Paula Machín

a golden life

Ecology of breeding waders in low Lapland

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CHAPTER 1

Introduction

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Arctic ecosystems

Waders form a characteristic and dominant part of the arctic breeding bird communities (Wetlands International 2012). In summer, these charismatic birds exploit a short but intense peak of food supply (Alerstam et al. 2003, Schekkerman et al 2003). However, at high latitudes, the breeding season is notably short, thus the birds need to adapt to tight schedules, with little leeway to deal with delays or set-backs (Newton 2008). Environmental and feeding conditions in the Arctic are too harsh to survive the winter (although there are some exceptions, see Ruthrauff et al. 2013), and therefore most waders have adopted migratory lifestyles, making long migrations, regularly even to southern hemispheres, to spend the winter (Piersma et al. 1996b, 2003).

Annual variation in the breeding success of waders in the Arctic is relatively well-studied. Breeding success of waders in the Arctic and Subarctic is influences by a plethora of factors (Figure 1). The main causal factors are believed to be predation by mammals and birds, and the extent of snow cover / timing of snow melt (Meltofte et al. 2007b).

Breeding success varies with the abundance of predators and their alternative prey (i.e. rodents and lemmings) (Rybkin 1998, Ims et al. 2013). The latter is known as the ‘alternative prey hypothesis’ (Roselaar 1979, Summers 1986, Underhill et al. 1993, Ebbinge and Spaans 2002, Quakenbush et al. 2004, Perkins et al. 2007), which states that predators forego to depredate wader nests when alternative prey are abundant. Consequently, breeding success of waders is high when predator numbers are low, but also when lemming/rodent numbers are high. Lemmings/rodent numbers fluctuate in a cyclic fashion with a period of 3-5 years. Predators abundance follows lemming/rodent fluctuations and normally peak the year after a lemming/rodent peak year. The second year after a lemming/rodent peak predator numbers are often very low.

Another factor that affects breeding success of arctic breeding waders is snow cover (Meltofte et al. 1981, Reneerkens et al. 2016). The amount of snow and timing of snow melt varies between years, which in combination determines the extent of the area covered by snow at the start of the breeding season. In a late year, when a large area of the tundra is still covered by snow at the beginning of the breeding season, waders delay breeding or even forego breeding at all (Meltofte et al. 2007b). Large snow cover area could also increase predation risk, especially in the beginning of the season, since birds will nest in the few snow free patches, and thus nests will be relatively easy to locate for predators (Byrkjedal 1980, Meltofte et al. 1981).

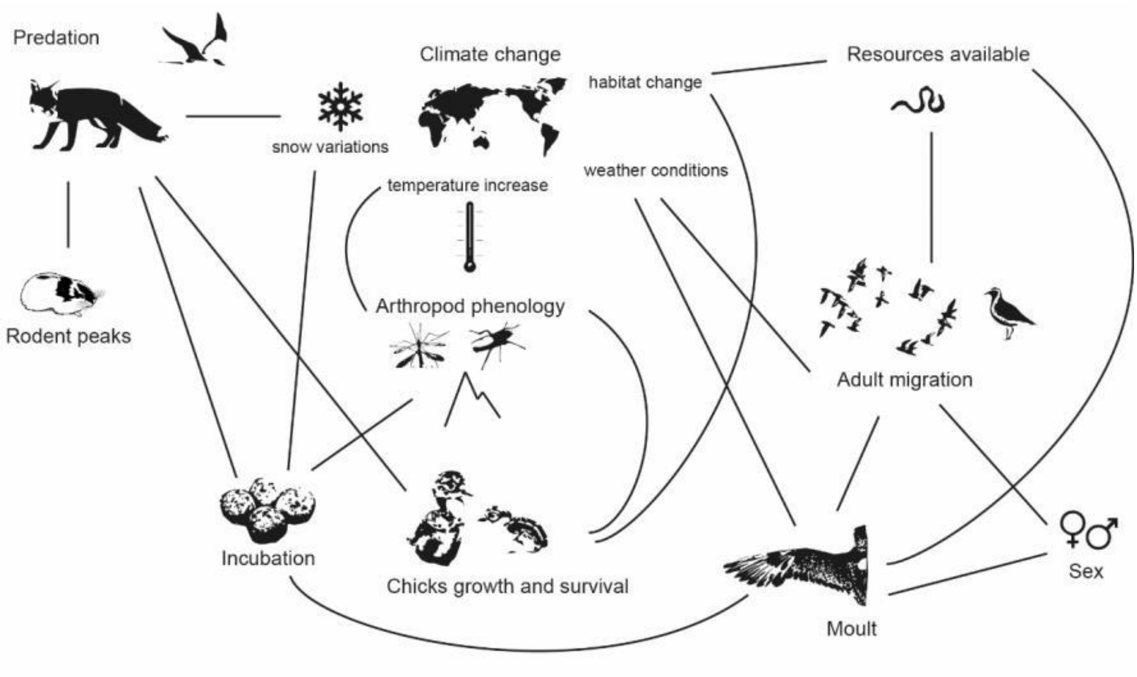

Figure 1. Environmental and biotic factors that influence on the performance of each stage of the life cycle of a Golden Plover.

Arctic ecosystems are believed to be sensitive to global warming due to humanity-induced climate change (Callaghan et al 2011), because (1) a relatively large change in temperature is predicted for these areas, and (2) one degree of warming has a much larger impact in the Arctic compared to temperate areas (IPCC 2014). The two most important negative effects of climate warming possibly are habitat change and a mismatch between the timing of nesting and the timing of the food peak (Saino et al. 2011). The latter occurs when the phenology of insects advances more rapidly than the phenology of nesting, for example because the waders are constrained by their spring migrations to arrive earlier at the breeding grounds (e.g. see Tulp and Schekkerman 2008). Both the change in weather conditions and the mismatch with food availability have direct negative consequences on the growth and survival of wader chicks (Schekkerman 1998, 2003, 2004, Pearce-Higgins et al. 2010, Kentie et al. 2013, Meltofte et al. 2007a, Tjørve et al. 2007)

However, arctic breeding waders might also benefit from climate warming because of a longer breeding season, creating leeway in their breeding period (Rehfisch and Crick 2003), higher prey abundance (Holmes 1966, Holmes & Pitelka 1968) or lower thermoregulatory costs (McKinnon et al 2013). Thus, the exact outcome of climate change on waders remains uncertain.

The Subarctic

The Subarctic is the climate zone immediately south of the Arctic (Geiger 1954). It is similar to the Artic in many aspects, such as darkness during most of the winter and snow cover for most of the year. Even the food web is very similar between arctic and subarctic ecosystems, with regular rodent and predator cycles (Hansson & Henttonen 1985, Hörnfeldt et al. 2005). Just as for the Arctic, waders are a dominant species group of the breeding bird community in the Subarctic. The main differences between the Arctic and Subarctic are that the Subarctic knows a longer growing season and higher temperatures during summer (Geiger 1954). A longer growing season might be beneficial for breeding waders as it creates some extra time to complete a breeding season, so that the Subarctic might accommodate species with relatively long breeding cycles. Greater proximity to the temperate wintering grouns, i.e. shorter migration distances, might be another advantage for waders breeding in the Subarctic.

Despite the fact that the Subarctic hosts a large number and variety of waders (e.g. Lindström et al. 2015 for Scandinavia), relatively little is known about their ecology. In fact, one could argue that arctic breeding waders have been studied more extensively than subarctic birds. The lack of information on the breeding ecology of subarctic breeding waders is of concern, as we have no idea how future climate change might affect these wader populations.

Effects of climate change might generally be similar for subarctic and arctic ecosystems, i.e. impact of climate warming might be relatively large, conform the idea of arctic amplification (Sukyoung 2014). One important difference is that in the Subarctic, tundra habitats are located on mountains, with birch forest habitats in the valleys. One effect of climate warming is the altitudinal shift of the tree line, resulting in the retraction of alpine tundra habitat (Kullman 2001, 2002, IPCC 2014). Furthermore, climate models predict relatively large increases in precipitation for the Subarctic (Popova 2004, IPCC 2014), and thus more now fall in winter (Serreze et al. 2007). It is difficult to predict how the breeding seasons of waders will look in the future, but a likely scenario is that there will be shorter but warmer snow-free summer periods. As knowledge on the breeding ecology is lacking, we cannot foresee how these changes would affect wader populations.

The annual cycle of migratory waders

Migration enables birds to exploit short temporal peaks in food abundance for breeding in areas that are unsuitable during the non-breeding season because of severe winter weather conditions (Alerstam 1999). There are three main energetically demanding phases in the annual cycle of a bird: breeding, migration and moult. Spring migration is scheduled in such a way that birds arrive at the breeding grounds to maximally benefit from the short but rich food supply (McNamara et al. 2011). Many waders are income breeders, meaning that they rely on local resources for the production of their eggs, and thus need some time between arrival and egg-laying (Klaassen et al. 2001, Morrison and Hobson 2004). This contrasts with 'capital breeders' like geese and ducks, which bring along resources for breeding from spring staging or even wintering sites (Bety and Hobson 2003). There is a short time window for incubation and chick rearing, and the birds generally have no leeway for a second breeding attempt in case the first attempt fails. Waders are precocial, i.e. chicks leave the nest a few hours after hatching. Chicks immediately forage on their own, but in order to retain homeostasis they need to be brooded regularly by their parents during the first weeks of their lives (Visser & Ricklefs 1994). Post-breeding migration is scheduled way before the conditions at the breeding grounds deteriorate and become too harsh to survive. Migrant waders normally moult during the non-breeding season, before or after autumn migration, to avoid overlapping of two energetically demanding activities (Ginn & Melville 1983, Newton 2009). However, some species, because of their tight annual schedules, do overlap moult with breeding and/or migration (Figure 2). Knowledge on the annual cycle of migrants provides insights in the ecological requirements of the species throughout the year, and enables to identify possible temporal and energetic bottlenecks (Buehler & Piersma 2008). Hence, it is important to not only conduct detailed studies on specific aspects of behavior, but to also place results within an annual cycle perspective (Marra et al. 2015).

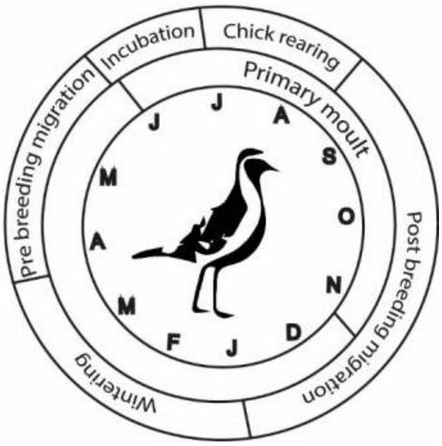

Figure 2. Example of schedule of the annual cycle of a Golden Plover from Ammarnäs population.

Aims and approach

Three main threats of climate change for migrant waders have been identified (Meltofte et al. 2007b, Sutherland et al. 2016): (1) habitat loss, for example through sea-level rise (Purkey & Johnson 2010) and latitudinal and altitudinal treeline migration (Soja et al. 2007, Sjögersten & Wookey 2009), (2) food web changes, in particular an increase in predators (and thus predation rates), related to the increase in rodent numbers (Krebs et al. 2002), and (3) trophic mismatches, in particular the mismatch between timing of breeding and peak food availability (McKinnon et al. 2012). In this context, detailed ecological knowledge of the species life cycles is required, but such data are unavailable for most species of conservation concern.

We recognized that especially waders breeding in the Subarctic remain understudied, thus the general goal of our study was to improve our knowledge on the ecology of waders breeding in the Subarctic. We focussed on two key life-history phases, incubation and chick rearing, as these are the two main drivers of reproductive output in waders (Roodbergen et al. 2012). The first aim was to describe the nesting success of waders in relation to environmental conditions like abundance of predators, abundance of alternative prey (lemmings and rodents), and weather conditions (e.g. snow cover). The second aim was to describe the ecology of the chicks, i.e. what they eat, their habitat use, and their growth, again in relation to environmental conditions (food abundance in different habitats, weather). Subsequently, we aimed to put these results in an annual cycle perspective, by describing the annual cycle, i.e. when the species moult and migrate. Finally, we aimed to make a comparison between waders breeding in the Arctic and Subarctic, highlighting differences and similarities.

To learn more about the ecology of waders breeding in the Subarctic, we studied waders in the Vindelfjällen Nature Reserve, Ammarnäs, Swedish Lapland, a typical subarctic breeding site, from 2009-2013. For the study on nesting success we made a general annual survey of the study area, locating as many wader nests as possible, and recording the fate of these nests at regular intervals. For this particular study, also data from 2008 collected in the area was used. At the same time abundance of predators, lemmings and rodents, and weather variables including snow cover were recorded. For the studies on the ecology of chicks, we focussed on one wader species, the Eurasian Golden Plover (*Pluvialis apricaria*) (hereafter: Golden Plover).

This study focused on Golden Plover because (1) it is representative for subarctic waders and does not occur in the Arctic, (2) it is a common species in the study area and thus a sufficient number of chicks could be studied, (3) it is a relatively large species, with chicks large enough to carry radiotransmitters, which was essential to be able to follow individual chicks during their development, (4) it is a species that is relatively easy to observe on the relatively open tundra habitats, and (5) the species has been studied rather intensively during the non-breeding period at stopover and wintering sites (Jukema 1982, Kirby and Lack 1993, Kirby 1997, Byrkjedal and Thompson 1998, Gillins et al. 2007, Jukema et al. 2001, Piersma et al. 2003, Lindström et al. 2010). This gave me the opportunity to study moult and migration of the Golden Plover. When studying moult, we included information from other breeding areas, Iceland and Russia, as this helped us to understand the timing of moult in the annual cycle of the Scandinavian plovers. For the comparison between arctic and subarctic waders, we reviewed the literature, extracting information about nesting success, chick growth, and moult.

Study area

Figure 3. Image from the study area

Ammarnäs is a small village located in southern Lapland, Sweden (65º57'N; 16º13'E) (Figure 3, 4), and lies in the middle of the vast Vindelfjällen Nature Reserve. This reserve was established in 1974, and is the largest protected area in Sweden covering 5500 km^2. Within the reserve different types of habitats are found, ranging from coniferous forest to high alpine tundra. The area is a Special Protected Area (SPA) for birds under the EU Birds Directive, as well as a designated Important Bird Area (IBA) according to Birdlife International (BirdLife International 2017).

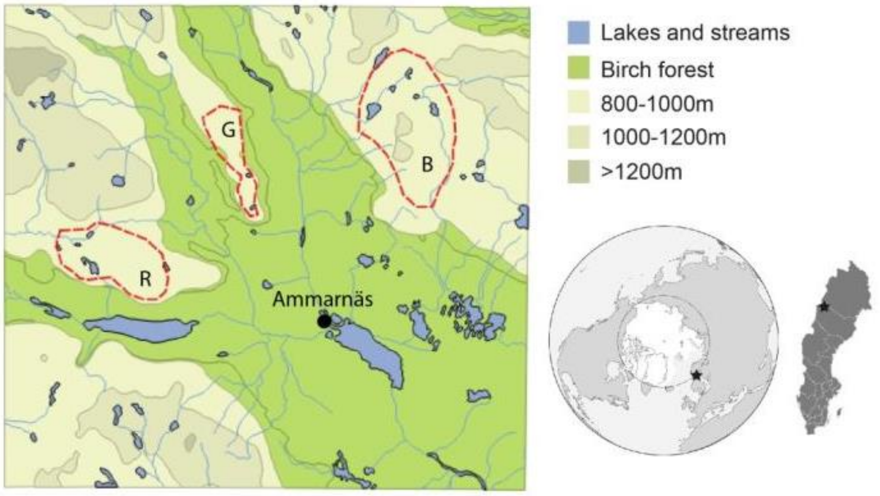

Figure 4. Location of the study area, and a map indicating main habitats. Location of the three main study plots are indicated by red lines. The most western area (R), is the Raurejaure area, the study plot where the in-depth studies on the Golden Plovers were conducted. The other study areas are Gelmetje (G) and Bjorkfjället (B).

Field work was conducted in the lower alpine zone, at altitudes ranging between 800 and 1000 m a.s.l., in three study plots (Figure 4). These areas are characterized by low Arctic mountain heath tundra above the birch zone with a high proportion of lakes, mires and areas with standing and running water (Svensson & Andersson 2013). Areas are largely snow covered from October/November until the beginning of May. The timing of snow melt varies between years. For example, 2009 was a relatively early year, when snow started to melt on the 8th of May. 2012 was a notably late year with snow melt starting on the 25th of May. In summer (May–August), average daily temperatures are relatively high, and varied between 8.1^{o} in 2012 and 10.7^{o} in 2013. The study area is notably wet during the breeding season. Mean rainfall fluctuated between 64.3 mm in 2012 to 82.64 mm in 2009.

Four main habitat types can be distinguished, heathland, willow shrubs, alpine meadow and wet areas. Heathland is a habitat characterised by mosses and lichens, and plants as *Betula nana*, *Empetrum nigrum Vaccinium myrtilllus* and *Salix herbaceae*. Willow shrubs are dominated by *Salix lapponum*, but also other willow species such as *Salix glauca* and *Salix lanata* are found. Alpine meadows are dominated by grasses such as *Deschampsia flexuosa*, *Anthoxanthum odoratum* and *Rumex acetosa*. Wet areas comprise of rich fens, vegetated with *Carex* species and mosses, often interspersed by small patches of *Salix lapponum*.

Breeding birds

The breeding bird community of the Vindelfjällen Nature Reserve has been studied since 1963 by the LUVRE project of the Lund University, Sweden (www.luvre.org). In total, 12 species of waders breed regularly in the area. Population trends are stable to positive (Table 1). The species with highest densities are Dunlin *Calidris alpina*, Golden Plover *Pluvialis apricaria*, Red-necked Phalarope *Phalaropus lobatus* and Redshank *Tringa totanus*. Other species present in lower densities are Temminck´s Stint *Calidris temminckii*, Ruff *Philomachus pugnax*, Ringed plover *Charadrius hiaticula*, Common snipe *Gallinago gallinago*, Dotterel *Charadrius morinellus*, and then there are other species present in very low numbers, with only a few pairs as Whimbrel *Numenius phaeopus*, Wood sandpiper *Tringa glareola*, Purple sandpiper *Calidris maritima*, Broad- billed sandpiper *Limicola falcinellus*, Common sandpiper *Actitis hypoleucos*.

Table 1. Number of nests found in each species during all years of study and population trends in breeding waders in the Vindelfjällen Nature Reserve (1972-2011) (data from Svensson & Andersson 2013).

Number of nests								**Population trend 1972-2011**	
Species	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**Total**	**Trend**	**p**
Broad-billed Sandpiper *Limicola falcinellus*		1		2		1	4		
Common Sandpiper *Actitis hypoleucos*	1	1					2		
Common Snipe *Gallinago gallinago*	3	4	3	1	1		12	0.9909	ns
Eurasian Dotterel *Charadrius morinellus*				1		1	2	1.0112	ns
Dunlin *Calidris alpina*	29	39	49	50	26	28	221	1.0292	<0.01
Golden Plover *Pluvialis apricaria*	19	35	43	60	36	37	230	1.0181	<0.01
Purple Sandpiper *Calidris maritima*		1					1		
Red-necked Phalarope *Phalaropus lobatus*	2	10	9	11	11	12	55	1.0189	ns
Redshank *Tringa totanus*	3	11	10	16	13	8	61	1.0532	<0.01
Common ringed Plover *Charadrius hiaticula*	1	2	2	1	2	3	11	1.0384	<0.01
Ruff *Philomachus pugnax*	1	7	4	11	5	7	35	0.9934	ns
Temminck's Stint *Calidris temminckii*	1	3	8	3	7	4	26	0.9926	ns
Whimbrel *Numenius phaeopus*		1					1	1.0453	<0.01
Wood Sandpiper *Tringa glareola*		1			1		2	1.0683	<0.01
Total	**60**	**116**	**128**	**156**	**103**	**101**	**664**		

During our own studies (2008-2013) a total of 664 wader nests of 14 species were located (Table 1). Most nests found were of Golden Plover, which is caused by them being the focal study species but also the most common one. The number of nests found varied between years because of nest searching effort (e.g. lower effort in 2008) and predation rates (i.e. high predation rates in 2012).

Lemmings and rodents

Two rodent species occur in the alpine tundra habitats in the study area, the Norwegian Lemming *Lemmus lemmus* and the Field Vole *Microtus agrestis*. Both species fluctuate in numbers in a 3-4 year cyclic fashion (Ecke and Hörnfeldt 2017. During the study period, a strong peak in lemming and vole numbers occurred in 2011 (chapter 2). This was the first lemming outbreak since the early 1980ties.

Predators

The two main mammalian predators occurring in the study area are Red Fox *Vulpes vulpes* and Stoat *Mustela erminea*. Red Foxes were observed on many occasions during fieldwork. Stoats were only seen occasionally. Although Wolverine *Gulo gulo* and Arctic Fox *Alopex lagopus* occur in the nature reserve, we have no indications that they occurred in our study area during the study period. Long-tailed skua *Stercorarius longicaudus* and Raven *Corvus corax* are the two most common avian predators. The number of breeding skuas fluctuated in concert with the number of lemmings and voles.

Golden Plover

Golden Plovers have a western Palearctic distribution. They breed in tundra habitats in the UK, Scandinavia and Russia. They are migratory, spending the winter in temperate coastal areas as the Netherlands and UK, and in southern Europe or eventually Morocco. Golden Plovers are renowned for their cold-spell movements, i.e. birds wintering in Western Europe are pushed southwards when cold fronts arrive (Jukema & Hulscher 1988).

The Golden Plover is the most abundant wader species in the study area. In the main study plot, the Raurejaure area, about 50 pairs occur. Golden Plovers are generally site faithful (Byrkjedal & Thompson 1998), something we could confirm on the basis of colour-ringed birds. 60-80% of adults came back each year to the same breeding area. Additionally, in 2012, two local recruits of chicks ringed in the previous year were recorded.

Golden Plovers are relatively easy to study as they occur in open tundra habitats, thus it is easy to observe the birds. Finding nests, however, was a challenge, especially because the plovers either remained at their nest relying on their camouflage, or left the nest from a large (500 m) distance. The latter birds often approached the observers, continuously calling their melancholic alarm calls. Most nests were found by chance walking through the area and many were found watching birds returning to their nest after they were flushed due to a disturbance (for example a second observer walking though the study plot).

Both parents incubate the eggs (Byrkjedal & Thompson 1998). Incubation takes a mean of 30 days. On the basis of sexual differences in plumage, where males have darker face and belly plumage than females, we could infer that generally males incubate during the day and females during the night. After chicks have hatched, both parents guide and brood the chicks for a few weeks. However, females desert the brood when the chicks are about three weeks old, leaving all parental care to the male. Chicks fledge at a mean of 30 days old.

During the study period, a total of 169 chicks and 71 adults (46 males and 25 females) were captured. Adult females tend to be slightly larger than adult males (Table 3).

Table 3. Biometry of adult Golden Plovers trapped in Ammarnäs. Table provides mean values (in mm) and standard deviation.

	Male	**Female**
Wing	188.9 ± 5.1	191.0 ± 3.4
3rd PP	126.1 ± 3.4	126.1 ± 4.0
Tarsus	41.1 ± 1.4	41.2 ± 1.4
Tail	73.3 ± 2.9	73.4 ± 2.7
Bill skull	29.1 ± 1.9	29.2 ± 1.5
Bill head	59.1 ± 5.3	59.5 ± 1.3
Bill feathers	22.3 ± 1.0	22.2 ± 0.9
Bill height	7.0 ± 0.4	7.0 ± 0.5
Bill width	5.1 ± 0.4	5.2 ± 0.4
Weight	187.2 ± 8.9	193.0 ± 10.4

Outline of the thesis

This thesis consists of five chapters on the ecology of waders breeding in the Subarctic. The first chapter, a general analysis of nest survival, includes information on different species. The subject of the other, more specialized chapters, is the Golden Plover. The order of the chapters follows the annual cycle of a migrant wader species; nesting (chapter 2), chick rearing (chapter 3-4), moult (chapter 5), and migration (chapter 6). The thesis is concluded with a synthesis on the differences between Arctic, Subarctic and temperate zones on some of the aspects underlined in the chapters before (chapter 7).

Chapter 2: Nest survival

The abundance of predators and their alternative prey (i.e. rodents and lemmings) have a dominant effect on nesting success of waders breeding in the Arctic. In addition, late snow melt (large snow cover) can enhance predation rates as nests are easier to locate in snow-free patches. Late snow melt also delays the start of incubation, which might cause problems to complete the whole breeding cycle during the short breeding season (Meltofte 2007). Less is known about nesting success in subarctic areas. In chapter two, we describe the breeding performance of four wader species breeding in the Subarctic during six years (2008-2013) in relation to the abundance of predators, lemming and rodents, and in relation to annual variation in snow cover.

Chapters 3 & 4: Chick rearing

The chick rearing period is one of the main drivers of reproductive output in waders (Meltofte et al. 2007), but it is also one of the life cycle stages least studied in detail in northern areas (with some memorable exceptions as Tulp 2007, Tjorve 2007, Tjorve et al. 2007,2009). The main aim of chapter three was to describe how Fennoscandian Golden Plover chicks use their environment by studying habitat use, diet and prey availability. The importance of food availability and weather on the survival and growth of the chicks was described in chapter four.

