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Article

Conditions at the breeding grounds and migration strategy shape different moult patterns of two populations of Eurasian golden plover *Pluvialis apricaria*

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Events in the life cycle of migrant birds are generally time-constrained. Moulting, together with breeding and migration, is the most energetically demanding annual cycle stages, but it is the only stage that can be scheduled at different times of the year. However, it is still not fully understood what factors determine this scheduling.

We compare the timing of primary feather moulting in relation to breeding and migration between two populations of Eurasian golden plover *Pluvialis apricaria*, the continental population breeding in Scandinavia and in N Russia that migrates to the Netherlands and southern Europe, and the Icelandic population that migrates mainly to Ireland and western UK. Moulting was studied at the breeding grounds (N Sweden, N Russia, Iceland) and at stopover and wintering sites (S Sweden, the Netherlands). In both populations, primary moulting overlapped with incubation and chick rearing, and females started on average 9 d later than males. Icelandic plovers overlapped moulting with incubation to a larger extent and stayed in the breeding grounds until primary moulting was completed. In contrast, continental birds only moulted the first 5–7 primaries at the breeding grounds and completed moulting in stopover and wintering areas, such as S Sweden and the Netherlands.

This overlap, although rare in birds, can be understood from an annual cycle perspective. Icelandic plovers presumably need to initiate moulting early in the season to be able to complete it at the breeding grounds. The latter is not possible for continental plovers as their breeding season is much shorter due to a harsher climate. Additionally, for this population, moulting all the primaries at the stopover/wintering site is also not possible as too little time would remain to prepare for cold-spell movements. We conclude that environmental conditions and migration strategy affect the annual scheduling of primary feather moulting in the Eurasian golden plover.

Keywords: primary moulting, moulting-breeding overlap, life cycle



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Introduction

Birds need to fit different events into their annual cycle in such a way that energy-demanding activities such as breeding and moult coincide with periods of favourable environmental conditions that imply, at the same time, good nutritional conditions (Newton 2008). This might be especially problematic for migratory birds as migration (including the preparation for migration) is time-consuming and entails high energy expenditure; migration thus poses a possible energy and time constraint on other annual cycle events (Newton 2009). Birds might overlap activities, e.g. breeding and primary feather moult (Holmes 1971, Rogers et al. 2014), which is believed to indicate a time, survival or energetic bottleneck (Buehler and Piersma 2008).

Birds organise their annual schedules in different ways, with a particularly high rate of variation in when and where they moult (Ginn and Melville 1983). Moult is the only main seasonal activity that birds can schedule at different times of the year (Noskov et al. 1999, Dawson et al. 2000, Helm and Gwinner 2006). Some species moult in the breeding grounds (normally directly after breeding), others moult during migratory stopovers, and others again moult during the winter period (Ginn and Melville 1983, Newton 2009). Some species split their moult over different periods/areas, for example, starting their moult in the breeding area, then suspending moult during migration, and completing their moult in wintering grounds (e.g. grey plover *Pluvialis squatarola* (Branson and Minton 1976)). Among all the scenarios, the least common case is to overlap moult with active breeding (Newton 2009). In spite of many studies describing the relationships between breeding, migration and moult of different species and all over the globe (Serra et al. 1999, 2006, Newton 2009, Remisiewicz 2011), we still do not fully understand which factors determine the scheduling of these different events in the annual cycle of a migrant bird, and why in some species there is overlap between energy-demanding activities.

Although the timing of moult seems to be, in general, under strict endogenous control (Pulido and Coppack 2004, Helm and Gwinner 2006), individuals still seem to be flexible in the start and extent of moult. This flexibility might arise from timing constraints caused for example by late or early breeding (Conklin et al. 2013, Tomotani et al. 2016).

Comparisons of annual schedules between species, sub-species and populations are a potentially powerful approach to understand the organisation of migrants' annual cycle. However, such comparative studies remain scarce (Serra et al. 1999, Barshep et al. 2013). In this study we compare the timing of primary feather moult in relation to breeding and migration between two populations of Eurasian golden plover *Pluvialis apricaria* (hereafter: golden plover), the continental population breeding in northern Sweden and in northern Russia that migrates to the Netherlands and southern Europe, and the population breeding in Iceland that migrates mainly to Ireland and western UK (Byrkjedal and

Thompson 1998, Wiersma et al. 2017). The golden plover is an interesting species in this respect because it is one of the unusual examples of a species in which primary feather moult overlaps with breeding activities (Jukema 1982, Jukema et al. 2001, Bridge 2006). Previous ringing studies suggest that Scandinavian birds may extend their wing moult over the first stages of their autumn migration (Lindström et al. 2010) whereas Icelandic birds apparently finish wing moult while still in the breeding area (Jukema et al. 2001). We describe how moult is scheduled within the annual cycles of these two populations, including details on the speed of moult. We also investigate the influence of sex in moult patterns. Subsequently we explore different explanations for the development of their moult strategies in relation to breeding and migration schedules and weather conditions during the breeding and non-breeding seasons.

