Photoperiod is the same at the equinoxes, the rate of change is greatest at the equinoxes, and the rate of change is minimal at the solstices. In theory, using such photoperiodic cues, birds could estimate calendar time irrespective of their latitude, although this would necessitate a sophisticated degree of perception and presumably a sufficiently long period of time resident at a given latitude. If birds were actively migrating, this would

complicate perception of calendar time. Helm and Gwinner (2005) exposed groups of stonechats *S. torquata* to different patterns of photoperiod during spring to simulate different migration strategies. This did affect the subsequent timing of testicular regression, moult and autumnal migratory restlessness. These three possibilities of control are not necessarily mutually exclusive and perhaps elements of all three are involved, and the relative importance of each may vary between species to reflect their differing ecologies.

Another striking finding from the study was the wide variation in all measured parameters within groups, whether the timing and duration of moult, the timing of reproductive regression and fat deposition with respect to moult, or the amount of fat deposited. Three points are relevant. Firstly, because our siskins were caught from winter flocks, their natal areas were unknown, but to judge from previous ringing recoveries, the birds could have been hatched further north in Britain, or in a wide area of northern Europe extending from Norway to Russia. Different birds could have originated from different areas, accounting for some of the individual variation found in all three experimental groups. Secondly, there is evidence from the wild that the timing of breeding and migration in siskins can vary from year to year in the same region, depending on the abundance of the tree-seeds that form their main foods (Svärdson 1957, Newton 2008). However, in captivity, our birds had continuous access to *ad lib* food. Thirdly, in the wild, the timing of breeding is likely to influence the timing of moult and subsequent migratory fat deposition. Although our captive birds showed reproductive development, they did not have facilities to breed in captivity and so this is unlikely to have contributed to the variation between individuals.

There was no significant difference in the duration of moult between the siskins on different simulated latitudes whereas in free-living birds of some other species, moult duration is less at

higher latitudes (Berthold 1993). This too may result from breeding activity. At higher latitudes breeding tends to start later (Berthold 1993) and so it may also finish later (at least in single brooded species). Moult is often delayed until breeding has finished (Newton 1966, Samson 1976, Morton and Morton 1990, Morton 1992, Hemborg 1999). Therefore, breeding birds at higher latitudes may start to moult later. Birds that start to moult late then moult more rapidly (Samson 1976, Morton and Morton 1990), because the rate of moult is influenced by the time that it starts (Dawson 2004). In individual siskins, moult duration decreased in birds that started to moult later (Fig. 4). However, in the absence of breeding activity, there was no difference in mean moult start dates between the simulated latitudes and so there was no difference in mean moult duration.

One other finding from out study concerns the fat scores which followed a similar pattern in all three groups, but were higher during late summer and autumn in the 70º N birds than in the 55 and 40º N birds. This difference may have been a response to the longer nights experienced by the 70º N birds, during which they had to survive on their body fat.

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Figure legends

Figure 1. Experimental protocol: Until 21 March, siskins were kept outdoors under a natural photoperiod at 52°N. Thereafter the three groups were held indoors and photoperiod was changed daily to simulate natural changes at 40°, 55° or 70°N. For the latter group, once photoperiod had decreased to 4h per day during November, it was held at 4h.

Figure 2. Changes in body mass, fat score and cloacal size in siskins kept from 21 March on simulated photoperiodic regimes appropriate to 40° (n=8), 55° (n=9) or 70°N (n=8). Each point represents the mean ± SE. The vertical dashed lines represent the mean start dates and end dates of moult.

Figure 3. Mean start and end dates of moult in three groups of siskins kept from 21 March on simulated photoperiodic regimes appropriate to 40°, 55° or 70°N respectively.

Figure 4. Relationship between start date and duration of moult for individuals in the three groups. Regression relationship for all three groups combined: Duration = 82.8 (SE 3.7) – 0.28*(date of start) (SE 0.11), $r^2 = 0.26$, F = 6.11, P = 0.024. Intercept on Y axis indicates estimated duration for moult starting on 31 May (day 0).

Table 1. Results of statistical analyses. Date on body mass, fat score and cloacal size were analysed with two-way ANOVA with repeated measures (latitude and date). Moult data were analysed with single factor ANOVA (latitude).