Chapter 5: Moult

Animals must fit different activities within their annual cycle, such as breeding, migration and moult. Species are flexible in the timing of moult, i.e. some moult after the breeding season, others during migratory stopovers, and others again during the winter period (Newton 2009). Species generally avoid overlapping moult with other energy demanding activities such as breeding and migration, as this would form a temporal or energetic bottleneck (Buehler & Piersma 2008). Studying differences in moult strategies between populations that perform different migration strategies helps to understand the organisation of the migrants' annual cycle. In chapter five, we compare moult patterns of two Golden Plover populations, one that breeds in Iceland and migrates to Ireland and West Britain, and one continental that breeds in northern Sweden and northern Russia and migrates to Western Europe and eventually to southern areas as southern Spain and Morocco.

Chapter 6: Migration

Waders breeding in the Arctic and Subarctic spend the winter at more southern latitudes as environmental conditions at the breeding grounds in winter are too harsh to be able to survive. In chapter six the migration pattern of a sample of Fennoscandian Golden Plovers is described. This study provides an annual cycle perspective of this subarctic breeding wader, which helps to understand the factors influencing the organisation of the species' annual cycle.

CHAPTER 2

On the role of ecological and environmental conditions on the nesting success of waders in Subarctic Fennoscandia

Paula Machín, Juan Fernández-Elipe, Johannes Hungar, Anders Angerbjörn, Raymond H. G. Klaassen, Jose I. Aguirre

Waders that breed in the Subarctic are one of the groups most threated by environmental change induced by climate change. At the same time, wader breeding success seems to vary annually in concert with fluctuations in numbers of predators and rodents (an alternative prey for the predators). How climate change could influence the food web interactions remains poorly studied. In this study we analysed the effects of ecological (e.g. vole/lemming and predator abundance) and environmental factors (e.g. snow cover) on the breeding success of waders in Subarctic low Lapland. We monitored more than 500 wader nests during six breeding seasons. During this period a full rodent cycle occurred, which enabled us to record wader breeding success during rodent crash to peak years. In addition, in one year snow melt was exceptionally late occurred. Surprisingly, nest predation rate, and thus wader breeding success, did not correlate with predator or rodent abundances. However, predation rate was exceptionally high in the year with the late snow melt. If indeed more precipitation resulting in late snow melt is the outcome of climate change in this region, rodent and predator numbers might fluctuate attending to these conditions and dictate wader breeding success also in the Subarctic in the future.

Submitted to Polar Biology

Introduction

Effects of climate change on ecosystems have been studied all-over the world (Walther et al. 2002, Rosenweig et al. 2007, Walther 2010). However, climate change scenarios indicate that global warming is expected to be most pronounced, both in absolute and relative terms, in the Arctic and Subarctic (IPCC 2014). In addition to temperature, changes in precipitation could also play an important role (Callaghan et al. 2011). This might be especially true for Arctic and subarctic ecosystems where an increase in precipitation means an increase in snow depth and snow cover (Popova 2004, Serreze et al. 2007). Effects of an increase in temperature could even been offset by effects of an increase in precipitation (snow), and one possible outcome of climate change could actually be a shorter snow-free period during a warmer summer (Radionov et al. 2004).

Climate change scenarios predict an increase in precipitation (IPCC 2014). Indeed, a long-term increase in snow depth has been observed for the Arctic and Subarctic (Callaghan et al 2011). These predictions and observations are supported by statements by Sámi reindeer shepherds from northern Sweden (Callaghan et al. 2010, Riseth et al. 2010). They for example have stated that "terrain elements that determined animal movements in the summer are now snow covered: reindeer now find new passes and roam over a wider area", "snow-covered areas and snow patches persist longer into the summer in high mountain areas", and "rapid thaws created problems when moving to summer grazing areas in 1938–1940".

In order to understand how climate change will affect arctic and subarctic ecosystems, it is thus essential to also study effects of an increase in precipitation (snow) in addition to effects of an increase in temperature. Waders are a prominent and characteristic species group of Arctic and subarctic ecosystems, and could be considered sentinels of changing ecosystems (Piersma & Lindström 2004, van Gils et al. 2016). Waders are expected to be sensitive to variation in snow cover as they have a limited time window for reproduction in these latitudes. A shorter growing season in connection to increasing in winter snowfall could be limiting for wader populations. It is therefore important to establish the relationships between snow cover and key annual cycle events such as the timing of the onset of incubation.

In addition, wader nesting success highly depends on predation (MacDonald and Bolton 2008). For waders breeding in the Arctic, it is well-established that nesting success is shaped by regular fluctuations in the number of voles/lemmings and predators (Meltofte et al. 2007). Many predator species take advantage of the cyclic small mammal populations, e.g. Arctic fox (*Alopex lagopus*), red fox (*Vulpes vulpes*), rough legged buzzard (*Buteo lagopus*) and mustelids. These predators can also switch from feeding on voles and lemmings when these are abundant to prey species such as waders, “the alternative prey hypothesis” (Roselaar 1979, Summers 1986, Underhill et al. 1993, Ebbinge and Spaans 2002, Quakenbush et al. 2004, Perkins et al. 2007). However, little is known about how predator-prey multi-specific relationships are affected by variation in snow cover (Gilg et al. 2009).

In this study we describe nesting success of waders breeding in subarctic southern Lapland in 2008-2013, in relation to variation in ecological (e.g. vole/lemming and predator abundance) and environmental conditions (e.g. snow cover). We describe how the timing of nesting (onset of incubation) and predator-prey relationships are affected by snow cover, providing new insights in how wader nesting success could develop under climate change scenarios.

Materials and methods

Fieldwork was conducted in the Vindelfjällen Nature Reserve (65°57' N and 16°12' E) during breeding seasons of 2008-2013. The area is a Special Protected Area (SPA) for birds under the EG Birds Directive (Natura 2000), as well as a designated Important Bird Area (IBA) (BirdLife International 2017). Almost the whole reserve lies within the alpine zone. The area is treeless above 800 m altitude, and characterized by tundra habitats such as dry heath, grass heath, dry fen, rocks and firn (Staafjord 2012). Within the nature reserve, we covered three different subareas (Björkfjället, Gelmetje and Raurejaure) located near the village Ammarnäs. The total area of the study area measures about 60 km^2.

Daily temperature data and information on snow cover were obtained from the nearest weather station in Boksjö, located 36 km south of the study area, at 470 m a.s.l. (Swedish Meteorological and Hydrological Institute, SMHI). In 2012, almost the whole area was still covered by snow upon arrival to the study area in the beginning of June. Therefore, in 2012, we estimated snow cover for the three subareas at each visit. In the other years snow cover was not estimated by us, since the area was not covered by snow upon arrival.

In the area, the main rodent species are the Norwegian Lemming *Lemmus lemmus* and the Field Vole *Microtus agrestis*. Their numbers fluctuate in cycles of about 3 to 5 years (Angerbjörn et al. 2001). Data on the abundance of voles and lemmings were obtained from the project "Environmental monitoring of rodents" from the Swedish University of Agricultural Sciences (www.slu.se/mo-smagnagare). Data is collected as density index based on captures performed two times per year, one in spring and another one in autumn. In Ammarnäs, a total of 2200 traps are used, at a rate of 50 traps per ha, and the total area covered is 40 ha.

Red Fox and Stoat *Mustela erminea* are the main mammalian predators of wader nests in the study area, and responsible for the great majority of predation events. Avian predators are Long-tailed Skua *Stercorarius longicaudus* and Common Raven *Corvus corax*. In a pilot study in 2011, when a number of automated trail cameras were placed near Golden Plover nests, two nests were depredated by Long-tailed Skuas, one by a Common Raven and one by a Red Fox. In addition, the cameras registered four predation events by Reindeer *Rangifer tarandus*. The latter occurred mainly when Reindeer herds gathered in high densities in the east of the Raurejaure area.

Data on the abundance mammalian predators were obtained from the Wildlife Triangle Scheme (Stoessel et al. 2017). This scheme comprises of snowtracking surveys that are conducted in March and April following Lindén et al. (1996). The number of tracks of predators were surveyed along transects in the shape of triangles, with a total length of 12 km (4 km per side of the triangle). Triangles were located in treeless tundra throughout the nature reserve. The exact same triangles were surveyed throughout the study period. Surveys were performed in good snow and weather conditions from a snowmobile. In order to ensure only fresh tracks were counted, surveys were timed the day after old tracks were erased by snowfall or wind (Lindén et al 1996). For each track, the species was identified and the exact location of the track was recorded by a handheld GPS-device. A track index was calculated for each year, as the mean number of recorded tracks of predators per triangle per year. For this study, we only used the data for three triangles located near the study area. Data on the abundance of Long-tailed Skuas were obtained from the LUVRE monitoring scheme (www.luvre.org).

Wader nests were searched in areas holding high densities of breeding waders according to the long-term LUVRE-project (www.luvre.org). These areas host relatively high densities of Dunlin *Calidris alpina*, Golden Plover *Pluvialis apricaria,* Red-necked Phalarope *Phalaropus lobatus* and Redshank *Tringa totanus*. Other species present in the area were Temminck´s Stint *Calidris temminckii*, Ruff *Philomachus pugnax*, Ringed plover *Charadrius hiaticula* and Dotterel *Charadrius morinellus*. Nests were located by following adults back to the nest, or by "rope-dragging" (Labisky 1957). For completed clutches, hatching dates were determined by the egg flotation method of Liebezeit et al. (2007). For incomplete clutches (i.e. found during laying period) hatching date was simply determined by adding the length of the incubation period (20 days for Red-necked Phalarope, 21 days for Dunlin and Temminck's Stint, 22 days for Ruff, 24 days for Common Redshank, 28 days for Golden Plover, cf. Harrison and Castell 2004).

Nests were checked every two to four days (occasionally nest visit were delayed up to seven days) until hatching or until the nest was preyed on or abandoned. Nests were considered still being active when the eggs were warm, but considered abandoned when the eggs were cold during two consecutive visits. Nests were considered as predated when eggs had disappeared before the estimated hatching date. Nests were considered as successfully hatched when the chicks were found in or close to the nest, or when there were clear signs of hatching (small egg fragments in nest, egg cap near the nest).

Daily predation rates (DPR) were calculated using the Mayfield method (Mayfield 1961, 1975), where the daily predation rate is defined as the probability for any nest to be predated on a single day. A species was only included in the analysis if at least five nests were found in that particular year.

Results

Weather and timing of incubation

Spring temperature (mean temperature during April and May) was low in 2012 (0.5 degrees), moderate in 2008 and 2010 (2.1 and 1.7 degrees, respectively) and high in the other years (>3 degrees). 2010 and 2012 were years with relatively a lot of snow (Figure 1), but only in 2012 a large part of the study area was still covered with an extensive amount of snow (>50%) upon arrival of the waders. On the 15th of June of that year, the subareas were still covered by 76% (Björkfjället), 40% (Gelmetje) and 68% (Raurejarure) (Figure 2).

A positive linear relationship existed between the timing of the start of incubation and the snow depth in spring (mean for April and May) (F=107.48, df=1, p=<0.001). The start of incubation was delayed by about two weeks in 2012, the year with the largest amounts of snow (Figure 1). Timing of the start of incubation differed also significantly between the species (F=3.32, df=3, p=0.02), with Dunlin breeding relatively early, and Red-necked Phalarope relatively late (Figure 1).

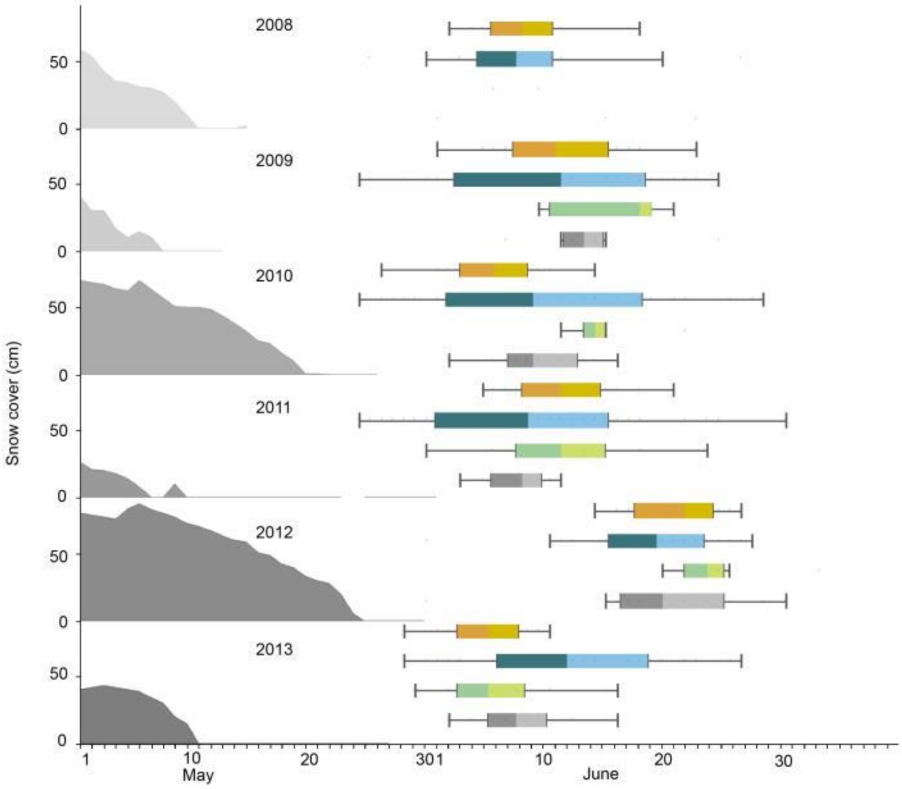

Fig 1. Snow cover in relation to breeding dates of each species for each year of study. Colors correspond to different species: orange= Golden Plover, blue= dunlin, green= red-necked phalarope, grey=redshank

Number of nests preyed in proportion with active nests during the first two weeks of incubation was very high for 2012, resulting in 32% of nests being preyed upon (Figure 2). It followed 2008 with 23%, 2013 and 2009 with 16%, 2011 with 13% and 2010 with 9% of nests ended by predation. The depredated proportion of nests decreased generally with time of season in all years combined (t=-1.67, df=42, p=0.10), with 2008 and 2012 showing significant negative seasonal trends (2008: t=0.01, df=6, p=0.01and 2012: t=-2.58, df=5, p=0.05).

Annual variation in predation rate

The numbers of voles and lemmings peaked in 2007 and 2011 (Figure 3). Lemming numbers in 2011 were actually the highest since 1980. Lemming and vole numbers were very low the years after the peak years, in 2008-2009, and 2012-2013. In 2008 lemming numbers crashed in early spring before the monitoring of rodents was conducted. Mammalian predators were abundant after the vole and lemming peak years, in 2008-2009 and 2012-2013. Also in 2011 a relatively large number of predator tracks were found. 2010 was the year with the least mammalian predators in the study area. The number of breeding pairs of Long-tailed Skua varied between the years, with 17 breeding pairs in 2007, 30 in 2008, none in 2009, 22 in 2010, 56 in 2011, none in 2012, 2 in 2013, 17 in 2014 and 39 in 2015.

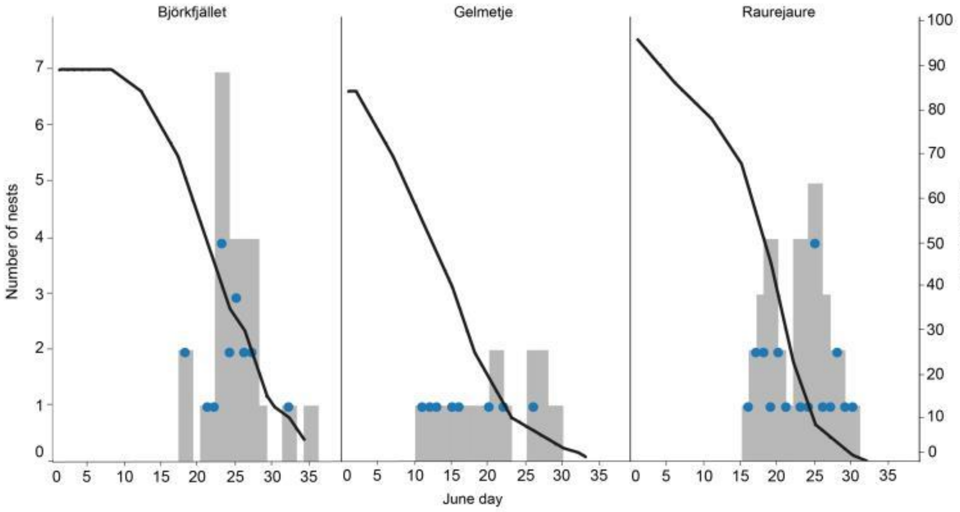

Fig 2. Number of nests starting incubation in each day in all subareas. Line refers to percentage of snow cover in the area (every visit estimate), grey bars are number of nests starting incubation and blue dots refers to number of nest that were preyed on.

Daily predation rates (DPR) of wader nests strongly varied between years and was lowest in 2011 and highest in 2012 (Figure 3, 4). Predation rate also vary between species, with Golden Plovers having relatively high predation rate in all years, and Redshanks relatively high predation rate in 2012-2013. 2012 was the only year in which the waders started to breed when a large part of the study area was still covered by snow (Figure 2). Predation rates were especially high during the first weeks of incubation: 32% of nests were preyed in 2012, compared to 15.4 % in the other years, this difference being significant (t=-1.67, df=42, p=0.10).

When analysing the relation between average predation rate per year and abundance of rodents (Figure 4), we did not find a significant correlation when accounting for all years (t=-1.00, df=4, p=0.37), or when excluding 2012 (t=-1.16, df=3, p=0.32). The relation between average DPR and predators in the area was also not significant when excluding the atypical snow year of 2012 (t=0.49, df=3, p=0.65), but it was slightly significant when including all years in the analyses (t= 2.78, df=4, p=0.049) (Figure 4).

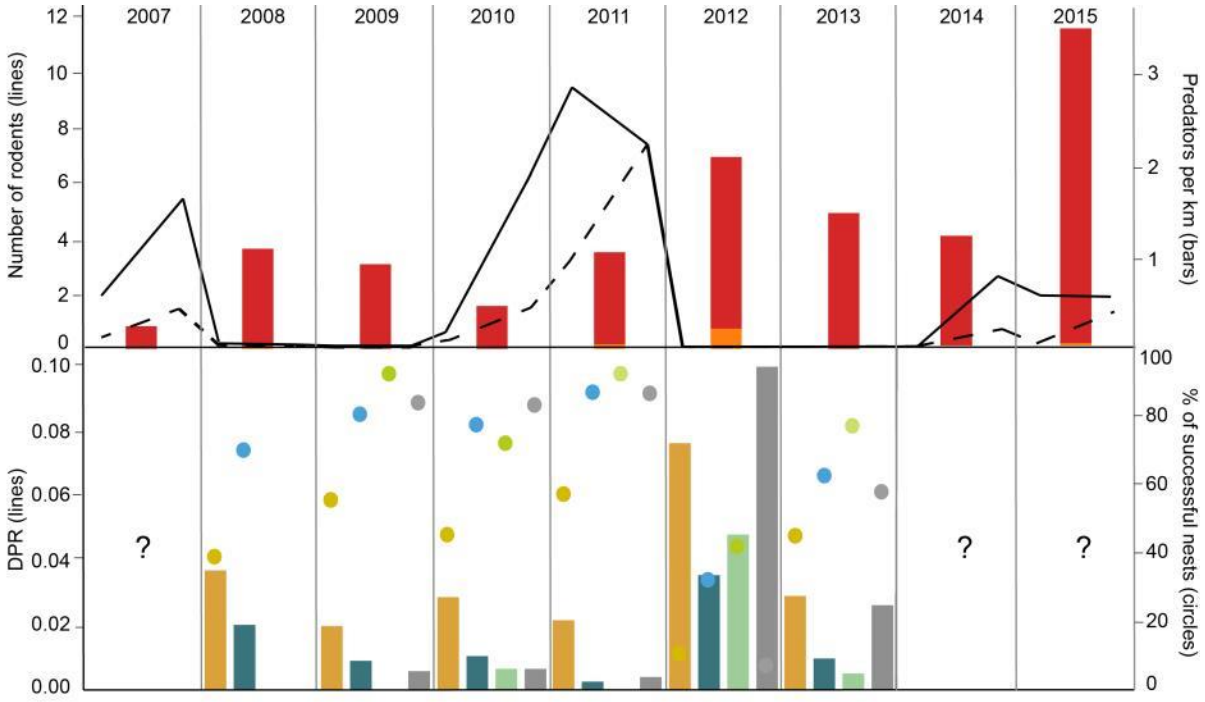

Fig 3. Abundance of rodents (upper lines, full corresponds to field voles and dash line to Norwegian lemmings) and predators (upper bars, red represent red foxes and orange stoats) Mean DPR (lower bars) and percentage of successful nests (lower circles) for each year and period and species. Colors correspond to different species: orange= Golden Plover, blue= dunlin, green= red-necked phalarope, grey=redshank.

Number of hatchlings differed between years and species. For every species 2012 was the year with the least hatchlings per pair (Table 1).

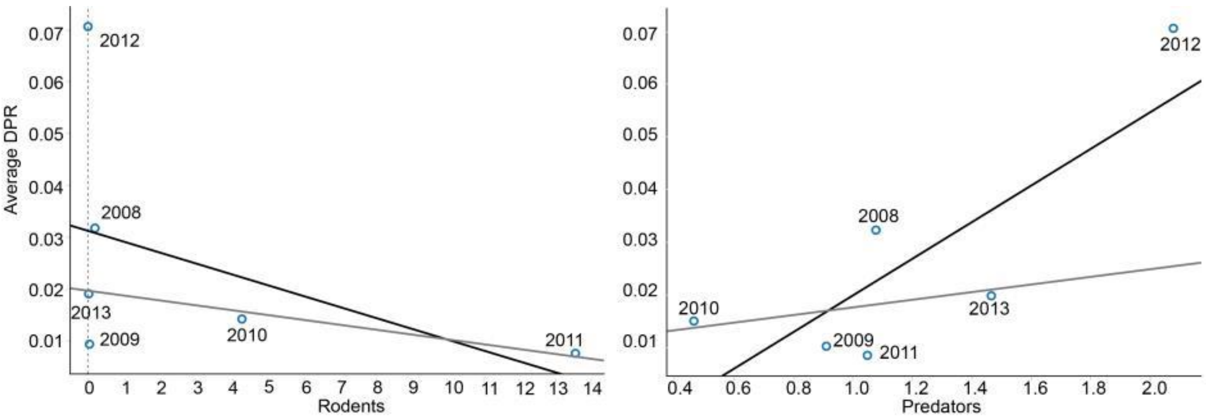

Fig 4. Correlation between average Daily Predation Rate of the main four species each year vs rodents (left) and vs predators (right). Black lines refer to regression lines including all years, and grey lines are regression lines excluding the exceptional year of 2012.

Table 1. Number of hatchling per pair for the different species in each year. Sample sizes are denoted between brackets (number of pairs).

Species	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**Total**
Dunlin	2.52	2.97	2.84	3.48	1.19	2.64	2.78
	(29)	(39)	(49)	(50)	(26)	(28)	(192)
Golden Plover	1.16	2.09	1.53	2.25	0.25	1.11	1.54
	(19)	(35)	(43)	(60)	(36)	(37)	(211)
Red-necked Phalarope	-	3.8	1.56	2.91	1.45	3.08	2.58
		(10)	(9)	(11)	(11)	(12)	(53)
Redshank	-	3.55	3.6	3.19	0.31	2.38	2.57
		(11)	(10)	(16)	(13)	(8)	(58)

Discussion

Although Fennoscandian alpine tundra habitats support large numbers of breeding waders (Lindstöm et al. 2015), wader breeding ecology is relatively understudied for the Subarctic, In this study, nesting success of waders breeding in subarctic southern Lapland was monitored during six years (2008-

2013). This included a full cycle of rodent numbers, and one season with an exceptionally high snow cover during early spring. critical, as

Climate change scenarios predict warmer summers but also more precipitation (Radionov et al. 2004). The latter would mean in subarctic areas an increase in snow depth and snow cover, and consequently a shorter breeding season (Callaghan et al. 2011).In fact, 2012 may be exemplary how future breeding seasons could look like, as this was a year with exceptional large amount of snow during winter, which resulted in the study area being still snow covered at the beginning of the breeding season. Late snow melt had a clear effect on the timing of breeding of the waders. In 2012, the start of incubation was delayed by about two weeks compared to the other seasons. Also for waders breeding in the Arctic a clear relationship between snow cover and timing of breeding was found (Meltofte et al. 2007b).