Methods

Study species

The golden plover breeds from Greenland, Iceland and Faroes in the west, through north Fennoscandia, to Taymyr Peninsula in the east (Cramp and Simmons 1983). Incubation and the chick rearing period each last 30 d. Both parents do incubate in equal bouts of 12 h, but females leave the chicks when they are about two weeks old, while males care for them until they fledge (unpubl.). Scandinavian breeding birds migrate southwards in short hops, with stopovers in southern Sweden and in Denmark, towards wintering areas mainly in the Netherlands and the UK (Cramp and Simmons 1983, Jukema et al. 2001). Depending on the severity of the winter weather they may continue to migrate southwards to France, Iberia or Morocco (Machín et al. 2015). Scandinavian golden plovers leave the breeding grounds from mid-July to August, in which females depart before males, and failed breeders before successful breeders (Machín et al. 2015). Russian birds possibly fly across taiga through west Siberia, Kazakhstan and River Yenisey to Caspian Sea and Mediterranean (Cramp and Simmons 1983). In the Netherlands birds with both Scandinavian and more eastern origin occur (Jukema et al. 2001). Golden plovers breeding in Iceland leave the island in September–early November. They then migrate to western UK and Ireland, and some individuals eventually move further on towards western France, Iberia, and Morocco (Cramp and Simmons 1983, Gunnarsson 2009).

Study sites and fieldwork

Golden plovers were trapped during the breeding season in N Sweden (Ammarnäs) and on Iceland (near Selfoss). Fieldwork in N Sweden was conducted from the first week of June until mid-July of 2010, 2011 and 2013, in the Vindelfjällen Nature Reserve, Ammarnäs (Machín et al. 2015, 2017). Fieldwork on Iceland was conducted in the first

half of June 2016, near the village of Selfoss. Adult golden plovers were caught on the nest using walk-in traps (Yalden and Pearce-Higgins 2002) or bownet-spring traps (Gratto-Trevor 2004). To reduce the risk of damaging the eggs, the plover eggs were replaced by dummy eggs during catching. Birds were trapped mostly during the second and third week of incubation, to avoid the risk of nest desertion. Female and male golden plovers share the incubation duties fairly equally, in which males typically incubate during the day and females during the night (Byrkjedal and Thompson 1998). Hence, trapping attempts were made during both the day and night to catch both the males and the females of the breeding pairs. In total 67 breeding birds were captured in N Sweden and 37 in Iceland (Table 1). The captures of adults in Ammarnäs was part of a more extensive research program on the breeding ecology and migration behaviour of golden plovers (Machín et al. 2015, 2017). During these studies the timing of autumn migration departure was recorded (Machín et al 2017).

Golden plovers were trapped after the breeding season in Iceland. Fieldwork was conducted at the end of August–beginning of September 2016, near the village of Sandgerdi, near the airport of Keklavik. Here the plovers gathered in flocks in meadow areas after the breeding period. Birds were captured using a traditional Dutch trapping system, which basically is a large clapnet ('wilsternet', Jukema et al. 2001). Birds were lured to the net by calls and decoys. 108 plovers were captured at this location (Table 1).

Golden plovers were trapped at a migratory stopover site close to the city of Lund, in S Sweden. Fieldwork was conducted from August to November in 2003, 2005–2007, in the agricultural areas surrounding the city (Lindström et al. 2010). Birds were trapped in mistnets that were erected in one or two long rows at arable fields where plovers were expected to forage during the night. Playback was used to attract birds to the field and nets. 133 plovers were caught at this stopover site (Table 1).

In addition, golden plovers were trapped in the Netherlands which is both a stopover and wintering site. Here golden plovers are trapped year-round by volunteers using the above mentioned traditional Dutch 'wilsternet' system (Jukema et al. 2001). We selected data for August–September, when plovers are moulting, for the years 2007–2013. This dataset contained 162 birds (Table 1).

Finally, data on the moult of Russian plovers was obtained from museum skins at the Zoological Inst. of the Russian Academy of Science in Saint Petersburg. Skins were collected

throughout Russia in 1843–1989. As it was not possible to determine the sex and breeding stage of these birds, the data was considered as a mixture of breeding and non-breeding birds. Thus, this data was only included in the overall analysis of moult patterns in continental birds, and excluded from the comparison between the sexes in breeding birds.

Measurements and scoring of moult

The incubation stage of every nest was determined by measuring the development of the eggs by using the egg floating method (Liebezeit et al. 2007). Breeding birds were sexed on the basis of plumage differences within the pair (Byrkjedal and Thompson 1998). Non-breeding birds were aged on the basis of plumage characteristics, in which we distinguished between juvenile 'first calendar year birds' (hatched that year) and adult 'after first calendar year birds' (hatched in the previous year or earlier). In this paper, only adult birds were considered. For every trapped bird, a standard set of biometric measurements was collected (Jukema et al. 2001, Lindström et al. 2010). Primary feather moult was described according to Ginn and Melville (1983), in which a score on a scale of 0 to 5 is assigned to every primary feather. A newly moulted and completely regrown feather scores 5, a missing feather scores 1 and an old, not yet shed feather, scores 0. Growing feathers score values between 1 and 4 (Ginn and Melville 1983).

Statistical analyses of moult patterns

Every moult score was transformed into a proportion of feather mass grown (PFMG) index (Underhill and Summers 1993), using the mean relative mass of each primary feather (Supplementary material Appendix 1 Table A1). For each region, the start and end of moult and moult duration were estimated using the package 'moult' ver. 2.0 (Erni et al. 2013) in R 3.3.2 (R Development Core Team). In order to use these moult models (Underhill and Zucchini 1988, Underhill et al. 1990), the range of observed PFMG values was rescaled to a range of 0–1, for each of the regions, cf. Remisiewicz et al. (2010).

The plovers moulted different feathers at different locations, and thus different moult models were required to analyse moult patterns (Underhill and Zucchini 1988, Underhill et al. 1990). In Ammarnäs birds that had not yet started moult and birds' moulting actively were observed, thus moult model type 5 was used. In Iceland, only actively

Table 1. Numbers of adult golden plovers, by site, breeding status and sex, used in the moult analyses.