	Body mass			Fat score			Cloacal size		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Date	22,484	8.254	<0.0001	22,484	8.639	<0.0001	14,322	30.801	<0.0001
Latitude	2,484	0.245	0.785	2,484	1.961	0.165	2,322	0.274	0.274
Interaction	44,484	1.204	0.179	44,484	1.466	0.031	28,322	1.398	0.091

	Moult start date			Moult end date			Moult duration		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Latitude	2,33	0.509	0.606	2,18	0.727	0.499	2,18	1.176	0.334

Figure 1

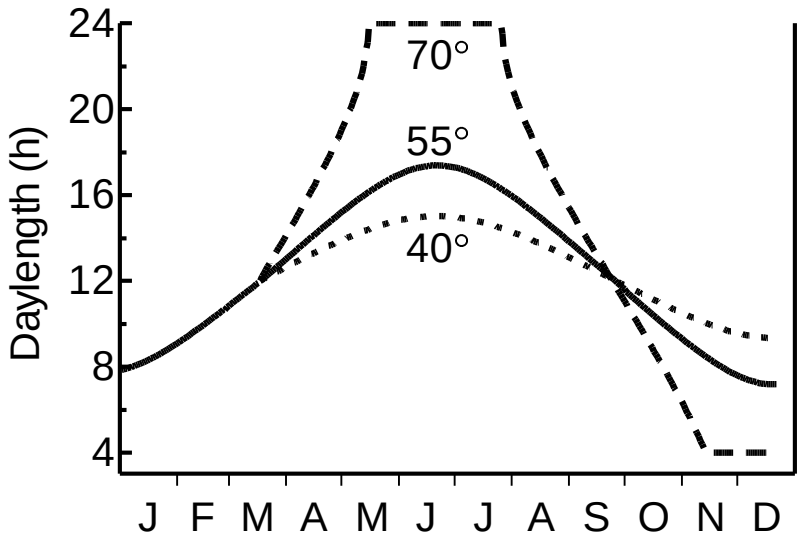

Figure 2

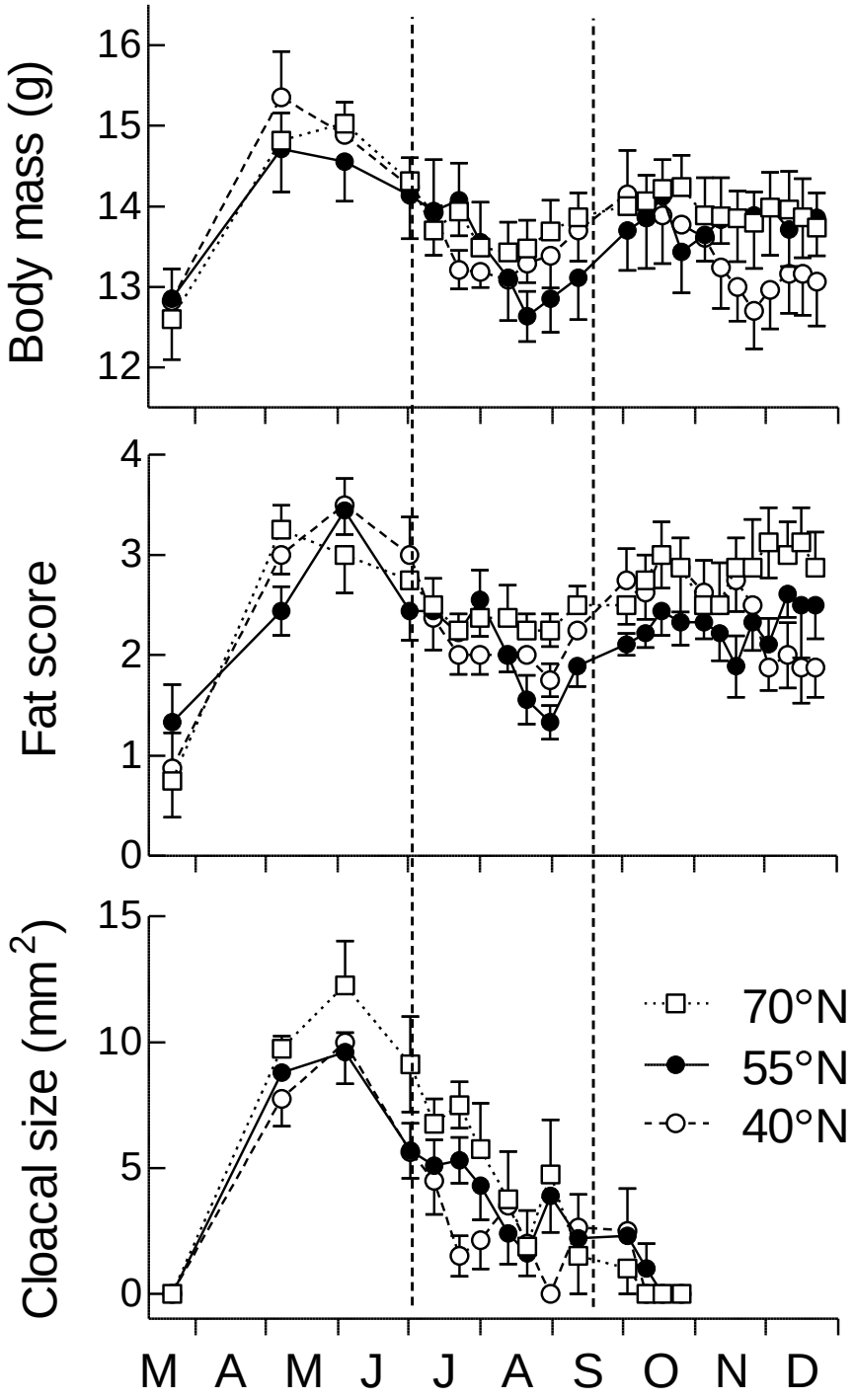
Body mass (g)
16
15
14
13
12
Fat score
4
3
2
1
0
Cloacal size (mm2)
15
10
5
0
70°N
55°N
40°N
M A M J J A S O N D