In the high Arctic, nesting success of waders is strongly shaped by the regular fluctuations in the abundance of predators and rodents (voles and lemmings) (Rybkin 1998, Ims et al. 2013). Predators heavily feed on wader eggs except when rodents are abundant. This prey-switching behaviour, with rodents being preferred, is known as the alternative prey hypothesis (Roselaar 1979, Summers 1986, Underhill et al. 1993, Ebbinge and Spaans 2002, Quakenbush et al. 2004, Perkins et al. 2007). However, here we showed that wader breeding success is not correlated with lemming or predator abundances, at least when excluding the exceptional breeding season of 2012 (see above). Instrumental in this respect is 2011; despite high lemming numbers (highest numbers since 1980), predation pressure was still relatively high for Golden Plover, and very comparable to the other years. One possible explanation for the difference between arctic and subarctic ecosystems could be that the Red Fox is now present in the Subarctic, being one of the main predators in the study area (Angerbjörn et al. 2013, Elmhagen et al. 2015). Here, the Red Foxes could move downwards into the valleys when prey is scarce at the tundra, which might completely change the predator-prey interactions. This contrasts to the Arctic where the Arctic Fox is the main predator, and they cannot easily switch to a different habitat when rodents are scarce at the tundra, forcing them to focus on wader nests.

2012 was an exceptional year when we could see the devastating effects of late snow melt on nesting success. At the beginning of the season, when few snow free patches were available for nesting, wader nests were easily found by the relatively many predators present in the area. Consequently, in 2012 nest predation rates were exceptionally high and considerable less chicks managed to fledge compared to other years. Predation pressure was especially high during the first two weeks of the breeding season, and much higher than in any other season.

Nesting success may become more strongly dependent on the lemming-predator cycle if snow cover is high, i.e. a situation more similar to high Arctic areas. To test this hypothesis also data on nesting success would be required for years with a late snow melt and a high abundance of predators and rodents, in order to see whether the alternative prey hypothesis applies in such situation. In this temporal series we have studied, we lack an important event; a late snow melt season with increasing or intermediate lemming abundance. We presume this event will have obvious consequences in the start of breeding of waders and probably will have higher predation rates, as shown in Meltofte et al. (1981), high snow cover in the beginning of the season despite a high lemming density resulted in high predation. However, if the snow event happens after a lemming crash year with also lower numbers of predators, the effects of predators will probably not be high.

Although 2012 may seem an exceptional year, 2015 was similar in snow conditions and it had even more predator numbers. It is important to note, that numbers of predators in 2015 were probably that high thanks to the accumulative survival rates from the very beneficial years of 2011-2012.

It is the question whether all species could deal with the scenario of a shorter snow-free period during a warmer summer (Radionov et al. 2004). For example, Golden Plovers have a relatively long breeding period, partly because of a long incubation period (Byrkjedal and Thompson 1998), and they might no longer be able to fit their breeding in a shorter season. In addition, higher temperature might change the phenology of the insects (Tulp and Schekkerman 2008), and it is unclear how this would affect chick condition and survival (Machin et al. 2018).

Differences in predation rate between species are observed in this study. Golden Plover is the most intensely depredated nesting species every year except for 2012. It is also the only species that breeds in heathland. This type of habitat might be the easiest to search by foxes and other predators, due to an open vegetation structure.

An increase in precipitation due to global climate change resulting in a later snowmelt, might thus be detrimental for these characteristic wader populations. However, we also suggest that a late snowmelt might change the interactions between waders, predators and their alternative prey (rodents), which makes it very difficult to predict the exact outcome of global climate change. We recommend running a long-term monitoring scheme of wader breeding success in place in order to better understand how the ecological and environmental interactions will change over time.

Acknowledgements

This research would had been impossible without the continuous encouragement of Martin Green and Åke Lindström. LUVRE project support us economically during the six years. We thank especially Rob van Bemmelen for all the help and support during the fieldwork campaigns. During the six years of work many people have been involved with this project. Thanks to all for many shared moments in the cold and sometimes too hot tundra.

Compliance with Ethical Standards

- Funding: Accommodation at Vindelfjällen Research Station and travel expenses were covered by the LUVRE-project (Lund University).

- Conflict of Interest: The authors declare that they have no conflict of interest.
- Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The fieldwork was carried out under permits from the Lund/Malmö Ethical Committee for Animal Experiments (M160-11, M27-10, M33-13).

CHAPTER 3

Habitat selection, diet, and food availability of European Golden Plover *Pluvialis apricaria* chicks in Swedish Lapland

Paula Machín, Juan Fernández-Elipe, Heiner Flinks, Maite Laso, Jose I. Aguirre, Raymond H. G. Klaassen

Fennoscandia alpine tundra habitats host large numbers of breeding waders, but relatively little is known about their breeding ecology, despite the fact that this habitat is threatened by climate change. We studied habitat selection, diet and prey availability of European Golden Plover chicks at the Vindelfjällen Nature Reserve, Ammarnäs, Sweden. Information from 22 chicks tracked using radiotransmitters was analysed. By analysing 149 faeces samples four main prey taxa were identified, Coleoptera (40 %), Bibionidae (31 %), Hymenoptera (13%) and Tipulidae (10 %). We found that plover chicks switched from feeding on Tipulidae to feeding on Bibionidae, and that this switch coincided with a shift from the use of the habitat where Tipulidae were abundant (Alpine meadow/ Heathland) to the use of the habitat were Bibionidae were abundant (Willow shrub). Although chicks track food availability to some extent, the link between prey availability and habitat use was not perfect, indicating that additional factors other than food abundance determine habitat selection (e.g. shelter from predators). Bibionidae are an important prey for the plover chicks as it is the only prey group that has a late summer flush in abundance, in contrast to the general decline of total arthropod biomass during the chick rearing period. However, Bibionidae imagoes only occurred in 2011 and were virtually absent in 2013, which relates to the species' ecology with 2-5 year cycles in mass occurrence. Extreme annual variation in an essential food source such as Bibionidae imago might have an important effect on the condition and survival of Golden Plover chicks, which is an important subject for future studies. We suggest that the foraging conditions for Golden Plover chicks in Fennoscandia are different compared to the UK where the chicks rely mainly on a Tipulidae flush only.

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Introduction

Effects of global climate change on species and ecosystems are diverse, in which birds have provided many of the biological examples now underpinning the evidence for climate change (Walther *et al.* 2002, Parmesan & Yohe 2003). Of particular concern are Arctic ecosystems, not only because of disproportional warming of these areas (IPCC 2007), but also as a few degrees of warming is expected to have much larger effects in these relatively cold environments compared to temperate and tropical climates (IPCC 2007). The Arctic forms the breeding range of a large number of wader species, and three different types of threats of climate change have been identified for this characteristic group (Meltofte et al. 2007b, Sutherland et al. 2012): (1) habitat loss, for example through sea-level rise (Purkey & Johnson 2010) and latitudinal and altitudinal treeline migration (Soja et al. 2007, Sjögersten & Wookey 2009), (2) food web changes, in particular an increase in predation rates related to the increase in rodent numbers (Krebs *et al* 2002), and (3) trophic mismatches, in particular the mismatch between timing of breeding and peak food availability (McKinnon *et al*. 2012). Given the multifaceted effects of climate change with direct, indirect, time-lagged, and nonlinear effects, it is difficult to make reliable inferences about consequences of (future) climate chance and to, ultimately, manage climate change effects. Detailed ecological knowledge on the vital phases of species' life cycles is required, but, disturbingly, such data are unavailable for most species of conservation concern.

The European Golden Plover *Pluvialis apricaria* (hereafter Golden Plover) is a characteristic breeding wader of open moorland, mountain heaths, alpine tundra and arctic tundra, with a breeding distribution ranging from Iceland/northern United Kingdom, Fennoscandia, to eastern Siberia (Byrkjedal & Thompson 1998). Golden Plovers are believed to be sensitive to climate change because climate warming has a negative effect on the abundance of a key prey species, Crane Flies (*Tipulidae*) (Pearce-Higgins 2010, Carroll *et al*. 2011), as well as on the extent of breeding habitat (Soja *et al*. 2007). Virtually all the information we currently have on the breeding ecology of Golden Plovers comes from the UK (e.g. Ratcliffe 1976; Whittingham *et al*. 1990, 2000, 2001, Pearce-Higgins & Yalden 2003, 2004, Douglas & Pierce-Higgins 2014) whereas information from for example the large Fennoscandian population is surprisingly scarce (Byrkjedal 1980, Byrkjedal & Thompson 1998). Similarly, conservation actions to manage effects of climate change have been designed based on specific problems identified for the UK. This raises the basic scientific question how representative the knowledge obtained for a certain study location is for other areas throughout the species' breeding range, especially in the case different countries and populations are involved. In particular, do Golden Plovers breeding in Fennoscandia have a similar breeding ecology and face the same problems as the birds in the UK? There clearly is a need for comparative studies throughout the breeding range.

Inspired by the detailed ecological studies on the breeding ecology of Golden Plovers in the UK (Whittingham *et al* 2001; Pearce-Higgins & Yalden 2004), we set out to study the breeding ecology of Golden Plovers at a core breeding population in Fennoscandia. We particularly focused on the chick phase as it is a critical phase in the waders' annual cycle, and an important factor explaining current declines of wader populations (Roodbergen *et al*. 2012; Kentie *et al*. 2013). The reason to focus on Fennoscandia was that it hosts large numbers of breeding waders (Svenson 2013; Lindström *et al*. 2015) whereas basic information about their breeding ecology such as habitat selection, diet, and food availability is lacking. At the same time, the alpine tundra habitats where these birds occur in Fennoscandia are expected to decline in extent as well as deteriorate in quality as a result of climate warming (see Moen *et al.* 2004; Sjögersten & Wookey 2009), which makes this ecosystem of great conservation concern.

The main aim of the study was to describe how Fennoscandian plover chicks used their environment by studying habitat use, diet and prey availability. As the ecological circumstances are similar to the UK, thus we expect Tipulidae form an important part of the chicks' diet, in addition to Coleoptera and Arachnida, and that the chicks select habitats with higher Tipulidae densities (i.e. tracking food abundance, cf. Whittingham *et al* 2001, Pearce-Higgins & Yalden 2004). In addition, we investigated whether there could be a potential for effects of climate change for our Fennoscandian study population by looking at seasonal availability of (main) prey in relation to the phenology of the plovers' breeding season. In seasonal environments it is essential for birds to synchronize their breeding with peaks in food availability (McKinnon *et al.* 2012). A common effect of climate warming is that species advance in their phenology, but as the magnitude of this advancement often varies between trophic levels, a mismatch between peak occurrence of the prey and peak requirements of the predator can occur (Both & Visser 2001, 2005, Both *et al.* 2006). Such mismatch was found in some wader species nesting in the High Arctic in the sense that the chicks hatched too late to profit from the peak in arthropods they rely on (McKinnon *et al.* 2012, see also Tulp & Schekkerman 2008) but not for Golden Plovers breeding in the UK (Pearce-Higgins *et al.* 2010). The latter was the result of a relatively moderate advancement of the timing of Tipulidae mass occurrence, which was even smaller than the magnitude of the advancement of laying dates in the Golden Plovers (Pearce-Higgins *et al.* 2005). Assuming ecological circumstances are similar between the UK and Fennoscandia, we expect no mismatch for our study population.

Materials and methods

Study syte

The study was performed in the breeding seasons of 2011 and 2013 at an area of 24 km^2 in the Vindelfjällen Nature Reserve, located next to a small village called Ammarnäs, in southern Lapland in Sweden (65° 59′ N, 15° 57′ E). The study area was visited also in 2012 but as nest survival was extremely low due to a combination of late snow melt (Machin 2012) and high nest predation rates, it was impossible to study the ecology of plover chicks in that year (only one chick hatched from 21 nests located). The area is a Special Protected Area (SPA) for birds under the EU Birds Directive as well as a designated Important Bird Area (IBA) according to BirdLife International. It is characterized by open low Arctic mountain heath tundra above the birch zone from 800 till 1000 m.a.s.l. with a high proportion of lakes, mires and areas with low standing and flowing water (Svensson and Andersson 2013) (see Table 1 for more information about the habitat).

The study area is largely covered by snow from October/November till the beginning of May.

The date of snow melt varies between years. In 2011 and 2013, extensive snow melt started almost at the same date, on the 10th and 9th of May, respectively. During the breeding season (May – August), average daily temperature was similar between years (10.0ºC in 2011 and 10.3ºC in 2013). The study area is notably wet during the breeding season. Mean rainfall varies between years, but, again, was fairly similar in 2011 and 2013, with 75 mm and 62.5 mm rain recorded during the two seasons, respectively.

The Golden Plover is the most abundant wader species breeding in the study area, at about 3 pairs per km^2 (LUVRE survey, Å. Lindström, Lund Univ., Sweden, personal information). Other waders as Dunlin *Calidris alpina* and Redshank *Tringa totanus* are also quite common. Temmink Stint *Calidris temminkii*, Ruff *Philomachus pugnax*, Ringed Plover *Charadrius hiaticula*, Dotterel *Charadrius morinellus*, Whimbrel *Numenius phaeopus*, Red-necked Phalarope *Phalaropus lobatus* and Broad-billed sandpiper *Calidris falcinellus* occur frequently in the area but in lower densities. The most important potential predators of Golden Plover eggs and chicks in the study area are Long-tailed Skua *Stercorarius longicaudus*, Red Fox *Vulpes vulpes* and Stoat *Mustela erminea*. Abundance of predators varies between years, as they mainly depend on cyclic lemming and vole populations. For an overview of the number of breeding birds in the study area see Svensson (2013).

Table 1. Characteristics of dominant habitats in the study area.

	Habitat type			
	Heathland	**Willow shrub**	**Alpine meadow**	**Wet areas**
Dominant plants	Several species of mosses and lichens. Mainly *Betula nana*, *Empetrum nigrum*, *Vaccinium myrtillus*, and *Salix herbaceae*	Mainly *Salix lapponum*, *Salix glauca* and *Salix lanata*	Dominated by grasses: *Deschampsia flexuosa*, *Anthoxanthum odoratum*, *Rumex acetosa*, *Ranunculus acris*, and *Alchemilla glomerulans*	Intermediate rich fens: *Carex rostrate* and mosses. Often combined with small examples of *Salix lapponum*,
Humidity	Dry	Variable, connecting wet and dry areas.	Variable, but wetter than Heathland.	Very wet

Snow	Early snow free	Late snow free	Very late snow free	Late snow free
Other characteristics	Very open areas, mainly slopes and windblown summits	Tight and close structures of difficult access.	Open areas on foot of slopes and ditches.	Low open areas dominated by water at different levels.

Tracking Golden Plover chicks

Golden Plover nests were searched for by walking and flushing incubating birds, by watching (flushed) birds returning to their nest or by flushing birds by dragging a 30 m long rope in between observers over the tundra. The incubation stage of each nest containing eggs was estimated by floating the eggs in water (Liebezeit *et al.* 2007). We increased nest-checking frequency (at least once per day) approaching the expected hatching date to avoid missing freshly hatched Golden Plover chicks, which usually leave the nest within 12-36 hours after hatching (Cramp *et al*. 1983). Chicks were caught on the nest a few hours after hatching and supplied with radio-transmitters (0.75g BD-2 tags, Holohil Systems Ltd, Ontario, Canada, expected lifetime ~4 weeks). As Golden Plover chicks are precocial and difficult to observe or relocate even in low vegetation tundra habitats, radio-transmitters are the best tool to monitor chick movement during the period from hatching to fledging. Additionally, one alphanumeric and one metallic ring were deployed on tarsus to allow individual recognition at distance.

A single chick was tagged per brood. Tags were glued to a small piece of gauze pad that was painted black and yellow to reduce visibility. Subsequently, the pad with the attached tag was glued to the lower back of the chick, with the aerial pointing backwards, using a latex based rubber cement (Copydex TM). Copydex is solvent free (water based) non-toxic glue. The total weight of the rings together with the tag plus attachment and glue was less than 4% of the weight of the hatched chick in all cases. When rump feathers start to grow, which is around an age of 30 days, the pad with attached radiotransmitter falls off with no subsequent harm to the bird.

Radio transmitters were tracked using a receiver (ICOM IC-R20, USA in 2011 and SIKA, UK in 2013) with an external hand-held directional antenna (Televilt, Sweden in 2011 and Yagi, UK in 2013). The radio-tagged chick was relocated the first day after hatching (age=1 day) to ensure that the bird and the attachment were fine, and thereafter every second day during the whole pre-fledging period. Attending to Pearce-Higgins *et al.* 2004, no effects from handling were observed at intervals between 1-4 days and we did not observed effects by handing the bird every second day. To relocate a chick, a triangulation from a larger distance (approximately >100 m) was made first to get a rough idea about the chick's approximate position and subsequently to quickly move towards this position to pinpoint the chick. This approach was adopted in order to avoid chick movement during the search, taking advantage of the innate anti-predator behaviour of Golden Plover chicks to press themselves to the ground and remain motionless as soon as a predator is nearby. Once located, the chick was weighted and measured (tarsus length, bill length, bill head length) as fast as possible, and habitat type (see below) and exact location (GPS position, Garmin-eTrex Vista HCx) were recorded. In a few cases chicks ran away upon approach of the observer (noticed by variation in the strength of the radio signal). In these cases, habitat type and GPS-position were recorded for the location where the chick was originally triangulated.

Habitat mapping

A Google Earth satellite image (© 2015 DigitalGLobe Quickbird 65cm pan-sharpened) was used as a background to create a digital habitat map of the study area. Habitats were mapped using QGIS 2.8.1 software. Initial maps were checked by ground observation and subsequently adjusted. Based on detailed local habitat descriptions by Eknert & Lemby (1991), Mossberg & Stenberg (2008) and Waldemarson (unpublished), four main habitat types were defined (see Table 1): Heathland (including Dwarf Birch-heath, Crowberry-heath, Blueberry-heath, Dwarf Willow-heath and Poor Grassy-heath), Willow shrub (meadow and heather-meadow type), Alpine meadow (grassland areas), and Wet areas (hummock-tussock-bog, raised heath-bog and sedge-brown-moss-fen).

Diet composition of chicks

When relocating chicks, faeces samples were collected by keeping the chick for a maximum of ten minutes inside a rubber cube. Fresh droppings were preserved in the field with a small amount of salt (to prevent bacterial or fungal growth) and later stored in a freezer at -18°C. For examination, a sample was dissolved by soaking it in water for 30 minutes after which arthropod and plant remains were collected on a filter paper. Arthropod remains were analysed under a binocular microscope at 20x to 40x magnification and epidermal tissue of plants at 400x magnification. For every individual sample, a minimum number of individuals was estimated based on the number of arthropod and plant remains (i.e. number of head, mandible, thorax, wing, leg or abdomen remains). Individual length of each prey was estimated using a reference collection from the study plot (cf. below) and information from the literature (Davies 1976, 1977, Calver & Wooller 1982, Ralph et al. 1985, Flinks & Pfeifer 1987, Jenni et al. 1989).

Food availability

Ground-dwelling arthropods were sampled using pitfall traps. These traps consisted of hard-plastic cups (250 ml, upper diameter 8 cm) dug into the ground until ground level, and filled with an approximately 1 cm deep mixture of water, salt and odourless detergent. In 2011, a large number of random points were created and one pitfall was placed at each random point, resulting in having 50 pitfalls in Heathland, 8 in Alpine meadow, 10 in Willow shrub and 7 in Wet areas (see Table 1 for details on habitat types). In 2013, pitfalls were more evenly distributed between habitats, having a total of 32 pitfall traps placed in four different habitats (8 pitfalls per habitat). In 2013 pitfall traps were placed in transects in which the distance between traps was 5 m. Traps were placed as soon as the snow had melted and were removed at the end of the breeding season, from 1 July to 6 August in 2011 and from 11 June to 18 August in 2013.

The content of every individual pitfall trap was collected every two to four days and brought to the laboratory for further processing. Individual arthropods were identified up to family level, and assigned to a size class (≤5 mm, 5-10 mm and ≥10 mm). Samples of individuals of the same families and size classes were stored in a freezer as a reference collection for the analyses of faeces samples (see below).

Analyses

Habitat selection

Home ranges of individual plover chicks were determined by calculating Minimum Convex Polygons (MCP), using all relocations of the radio-tracked chicks. Habitat within this MCP was considered to reflect the habitat availability for each particular chick. Habitat used was calculated by the proportion of each habitat from the total number of locations of the chick. Subsequently, habitat selection of chicks was determined by comparing habitat use with habitat availability (by calculating the Jacobs Index, Jacobs 1974) and by ranking which habitat was preferred over the other (by conducting a compositional analysis, Aebischer et al. 1993). The Jacobs index was calculated according to the formula: $D = (r - p)/(r + p – 2rp)$, where r is the proportion of habitat used and p the proportion of habitat available. D varies from -1 (strong avoidance of that specific habitat) to +1 (strong preference), and values around zero indicate that the habitat is used in proportion to its availability. Compositional analyses were conducted using the R-package AdehabitatHS (Calenge 2006) and differences between habitats were addressed by randomization analyses. Additionally Jacobs index and compositional analyses were performed for two groups of age, below 10 days (5 first location points) and above ten days (the next 5 or more location points).

Diet

To describe the diet of the chicks throughout the season, and for different habitats, the proportion of biomass for the different taxa was calculated per faeces sample by dividing the total biomass of a certain taxa in the faeces by the total biomass of the faeces (sum of biomass for all taxa). This approach was adopted to correct for a natural increase in faeces size with chick age (cf. Pearce-Higgins & Yalden 2004). Proportion of biomass was subsequently modelled in a General Mixed Model (GLMM) with chick ID as a random factor, using a binomial error distribution. Response variable was then the proportion of biomass of each taxa and explanatory variables were habitat, date, chick age and year. For date and chick age also quadratic effects were included in order to allow for possible curvilinear relationships. Bibionidae imagoes only occurred in 2011 and was practically absent in 2013, and larvae were only present in 2013 (see Results). Therefore, after establishing the effect of year, the model was run with the data for only 2011 and 2013, respectively. Analyses were only performed for prey taxa that constituted a minimum of 5% of the diet by biomass, in one or more of the 6-day age classes. Model selection was performed using glmulti package from R software (Calcgno & de Mazancourt 2010). Possible collinearity between the date and chick age were evaluated by the variance inflation factor (VIF). VIF values were lower than 3 in all cases, thus both variables were retained in the analyses (Zuur et al. 2010).

Food availability

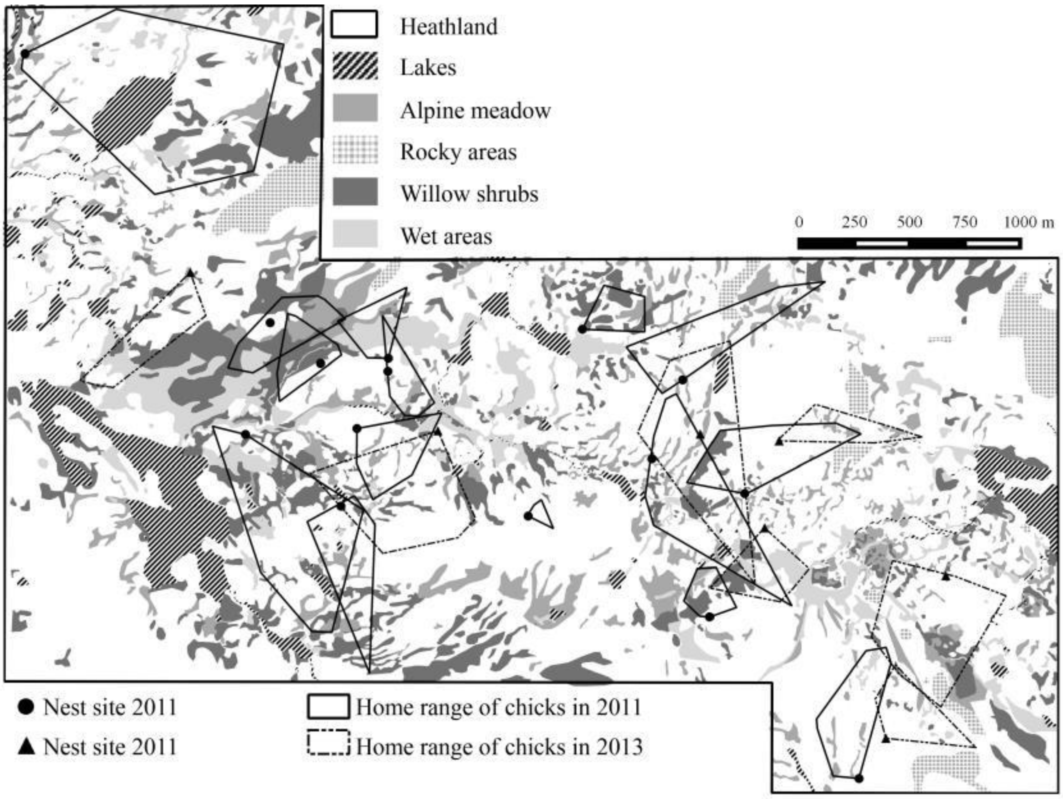
In order to describe the abundance of prey in different habitats, and over time, total biomass of a taxon was calculated per pitfall trap and per sampling occasion. From our own measurements of arthropods, different size classes were created (see food availability in Material and Methods). Afterwards, biomass of individual prey was calculated from its size using a conversion factor suggested by Rogers et al. 1976. Prey abundance was modelled separately for the four representative main (sub)orders: Coleoptera, Hymenoptera, Diptera Nematocera Bibionidae (hereafter Bibionidae) and Diptera Nematocera Tipulidae (hereafter Tipulidae). For Coleoptera, only families that were considered suitable prey for the Golden Plovers (i.e. were found in the faeces samples) were included, therefore Carabidae, Staphylinidae, Byrrhidae and Curculionidae, and the families Dysticidae and Silphidae were excluded since they were not present in the faeces samples. The relationship between arthropod biomass, habitat type and date was analysed using a GLM, including the interaction between habitat type and date. Data were transformed in order to meet model assumptions (i.e. Levene´s and Non-additivity tests originally failed) following Little and Hills (1978). For the orders Coleoptera and Tipulidae, a power transformation performing a regression of the logarithms of the variances versus the logarithms of the means of the original data, was used. There was no need of data transformation for Bibionidae and Hymenoptera. If for a certain habitat and sampling event, data from less than three pitfalls was available (because pitfalls were trampled by Reindeer Rangifer tarandus, got flooded, or had a Norwegian Lemming Lemmus lemmus carcass in or next to the cup), this data point was removed. Differences of abundance measured as biomass in habitat types were subsequently analyzed using a Tukey HSD test.