	Iceland			Continental Europe			Total
	Iceland breeding	Iceland non-breeding	Ammarnäs (N Sweden) breeding	Russia unknown	Lund (S Sweden) non-breeding	The Netherlands non-breeding	
Male	18	0	43	29	0	0	90
Female	19	0	23	16	0	0	58
Sex unknown	0	108	1	2	133	162	406
Total	37	108	67	47	133	162	554

moulting birds were observed and thus moult model type 3 was applied. In both Lund and the Netherland most birds were moulting actively, although some birds had already completed moult. Moult model type 3 was used because the latter birds were excluded as their moult pattern departed from normal. For the breeding sites, separate moult models were run for the different sexes, in order to be able to compare moult patterns between sexes. In addition moult models were run in which data for the sexes was combined, in order to allow comparisons between regions and populations.

The mean daily rate of the primary feather material growth (% PFMG d^{-1}) was calculated for each region by dividing the maximum PFMG by the estimated duration of the part of moult observed in that area (Remisiewicz et al. 2010). We then compared these mean daily rates of moult by a Z-test (Remisiewicz et al. 2014), in which a critical significance level of $p = 0.0167$ was adopted according to Bonferroni correction for combining three pairwise comparisons (Dunn 1961). To determine if the timing of primary moult differed between the sexes at Ammarnäs and Iceland breeding grounds, we applied moult models with and without the sex as a covariate (Remisiewicz et al. 2014). We ranked these models using the Akaike information criteria corrected for small sample size (AIC_c) (Burnham and Anderson 2002).

Results

A total of 69 golden plovers were measured at their breeding grounds in Ammarnäs, and 45 in Iceland. At both locations, females were generally larger than males, but this difference was only significant for Ammarnäs ($t = -2.42$, $df = 1$, 67 , $p = 0.018$). Birds from Iceland were generally larger than birds from Ammarnäs. Size differences were significant for wing length ($t = -4.87$, $df = 106$, $p < 0.01$), tarsus length ($t = -3.87$, $df = 108$, $p < 0.01$) and weight ($t = -10.26$, $df = 112$, $p < 0.01$) but not for total head or bill length.

Timing of moult of males and females in Sweden and in Iceland during breeding

The breeding birds in Ammarnäs moulted at least the four innermost primaries (P1–P4), and some begun moulting P5 or P6. One out of 23 females (5%) had started to moult P5. Among 43 males, 26% moulted primaries up to P5 (10 birds) or P6 (1 bird). The mean moult index was higher for males (mean PFMG = 0.090, range = 0.004–0.300, $n = 43$) than for females (mean PFMG = 0.040, range = 0–0.182, $n = 23$, $t_{130} = 16.34$, $p < 0.001$). In Iceland most birds trapped on the nests were moulting primaries up to P4, and three males (8.1% of males) just started to grow P5. The mean moult index for males (mean PFMG = 0.106, range = 0.028–0.206, $n = 18$) was higher than for females (mean PFMG = 0.072, range = 0.004–0.154, $n = 19$; $t = 2.18$, $df = 35$, $p = 0.02$).

For Ammarnäs, one male with an advanced moult score (PFMG = 0.300) was considered an outlier. Timing of moult was subsequently estimated for a PFMG range of 0–0.228,

for primaries P1–P5 combined. For Iceland timing of moult was estimated for a PFMG range of 0–0.206, for P1–P6 combined. For both populations, the best fitted moult model indicated that sex had an effect on the start of moult, but not on moult duration (Supplementary material Appendix 1 Table A1). According to these models, males started to moult on average 9 d earlier than females in Ammarnäs and in Iceland (Table 3, Fig. 1).

In Iceland, the incubation period started on average on the 28 May (16 May–13 June). In Ammarnäs the incubation period started 8 d later, on the 6 June (26 May–15 June) (Fig. 1). This means that in Ammarnäs, males started primary moult on average 3 d, and females 12 d after the beginning of incubation (Fig. 1). In Iceland, males started moult on average 9 d before the start of incubation, and females at the day incubation begun (Fig. 1). In Ammarnäs the plovers reached a moult stage of PFMG = 0.228 on average on the 18 July in males, and the 26 July in females. In both sexes, it took 47 d to reach this moult stage (Table 2, Fig. 1). For Iceland, moult duration was estimated to be 45 d, but for a smaller PFMG range, thus the rate of moult was similar for the two breeding areas (Table 3, $Z = 0.194$, $p = 0.42$). In Iceland breeding males reached a moult stage of PFMG = 0.206 on average on the 3 July, and females on average on the 13 July (Fig. 1). Females left Ammarnäs at the end of July, usually after two weeks of chick rearing. Males stayed in Ammarnäs at least two weeks longer than the females, until chicks fledged, and the earliest date when a male left was 18 August. Because males left the breeding grounds about three weeks later, and begun moult 9 days earlier than the females, it is likely that males had progressed much further in their moult than females upon departure from Ammarnäs (Fig. 1).

Comparison of moult patterns between continental and Icelandic populations

Data from the birds from Ammarnäs, Russia, Lund and the Netherlands were analysed jointly, assuming these birds belong to the same continental population. Moult is similar between both breeding populations (Scandinavian and Russia), moulting some primary feathers at the breeding grounds (Table 3), and Russian and Scandinavian breeding birds share stopover and wintering sites as shown by ringing recoveries. No birds with suspended moult were observed in Ammarnäs, the Netherlands, and among the Russian specimens. In Lund, 5.2% of 133 golden plovers had suspended their moult after they had replaced six (P1–P6, two birds) or seven (P1–P7, five birds) primaries. These birds were trapped between the 23 August and the 8 September (Fig. 2), and were excluded from estimating moult duration and speed. In Lund and the Netherlands golden plovers moulted almost twice as fast as compared to the birds in Ammarnäs (Table 3).