Figure 3

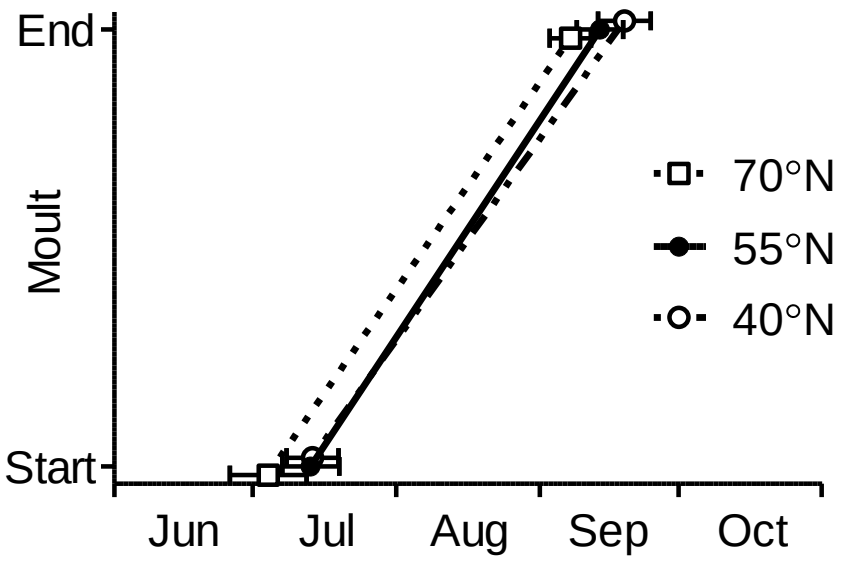
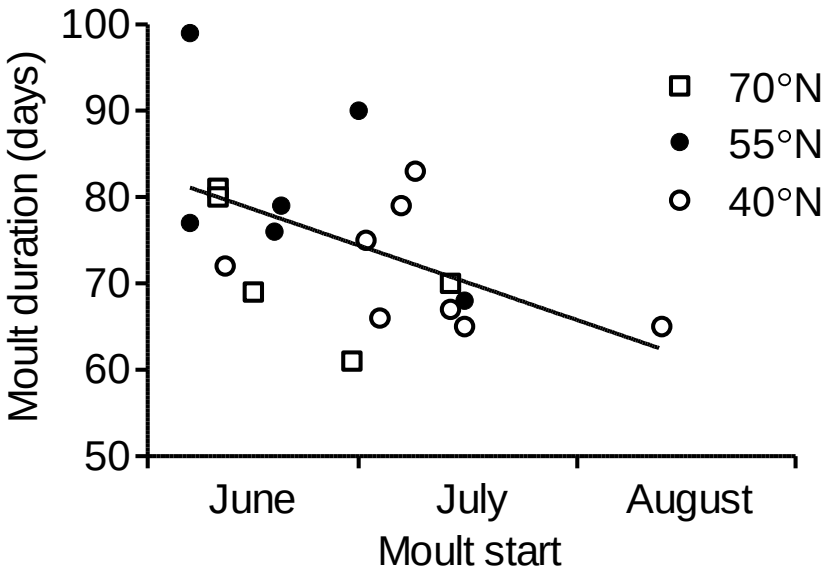
Figure 4