Results

Habitat selection

A total of 32 chicks were radio-tagged. Data from ten chicks were discarded for further analysis on habitat location as too few positions were obtained (5 chicks in 2011 and 5 in 2013), either because the chick dropped the radio-transmitter (n = 3), the chick was found dead (n = 5), or the chick was predated (n = 1). Additionally, data from one tagged chick were discarded as it had moved outside the study area at an age of 10 days. The final dataset consisted of 22 Golden Plover chicks, 15 in 2011 (number of locations varied from 5 to 16, mean = 12.2, median = 13) and 7 in 2013 (number of locations varied from 7 to 16, mean = 11.5, median =11). Home ranges (minimum convex polygons) varied in size, ranging from 0.034 to 0.640 km2 (MCP area is not correlated with maximum age of the chick F = 0.53, df = 1, 17 P = 0.478). Interestingly, the position of the nest was always at the edge of the home range, except in the case of one home range in 2013 (Figure 1).

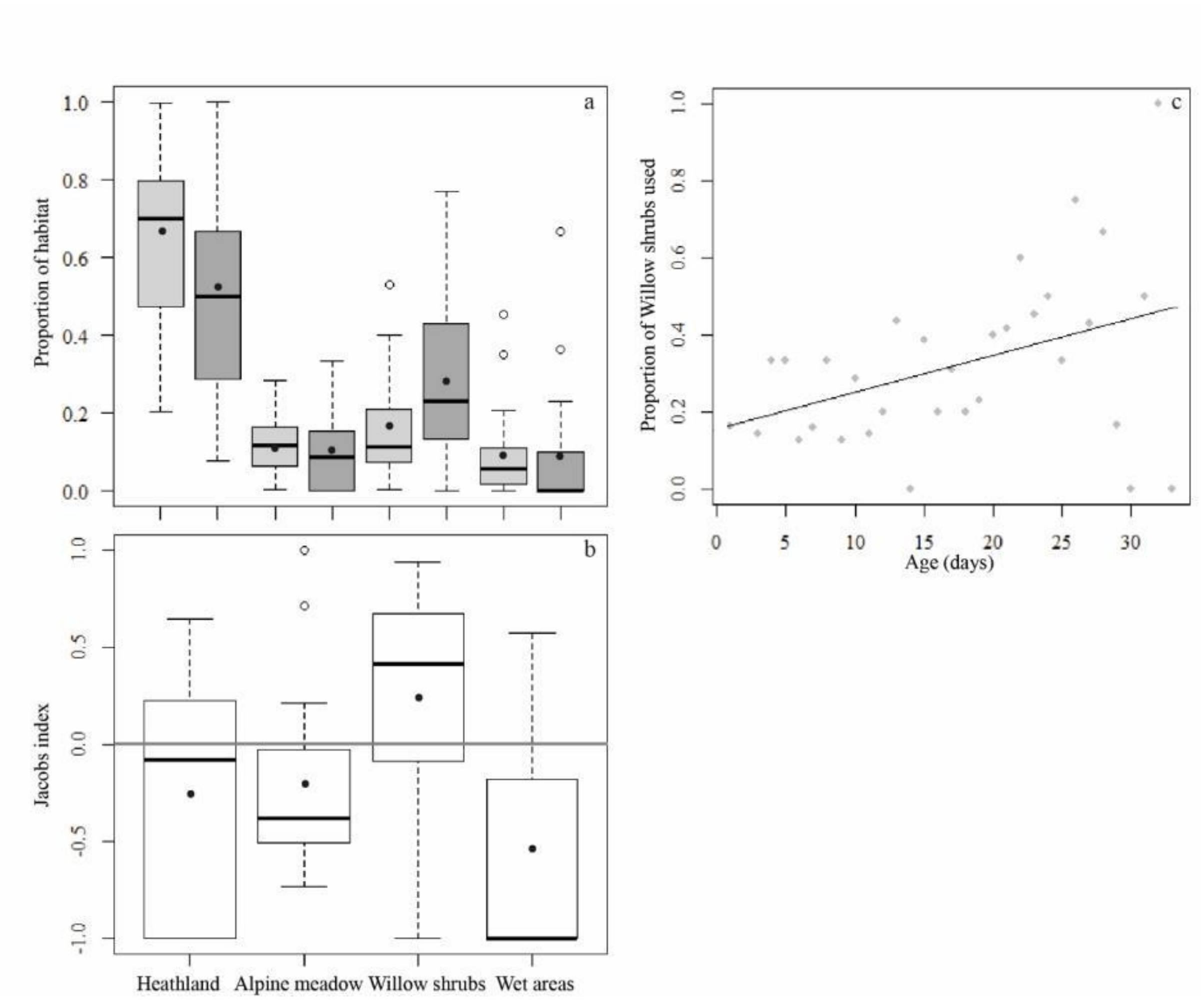
Figure 1. Nest positions and home ranges (Minimum Convex Polygons) for chicks tracked by radio transmitters.



Heathland was the most common habitat within home ranges, covering on average 64% of the area. Willow shrub, Alpine meadows and Wet areas all covered between 8% and 15% of the area (Figure

2a). Chicks were most frequently relocated within Heathland (52%) and Willow shrub (28%), less often in Alpine meadows (10%) and rarely in Wet areas (8 %) (Figure 2a). A compositional analysis revealed that habitat availability and habitat use differed significantly (Lambda = 0.38, df = 3, P < 0.001). Willow shrub habitat was significantly selected over all other habitats, and Wet area habitat was significantly avoided compared to all other habitats (Table 2). Correspondingly, the average Jacobs selection index was positive for Willow shrub (mean = 0.24) and negative for the rest of the habitats (Wet areas mean = -0.57, Alpine meadow mean = -0.20 and Heathland mean = -0.24), indicating that

Figure 2 a) Habitat availability (light grey boxplots) and habitat use (dark grey boxplots) for Golden Plover chicks. b) Jacobs habitat selection index values for different habitat types. In a and b, boxplots illustrate 95% confidence interval (whiskers), 25-75 percentiles (box), median (horizontal line) and mean (black dot). c) Proportion of the use of Willow shrub habitat in relation to chick age (in days).



Willow shrub is the only habitat preferred by the chicks (Figure 2b). The use of Willow shrub increased significantly over time (i.e. with chick age) (F = 5.90, df = 1, 30, P = 0.021) (Figure 2c).

That habitat selection varies with chick age also became apparent from separate analyses for young (<10 days) and older (>10 days) chicks. For young chicks, the compositional analysis revealed that habitat availability and habitat use differed significantly (Lambda = 0.39, df = 3, P < 0.001), with wet areas being avoided over all other habitats (results not shown). Correspondingly, the average Jacobs selection index was strongly negative for Wet areas, indicating strong avoidance (mean = - 0.77), slightly negative for Heathland and Alpine meadow, indicating moderate avoidance (mean = -0.22 and -0.17, respectively), and close to zero for Willow shrub, indicating no avoidance nor preference for this habitat (mean = 0.06). Also for older chicks, habitat availability and habitat use differed significantly (Lambda = 0.13, df = 3, P < 0.001), but now with Willow shrub being selected over all other habitats (results not shown). Correspondingly, the average Jacobs selection index was highly positive for Willow shrub, indicating strong preference (mean = 0.43), and negative for Wet areas, Alpine meadow and Heathland, indicating moderate to strong avoidance of these habitats (mean = -0.87, -0.61 and -0.23, respectively).

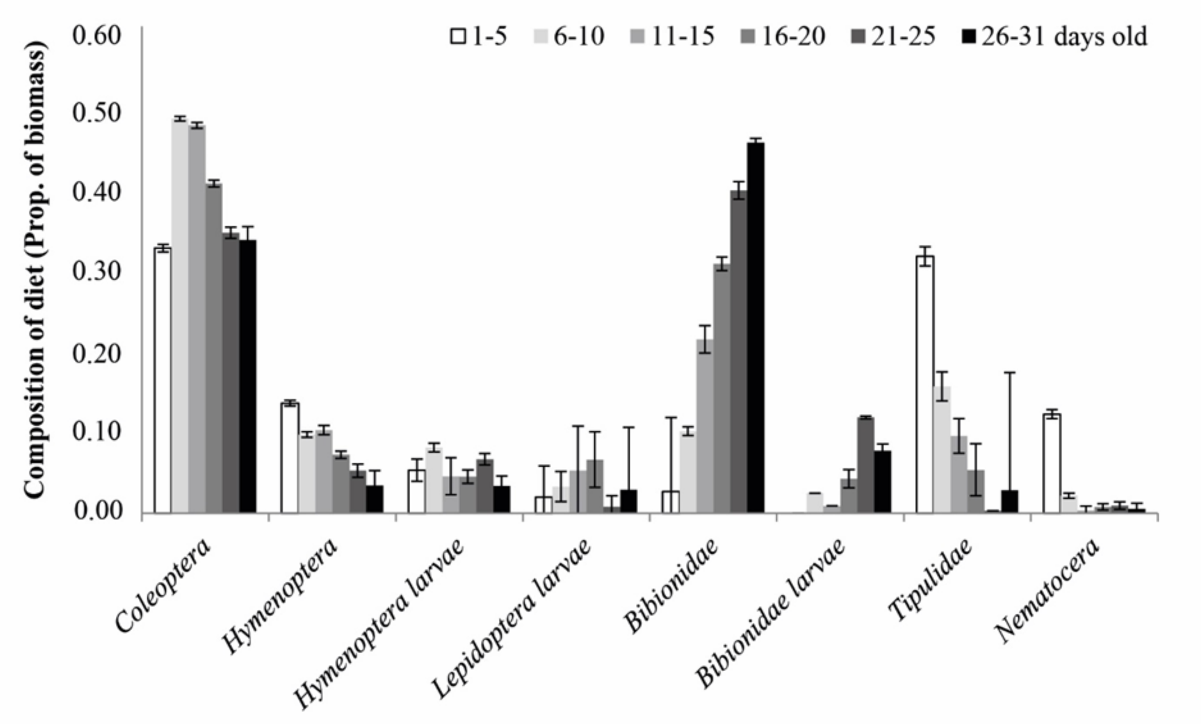
Table 2. Matrix of habitat preferences. Preferences are indicated for habitats listed at the left relative to those listed on top. Thus, for example, Willow shrub habitat is strongly preferred over Wet areas. + reflects preference, - avoidance. When three symbols are shown, preference/avoidance is significant (*P* < 0.05, Wilk's lambda test) when a single symbol is shown, preference/avoidance is not significant.

Habitat preference within Home range				
	Heathland	**Willow shrub**	**Alpine meadow**	**Wet areas**
Willow shrub	+++	0	+++	+++
Alpine meadow	-	---	0	+++
Wet areas	---	---	---	0
Heathland	0	---	+	+++

Diet composition

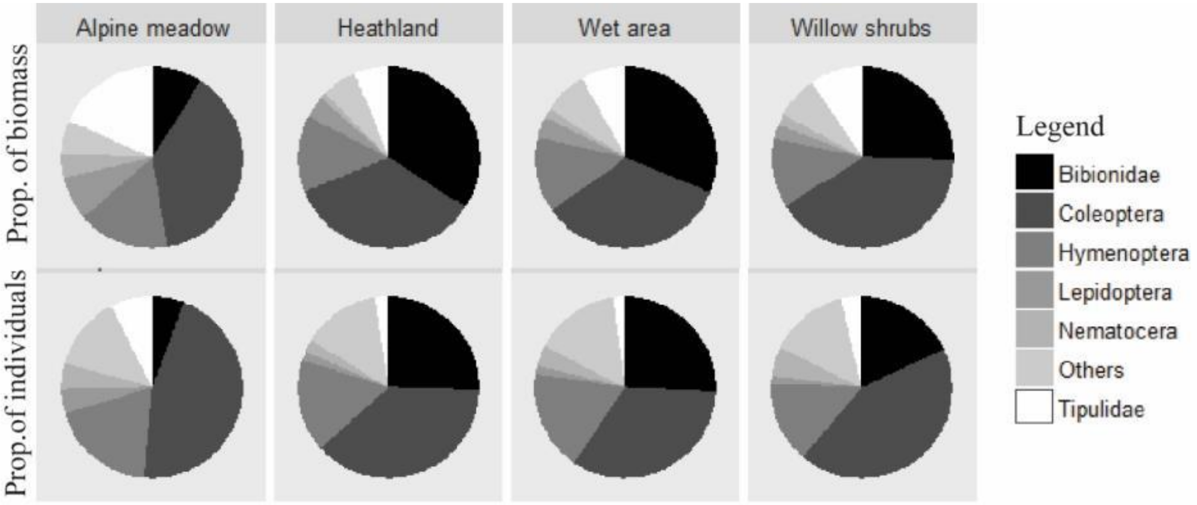
A total number of 149 faecal samples were collected from Golden Plover chicks. In these samples, remains from 10 different arthropod orders and 16 families were found. However, in both years, and in the four different habitats, the diet was generally dominated by only two orders, Coleoptera and Diptera (Bibionidae and Tipulidae) (Figure 3 and 4). These two groups comprised about 70% of the diet of the chicks. Another relatively important order in the diet was Hymenoptera (Figure 3 and 4). The rest of the orders present in the diet were Araneae, Hemiptera, Homoptera, Lepidoptera and Opiliones. Acari (subclass) was also found in the faeces.

Figure 3. Diet of Golden Plover chicks, as expressed as the proportion of different prey taxa in individual faeces (proportion of biomass), for different age classes.



Chick diet varied between years (Table 3, Figure 3). Bibionidae imagoes were very common and abundant in 2011, but almost absent from the diet in 2013. The opposite was true for Bibionidae larvae that were more common in 2013 but completely absent from the diet in 2011. Also Coleoptera and Hymenoptera larvae were more common in 2013 compared to 2011. In addition, chick diet was not constant within seasons but varied with chick age, date and habitat (Table 3, Figure 3). Coleoptera formed the most important prey for chicks at all ages, presenting between 32 and 49% of the diet at every age class (Figure 3). The proportion of Coleoptera in the diet differed significantly during the season, peaking at intermediate dates and increased with chick age (Table 3). Bibionidae imagoes was the second most important group, although almost only present in the diet in 2011. In 2011, the proportion of Bibionidae imagoes increased with date and chick age, from 3% in young to 46% in older chicks. Similarly, Bibionidae larvae which were only present in the diet in 2013, significantly increased in abundance with date and chick age in that year (Table 3). Tipulidae imagoes were eaten relatively much by young chicks (up to 32% of the faeces content, Figure 3), but the proportion of Tipulid imagoes in the faeces strongly decreased with date (Table 3). Hymenoptera was the fourth most important prey eaten by the chicks, in which consumption decreased with chick age. The proportion of Hymenoptera larvae increased with date but decreased with chick age. Nematocera were of relative importance for very young chicks, presenting up to 15% of the diet of chicks younger than 5 days, but were almost absent in older ages. The presence of Lepidoptera larvae in the diet did not follow any pattern. Diet composition only varied between habitats for Bibionidae larvae, occurring more frequently in the faeces of chicks that were relocated in Wet areas (Table 3). In all habitats, the most abundant prey group was Coleoptera and the second abundant one Bibionidae, except for Alpine meadow, where Hymenoptera was most abundant (Figure 4).

Figure 4. Diet of Golden Plover chicks, as expressed as the proportion of different prey taxa in individual faeces (proportion individuals (top), proportion of biomass (bottom)), for different habitats.



In addition to arthropod remains, plant material was found in the faeces of the Golden Plover chicks in 2011. These were mainly Crowberry Empetrum nigrum remains. Consumption of berries was not evenly distributed among chicks but was present in 13 of them (one chick with remains of 20 berries, one with 12 berries, one with 9, one with 5, three with 2 remains and 6 chicks with only 1 remain). Berries were mostly consumed in the later chick phase, although later hatched chicks consumed berries in earlier stage. The first berry was consumed on the 1st of July, but the mean date for consumption was the 19th of July, the latest being the 18th of August.

Table 3. Summary of significant effects of year, date, and chick age (column “Temporal”) and effect of habitats (column “Habitat”) on the abundance of different arthropod taxa in the diet of Golden Plover chicks (expressed as proportions of biomass per faeces sample), as based on GLMM-modelling. Symbols indicate directions of quadratic correlations, within the central 90% of values of the independent variable (following Tharme *et al* 2001) and the number of symbols indicates their significance (1 symbol: $P < 0.05$; 2: $P < 0.01$; 3: $P < 0.001$; 4: $P < 0.0001$). Habitats and results of a Tukey HSD posthoc test were only mentioned if habitat had a significant effect on the proportion of biomass of that taxa. NS=Not significant. See also Figure 3 and 4 for corresponding graphs of age and habitat effects, respectively.

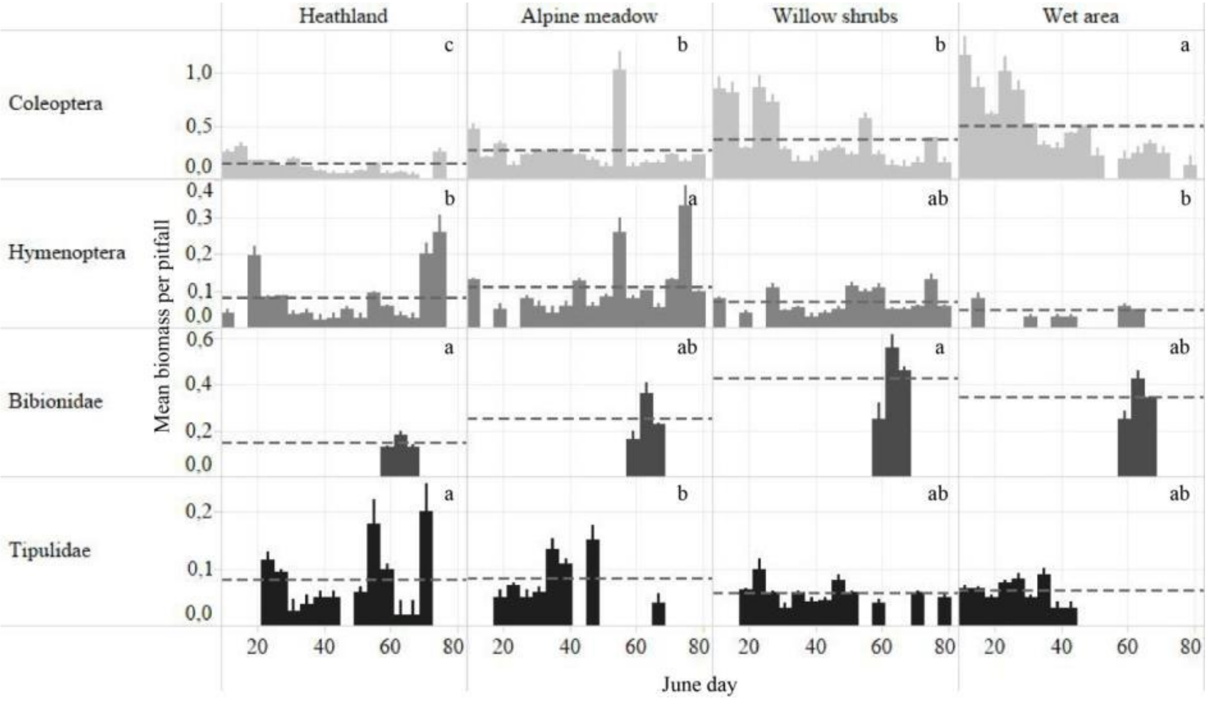
	Temporal	Habitat
Coleoptera	Date ∩∩∩	
	Age + +	NS
	Year 2013>2011*	
Hymenoptera	Age - - - -	NS
Hymenoptera larvae	Age - - -	
	Date + + +	NS
	Year 2013>2011*	
***Bibionidae* (2011)**	Date ╯╯╯╯	
	Age ++	
***Bibionidae larvae* (2013)**	Date ╯╯	Wet area ^{a}
		Willow shrubs ^{b}
	Age ╯	Heathland ^{b}
		Alpine meadow ^{b}
Tipulidae	Date ╰╰╰	
Nematocera	Age - -	NS
Lepidoptera larvae	NS	NS

Food availability

Arthropod sampling presented 10 different orders, although the three most abundant ones were Coleoptera, Hymenoptera and Diptera (Bibionidae and Tipulidae). The rest of the orders found were

Collembola, Diplura, Ephemenoptera, Hemiptera and Plecoptera. Also Acari (subclass) and Ixodidea (family) were present in the pitfalls.

Figure 5. Abundance of different arthropod taxa, as expressed as biomass per pitfall trap and per day, over time, for different habitat types. Here, only graphs for the most abundant taxa are presented. Error bars represent standard deviation. Small letters in each box show significant differences in abundance according to a Tukey HSD tests. Dashed horizontal lines show mean biomass values.



Patterns in the abundance of arthropods, between habitats and over time, differed for the four main (sub) orders found in the pitfall traps (Coleoptera, Hymenoptera, Bibionidae, and Tipulidae, Figure 5). Coleoptera were most abundant in Wet areas, where they declined in abundance during the season (F = 94.27, df = 1, 583, P <0.001). Hymenoptera were most abundant in Alpine meadow with no trend over time (F = 2.152, df = 1,274, P = 0.143), Bibionidae were most abundant in Willow shrub habitat and increased in abundance (F = 63.97 , df = 1,127, P = 0.02), and Tipulidae were most abundant in Alpine meadow with no trend over time (F = 0.12, df = 1,111, P = 0.72).

Overall food availability, in terms of the average total biomass per pitfall trap per day, did not differ between 2011 and 2013, despite the absence of Bibionidae imagoes in 2013 (F = 0.238, df = 1, 25, P

= 0.63, Figure 6a). In both years, overall food availability decreased throughout the chick-rearing period (from 1st of July till 6th of August, Figure 6). Note that Tipulidae and Bibionidae larvae live in the ground, and thus pitfall trapping does not provide information about their abundance.

Discussion

Habitat selection, diet and prey abundance

We radio-tracked Golden Plover chicks from hatching to fledging to study their habitat selection, diet and food abundance in a Fennoscandian breeding population. One of the main findings of our study is that plover chicks switched from feeding on Tipulidae to feeding on Bibionidae, and that this switch coincided with a shift from the use of the habitat where Tipulidae were abundant (Heathland) to the use of the habitat were Bibionidae were abundant (Willow shrub). This observation suggests that the chicks are tracking food abundance, at least to some extent. However, if the distribution of chicks would solely be determined by food abundance we may have expected that Wet areas, being rich in Coleoptera - a main prey type, would had been used more intensively. That Wet areas form a potentially favourable feeding habitat for wader chicks is illustrated by the fact that chicks from several other wader species intensively use this habitat (for example Dunlin, Redshank, Ruff, Broad-billed Sandpiper and Red-necked Phalaropes; P. Machin & J. Fernández-Elipe, pers. obs). However, these species might search for other prey which they feed on by probing in the soil, an uncommon and possibly inefficient feeding mode for Golden Plover given their short and stout bill. In addition, Bibionidae imagoes were virtually absent in 2013 whereas the plover chicks still made the same switch from Heathland to Willow shrub. Thus, it is likely that, in addition to food abundance, other factors like for example predation risk are important for habitat selection. Willow shrub seem to form an optimal habitat in terms of predation risk as the dense leaves provide cover from aerial predators (Long-tailed Skua, Raven Corvus corax, Common Gull Larus canus). At the same time, the vegetation seems not too dense to be in-penetrable as was suggested for example for Heathland habitat in the UK (Wittingham et al. 2001, Pearce- Higgings and Yalden 2004)

It should be noted that also the match between diet and prey abundance was far from perfect. For example, Tipulidae were most abundant in Heathland, but were mainly found in faeces of chicks found in Alpine meadow habitat. In addition, the proportion of Tipulidae in the diet strongly decreased throughout the season (Figure 3) whereas Tipulidae abundance was more or less constant over time (Figure 5). Partly, such differences could be a result of prey selection, but at the same time we cannot exclude methodological issues. In particular, pitfall traps are designed to sample surface dwelling arthropods, but it is an unsuitable methods to reliably sample flying insects such as Bibionidae and Tipulidae, which will be underrepresented in pitfall trapping. Although we believe that the differences within prey types in abundance between habitats, and changes in abundance throughout the season as presented in this paper are genuine, the difference in capture probabilities between groups makes it impossible to make interspecific comparisons. Hence, we strongly suggest to also apply methods which capture the abundance of flying insects in future studies (e.g. flight intersection traps).