In Iceland, golden plovers stayed at the breeding grounds until primary moult was completed on average on the 12 September (Table 3). No birds with suspended moult were observed in Iceland.

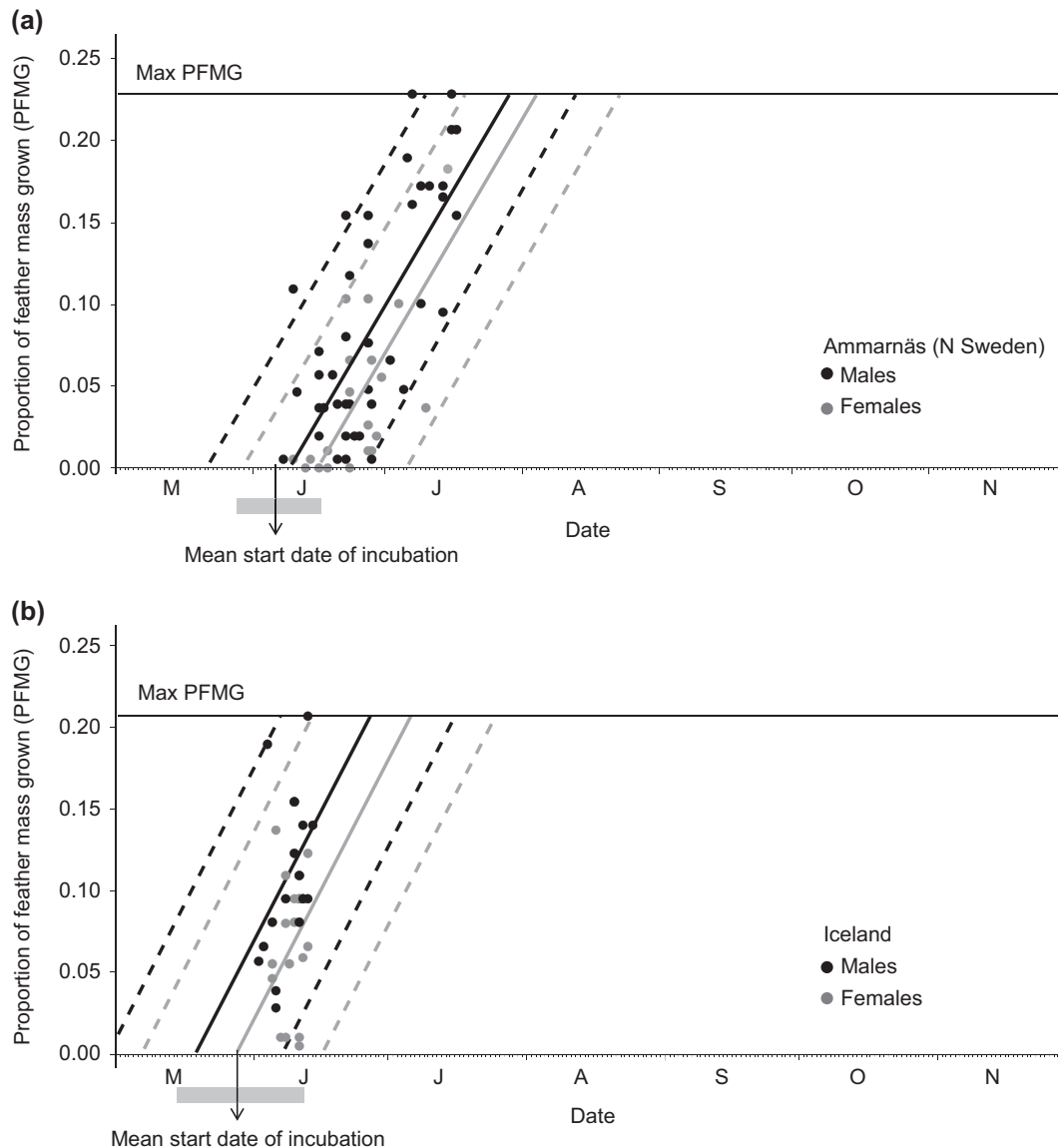


Figure 1. Proportion of feather mass grown (PFMG) over time, by sex, for golden plovers breeding in Ammarnäs (N Sweden) (a) and Iceland (b). Black refers to males and grey to females. Continuous lines = the estimated mean progress of primary moult, dashed lines = 95% confidence intervals for each sex. Grey bars below the x axis = the range of breeding dates for each population, the arrows = the mean start of incubation.

Icelandic golden plovers started to moult 17 d earlier and completed moult 37 d earlier compared to the continental plovers. Overall, they took 16 d less to moult their primaries than the continental birds that split moult between different sites (Table 3, Fig. 2) and this difference was significant ($Z = -5.14$, $p < 0.01$, Table 3).

Discussion

Moulting primaries during incubation

In birds, the most common moult strategy is that adults start to replace primary feathers after the chicks have fledged

(Newton 2008). Moulting flight feathers during chick provisioning is believed to be too costly energy-wise (Newton 2008), also because flight feather moult impairs flight efficiency (Hedenström and Sunada 1999). However in some species, especially among waders, raptors and marine birds, moult and breeding overlap more extensively (Cramp and Simmons 1983, Ginn and Melville 1983, Kjellén 1994, Bridge 2006). Overlap between primary moult and breeding has been described for petrels, shearwaters, sulids, cormorants, pelican, alcids, terns, gulls and one species of skua, skimmer, prion and frigatebird, although it varies the extent of overlap between incubation and the rearing period and many of the species are sedentary (Bridge 2006). Moulting primary feathers during incubation is a relatively rare strategy,

Table 2. Molt parameters for male and female golden plovers caught during breeding seasons in Ammarnäs, N Sweden (PFMG range 0–0.228) and Iceland (PFMG range 0–0.206) estimated for primaries P1–P6 combined. Molt estimates are according to the best-fitted molt models with the sex as a covariate (Supplementary material Appendix 1 Table A1). 95% CI = 95% confidence interval, %PFMG d⁻¹ = the estimated daily rate of the primary feather material growth. * = values refer to the analysed range, not to the molt duration of all primaries.