Timing of breeding of plovers in relation to temporal changes in arthropod abundance

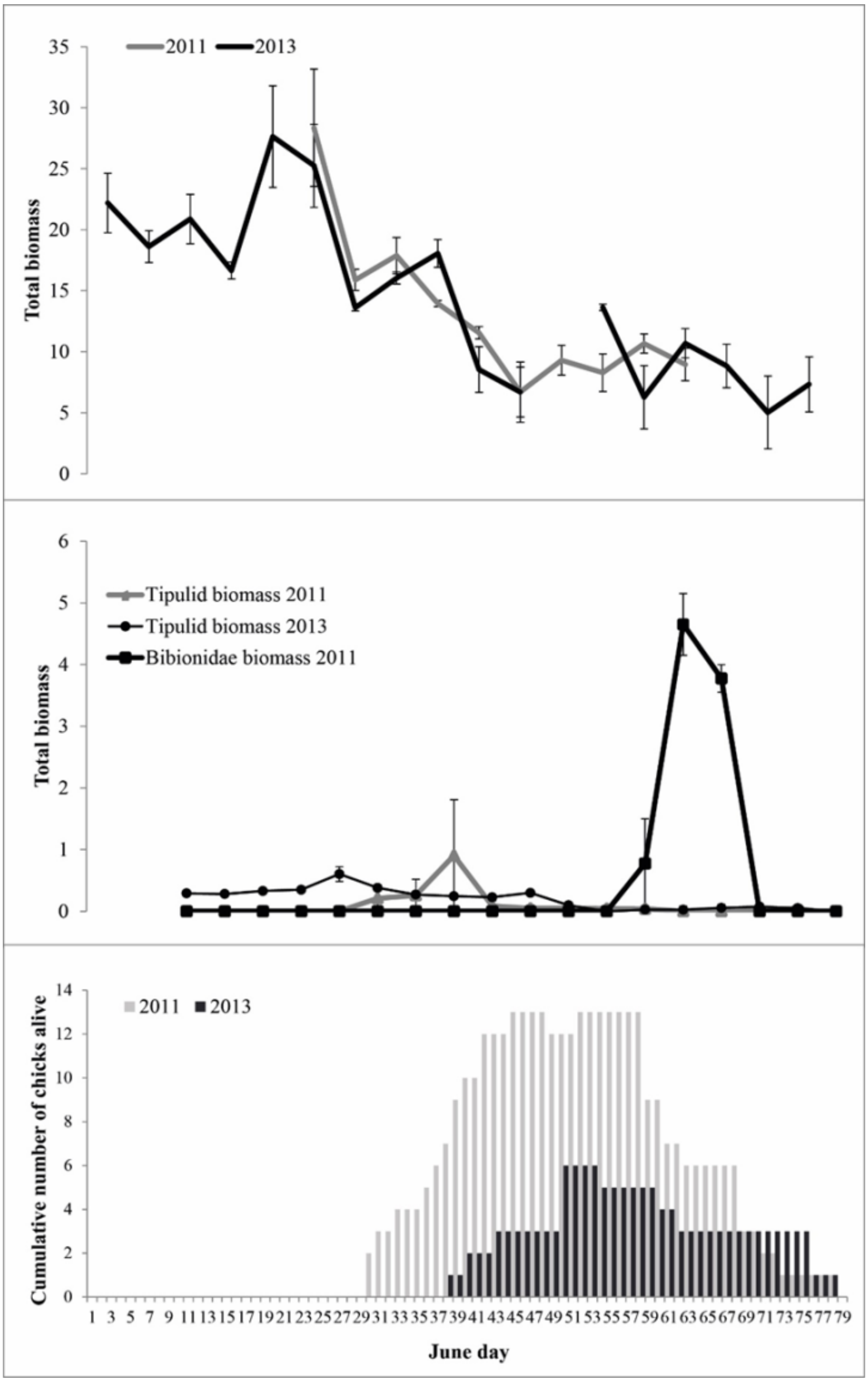
In accordance with studies from Greenland (Meltofte et al. 2007a), overall arthropod abundance decreased throughout the chick rearing period in our study area (Figure 6) suggesting that the late chick rearing period might be a critical phase for Golden Plovers breeding in Fennoscandia. In the UK, hatching roughly coincides with the mass emergence of adult Tipulidae (Whittingham et al. 2001, Pearce-Higgins & Yalden 2004), whose abundance correlates with the growth and survival of young chicks (Pearce-Higgins & Yalden 2004) as well as with the success of the fledglings (Douglas & Pierce-Higgins 2014). In our study, chicks generally hatched too late to profit from the Tipulidae-peak, which is for example illustrated by the steep drop in the occurrence of Tipulidae in the diet with increasing chick age. This suggests that, in this case, a mismatch exists between the timing of breeding and Tipulidae emergence. However, in Sweden, older chicks seem to profit from a late-season flush in Bibionidae flies (Figure 6). Because of this Bibionidae-peak in the second half of the chick rearing period, we believe there currently is no food shortage throughout the chick rearing period, and thus also that the timing of breeding of Golden Plovers currently is not mismatched with the phenology of their prey.

Whether the timing of breeding of Golden Plovers and timing of Tipulidae and Bibionidae emergence have shifted over time as an effect of climate warming is unknown. It is possible that in former times, the plover chicks relied on a later occurring Tipulidae peak, resembling the current situation in the UK (Pearce-Higgins et al. 2005) and southern Norway (Byrkjedal 1980). I.e. it is unclear whether the importance of Bibionidae is something 'new' or whether Bibionidae always have been important for Fennoscandian Golden Plovers. It is in this respect unfortunate that no long-term time series on the timing of breeding of plovers, and the seasonal occurrence of insects, are available (Thompson & Thompson 1991).

Given the importance of Bibionidae for the plover chicks it is worthwhile to review the information on this species. The species of Bibionidae occurring in our study area is Bibio pomonae (Fabricius, 1775). According to Skartveit 1995, imagoes occur from late July till early September, in which mass occurrences might appear in August, particularly in Scandinavia. Although the species is found throughout continental Europe, it only occurs at higher altitudes, up to 1440 m. The species is typically common above the timberline among Willow shrub (Fitzgeral & Skartveit 1997). Intriguingly, Bibio pomonae have been found to vary in abundance between years, ranging from mass emergences in some years and virtual absence in others (Skartveit 1995). Indeed, Bibionidae imagoes were only found in the pitfall traps in 2011 and absent in 2013, and in 2011, Bibionidae represented 30% of the chicks' diet compared to 17% in 2013 (in which all Bibionidae consumed in 2011 were imagoes whereas in 2013 the chicks almost exclusively ate Bibionidae larvae; 0.12 % imagoes).

Extreme annual variation in an essential food source such as Bibionidae imago might have a dramatic effect on the condition and survival of Golden Plover chicks during the second half of the chick rearing period, and thus on breeding success in general, as was found for Tipulidae in the UK (Pearce-Higgins et al. 2010). In fact, we could expect that breeding success closely varies with annual fluctuations in Bibionidae abundance, similar as to how breeding success of arctic-breeding waders vary with Lemming cycles (Summers et al. 1998) or annual variation in snow cover (Byrkjedal 1980, Meltofte et al. 2007b). The link between annual variation in Bibionidae and breeding success in Golden Plovers and other waders is an important subject for future studies.

Figure 6. Overview of the timing of breeding of Golden Plover chicks in relation to the phenology of arthropods. a) Abundance of different arthropod (total biomass per pitfall and per day) over time. Erros bars reflect standard deviation. b) Abundance (biomass per pitfall and per day) of the two main arthropod groups (Bibionidae and Tipulidae) over time, in 2011 and 2013. Error bars represent standard deviation. c) Cumulative number of plover chicks alive on each day of the breeding season, for 2011 and 2013.



Given the importance of Bibionidae for the plover chicks it is worthwhile to review the information on this species. The species of Bibionidae occurring in our study area is Bibio pomonae (Fabricius, 1775). According to Skartveit 1995, imagoes occur from late July till early September, in which mass occurrences might appear in August, particularly in Scandinavia. Although the species is found throughout continental Europe, it only occurs at higher altitudes, up to 1440 m. The species is typically common above the timberline among Willow shrub (Fitzgeral & Skartveit 1997). Intriguingly, Bibio pomonae have been found to vary in abundance between years, ranging from mass emergences in some years and virtual absence in others (Skartveit 1995). Indeed, Bibionidae imagoes were only found in the pitfall traps in 2011 and absent in 2013, and in 2011, Bibionidae represented 30% of the chicks' diet compared to 17% in 2013 (in which all Bibionidae consumed in 2011 were imagoes whereas in 2013 the chicks almost exclusively ate Bibionidae larvae; 0.12 % imagoes). Extreme annual variation in an essential food source such as Bibionidae imago might have a dramatic effect on the condition and survival of Golden Plover chicks during the second half of the chick rearing period, and thus on breeding success in general, as was found for Tipulidae in the UK (Pearce-Higgins et al. 2010). In fact, we could expect that breeding success closely varies with annual fluctuations in Bibionidae abundance, similar as to how breeding success of arctic-breeding waders vary with Lemming cycles (Summers et al. 1998) or annual variation in snow cover (Byrkjedal 1980, Meltofte et al. 2007b). The link between annual variation in Bibionidae and breeding success in Golden Plovers and other waders is an important subject for future studies.

Comparison between Fennoscandia and the UK

One of the main differences in the diets of Golden Plover chicks between the UK and our study site is the importance of Tipulidae larvae (Table 4). In the UK, chicks initially feed to a large extent on adult Tipulidae and then switch to feeding on Tipulidae larvae (Wittingham et al. 2001, Pearce- Higgings & Yalden 2004). In Sweden, Tipulidae larvae form only a minor part of the chicks' diet; after feeding on adult Tipulidae the chicks switch to feeding on Bibionidae flies (in years these flies are abundant) or Bibionidae larvae (in years flies are almost absent). Why this difference arises between populations is unclear. One possible explanation could be that Tipulidae larvae are less accessible at our study site for example because vegetation structure is different. Clearly, more information on the ecology of Tipulidae larvae and the abundance in different habitats is needed. An alternative explanation for the difference in prey choice between the populations is that Bibionidae would be rare or absent in the UK. However, mass emergences of adult Bibionidae have been reported from Scotland, where they form an important prey for the Common Pheasant Phasianus colchicus in autumn (Skartveit et al. 2013). Additionally, in 2 of 96 faeces of Golden Plover chicks in the Peak District (UK) Bibionidae were recorded, confirming that Bibionidae do occur in the UK (J. W. Pearce-Higgins pers.comm.).

Table 4. Comparison of habitat selection, diet and prey availability between three studies on the breeding ecology of Golden Plover chicks.

	Ammarnäs, Sweden	**Northern Pennines, UK[1]**	**South Pennines, UK[2]**
Selected habitat	Willow shrub	Small patches of heather mixed with grass, marshes, grasslands and Cotton grass*(Eriophorum vaginatum)* mire	Cotton grass, bare peat, crowberry, bilberry.
Avoided habitat	Wet areas and Alpine meadows	Heather	Heather and grasslands
Prey availability	Higher biomass and number in Willow shrub and Heathland	Depends on the year, but always high in *Cotton grass* mire and upland grasslands.	Higher number in Cotton grass
Most selected prey items	*Coleoptera* and *Bibionidae*	*Tipulidae* and *Coleoptera*	*Tipulidae, Lepidoptera, Coleoptera*

[1] Wittingham *et al.* 2001

[2] Pearce- Higgins & Yalden 2004

The difference in the diet of the Golden Plover chicks between the two populations also seems to be reflected by their habitat use. In the UK, plover chicks predominantly access Tipulidae larvae from areas of cotton grass and bare peat, whereas dense heather stands are avoided, possibly as the vegetation structure is so dense that it impedes chick movement (Wittingham et al. 2001, Pearce-Higgins & Yalden 2004) (see Table 4 to compare habitat types of the different studies). In contrast, at our study site, the plover chicks strongly selected for the densest available habitat, Willow shrub, possibly as it is rich in food (Bibionidae) and at the same time provides cover for aerial predators. Thus, the ecology of Golden Plover chicks differs between breeding populations in essential aspects such as prey choice and habitat use. Whether these differences arise from phenotypic plasticity, or whether the birds have adapted to the local environmental conditions, remains an open question.

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CHAPTER 4

The relative importance of food abundance and weather on the growth of a sub-arctic shorebird chick

Paula Machín, Juan Fernández-Elipe, Raymond H. G. Klaassen

Understanding how environmental conditions affect growth is important because conditions experienced during early development could have immediate as well as long-term fitness consequences. Annual fluctuations in (environmental) conditions may influence life-histories of entire cohorts of offspring. In birds, food availability and weather have been identified to affect chick growth. However, the relative importance of these factors in explaining growth in different years is poorly understood. We studied the growth of Golden Plover Pluvialis apricaria chicks by radio-tracking individuals from hatching till fledging, and related variation in chick growth to food availability (as sampled by pitfall trapping) and weather conditions. 2011 appeared to be a favorable season in which the chicks achieved notably fast growth rates. In 2013, in contrast, chicks were lagging behind in growth and possibly even achieved smaller ultimate sizes. Food abundance had a dominant effect on growth, whereas temperature only had short-term effects (at least in body weight). Thus, variation in food availability rather than variation in weather could explain the marked difference in growth of the plover chicks between the years. A short but intense flush of Bibio pomonae flies late in the breeding season in 2011 seems the reason why the plover chicks managed to achieve high growth rates in that year, despite hatching after the main arthropod peak. Thus, understanding cohort effects in the growth of plover chicks, for example in relation to climate change, requires an understanding of the seasonal dynamics of individual prey species.

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Introduction

Conditions experienced during early development may have immediate effects as well as long-term fitness consequences for individual animals (Lindström 1999; Metcalfe and Monaghan 2001; van de Pol et al. 2006). The latter has been coined the 'silver-spoon effect' (Grafen 1988) and is important for life history evolution (Roff 1992; Stearns 1992; Lindström 1999). At the population level, annual fluctuations in (environmental) conditions may influence the life-histories of entire cohorts of offspring, with groups of individuals raised under good conditions are more likely to survive, recruit and reproduce compared to offspring raised under poor conditions ("cohort effects", e.g. Reid et al. 2003; van de Pol et al. 2006).

Many of the examples of how conditions during early development affect survival and fitness originate from studies on free-living birds in the wild (e.g. Reid et al. 2003; van de Pol et al. 2006; Kentie et al. 2013). Food abundance and weather turn out to have dominant effects on the growth of young birds, but studies that determine the relative roles of these factors remain scarce (Schekkerman et al. 1998, 2003; Pearce-Higgins et al. 2010; McKinnon et al 2013). A relevant species group in this respect are Arctic shorebirds because (1) seasonal peaks in food abundance (arthropods) are relatively short at high latitudes, in which the timing and amplitude of the food peak vary between years (Tulp and Schekkerman 2008), and growing up before or after the food peak could negatively affect growth, and because (2) thermoregulatory costs are relatively high in the Arctic due to low ambient temperatures, and thus small temperature changes can already have large effects on energy expenditure and therefore growth (Schekkerman et al. 2003; Tjørve et al. 2009). Hence, both annual variation in food abundance and temperature could easily lead to cohort effects. Cohort effects might be especially important in Arctic breeding shorebirds because they are amongst the sort of bird species that produce a large output of offspring in occasional favourable years (Saether et al. 1996; Saether and Bakke 2000).

The relative importance of food and weather on the growth of young birds is also relevant from a conservation perspective, given the fact that Arctic regions have experienced the greatest and fastest climate warming in recent decades (Callaghan et al. 2005; Parmesan 2007). Climate warming might be beneficial for the growth of shorebird chicks as thermoregulatory costs will be lower (e.g. McKinnon et al. 2013). However, another effect of climate warming is that the seasonal food peak has advanced (Tulp and Schekkerman 2008). Since it appears problematic for birds to advance the timing of breeding to the same extent, a phenological mismatch between the timing of reproduction and the timing of food peaks occurs (Saino et al. 2011), which subsequently has direct and indirect negative effects on the growth of shorebird chicks (Schekkerman et al. 1998, 2003; Pearce-Higgins et al. 2005) and ultimately populations size (van Gils et al. 2016).

Several studies underline the importance of arthropods on the survival and growth of shorebird chicks (Schekkerman et al. 1998, 2003, 2004; Pearce-Higgins et al. 2010; Kentie et al. 2013). When arthropods are scarce, chicks grow slower but also attain smaller adult size (van Gils 2016). Others studies highlight effects of weather, mainly temperature, on the growth of shorebird chicks (Handel and Gill 2001; Krijgsveld et al. 2003; Meltofte et al. 2007a; Tjørve et al. 2007). It is important to note that weather can affect growth in different ways. First, energy expenditure is expected to increase with decreasing temperatures (thermoregulation), having a negative impact on growth (Piersma et al. 2003). Second, chicks have less time to feed on colder days as they need to be brooded more often and for longer time periods, which would also negatively affect growth (Meltofte et al. 2007a). Third, arthropods might be less active on colder days, negatively affecting growth (Meltofte et al. 2007a).

We studied growth and apparent survival of individual Golden Plover Pluvialis apricaria chicks in Swedish Lapland (low arctic tundra) using radio telemetry during two breeding seasons. Chick growth appeared to differ markedly between the two years. As we followed the growth of individual chicks over time, repeatedly measuring the same individuals as they were growing up, we were able to determine the short- and long-term effects of arthropod abundance and temperature on growth. These results provide novel insights in factors causing cohort effects in the development of shorebirds chicks.

Material and methods

Study area

Fieldwork was conducted in the Vindelfjällen Nature Reserve, Ammarnäs, Sweden (65°57' N, 16°12' E). The area is a Special Protected Area (SPA) for birds under the EG Birds Directive as well as a designated Important Bird Area (IBA) according to BirdLife International. Vindelfjällen is located in the lower alpine zone of the Swedish mountain range in the southern part of Lapland. The habitat is characterized as open low Arctic mountain heath tundra above the birch zone with a high proportion of lakes, mires and areas with low standing and flowing water. Fieldwork was concentrated in a 16 km2 study plot east of Lake Raurejaure (see Machín et al. 2017). The Golden Plover is the most abundant shorebird breeding in the study plot, at a density of three pairs/km2 (LUVRE survey, Å. Lindström personal communication).

The study was performed in the breeding seasons of 2011 and 2013. The study area was visited also in 2012 but as nest survival was extremely low due to a combination of late snow melt (Machín and Fernández-Elipe 2012) and high nest predation rates, it was impossible to study growth of Golden Plover chicks in that year (only one chick hatched from 21 nests located).

Abundance of arthropods

To estimate the abundance of arthropods during the chick-rearing period, arthropods were sampled using pitfall traps (250 ml, upper diameter 8 cm). In 2011 a total of 50 pitfall traps randomly distributed among habitats, in 2013 eight pitfall traps were placed in the four main habitats (32 pitfall traps in total). Content of the traps was collected every 2-4 days and brought to the laboratory for processing. Individual arthropods were identified to family level, and assigned to a size class. The biomass of each individual prey was calculated from its size using a conversion factor suggested by Rogers et al. (1976). Abundance of prey was then calculated per pitfall and per sampling occasion. For further details on arthropod sampling see Machín et al. (2017).

Weather conditions

Daily mean and minimum temperature data and daily information on snow cover were obtained from the nearest weather station (Boksjö, located 36 km south of the study area, at 100 m lower elevation), as provided by the Swedish Meteorological and Hydrological Institute (SMHI).

Radio-tracking

Golden Plover nests were located during the incubation period by walking and flushing incubating birds, by watching flushed birds returning to their nest or by flushing birds by dragging a 30-m-long rope between observers over the tundra. Incubation stage was determined by floating the eggs in water (Liebezeit et al. 2007). Nests were checked every day around the expected time of hatching. Freshly hatched Golden Plover chicks were caught on the nest, and supplied with radio-transmitters (0.75g BD-2 tags supplied by Holohil Systems Ltd, Ontario, Canada). The radiotagged chick was relocated the day after hatching (age = 1 day) to ensure that the bird was fine and transmitter attached properly, and thereafter every second day during the whole pre-fledging period. No effects of handing the birds every second day were observed, as was also concluded by Pearce-Higgins and Yalden (2004) who handled Golden Plover chicks at intervals of one to four days. To relocate a chick, a triangulation from a larger distance (approximately 100 m) was made first to get a rough idea about the chick's approximate position and subsequently to quickly move towards this position to pinpoint the chick. Once located, the chick was weighed and measured (tarsus length: length from the inner bend of the tibiotarsal articulation to the base of the toes, bill length: from tip of bill to feathering on forehead, total head length: from tip of bill to end of skull) and exact location (GPS position, Garmin-eTrex Vista HCx, Garmin International, Inc., Olathe, KS, USA) was recorded. For further details on radio-tracking see Machín et al. (2017). As a result, data blind was not possible to record because our study involved focal animals in the field.

The fieldwork was carried out under permits from the Lund/Malmö Ethical Committee for Animal Experiments (M160-11, M27-10, M33-13).

Analyses

All analyses were conducted in R version 3.2.1. (R Development Core Team 2008)

Apparent survival

Proportional hazard model reformulated as a counting process (Andersen and Gill 1982) was used to estimate the apparent survival of chicks in relation to age in each year using the function “coxph” and “survfit” from the R-package “survival” (Therneau and Grambsch 2000).

Growth curves

Data were selected from 23 chicks from 23 different broods (14 from 2011 and 9 from 2013) that did not die for unknown reasons (presumably starvation or cold), i.e., this sample will represent the normal growth of Golden Plover chicks in the study area. Growth curves for every measurement (weight, bill, total head, and tarsus length) were described by Gompetz growth equations, which were fitted using the R-package “drc” (Ritz and Streibig 2005). Gompertz growth equations were chosen as they fitted the data best (compared to Logistic, Log-logistic, Exponential and Weibull equations), and also to facilitate comparisons with other studies (Ricklefs 1973; Beintema and Visser 1989; Pearce-Higgins 2002). For all measurements we fitted three parameters Gompertz growth equations, except for weight for which a four-parameter Gompertz growth equation fitted better (i.e. lower AIC value). The Gompertz growth equation is described by:

$y= A(\exp(-\exp(K(x-t))))$ (3-parameter Gompertz growth equation)

$y= c + (A-c)(\exp(-\exp(K(x-t))))$ (4-parameter Gompertz growth equation)

Where y= biometric measurement, A = asymptote or upper limit, K = growth coefficient, t = time of inflexion and c is the lower limit (only relevant for the four parameter Gompertz growth equation). Owing to problems of weight loss in chicks between hatching and day one of age, the growth curve for weight was fitted only to data from chicks older than one day (Thomson 1994). Growth curves for different years were compared using R- package “statmod” 1.2.4. (Giner and Smyth 2016).

Factors affecting growth

For this analysis, data from chicks that were not controlled more than two times were excluded. General linear mixed models (GLMM) were used to analyze growth of chicks following Schroeder et al. (2008) and using R-package “nlme” (Pinheiro et al. 2017) and model selection was performed with “glmulti” package using AICC criteria (small-sample corrected AIC). Chick growth was analyzed in two different ways. First we modeled residuals of every measurement, which is the difference between the observed value at a certain chick age minus the expected value taken from the fitted Gompertz equation for that chick age. These growth residuals represent cumulative long-term effects of factors affecting growth. Second, we modeled residual growth change, which is the observed growth in a certain age interval minus the expected growth from the fitted Gompertz equation for that interval. These growth change residuals represent short-term effects of factors influencing growth.

Measurements analysed included one measure for condition (weight) and different measures for structural size (tarsus, bill, and bill-head length). Independent variables included for the model selection were ‘year’ and ‘sex’ as factors, and ‘June day’ and ‘age’ as continuous variables. Furthermore, we studied possible effects of ‘mean minimum temperature’ and ‘mean biomass’, using means of the previous two days in the analyses of growth residuals, and means for the specific age intervals for the analyses of growth change residuals. Mean minimum instead of mean temperature was chosen (cf. Pearce-Higgins and Yalden 2002).

These analyses were repeated for three classes, the whole dataset including data from hatching to fledging, data from chicks younger than nine days (the estimated age at which plover chicks become thermo-independent, during this phase chicks still strongly depend on brooding by the parents), and data from chicks older than nine days (chicks considered thermo-independent) (Byrkjedal and Thompson 1998).

Sex analysis

Upon capture, a small droplet of blood (~10 µl) was obtained from the chick by venepuncture of the medial metatarsal vein and the sample was subsequently stored in 96% ethanol. In the lab, chicks were sexed using PCR-based molecular techniques, as described in Fridolfsson and Ellegren (1999) and van der Velde et al. (2017). For the chicks captured in 2011 we used primers 057F/002R

(Fridolfsson and Ellegren 1999) and for the birds caught in 2013 primers 2602F & 2669R were used (van der Velde et al. 2017).

Results

Apparent survival

A total of 32 chicks were radio-tagged, 20 chicks from 20 broods in 2011 and 12 chicks from 12 broods in 2013. In 2011, six chicks were tracked until fledging and seven were found dead (Table 1). One of the dead chicks was predated, probably by a raven Corvus corax, whereas the other six chicks presumably died of starvation. The fate of the seven remaining chicks was unclear, for five individuals suddenly no radio signals were received anymore (chick either disappeared, for example because it was taken by a predator, or battery of the transmitter failed prematurely) and two individuals lost their tags (Table 1). In 2013, three chicks were tracked until fledging and three were found dead (Table 1). The fate of six birds was unknown as the signal was lost (four birds) or the birds lost the transmitter (two birds) (Table 1).

Table 1. Fate of individual Golden Plover chicks that were tracked by radio-transmitters in 2011 and 2013

Year	**Survived till fledging**	**Lost signal**	**Lost tag**	**Dead**	
				Predated	**Unknown**
2011	6 (30%)	5 (25%)	2 (10%)	1 (5%)	6 (30%)
2013	3 (25%)	4 (33.3%)	2 (16.6%)	0	3 (25%)

Ages at which the chicks lost their tag were 12, 25, 22 and 28 days. Ages at which no radio signals were received anymore were 2, 2, 4, 11, 22, 24, 25 and 28 days. When analyzing apparent survival, chicks that lost the tag because the glue did not hold, or because the (down) feathers the tag was attached to were moulted, were considered as survivors, whereas chicks that could not be relocated because the radio signal was lost were considered predated if chicks were smaller than 3 weeks. For older chicks malfunction of the tag was assumed. Apparent survival was slightly higher in

2011 (56%) compared to 2013 (44%) but did not differ between the years (Wald Z= 0.64, df=1, p=0.42) (Figure 1). Also, the percentage of individuals that survived until fledging was higher in 2011 (30%) than in 2013 (25%) (Table 1). Finally, weight at hatching was not related to chick apparent survival (Wald Z=1.61, df=1, p=0.20).

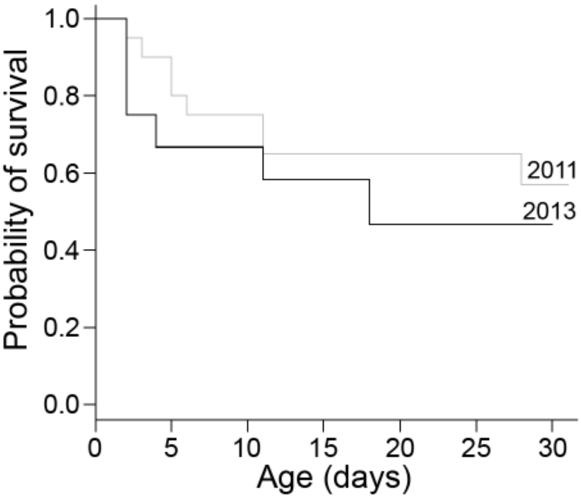

Figure 1 Apparent survival of Golden Plover chicks throughout the breeding season. Relative apparent survival plots are shown for 2011 (n=20 chicks) and 2013 (n=12 chicks)

Biological and environmental conditions

36 Golden Plover nests were located in 2011 and 29 in 2013, of which 22 (61%) and 14 (48%) hatched, respectively. Norwegian lemming *Lemmus lemmus* was present in the study in low to moderate numbers in 2011 but absent in 2013 (Machín and Fernández-Elipe 2012). Consequently, mammalian predators like red fox *Vulpes vulpes* and least weasel *Mustela nivalis* were occasionally encountered only in 2011, and the most abundant avian predator, long-tailed skua *Stercorarius longicaudus*, only nested in 2011 (with 27 pairs in the study plot, R. van Bemmelen personal communication). The two breeding seasons differed little in timing of snow melt in spring (extensive snow melt starting almost at the same date, on 10 and 9 May, respectively, Figure 2), average daily temperature in May–August (10.0 °C in 2011, 10.3 °C in 2013), and precipitation (75 and 62.5 mm rain recorded in 2011 and 2013, respectively, in May–August).

Mean minimum temperature was significantly lower in 2013 compared to 2011 (*t*=3.33 *p*<0.01) due to much longer periods of cold weather (<8 °C during 17 days) from 14th July and 15th August, than in 2011, when cold weather only occurred on 13th July and 10th August (Figure 2).

Arthropod abundance generally declined throughout the season, suggesting that plover chicks generally occur after the main arthropod peak. In 2011, a late peak in arthropods occurred, which could be contributed to a late season flush of the March fly *Bibio pomonae* (Fabricius, 1775), a much preferred and consumed prey item by plover chicks in the study area (see Machín et al. (2017) for a detailed account on arthropod abundance and plover chick diet) (Figure 2).

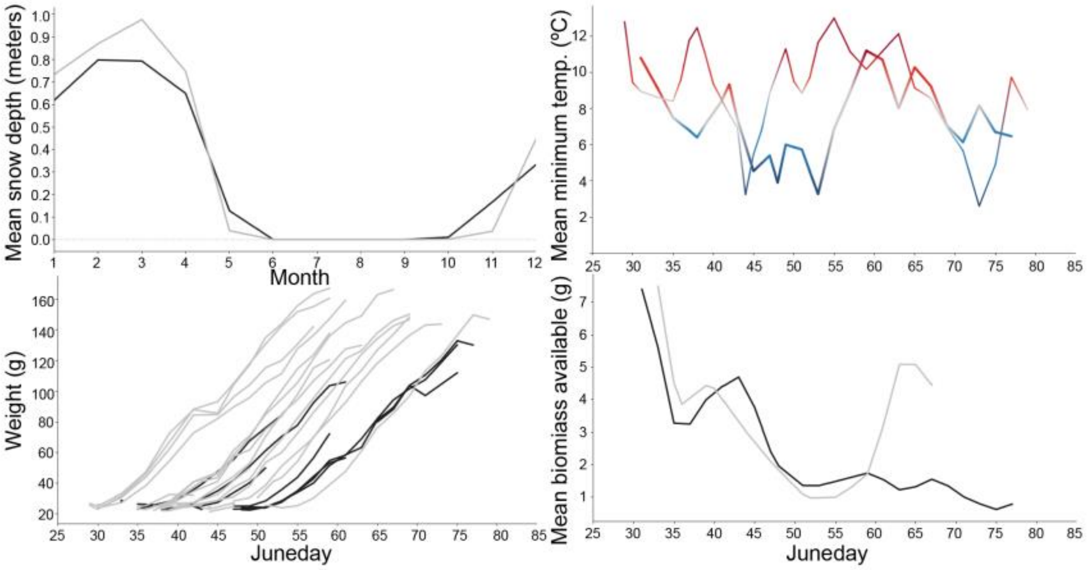

Figure 2 Environmental conditions (snow cover, temperature, and arthropod abundance) and growth of individual Golden Plover chicks, in 2011 (grey lines) and 2013 (black lines). In the plot depicting temperature, the thicker line refers to 2013. In the plot showing growth of individual chicks, only data for chicks that were relocated at least three times are shown.

Differences at hatching

Mean hatching dates of nests from which chicks were radio-tracked differed only five days between years, being 7 July in 2011 and 12 July in 2013, and there was no difference in mean egg volume between years (means 2011 and 2013, 35.05 and 34.15 cm^3, respectively, *F*=-0.24, df=1, 27, *p*=0.62).

There were also no differences between years in weight, tarsus, bill, and bill-head length at hatching (Table 2), thus the starting point for the plover chicks seemed very similar in the two seasons. Finally, we could not detect any correlation between mean clutch egg size and weight, tarsus, bill and bill-head length of the newly hatched chicks, probably due to a large variation in egg size within clutches (Table 2).

Table 2 Weight, tarsus, bill, and total head length of Golden Plover chicks, in relation to the mean egg volume of the clutch. Provided are correlations between mean egg volume and measurements at hatching

		Measurements at hatching			
		Weight	Tarsus	Bill	Total head
Year	*Estimate* ± SD	-0.86±0.49	-0.43±0.44	-0.08±0.22	-0.69±0.48
	t	-1.73	0.96	-0.37	-1.43
	p	0.09	0.34	0.70	0.17
Mean clutch egg volume	*Estimate* ± SD	-0.14±0.13	-0.20±0.10	0.08±0.05	0.26±0.10
	t	-1.11	-1.99	1.61	2.41
	p	0.27	0.05	0.11	0.03

Growth curves

Growth decelerated from hatching for all structural measurements (tarsus, bill, and bill-head length), whereas growth initially accelerated for weight until the deflection point at an age of 16 days where the maximum weight gain was achieved (Figure 3, Table 3, supplementary material 1). Hence, Gompertz growth curves with three parameters could describe growth of the structural measurements, whereas a Gompertz growth curves with four parameters had a better fit for weight (Table 3, supplementary material 1). Golden Plover chicks lost a bit of weight between hatching and day 1 (Figure 3). Tarsus grew at a faster rate than any other structural measurements (K= -0.076), but weight was the variable with the highest growth speed (K= -0.083, Table 3).

Growth curves fitted significantly better when adding year as a covariate in all the cases, as well as with sex as a covariate, meaning that growth curves did differ between years (Figure 3) and sexes (supplementary material 1). However individual growth parameters themselves were not significantly different between years or sexes, although in 2011 males had higher K-values for all measurements (supplementary material 1).

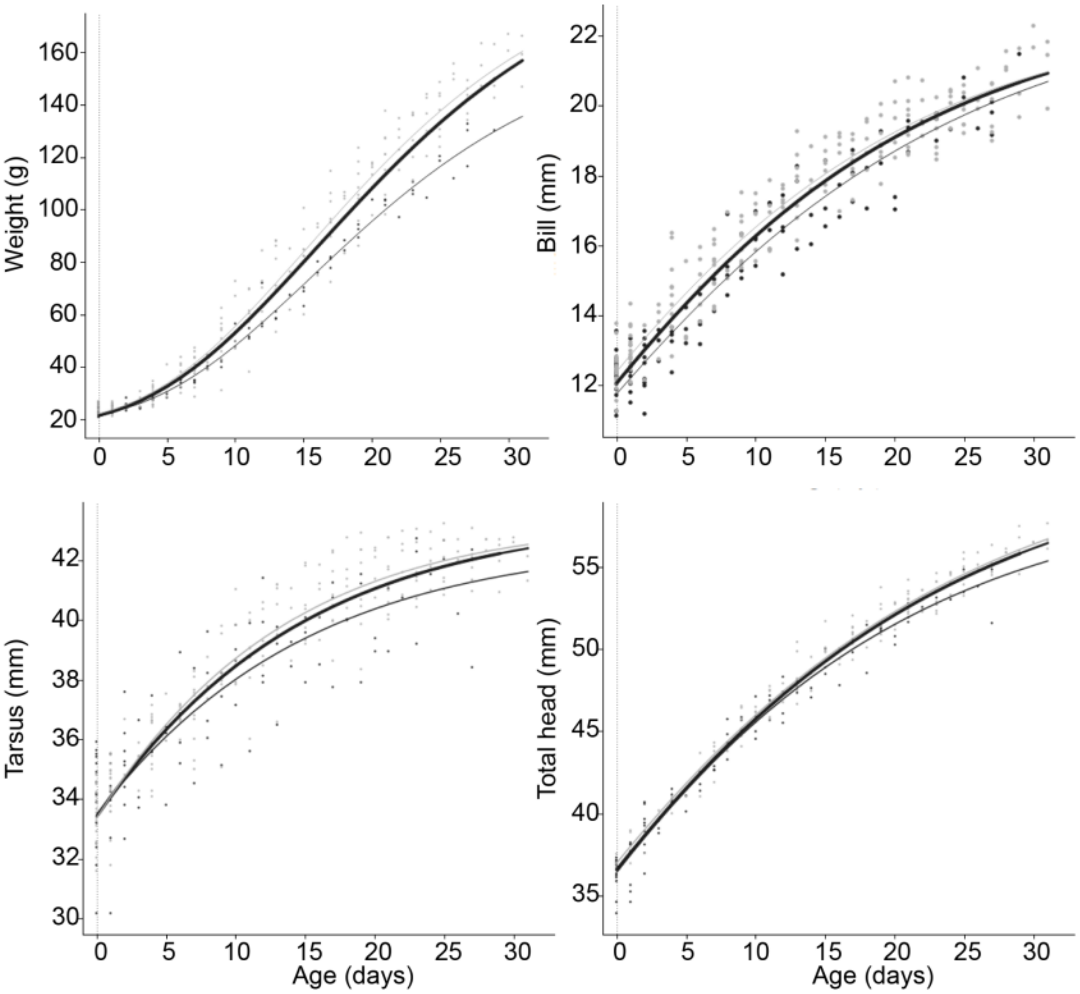

Fig .3 Growth curves for weight, tarsus, bill and total head length. Solid lines depict fitted Gompertz growth curves. Grey lines refer to 2011, black lines to 2013, thick black lines to both years combined

Factors affecting growth

For this analysis, only chicks that were tracked for at least 5 days were included (i.e. measured at least two times). The final dataset consisted of 17 chicks in 2011 and 7 chicks in 2013.

Generally, growth of the plover chicks differed markedly between the years. More specifically, growth lagged behind in 2013 compared to 2011, which was most pronounced for older chicks. For example, residuals of weight, a measure for condition of the chick, were stable in 2011 but decreased with age in 2013 (Figure 4, significant interaction between year and age: supplementary material 2). For structural measurements, residuals were generally higher in 2011 compared to 2013 throughout the whole season, which was significant for bill length, and for bill-head length but only for older chicks (Figure 4, supplementary material 2).

Temperature generally had no effect on the growth of the plover chicks (residuals, supplementary material 2), thus temperature cannot explain the difference in growth between the years. The only case where some effect of temperature was picked-up was for bill length of older chicks, for which the relationship between residual bill length and temperature seems to differ between years (significant interaction between year and temperature; Figure 4, supplementary material 2). Instead, biomass had a dominant effect on growth, with residual weight, tarsus, bill, and bill-head lengths being larger when more biomass was available. Correlations between residuals and biomass seem to differ between years, at least for weight and bill-head length in older chicks, for which also the interaction between year and biomass was significant.

Another factor that turns out to affect residual growth is sex of the chick. In older chicks males were heavier and had longer tarsus lengths (supplementary material 2).

Table 3 Estimates ± SD for parameters of Gompertz growth curves for weight, tarsus, bill and total head length of Golden Plover chicks. For weight, a four parameter Gompertz curve was fitted, whereas for tarsus, bill and total head length three parameter Gompertz growth curves were fitted (see main text)

Variable	**Growth parameters**	**Estimate±SD**		
		All chicks	2011	2013
Weight	K	-0.08±0.01	-0.08±0.01	-0.09±0.02
	t	15.95±4.06	15.22±0.62	15.53±1.57
	A	203.05±15.22	200.89±11.67	169.36±23.20
	c	17.45±0.83	18.20±4.05	19.06±4.84
Tarsus	K	-0.08±0.01	-0.08±0.01	-0.07±0.02
	t	-17.52±1.68	-16.06±1.78	-19.15±3.60
	A	43.47±0.48	43.39±0.46	42.65±1.03
Bill	K	-0.06±0.00	-0.06±0.01	-0.06±0.01
	t	-7.07±0.42	-7.77±0.60	-6.75±0.58
	A	22.97±0.56	22.85±0.58	23.23±1.23
Total head	K	-0.05±0.00	-0.05±0.00	-0.06±0.00
	t	-11.56±0.41	-12.01±0.70	-11.69±0.60
	A	62.28±0.86	62.91±1.13	59.86±1.26

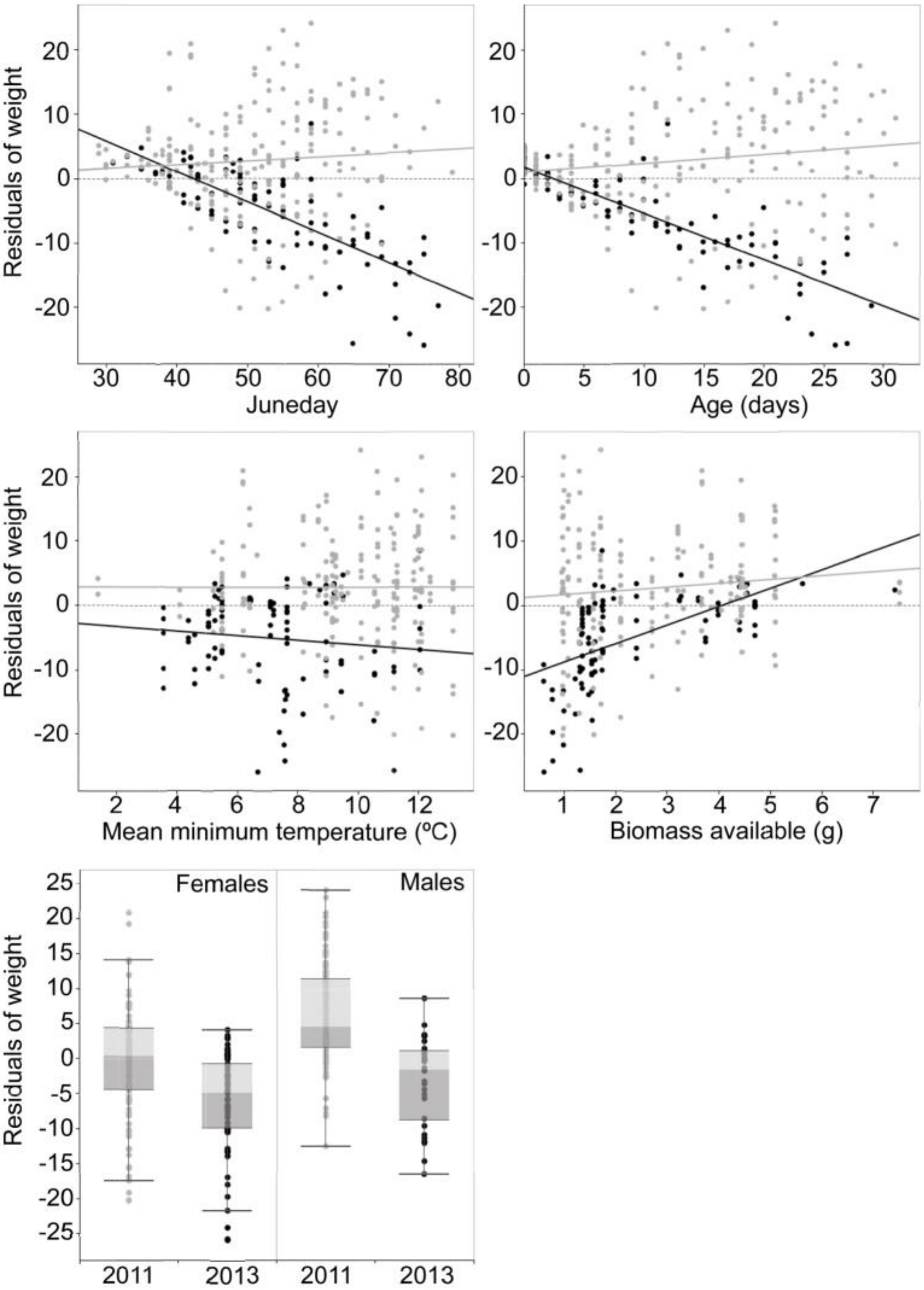

Figure 4 Factors affecting growth. Absolute residuals of weight in relation to juneday, age, temperature, arthropod biomass and sex of the chick. Light grey represents 2011 and dark grey 2013. Last figure is a Tukey boxplot where central line is the median, upper and lower line in the box correspond to the first and third quartiles and upper and lower whiskers correspond to 1.5 IQR of the lower and the upper quartile. The data not included between the whiskers are outliers.

In addition to growth residuals, we also modelled residual growth change, which should capture more short-term changes. This analysis sketches a different picture (supplementary material 3). Mainly, residual growth change did not differ between the years. Also, although biomass was retained in most models, it never had a significant effect on residual growth change, for any chick age or measurement (supplementary material 3). Instead, for weight, temperature had a strong positive effect on residual growth change, suggesting that temperature affects short-term changes in condition of the growing chicks (Figure 5, supplementary material 3).

Measurements of chicks at fledging, i.e. at the last check the chick could not yet fly off, are provided in Appendix 4, along with measurements of breeding adults from the same study area (Machín et al. 2012). The mean age of fledging in 2011 was 30.7 days (SE=1.7, N=6). Plovers chicks fledged with full-grown tarsus (101%), and nearly full-grown bill (97%) and total head (94%). Weight and wing were not fully developed at fledging, reaching only 80 and 76% of adult size, respectively. No chicks were tracked until fledging in 2013, which, unfortunately, excludes the possibility of a comparison between years. However, a single chick that was tracked until 29 days old weighted only 130.2 grams at that moment, which is the weight expected for a 24 day old chick.

Discussion

The growth of the Golden Plover chicks in our study area in Swedish Lapland differed markedly between years. 2011 appeared to be a favorable season in which the chicks achieved fast growth rates (see below for a comparison with other studies). This strongly contrasted with 2013, when residuals for weight decreased with age, suggesting that the condition of the chicks steadily deteriorated throughout the season. In addition, residuals for structural measurements (tarsus, bill, and total head length) were consistently lower in 2013 compared to 2011, independent of chick age, suggesting that chicks were lagging behind in growth and possibly even achieved smaller ultimate sizes. The latter could however not been confirmed by comparing measurements of chicks at fledging, as no birds were tracked until fledging in 2013. Nevertheless, the notable difference in growth between the two years suggest a strong cohort effect with the plovers fledged in 2013 being less fit compared to plovers fledged in 2011. An underdeveloped growth is known to have knock-on effects on for example post-fledging survival, dominance rank, adult body size, recruitment in the breeding population, and longevity (Newton 1989; Metcalfe and Monhagan 2001; van de Pol 2006), which ultimately accumulates in population effects (Reid et al. 2003; Cam and Aubry 2011; Kentie et al. 2013; van Gils et al. 2016). Hence, understanding factors causing these cohort effects is pivotal.

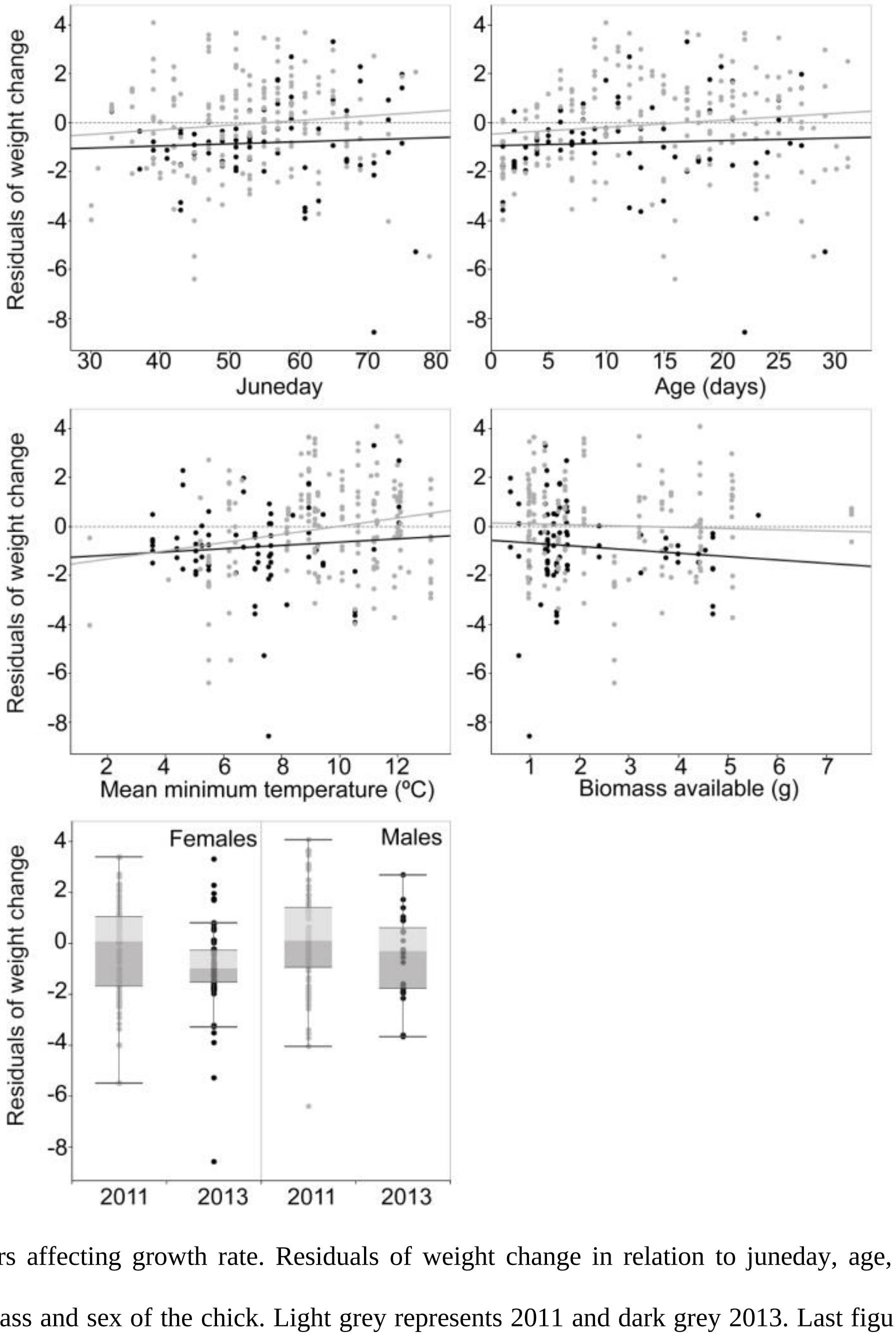

Figure 5 Factors affecting growth rate. Residuals of weight change in relation to juneday, age, temperature, arthropod biomass and sex of the chick. Light grey represents 2011 and dark grey 2013. Last figure is a Tukey boxplot where central line is the median, upper and lower line in the box correspond to the first and third quartiles and upper and lower whiskers correspond to 1.5 IQR of the lower and the upper quartile. The data not included between the whiskers are outliers.