Region	Sex	Molt parameters				Sample sizes				
		Mean start date (SE) and 95% CI	Common duration in days (SE)	Common SD of start date (SE)	Mean end date at max PFMG for region (SE)	Pre-molt	In molt	Post-molt	Data type	%PFMG d ⁻¹ (SD)
Ammarnäs (range 0–228)	Males	9 Jun (2.9) 21 May–28 Jun	47 (6.4)*	9.7 (3.8)	26 Jul (2.9)*	0	42	0	Type 5	0.48 (0.20)*
	Females	18 Jun (3.0) 30 May–7 Jul			4 Aug (3.0)*	4	18	0		
Iceland (range 0–206)	Males	19 May (16.3) 27 Apr–10 Jun	45 (32.1)*	11.1 (9.2)	3 Jul (19.5)	0	17	0	Type 3	0.46 (0.24)*
	Females	28 May (7.5) 6 May–19 Jun			13 Jul (14.7)	0	20	0		

Table 3. Molt parameters for golden plovers estimated for the stages of molt conducted in each location, and for the Scandinavian and Icelandic birds for all primaries. 95% CI = 95% confidence intervals, %PFMG d⁻¹ = the estimated daily rates of the primary feather material growth in the PFMG range of each population. * = difference in the molt rate between that and each other continental regions significant (Z-test, p < 0.0001), ** = difference in the molt rate between the continental and the Icelandic populations significant (Z-test, p < 0.0001).

Region	PP in moult/PFMG range	Molt parameters				Sample sizes				
		Mean start date (SE) and its 95% CI	Duration in days (SE)	SD of start date (SE)	Mean end date at max PFMG for region (SE)	Pre-molt	In molt	Post-molt	Data type in moult model	%PFMG d ⁻¹ (SD)
Ammarnäs (N Sweden)	P1–P6	13 Jun (2.3) 24 May–2 Jul	45 (6.2)	10.0 (3.9)	28 Jul (2.3)	4	60	0	Type 5	0.51* (0.24)
	P1–P7	26 Jun (6.8) 8 Jun–15 Jul	60 (6.8)	9.4 (3.7)	26 Aug (6.8)	19	28	0	Type 5	0.80 (0.25)
Lund (S Sweden)	P4–P10	12 Jul (3.1) 26 Jun–28 Jul	100 (4.8)	8.3 (2.2)	19 Oct (3.1)	0	126	7	Type 3	1.00* (0.17)
	0.195–1	7 Jul (4.6) 15 Jun–28 Jul	91 (6.6)	11.1 (3.2)	5 Oct (4.6)	0	162	0	Type 3	1.10* (0.27)
The Netherlands	P3–P10	24 Jun (1.2) 31 May–18 Jul	116 (2.2)	12.33 (2.5)	18 Oct (1.2)	23	376	7	Type 5	0.86** (0.18)
	0.108–1	4 Jun (2.7) 18 May–22 Jun	100 (3.8)	8.7 (2.6)	12 Sep (2.67)	0	147	0	Type 3	1.00 (0.18)