Differences at fledgling

In this study, we followed the growth of individual plover chicks, which, uniquely, allowed us to quantify the relative importance of food availability and temperature on chick growth and chick growth rate. Although chick growth was monitored in only two years, we could show that food availability had a dominant effect on growth, whereas temperature affected short-term changes (at least in weight). This is an important result because variation in food availability rather than variation in weather apparently seems the cause for the cohort effect. Previous studies have shown effects of both food availability (e.g. Schekkerman et al. 2003; Tulp and Schekkerman 2008) and temperature (e.g. Schekkerman et al. 1998; Pearce-Higgins and Yalden 2002; Meltofte et al. 2007a; Tjørve et al. 2009) on the growth of shorebird chicks. However, how general our notion, that food availability rather than temperature causes cohort effects, is, remains to be established. Pearce-Higgins et al. (2010) also found that food availability rather than temperature had a dominant effect on, in their case, variation in Golden Plover population growth rates.

It should be stressed that in this study we focused specifically on food availability and temperature in explaining differences in growth, whereas many other factors could influence growth and thus cause cohort effects (Cam and Aubry 2011). For example, 2011 and 2013 differed in the abundance of predators, with more mammalian and avian predators present in 2011. The presence of predators alone could already have a negative effect on the growth of the chicks, for example because chicks hide more often and thus have less time left for foraging, or because chicks move to safer habitats where less food is available (Dunn et al. 2010). No indication exists that the difference in predator abundance had a negative effect on chick growth in our study. Instead, chick growth was better in 2011, when more predators were around. However, predation does play an important role in breeding success in the long term, as in some years plovers and other shorebirds fail to reproduce due to a natural cycle in predator abundance and thus predation pressure (Meltofte et al 2007). We experienced such ‘predation year’ in 2012 when most nests were predated before hatching, and the overall production was 0.25 chicks per pair (in comparison to 2.25 and 1.11 in 2011 and 2013 respectively). In such year, predation overrules any effect of food availability and temperature.

Other weather factor such as precipitation could also affect chick growth. In a preliminary analysis, we could not detect an effect of precipitation on growth (data not shown), presumably because more data and possibly also more accurate precipitation data would be needed to pick-up subtle additional effects. However, we did observe that residual weights of chicks (n=3) had dropped to almost -5 after a long-lasting period of rain (13 mm recorded), suggesting that rain indeed could play a role.

In 2011, the Golden Plover chicks ‘performed’ relatively well, in both chick apparent survival and growth. Apparent survival of the radio-tracked chicks was 60% in 2011 (and 50%, i.e. only slightly lower, in 2013), which is about three times higher compared to a similar study in the UK, where the proportion of chicks that survived up to 20 days was about 20% (Pearce-Higgins and Yalden 2002). It was shown before that shorebirds breeding at higher latitudes generally have higher growth rates (Schekkerman et al. 2003; Tjørve 2007; Tjørve et al. 2009). The observation that the Golden Plover chicks in this study achieved higher growth rates (K=-0.083 for weight) than in the UK (K=0.079, Pearce-Higgins and Yalden 2002) and Germany (K=0.059, Glutz et al. 1979) fits this hypothesis. In comparison to other precocial species, the growth rate of Golden Plovers in Ammarnäs is also relatively high given their body size and breeding location. For example, growth rate of the plovers is comparable to the growth rate of Bar-tailed godwits Limosa lapponica breeding in Taimyr (K=0.085, Tjørve 2007), despite the more northern breeding location and higher weight of the godwits.

The relatively high growth rate of the Golden Plover chicks in our study is surprising from the perspective that in both years the chicks hatched after the main arthropod peak. Tulp and Schekkerman (2001) for example showed that little stint Calidris minuta chicks that hatched when arthropods were already declining were less likely to be re-sighted than the ones born earlier, illustrating that a mismatch between hatching and the peak in food availability can have severe fitness effects (Meltofte et al. 2007a). The reason the plover chicks managed to achieve a high growth rate in 2011, despite hatching after the main arthropod peak, seems a short but intense flush of Bibio pomonae flies late in the breeding season. This flush occurred only in 2011, which relates to the specific ecology of the Bibio pomonae flies with mass occurrences every three to four years (Skartveit 1995).

Because of the late season flush in Bibio pomonae flies, the plover chicks do not experience a seasonal decline in food abundance, and thus we cannot consider this as a mismatch between hatching and the peak in food availability anymore, at least in such year. Intriguingly, the flush in Bibio pomonae flies might buffer possible effects of climate change in this particular case. A common effect of climate warming seems an advancement of the timing of the seasonal arthropod peak. However, in this particular case such advancement might have only a small or negligible effect on the growth of the plover chicks in years when mass emergence of Bibio pomonae flies occurs.

An increased mismatch between hatching and the peak in food availability might still have an important negative effect on the plover chick growth and survival in years without the Bibio pomonae peak. Thus, one possible effect of climate change could be strong cohort effects of years with and without Bibio pomonae mass emergence. It is unknown how this would impact the general trend of the species, i.e. whether sufficient relatively fit young are produced in the favourable years to compensate for the fewer and underdeveloped young being produced in the unfavourable years. Given the dominant effect of food availability rather than temperature on the growth of the plover chicks, we believe that a possible positive effect of climate warming, a reduction in thermoregulation costs (cf. McKinnon et al. 2013), is negligible compared to the changes in food availability.

They key question for our study system might be how the pattern of Bibio pomonae flies mass emergence will be affected by climate change. Qvenild and Rognerud (2017) indicate that in southern Norway mass swarming of Bibio pomonae has increased due to climate change, and that swarming occurs at higher elevations, which seems a favourable development for shorebirds breeding in the sub-arctic. It is unclear whether Bibio pomonae is at the same time also spreading to more northern altitudes, and thus whether arctic shorebirds could also profit from this additional food source. Certainly, predicting the precise effects of climate change on a species not only requires detailed ecological knowledge on prey species, but also how individual prey species might be affected by climate change.

Acknowledgements

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Supplementary material

Supplementary material 1. Estimates and standard deviation (sd) of growth parameters for all measurements per sex.

Variable	Growth parameters	Estimate ± sd	
		males	females
Weight	K	-0.085±0.000	-0.084±0.013
	t	14.648±0.902	17.025±1.168
	A	203.046±18.213	202.186±19.642
	c	15.104±6.862	19.455±3.944
Tarsus	K	-0.092±0.013	-0.064±0.010
	t	-14.815±1.996	-20.351±2.542
	A	43.239±0.515	43.867±0.823
Bill	K	-0.071±0.008	-0.056±0.007
	t	-6.553±0.666	-7.387±0.535
	A	22.351±0.655	23.640±0.949
Total head	K	-0.061±0.005	-0.050±0.004
	t	-11.368±0.657	-11.725±0.456
	A	60.901±1.012	63.650±1.306
Wing	K	-0.074±0.023	-0.082±0.028
	t	17.422±2.985	18.223±2.911
	A	215.943±46.931	202.756±48.128

Supplementary material 2. Models with residual growth as dependent variable. Significant variables are in bold. Standard deviation (sd), degrees of freedom (df) and statistical parameters (F and p values) are shown.

			Estimate ± sd	**df**	**F**	**p**
Older chicks	weight	intercept	-5.69 ± 2.72	137	0.02	0.87
		year	**1.19 ± 4.05**	**19**	**12.57**	**0.00**
		sex	**8.54 ± 3.16**	**19**	**7.47**	**0.01**
		age	0.07 ± 0.07	137	0.76	0.38
		biomass	**1.83 ± 0.30**	**137**	**48.83**	**0.00**
		year:age	**-0.61 ± 0.14**	**137**	**17.68**	**0.00**
	tarsus	intercept	-1.19 ± 0.35	139	0.04	0.82
		sex	**0.84 ± 0.42**	**19**	**4.77**	**0.04**
		temperature	0.05 ± 0.02	19	2.35	0.12
		biomass	**0.18 ± 0.03**	**139**	**18.17**	**0.00**
	total head	intercept	-0.53 ± 0.22	128	0.06	0.79
		sex	**0.69 ± 0.31**	**20**	**5.07**	**0.03**
		biomass	**0.14 ± 0.04**	**128**	**11.28**	**0.00**
	bill	intercept	0.86 ± 0.33	139	0.05	0.81
		year	**-2.06 ± 0.45**	**20**	**6.33**	**0.02**
		temperature	**-0.08 ± 0.02**	**139**	**3.96**	**0.04**
		biomass	**0.10 ± 0.03**	**139**	**14.47**	**0.00**
		year:temperature	**0.16 ± 0.04**	**139**	**15.80**	**0.00**
Younger chicks	weight	intercept	1.01 ± 1.82	51	0.05	0.81
		year	**-1.03 ± 1.74**	**21**	**5.09**	**0.03**
		sex	1.29 ± 1.17	21	1.19	0.28
		age	**-0.28 ± 0.16**	**51**	**11.52**	**0.00**
		biomass	0.07 ± 0.29	51	0.00	0.96
		year:age	-0.29 ± 0.25	51	1.36	0.24
	tarsus	intercept	-1.26 ± 0.44	54	0.04	0.83

		sex	0.52 ± 0.39	22	1.79	0.19
		temperature	**0.08± 0.04**	**54**	**5.68**	**0.02**
		biomass	0.10 ± 0.07	54	1.95	0.16
	total head	intercept	-0.18 ± 0.39	32	0.75	0.39
		sex	0.31 ± 0.36	12	1.10	0.31
		biomass	-0.03 ± 0.13	32	0.04	0.82
	bill	intercept	0.39 ± 0.48	51	0.85	0.36
		year	**-1.74 ± 0.72**	**22**	**11.37**	**0.00**
		temperature	-0.02 ± 0.04	51	0.03	0.85
		biomass	0.06 ± 0.06	51	1.69	0.19
		year:temperature	0.15 ± 0.09	51	2.29	0.13
All chicks	weight	intercept	-5.65 ± 2.08	213	0.01	0.92
		year	**2.24 ± 2.76**	**21**	**11.60**	**0.00**
		sex	**5.37 ± 2.34**	**21**	**5.01**	**0.03**
		age	0.20 ± 0.05	213	2.95	0.08
		biomass	**1.06 ± 0.22**	**213**	**26.32**	**0.00**
		year:age	**-0.76 ± 0.09**	**213**	**69.76**	**0.00**
	tarsus	intercept	-1.14 ± 0.31	217	0.00	0.97
		sex	0.66 ± 0.37	22	3.40	0.07
		temperature	**0.05 ± 0.01**	**217**	**4.79**	**0.02**
		biomass	**0.14 ± 0.02**	**217**	**22.73**	**0.00**
	total head	intercept	-0.48 ± 0.19	174	0.03	0.84
		sex1	0.52 ± 0.26	21	3.49	0.07
		biomass	**0.14 ± 0.04**	**174**	**12.51**	**0.00**
	bill	intercept	0.66 ± 0.26	215	0.85	0.35
		year	**-1.91 ± 0.37**	**22**	**10.39**	**0.00**
		temperature	-0.06 ± 0.02	215	1.38	0.24
		biomass	**0.09 ± 0.02**	**215**	**19.59**	**0.00**
		year:temperature	**0.15 ± 0.03**	**215**	**18.48**	**0.00**

Supplementary material 3. Model results using residuals change (residuals of differences in measurements between visits) as dependent variable. Significant variables are in bold. Standard deviation (sd), degrees of freedom (df) and statistical parameters (F and p values) are shown.

			Estimate ± sd	**df**	**F**	**p**
Older chicks	weight	intercept	-3.88 ± 0.96	124	0.00	0.94
		sex	**0.37 ± 0.32**	**18**	**5.19**	**0.03**
		temperature	**0.43 ± 0.09**	**124**	**10.02**	**0.00**
		biomass	0.16 ± 0.13	124	0.44	0.50
		precipitation	**-0.27 ± 0.06**	**124**	**16.83**	**0.00**
		year:precipitation	0.04 ± 0.05	124	0.85	0.35
	tarsus	intercept	-0.01 ± 0.02	139	0.05	0.81
	total head	intercept	-0.01 ± 0.05	110	1.74	0.18
		biomass	-0.01 ± 0.02	110	0.32	0.56
	bill	intercept	-0.05 ± 0.05	127	0.02	0.86
		biomass	0.02 ± 0.02	127	1.23	0.26
Younger chicks	weight	**intercept**	**-1.79 ± 0.77**	**57**	**4.47**	**0.04**
		sex	0.43 ± 0.41	22	1.92	0.18
		temperature	**0.19 ± 0.07**	**57**	**6.31**	**0.01**
		biomass	-0.04 ± 0.15	57	0.07	0.79
		precipitation	-0.12 ± 0.11	57	1.00	0.31
		year:temperature	-0.03 ± 0.06	57	0.26	0.60
	tarsus	intercept	-0.15 ± 0.15	64	0.93	0.33
		biomass	0.03 ± 0.08	64	0.44	0.50
	total head	intercept	-0.02 ± 0.08	34	0.08	0.77
	bill	intercept	-0.18 ± 0.12	58	0.24	0.62
		biomass	0.05 ± 0.04	58	1.73	0.19
All chicks	weight	intercept	-2.90 ± 0.65	190	1.06	0.30
		sex	**0.39 ± 0.25**	**22**	**7.45**	**0.01**

	temperature	**0.33 ± 0.05**	**190**	**15.69**	**0.00**
	biomass	0.06 ± 0.09	190	0.77	0.38
	precipitation	**-0.22**	**190**	**17.69**	**0.00**
	year:temperature	0.01	190	0.08	0.77
tarsus	intercept	-0.02 ± 0.02	212	1.25	0.26
total head	intercept	-0.02 ± 0.05	152	0.71	0.39
	biomass	0.00 ± 0.02	152	0.01	0.91
bill	intercept	-0.06 ± 0.04	191	0.01	0.89
	biomass	0.02 ± 0.01	191	2.44	0.11

Suplemmentary material 4. Mean measurements from chicks at hatching and fledging, and its proportion with breeding adults.

	Hatching (n=63)	**Date before fledging (n=6)**	**Breeding adult (n=37)**	**Proportion of adult size at fledging (%)**
Weight (g)	24.03±0.21 (n=60)	156.88±3.68	195.48±1.58	80.26
Bill (mm)	12.43±0.07	21.14±0.46	21.80±0.14	96.96
Tarsus (mm)	33.42±0.14	42.12±0.26	41.68±0.25	101.05
Total head (mm)	37.18±0.28 (n=10)	56.47±0.35	60.12±0.93	93.92
Wing (mm)		143.17±3.09	189.37±0.82	75.60

*****All data is from 2011, since in 2013 no chicks were observed fledging

CHAPTER 5

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 a life cycle of migrant birds are generally time-constrained. . Moult, together with breeding and migration are the most energetically demanding annual cycle stages, but 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 moult 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 that migrates mainly to Ireland and western UK. Moult 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 moult overlapped with incubation and presumably with chick rearing, in which females started on average 9 days later than males. Icelandic plovers overlapped moult with incubation to a larger extent and stayed in the breeding grounds until primary moult was completed. In contrast, continental birds only moulted the first 5-7 primaries at the breeding grounds and completed moult in S Sweden and The Netherlands. This overlapping, although rare in birds, can be understood from an annual cycle perspective. Icelandic plovers presumably need to initiate moult early in the season to complete moult 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 moult in the Eurasian Golden Plover.

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Introduction

Birds need to fit different events in their annual cycle in such a way that energy-demanding activities as breeding and moult coincide with periods of favourable environmental conditions that implies, at the same time, good nutritional conditions (Newton 2008). This might be especially problematic for migratory birds as (preparation for) migration is time-consuming and entails high energy expenditure, and thus migration 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 and/or energetic bottleneck (e.g. Buehler & Piersma 2008).

Birds organise their annual schedules in different ways, in which they particularly vary 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 (Dawson et al. 2000, Helm and Gwinner 2006, Noskov et al. 1999). 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 between different periods. They for example start to moult in the breeding area, then suspend moult during migration, and only complete moult in winter (e.g. Grey plover *Pluvialis squatarola* (Branson and Minton 1976). Among all the scenarios, the less 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 (e.g. Newton 2009, Remisiewicz 2011, Serra et al. 1999, 2006), we still do not fully understand what factors determine the schedule 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 generally be under strict endogenous control (Helm and Gwinner 2006, Pulido and Coppack 2004), individuals still seem to be flexible in the start and extent of moult. This flexibility might arise from timing constrains 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). Here 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. 2016). The Golden Plover is an interesting species in this respect because it is one of the rare examples of a species in which primary feather moult overlaps with breeding activities (Jukema 1982, Jukema et al. 2001). One major difference between the continental and Icelandic birds is that previous ringing studies suggest that Scandinavian birds may extend their wing moult over the first stages of their autumn migration, whereas Icelandic birds finish wing moult while still in the breeding area before the onset of autumn migration (Jukema et al. 2001, Lindström et al. 2010). We describe how moult is scheduled within the annual cycles of these two populations, including details on the speed of moult. Also, we describe differences in moult patterns between sexes. Subsequently we discuss how different moult strategies could have developed in relation to breeding and migration schedules and weather conditions during breeding and non-breeding season.

Materials and methods

Study species

The Golden Plover breeds from Greenland, Iceland and Faroes in the west, through north Fennoscandia, to Taymyr Peninsula in the east. The incubation and the chick rearing period each last 30 days. Both parents do incubate in equal bouts of 12h, but females leave the chicks when they are about two weeks old, while males care for them until they fledge. 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 Simons 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 (see 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 Pierce-Higgins 2002) or bownet-spring traps (Gratto-Trevor 2004). To reduce the risk at damaging the eggs the plover eggs were replaced by dummy eggs during catching. Birds were trapped mostly during the second and third weeks of incubation, to avoid the risk of nest abandonment. Female and male Golden Plovers share the incubation duties fairly equally, in which males typically incubates 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 sexes from the same breeding pair. In total 67 breeding birds were captured in N Sweden and 37 in Iceland (Table 1).

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”, see Jukema et al. 2001). Birds were lured to the net by calls and decoys. 108 plovers were captured on Iceland (Table 1).

Table 1. Numbers of adult Golden Plovers, by site, breeding status and sex, used in the 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	61
Female	19	0	23	16	0	0	42
Sex unknown	0	108	1	2	133	162	404
Total	37	108	67	50	133	162	507

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 of Lund (see 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 at migratory stopover or/and wintering site in The Netherlands. 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 Institute 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 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 (see Lindström et al. 2010, Jukema et al. 2001). Primary feather moult was described according to Ginn and Melville (1983), in which a score at 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 (Table 2). For each region, the start and end of moult and moult duration were estimated using the package “moult” version 2.0 (Erni et al. 2013) in R 3.3.2 (R Development Core Team 2016). 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 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 distribution departed from normal. For the breeding sites, separate moult models were ran for the different sexes, in order to be able to compare moult patterns between sexes. In addition moult models were ran in which data for the sexes was combined, in order to allow making comparisons between regions and populations.

Table 2. Actual and relative mass of individual primaries of Golden Plovers. Feathers were obtained from two trapping casualties in Lund, Sweden.

Primary	Actual mass (mg)	Relative mass (%)
P1	27	3.62
P2	32	4.29
P3	42	5.63
P4	51	6.84
P5	66	8.85
P6	82	10.99
P7	94	12.60
P8	107	14.34
P9	117	15.68
P10	128	17.16

The mean daily rate of the primary feather material growth (% PFMG/day) 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

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; $t_{35} = 2.18$, $p = 0.02$).

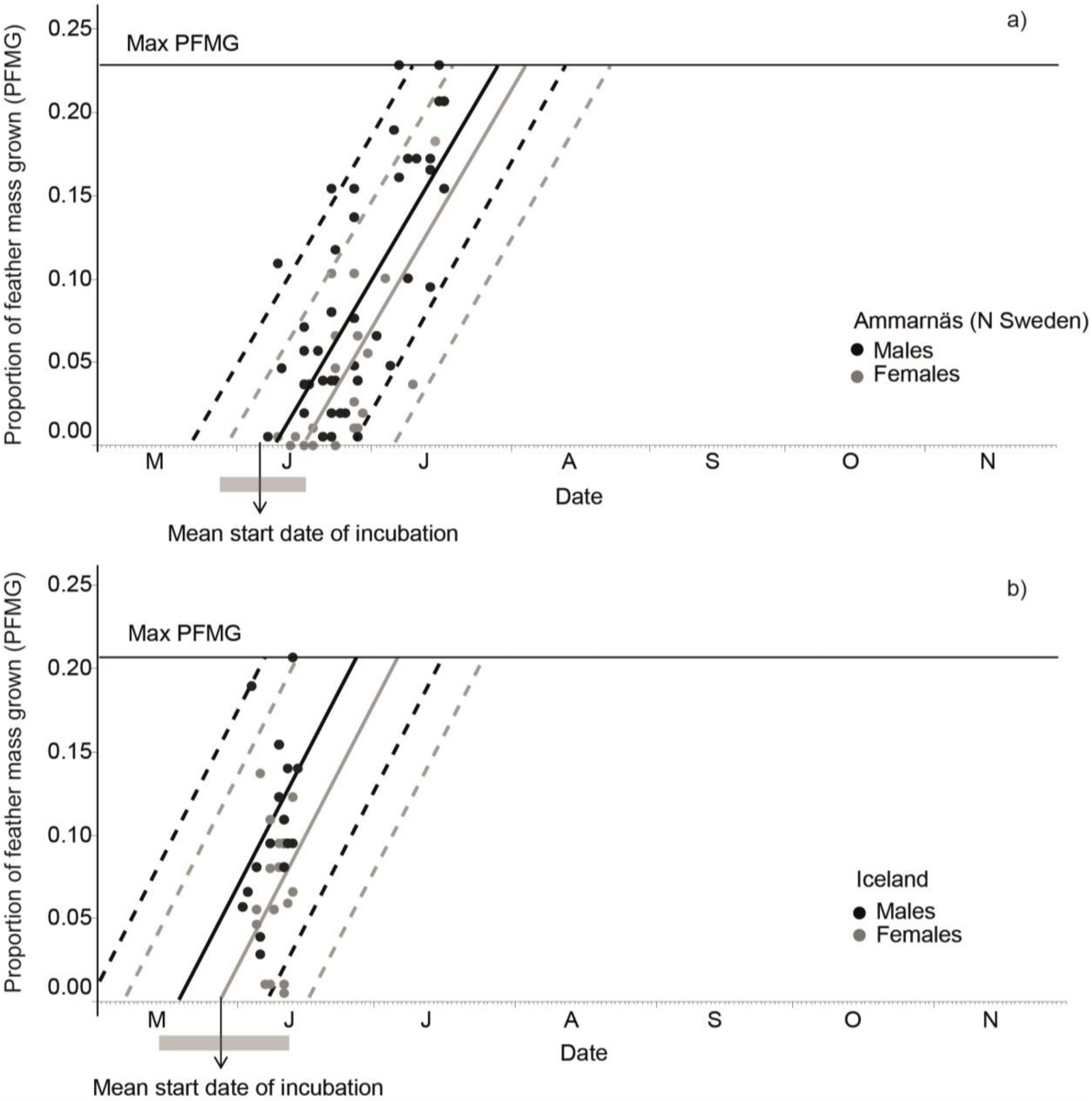
For Ammarnäs, a male with an advanced moult score (PFMG = 0.300) was considered an outlier. Timing of moult was subsequently estimated for a PFMG range of 0–0.228, for primaries P1–P5 combined. For Iceland timing of moult was estimated for a PFMG range of 0–0.206, for P1–P6 combined. For both populations, 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 days earlier than females in Ammarnäs and in Iceland (Table 3, Figure 1).

In Iceland, the incubation period started on average on the 28th of May (16th May–13th June). In Ammarnäs the incubation period started 8 days later, on the 6th of June (26th May–15th June) (Figure 1). This means that in Ammarnäs, males started primary moult on average 3 days, and females 12 days after the beginning of incubation (Figure 1). In Iceland, males started moult on average 9 days before the start of incubation, and females at the day incubation begun (Figure 1). In Ammarnäs the plovers reached a moult stage of PFMG = 0.228 on average on the 18th of July in males, and the 26th of July in females. In in both sexes, it took 47 days to reach this moult stage (Table 3, Figure 1). For Iceland, moult duration was estimated to be 45 days, 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 3rd of July, and females on average on the 13th of July (Figure 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 8 days earlier than the females, it is likely that males had progressed much further in their moult than females upon departure from Ammarnäs (Figure 1).

Table 3. Moult 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. Moult estimates are according to the best-fitted moult models with the sex as a covariate (Supplementary material Appendix 1, Table A1). 95% CI = 95% confidence interval, %PFMG/day = the estimated daily rate of the primary feather material growth. * = values refer to the analysed range, not to the moult duration of all primaries.