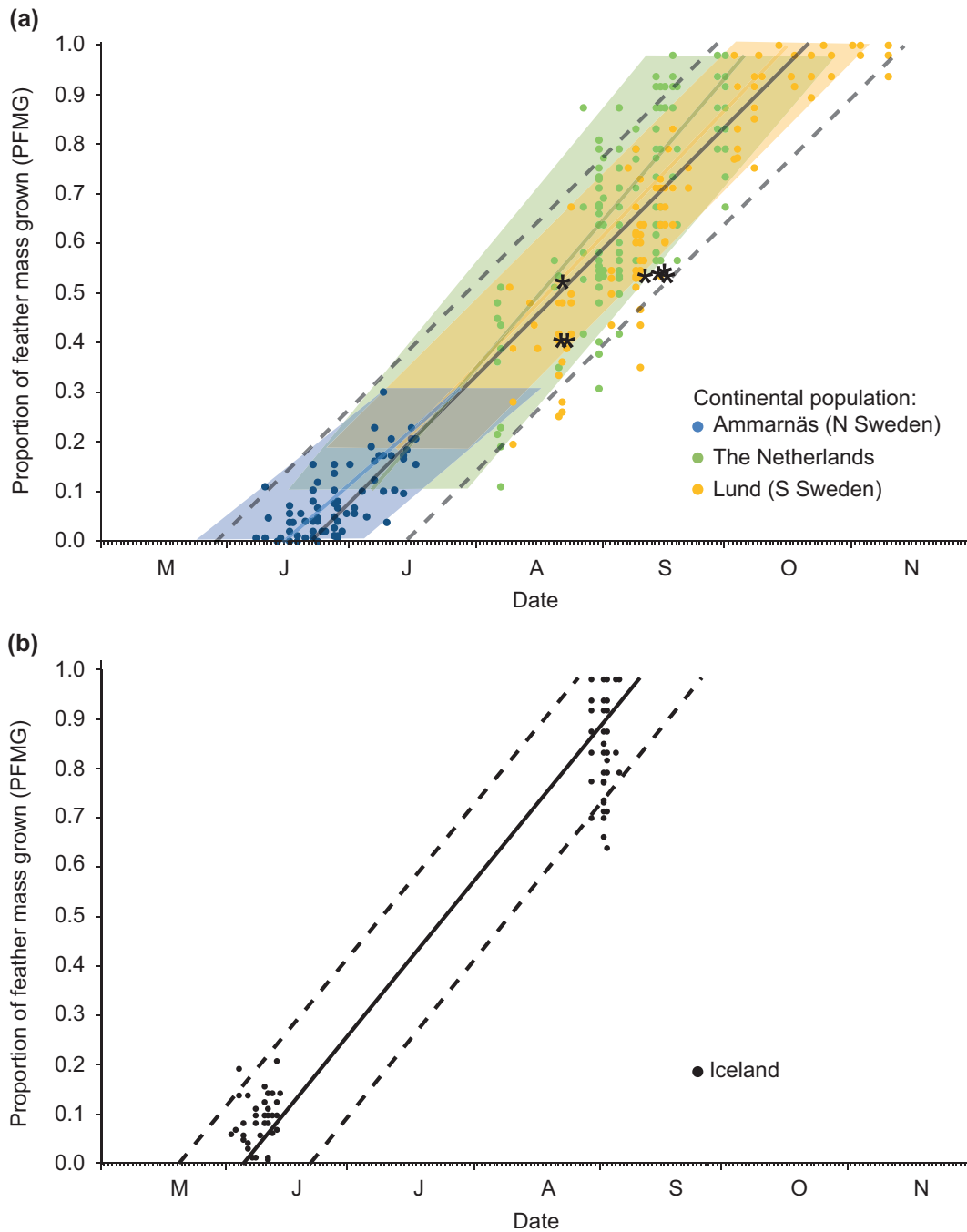


Figure 2. Proportion of feather mass grown over time for Scandinavian golden plovers (above), as estimated for the three locations separately (in colour) and for these locations combined (in black), and for Iceland golden plovers (below). Asterisks=7 birds in Lund with suspended moult, continuous lines=the estimated mean progress of primary moult, dashed lines=95% confidence intervals.

but occurs in some migratory waders (e.g. dunlin *Calidris alpina* (Holmes 1971, Kania 1990, Holmgren et al. 1993, 2001) and purple sandpiper *Calidris maritima* (Morrison 1976, Summers and Nicoll 2004)), sedentary waders (e.g. the hooded plover *Thinornis rubricollis* (Rogers et al. 2014) and a sedentary passerine (pale-winged starling *Onychognathus naboroupp* (Craig 2012)). Overlap between primary moult and incubation is also observed in raptors, in females of species

where the males provision food during the incubation period (e.g. sparrowhawk *Accipiter nisus* (Newton and Marquiss 1982) and Montagu's harrier *Circus pygargus* (Arroyo and King 1996)).

There are many factors that could contribute to the development of overlap between moult and incubation. In raptors, overlap between incubation and moult could readily be understood as the female raptors exhibit almost no

flight activity during the incubation period (Schlaich et al. 2017), providing a unique opportunity to moult a few primary feathers. High food abundance during the incubation period possibly is an important general prerequisite for overlap between incubation and moult (Newton 2008). The tight annual schedule of long-distance migrants could be another factor promoting moult during incubation (Holmgren et al. 2001). This might be particularly relevant for larger birds that need more time to breed (Heinroth 1922) and to grow primaries (Remisiewicz 2011). Finally, studies have also highlighted the possible role of flight performance (Williams and Swaddle 2003) and the species' breeding strategy (Giunchi et al. 2008). Extensive overlap between flight feather moult and incubation was observed in both golden plover populations we studied and in both sexes. What could favour this overlap between primary feather moult and incubation in golden plovers?

In Ammarnäs arthropod abundance was studied by pitfall trapping which showed that arthropods were already relatively abundant by mid-June (Machín et al. 2017) when the plovers initiated primary feather moult; thus the condition of high food availability seems satisfied. The only time arthropod abundance could constrain moult could be at the end of the breeding season, in July, when arthropods had dwindled (Machín et al. 2017). No detailed information on arthropod abundance is available from Iceland. Although Iceland and Ammarnäs lay at the same latitude, Iceland has a much milder climate because of the Gulf Stream effect (Fig. 3), and feeding conditions seem already favourable by May (T. Gunnarson pers. comm.). Although quantitative information on arthropod abundance is lacking, there is no indication that the plovers on Iceland are constrained by food abundance when they start to moult their primary feathers by the beginning of June. Similar moult rates in Ammarnäs and on Iceland

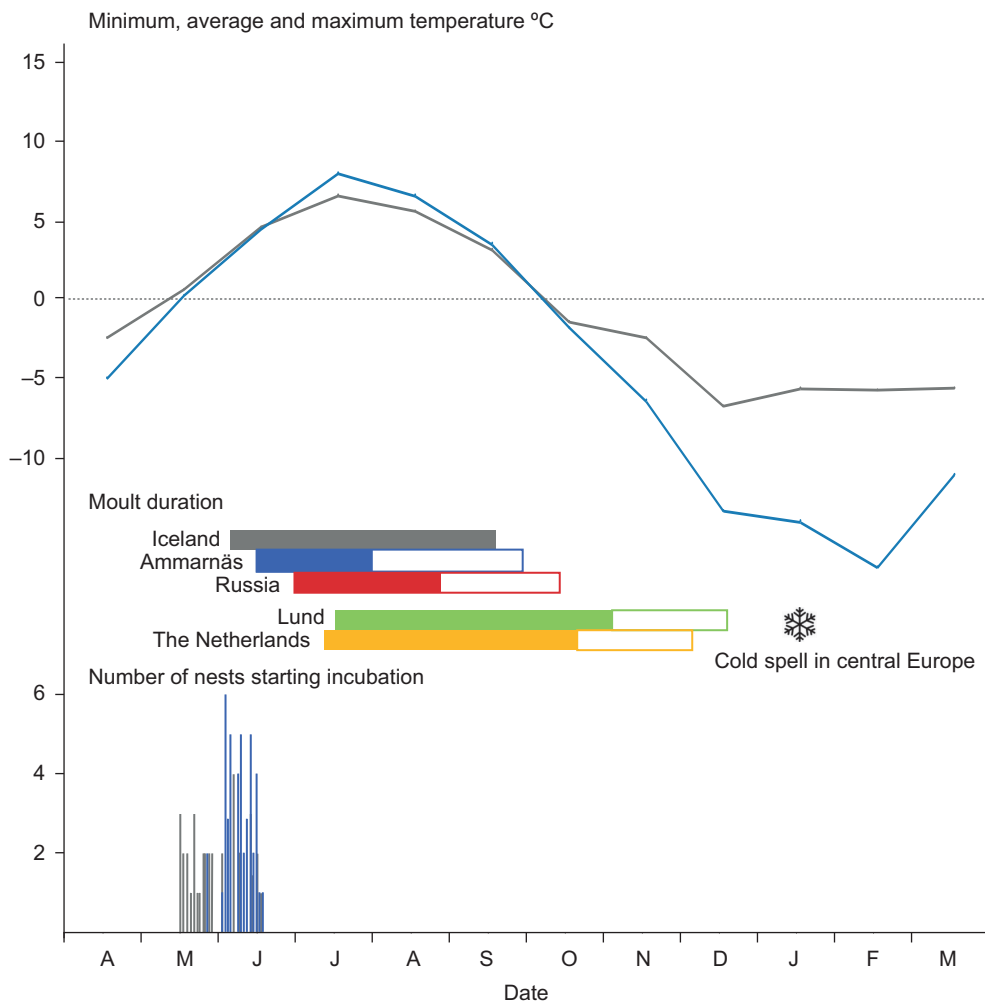


Figure 3. The timing of the start of incubation (vertical bars), timing of moult (horizontal bars), and temperature over time, for two breeding sites of golden plovers. Filled bars show the duration of moult as estimated for every region, transparent bars show hypothetical scenarios of moulting all feathers at that region. Grey = Iceland, blue = Ammarnäs, N Sweden, red = Russia, green = Lund, S Sweden and yellow = the Netherlands. Temperatures come from the closest weather stations to the breeding sites, Boskjö for Ammarnäs and Staðarhóll for Iceland from <www.smhi.se> and <www.vedur.is> open climate data. Snow flake shows the mean cold spell in central Europe.

(Table 3) suggest that at both locations the birds were able to meet the combined daily energy expenditure of incubation and growing primary feathers, among other activities.

At the golden plover's subarctic breeding grounds access to food is facilitated by almost 24-h of daylight during the breeding period. Golden plovers share incubation efforts, thus each sex would have plenty of time to forage between incubation bouts (Steiger et al. 2013). At the same time, golden plover chicks are precocial and forage on their own a few hours after hatching (Cramp and Simmons 1983). Energy expenditure of parents guiding independent chicks might be low enough to enable the adults to moult the primaries. This might be very different for adults provisioning altricial chicks, which might be the main reason why most birds moult only after their offspring has fledged.

Differences in timing of moult between males and females

In Ammarnäs and in Iceland, females started moult nine days later than males. This is explained by the fact that the females spend a lot of energy on producing a clutch (Carey 1996), which prevents them from starting the moult at the same time as males (Newton 2008). It is unknown whether the females are able to 'catch-up' with the males, either by moulting faster or longer at the breeding area, or by moulting faster at the stopover sites, or whether their moult will lag behind until completion.

Timing of moult is controlled by hormones. High levels of the sex-hormones prolactin and testosterone inhibit moult (Dawson 2004). Secretion of prolactin is controlled by increasing photoperiod at the beginning of the nesting season, and birds usually start to moult in response to a post-breeding decrease in the level of prolactin (Dawson 2006, 2008). A high level of testosterone can also prevent moult until gonadal regression (Dawson 1994, 2004). However, parental behaviour may affect the levels of the sex-hormones, and thus timing of moult (Dawson 2008). If the level of prolactin decreases soon after mating, this would allow birds to start moulting during incubation. Females laying eggs might retain high level of prolactin, causing a delay in the onset of moult compared to males.

Migration and moult

A small sample of golden plovers tracked by geolocators from Ammarnäs revealed that continental breeding birds make a stopover in autumn in S Scandinavia (Denmark) and the Netherlands, before moving to their final wintering areas (Machín et al. 2015). Thus, the data collected on moult of golden plovers in S Sweden near Lund (Lindström et al. 2010) and in the Netherlands (Jukema et al. 2001) seems representative for this population, although birds with a more eastern breeding origin might also occur at these sites (Jukema et al. 2001). If the data collected in Ammarnäs and Russia is combined with the data collected in S Sweden and the Netherlands (Fig. 3) a picture arises suggesting that the

continental birds initiate their primary moult at the breeding grounds but complete it at the S Scandinavian and Dutch stopover sites. Combining the moult data for Russian birds with those from the three other continental sites resulted in a better fit of the moult models than when only the N Scandinavian breeding birds were considered. It remains unknown what the exact ratio is at the stopover and wintering sites between birds with a Scandinavian and Russian breeding origin, mainly because of uneven ringing and recovering efforts for these populations. However, as the estimates for the start and duration of moult differed by only three days, an effect of a possible skewed proportion of Scandinavian to Russian birds is believed to be very small.

The first step of the Scandinavian plovers' autumn migration is a few hundred kilometres, which the birds cover in one-two days (Machín et al. 2015). The question arises whether these plovers interrupt their moult for this relatively short migratory flight, or whether they continue primary moult and thus migrate while still moulting actively. The latter is observed in another continental short-distance migrant, the common snipe *Gallinago gallinago* (Minias et al. 2010, Podlasczuk et al. 2017). In S Sweden a few birds with suspended moult were captured (Fig. 2). This was observed also in a small proportion of golden plovers with suspended moult in a more extensive dataset from the Netherlands (Jukema unpubl.) and in a sample of plovers shot in Denmark. The birds from Sweden had suspended their moult at a later stage than we would expect for N Scandinavian breeding birds. On the basis of these data and observations, it is impossible to draw a conclusion about whether the Scandinavian plovers interrupt their primary moult for the migratory flight or not.

Golden plovers moulted their primary feathers almost two times faster in S Sweden and the Netherlands compared to Ammarnäs (Table 3). This could be an effect of the fact that in Ammarnäs the birds overlap breeding and moult, and thus have to divide energy resources between these two activities. It should be noted here that during the stopovers, the plovers did not overlap energy-demanding activities as the birds only started to take on fuel after primary feather moult had been completed (Lindström et al. 2010). The agricultural areas in S Sweden and the Netherlands where the plovers stop over seem to provide favourable feeding conditions due to a high abundance of earthworms (Lindström et al. 2010). Russian birds moulted at an intermediate rate compared to birds from Ammarnäs and S Sweden and the Netherlands. This could be explained by the fact that this sample included both breeding and non-breeding birds.

Different moult strategies of different plover populations

The golden plovers breeding in Iceland replaced all primaries before autumn migration. These birds spend about half a year at the breeding grounds, from early April to September, which is much longer than the four months the continental birds spend at their breeding grounds. A longer season of mild weather in Iceland enables the plovers not only to

start breeding earlier there but also stay longer and moult all primary feathers. However, the fact that these golden plovers show the largest overlap between moult and incubation suggests there is little leeway in this schedule of completing moult at the breeding grounds. In other words, the advantage of completing primary moult at the breeding grounds comes at the cost of a larger overlap between moult and incubation. Golden plovers have a relatively long incubation period (30 d) among Palearctic waders (Cramp and Simmons 1983), which might be another factor contributing to their tight seasonal schedule and consequently an overlap between moult and incubation.

Would it be possible for continental breeding birds to moult all primary feathers at the breeding grounds? Take the hypothetical case of a plover moulting all primary feathers in Ammarnäs. If we assume it takes 100 d to complete moult (duration of moult for the Icelandic birds), this bird would finish around the end of September/beginning of October. This is about the time that the temperatures drop to freezing point in Ammarnäs (Fig. 3). Thus there would be no time left to feed up for the first stage of migration, because fuelling rates of the plovers during stopover in S Sweden were about 0.5% of LBM d⁻¹, thus gaining about 25% of LBM would require 50 d (Lindström et al. 2010). It should be noted that food availability had decreased dramatically already at the end of July (Machín et al. 2017), thus completing flight feathers moult at the breeding ground certainly only seems a hypothetical case.

Would it be possible for continental breeding birds to moult all primary feathers at the stopover sites in S Sweden or the Netherlands, i.e. not to moult primary feathers at the breeding ground at all? If we again assume that primary feather moult takes 100 d, a bird that moulted all primary feathers in Lund would not finish until mid- to end-December (Fig. 3). Cold spells in NW Europe are common in late December, but might occur earlier. Again, this would leave no time for fuelling for the next stage of migration. Golden plovers only leave the stopover sites when a cold spell occurs (Machín et al. 2015), but they should be ready to flee already by the end of October.

Thus it seems that the only option the continental golden plovers have is to adopt a strategy of split moult, i.e. to start to moult in the breeding area, and to complete moult during the stopover in S Sweden or the Netherlands. The overlap between moult and incubation suggests that with this strategy there is also little leeway in the schedule. Total moult duration was estimated to be 116 d for the continental plovers; thus it seems that split moult takes more time than moulting all feathers at one location (moult took 100 d for the Icelandic birds), possibly because the birds suspend or slow down moult during migration.

We conclude that in the golden plover the scheduling of the primary feather moult is determined by conditions at the breeding grounds (the length of the summer season) as well as the migration strategy (cold-spell movements). Also in the Pacific golden plover *Pluvialis fulva*, the scheduling

of primary feather moult seems determined by migration patterns (Jukema et al. 2014). Pacific golden plovers breeding in Alaska make long transoceanic flights to nonbreeding destinations on the Pacific Islands. These birds almost always postpone the initiation of primary moult until they reach their winter quarters. Pacific golden plovers breeding in Siberia spend winter in E Asia, which they can reach by shorter migratory flights over land. These birds instead start primary moult in the breeding areas.

Our results show that for the Icelandic and continental breeding populations of golden plovers it is crucial to 'be at the right place at the right time' (Leyrer 2011). Meeting the energy demands of breeding, moult, and migration calls for different timing and spacing of these events in their annual cycle, adjusted to conditions at their breeding and stopover sites, and to their migration strategy.

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Supplementary material (Appendix JAV-01709 at <www.avianbiology.org/appendix/jav-01709>). Appendix 1.