		Moult parameters				**Sample sizes**				
Region	**Sex**	**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-moult**	**In moult**	**Post-moult**	**Data type**	**%PFMG /day (SD)**
Ammarnäs (range 0-228)	**Males**	09 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 – 07 Jul			04 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)	03 Jul (19.5)	0	17	0	Type 3	0.46 (0.24)*
	Females	28 May (7.5) 06 May – 19 Jun			13 Jul (14.7)	0	20	0		

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.



Comparison of moult patterns between continental and Icelandic populations

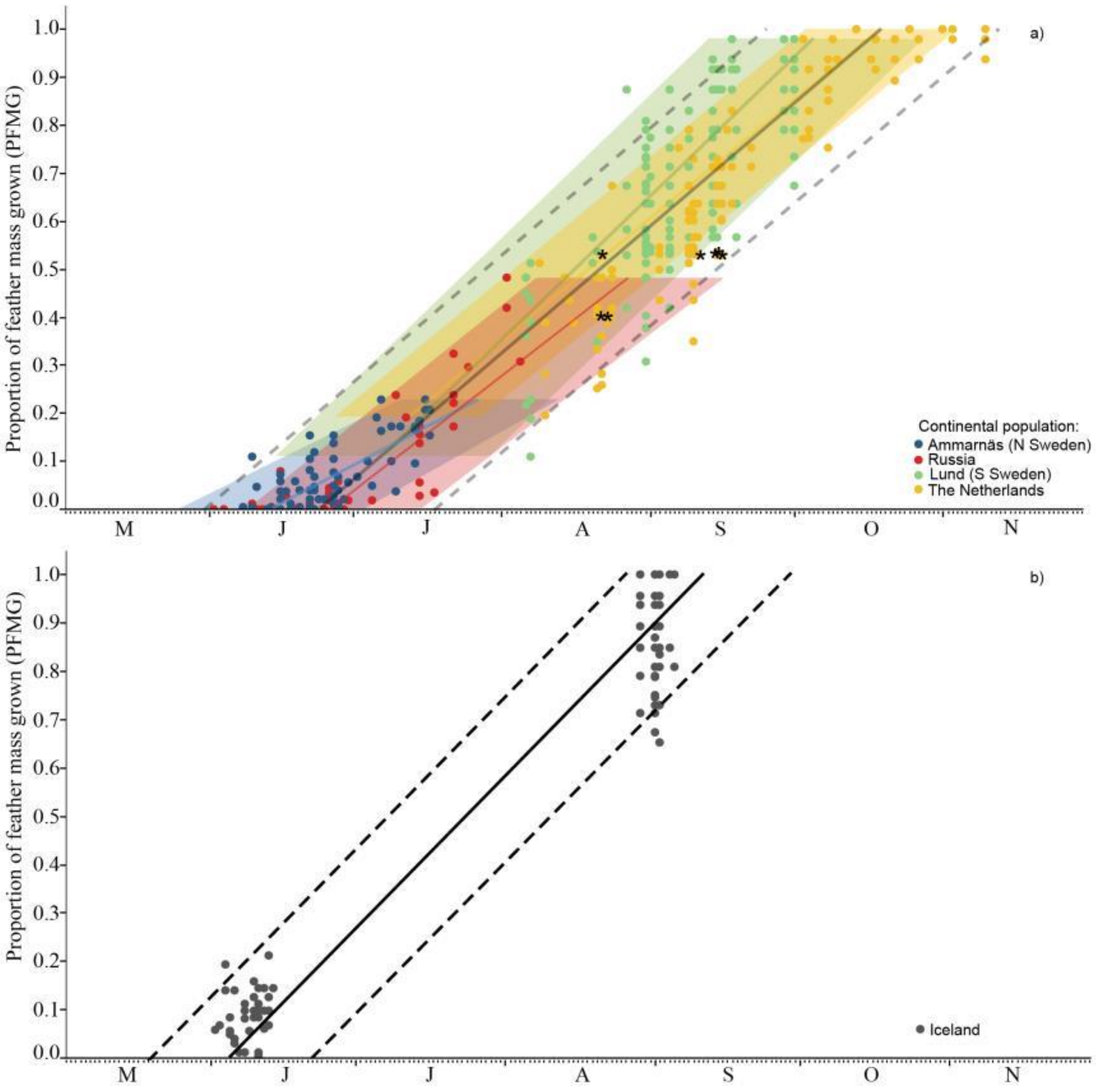
Data from the birds from Ammarnäs, Russia, Lund and The Netherlands were analysed jointly, assuming these birds belong to the same continental population. Moult is similar between both breeding populations (Scandinavian and Russia), moulting some primary feathers at the breeding grounds (Table 4), and 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 23rd of August and the 8th of September (Figure 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 4).

Table 4. Moult parameters for Golden Plovers estimated for the stages of moult conducted in each location, and for the Scandinavian and Icelandic birds for all primaries. 95% CI = 95% confidence intervals, %PFMG/day = the estimated daily rates of the primary feather material growth in the PFMG range of each population. * = difference in the moult rate between that and each other continental regions significant (Z-test, p<0.0001), ** = difference in the moult rate between the continental and the Icelandic populations significant (Z-test, p<0.0001).

	Moult parameters					**Sample sizes**				
Region	**PP in moult/ PFMG range**	**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-moult**	**In moult**	**Post-moult**	**Data type in moult model**	**%PFMG /day (SD)**
Ammarnäs (N Sweden)	P1–P6 0–0.228	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)
Russia	P1-P7 0-0.481	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 0.195–1	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)
The Netherlands	P3–P10 0.108–1	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)
Continental population	**P1–P10 0–1**	**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)**
Iceland population	**P1–P10 0–1**	**04 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)**

In Iceland, Golden Plovers stayed at the breeding grounds until primary moult was completed on average on the 12th of September (Table 4). No birds with suspended moult were observed in Iceland.

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.



Icelandic Golden Plovers started to moult 17 days earlier and completed moult 37 days earlier compared to the Scandinavian plovers. Overall, they took 19 days less to moult their primaries than the Scandinavian birds that split moult between different sites (Table 4, Figure 2). Similarly, moult was faster for Icelandic Golden Plovers than for Scandinavian birds ($Z = -5.14$, $p<0.01$, Table 4).

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 energetically costly (Newton 2008), also because flight feather moult impairs flight efficiency (Hedenström and Sunada 1999). However in some species, especially waders and raptors, moult and breeding overlap more extensively (Cramp and Simmons 1983, Ginn and Melville 1983, Kjellén 1994). Moulting primary feathers during incubation is a relatively rare strategy, but occurs in some migratory waders (e.g. dunlin *Calidris alpina* (Holmes 1971, Holmgren et al. 1993, 2001, Kania 1990) and purple sandpiper *Calidris maritima* (Morrison 1976, Summers 2004)), sedentary waders (e.g. the hooded plover *Thinornis rubricollis* (Rogers et al. 2014) and a sedentary passerine (pale-winged starling *Onychognathus nabouroup* (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 longer 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?

A prerequisite for overlap between moult and incubation is good nutritional condition (Newton 2008). 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 knows a much milder climate because of the effect of the Gulf Stream (Figure 3), and feeding conditions seem already favourable in 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 (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-hours 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 on 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 constrains them to start to 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 also birds with a more eastern breeding origin might 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 (Figure 3) the picture arises that the continental breeding 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 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, Podlaszczuk et al. 2017). None of the Golden Plovers captured in Ammarnäs had suspended moult, but as plovers were captured on the nest during the incubation period we actually have not sampled any bird that would have been close to departure on autumn migration. In S Sweden a few birds with suspended moult were captured (Figure 2). These birds had suspended their moult at a later stage than we would expect for N Scandinavian breeding birds, thus they might have originated from more eastern breeding grounds. In a sample of plovers shot in Denmark, a larger proportion of birds had suspended primary feather moult (Henriksen 1985). It is likely that these plovers were shot soon after arrival, whereas during catching a mixture of newly and earlier arrived birds would be sampled. If birds resume moult quickly after arrival, the probability to capture a bird with suspended moult might be small. No birds with suspended moult occurred in the sample of Dutch birds we analysed, but a small proportion of Golden Plovers with suspended moult were observed in a more extensive dataset from The Netherlands (Joop Jukema, pers.comm.).

Golden Plovers moulted their primary feathers almost two times faster in S Sweden and The Netherlands compared to Ammarnäs (Table 4). 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 is important to mention that during the stopovers, the plovers did not overlap energy demanding activities as the birds only started to 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.

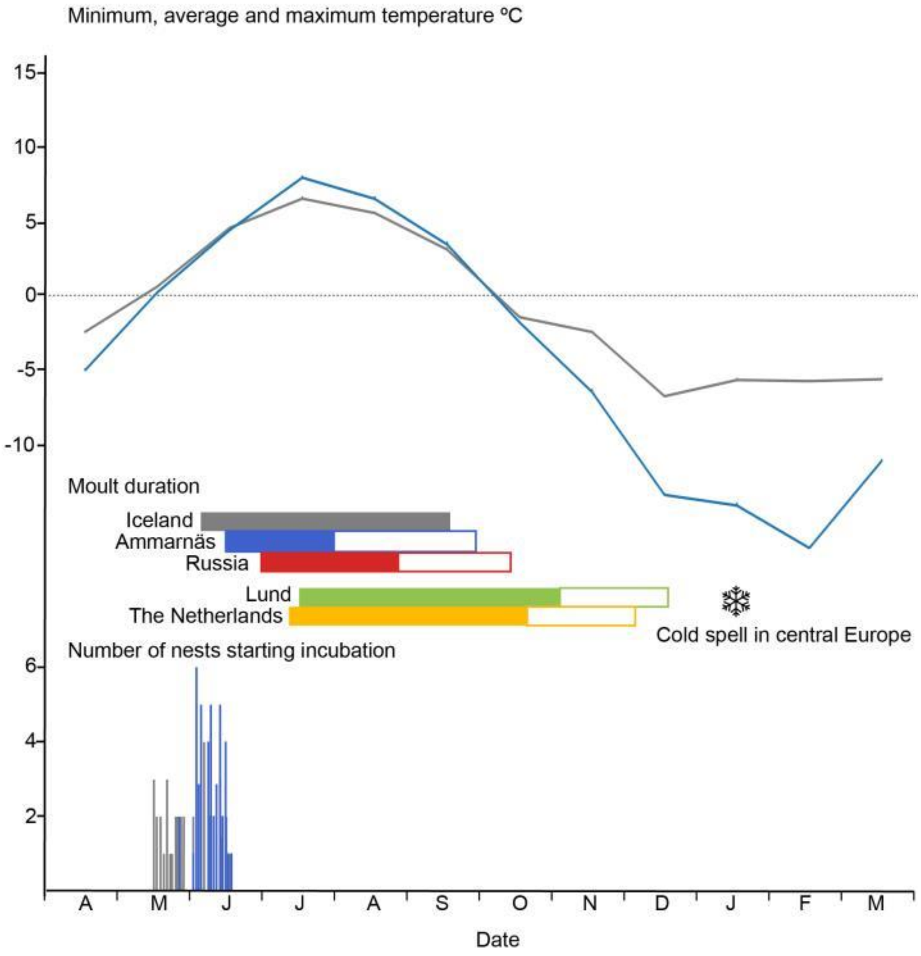
Different moult strategies of different plover populations

The Golden Plovers breeding on 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. Longer season of mild weather in Iceland enables the plovers to not only 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 days) among Palearctic waders (Cramp and Simons 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? Let us consider the hypothetical case of a plover moulting all primary feathers in Ammarnäs. If we assume it takes 100 days 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 (Figure 3). Thus there would be no time left to fuel for the first stage of migration, because fuelling rates of the plovers during stopover in S Sweden were about 0.5% of LBM per day, thus gaining about 25% of LBM would require 50 days (Lindström et al. 2010). It should be noted that food availability had decreased dramatically already at the end of July (Machin 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. to not moult primary feathers at the breeding ground at all? If we again assume that primary feather moult takes 100 days, a bird that would moult all primary feathers in Lund would not finish until mid- to end-December (Figure 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.

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 show the mean cold spell in central Europe.



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 also is little leeway in the schedule. Total duration of moult was estimated to be 119 days for the continental plovers, thus it seems that split moult takes more time than moulting all feathers at one location (moult took 100 days 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). To meet the energy demands of breeding, moult, and migration, it requires 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 1

Table A1. Models used to determine the effect of sex on moult parameters estimated for five primaries combined in adult Golden Plovers caught during breeding seasons 2010–2013 at Ammarnäs (N Sweden) (above) and Iceland (below). The models were ranked by Akaike's Information Criteria corrected for small cample (AIC_c), *df* is the number of parameters in a model, ΔAIC_c gives the difference in AIC_c from the best model, the Akaike weights (wi) assess the relative support that a given model has from the data compared with the other models. Best fitted models in bold face.

Model	**Moult parameters affected by the sex used as a covariate**	**Moult parameters assumed constant**	**df**	**AIC_c**	**ΔAIC_c**	**wi**
1	**start date**	**SD, duration**	**4**	**311.40**	**0.00**	**0.27**
2	duration	start date, SD	4	312.30	0.90	0.17
3	start date and SD	duration	5	313.84	2.44	0.08
4	start date, duration	SD	5	314.00	2.60	0.07
5	SD	start date, duration	4	313.75	2.35	0.08
6	SD, duration	start date	5	314.89	3.49	0.05
7	start date, SD, duration	none	6	316.52	5.12	0.02
8	none	start date, SD, duration	3	319.80	8.40	0.00

Model	**Moult parameters affected by the sex used as a covariate**	**Moult parameters assumed constant**	**df**	**AICc**	**ΔAICc**	**wi**
1	**start date**	**SD, duration**	**4**	**224.88**	**0.00**	**0.26**
2	start date and SD	duration	5	226.39	1.51	0.12
3	SD, duration	start date	5	226.40	1.51	0.12
4	start date, duration	SD	5	226.50	1.61	0.12
5	duration	start date, SD	4	227.17	2.28	0.085
6	none	start date, SD, duration	3	226.74	1.86	0.10
7	SD	start date, duration	4	229.08	4.20	0.03
8	start date, SD, duration	none	6	233.78	8.89	0.00

CHAPTER 6

Individual migration patterns of Eurasian Golden Plovers *Pluvialis apricaria* breeding in Swedish Lapland; examples of cold spell-induced winter movements

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Tracking studies normally focus on long-distance migrants, meaning that our understanding about short-distance migration remains limited. In this study, we present the first individual tracks of the Eurasian Golden Plover *Pluvialis apricaria*, a short-distance migrant, which were tracked from a Scandinavian breeding population using geolocators. In addition, Golden Plovers are known for their cold spell-induced winter movements, and this study provides some first individual tracking data on this type of movements. In three cases the plovers spent the winter in NW Europe and in four cases they departed during winter from NW Europe to spend the rest of the winter in Iberia or Morocco (one bird that was tracked during two subsequent migration cycles moved to Iberia in the first winter but remained in NW Europe during the second winter). The four winter departures were associated with a cold spell in NW Europe during which maximum temperatures dropped to freezing. Cold spell-induced winter movements were notably long and fast. The birds that remained at their NW European wintering site did not experience such cold spell. However, the plovers did not always move in response to freezing temperatures, as demonstrated by the individual that was tracked for a second season, when it experienced four cold spells at its wintering site in NW France without leaving. Little information was obtained about spring migration, but one bird had a prominent counter-clockwise loop migration pattern through E Europe. Due to their cold spell winter movements, Golden Plovers exhibit great flexibility in migration patterns, resulting in a notably large spread in final wintering areas.

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Introduction

An intriguing difference between short- and long-distance migrants is that the timing of migration of long-distance migrants is under endogenous control (Gwinner 1996, Berthold 1996), whereas short-distance migrants more often show facultative movements, i.e. only migrate when conditions deteriorate (Newton 2008). Facultative weather-induced escape movements can be rather spectacular in terms of the numbers of birds involved, and mass-migration events in response to cold spells and snowfall are for example known from Lapwings (*Vanellus vanellus*) and Eurasian Skylarks (*Alauda arvensis*) (Kirby and Lack 1993, Del Hoyo et al. 1996, Donald 2004, Newton 2008). Although weather-induced escape movements have been described in detail at the level of the population, little is known about the details of individuals taking part in these mass migration events, possibly as tracking studies normally focus on long-distance migrants (Strandberg et al. 2009b). Consequently, we have a rather limited understanding about the details of weather-induced escape movements such as for example the distances birds travel when pushed out by bad weather and whether and how long birds remain in their secondary wintering sites (Wernham et al. 2002). Here we aim to fill this lacuna by presenting the results of a tracking study of a short-distance migratory wader, known for its cold spell-induced winter movements (Jukema and Hulscher 1988, Kirby 1997, Yeatman et al. 1991), the Eurasian Golden Plover (*Pluvialis apricaria,* hereafter Golden Plover).

The Golden Plover is a medium-sized wader that breeds in N Europe on open moorland, montane heaths, and northern tundra, its distribution extending far into Siberia (Byrkjedal and Thompson 1998). They spend the winter mostly in West and Southwest Europe, often using agricultural habitats such as grasslands and arable fields (Byrkjedal and Thompson 1998, Gillings et al. 2007, Gillings et al. 2012). The Netherlands and S Scandinavia are two examples of prime non-breeding areas where Golden Plovers stay to complete their moult from the end of July until September/October (Poot et al. 1996, Jukema et al. 2001, Lindström et al. 2010). Plovers leave these areas when temperatures drop below freezing point, presumably as their main prey, earthworms, becomes unavailable (Jukema et al. 2001, Lindström et al. 2010). Only in very mild winters Golden Plovers may remain at these northern sites.

The general migration pattern of Golden Plovers has been inferred from ringing recoveries and observations (Jukema et al. 2001, Wernham et al. 2002, Fransson et al. 2008, Gillings et al. 2012, Saurola et al. 2013,). The birds arriving in northwest Europe in autumn seem to have a northern (Scandinavia) and north-eastern (Russia) origin. During autumn and winter, these birds move on, depending on the severity of the winter (Jukema and Hulscher 1988), to sites in the UK, France, Iberian Peninsula and even N Africa. Some British breeders remain in the UK in the winter whereas others travel as far as Morocco (Wernham et al. 2002). Golden Plovers originating from Iceland winter mainly in Ireland (Wernham et al. 2002). In spring, part of the birds wintering in S Europe and N Africa seems to follow a more eastern migration route via Italy to return to their northern breeding sites (Del Hoyo et al. 1996, Jukema et al. 2001).

In this paper we describe the migration patterns of seven Golden Plovers that we tracked using geolocators from a breeding population in Swedish Lapland. In our analyses, we focus explicitly on cold spell-induced winter movements by relating movements to local weather conditions (temperature). This study provides a first description of the migration patterns of a population of Golden Plovers breeding in N Sweden, and is a first study providing tracking data on cold spell-induced winter movements of Golden Plovers.

Materials and methods

Study system and fieldwork

Fieldwork was performed in the Vindelfjällen Nature Reserve, Ammarnäs, Sweden (65°59' N, 15°57' E) an area in Swedish Lapland characterized by open mountain heath tundra. Nests were found while walking through the area by locating incubating birds flushed from the nest or by watching adults returning to their nest from a high vantage point using a spotting telescope. For each nest, the fate was followed until eggs hatched, were predated or the nest was abandoned.

Adult Golden Plovers were caught on the nests using a walk-in trap (Yalden and Pierce-Higgins 2002) or a bownet-spring trap (Gratto-Trevor 2004). Trapping was mostly performed in the second and third week of incubation, in order to avoid the risk of nest abandonment. Trapped birds were fitted with colour ring combinations to facilitate individual identification in the field. Individuals were sexed on the basis of plumage characteristics (Byrkjedal and Thompson 1998).

In the 2011 breeding season 30 individuals (15 males and 15 females, including 13 pairs) were fitted with light-level geolocators. Geolocators were attached to a 10 mm high plastic colour ring on the leg of the bird with an additional 5 mm high plastic colour ring underneath (Figure 1). We used geolocator model Mk10 produced by the British Antarctic Survey (BAS), Cambridge, UK (www.birdtracker.co.uk). This geolocator weighed 1.1g and stored light data every 10 minutes. In the breeding seasons of 2012 and 2013 individuals carrying geolocators were recaptured.

Geolocator data analysis

Archived light-level data was downloaded from loggers and decompressed using BASTrak software ‘Communicate’ and ‘Decompressor’ (BAS). TransEdit2 (BAS) was used to inspect raw data and to identify times of sunrise and sunset, using a single light threshold value of 2. False sunrise and sunset events, i.e. caused by shading of the light sensor by for example feathers and vegetation (Lisovski et al. 2012), were removed by hand. Locations were calculated using Locator (BAS), in which estimates for latitude are based on the length of the solar day (or night) and estimates for longitude on the time of local solar noon (or midnight).

The sun angle corresponding to a light-level of 2 was found by Hill-Ekstrom calibration. This procedure is based on the effect that the error in latitude increases with an increasing mismatch between true and used sun angle, in particular near periods of equinox (Ekstrom 2004, Lisovski et al. 2012). Hill-Ekstrom calibration was performed for stationary periods that included an equinox. We chose the sun angle that minimized the difference in the estimate for latitude just before and after equinox. In the case the bird had moved during equinox we picked the sun angle that minimized the variation in latitude. This single sun angle was subsequently used to calculate positions throughout the rest of the year.

Stationary periods were identified by inspecting plots of latitude and longitude over time, alongside with plots of tracks on a map. To identify stopovers we mainly relied on patterns in longitude as the error in longitude is relatively small (Fudickar et al. 2012), and its estimation is not affected by calibration or equinox. Movements between stopover sites can readily be identified from plots of longitude over time (supplementary material), as the plovers' general migration axis has a SSW orientation, i.e. birds only rarely move due south or due north. Furthermore, movements between stopover sites were notably fast, thus it was straightforward to recognize different stationary periods. Mean coordinates were calculated for each stationary period.

Data analysis

Cold spell-induced winter movements were defined as movements from the wintering site in NW Europe (see results), that were advanced by a notable drop in temperature. For the individuals that made a cold spell-induced winter movement, autumn migration was subdivided in two parts: 'regular' autumn migration and 'cold spell-induced winter movement'. Regular autumn migration includes all movements from the departure from the breeding area until arrival to the NW European wintering site. Cold spell-induced winter movements include all movements from the departure from the NW European wintering site until arrival to the wintering site in S Europe / N Africa (see also results).

Travel distances were calculated as loxodrome distances between subsequent stationary sites, i.e. not considering exact flight paths and excluding local movements on stopovers. Duration simply was the time between departure and arrival (e.g. for regular autumn migration the time from the departure from the breeding site to arrival to the NW European wintering site), and migration speed was subsequently calculated by dividing total distance by total duration. Temperature data (daily minimum and maximum temperature) for the different stationary sites were obtained from the nearest weather stations from www.wunderground.com. Differences in frequencies (e.g. return rates of plovers carrying geolocators and plovers fitted with colour rings only) were compared using Chi-square tests. Differences in performance (e.g. timing of migration, migration speed, latitude of wintering site) between sexes, seasons and successful versus unsuccessful breeders were explored by t-tests.

Results

Return rates

In 2012, at least 17 out of 30 Golden Plovers fitted with geolocators were observed in the study area. The return rate of geolocator-birds (57 %) was similar (Chi-square=0.07, df=1, P=0.78) to the return rate of individuals not fitted with geolocators but only carrying colour rings (52 %, 10 out of 19 birds). In 2013, there were no extra observations of individuals carrying geolocators different from 2012. Nine out of the seventeen birds seen in 2012 (53%) were seen in the study area and all nested. Although a fairly good sample of birds carrying geolocators returned to the study area we had great difficulties in recapturing these birds as breeding conditions in the two seasons we tried to recapture birds were very unfavourable, and nest predation pressure was very high. In total only seven geolocators could be recovered, four in 2012 and three in 2013.

Three of these geolocators had been placed on males and four on females. Individual #1 and #7 (Figure 2 and Table 1) were a breeding pair in 2011 but bred with other partners in 2012. Nest fate in 2011 varied between geolocator birds. Four individuals bred successfully, two birds abandoned their nest (pair of the same nest), and one nest was predated. Successful nests hatched between 30 June and 10 July.

Geolocator issues

From the seven geolocators that were retrieved, four contained incomplete data as the batteries had failed prematurely. Loggers had failed on 2 February, 4 March, 4 March and 8 March respectively. Two of the loggers that did not fail prematurely contained data for a full annual cycle and one logger had data of two full annual cycles. In total we obtained partial or complete data for eight migration routes (Figure 2 and Table 1).

One of the geolocator-birds (ID #4, Table 1) was observed at its wintering site at Cley Marshes NWT Reserve, UK (52°57' N, 1°3' E) from 18th November 2011 to 2nd January 2012 and once again on the 4th November 2014 at the same area (David and Pat Wileman, pers. comm). Before arriving at this site, this bird made a stopover in Denmark from 11 August – 1 Nov (Figure 3). Equinox occurred during this stopover on Denmark, hence the Hill-Ekstrom calibration was conducted for this site. The obtained sun angle (-1.4°) was used to calculate the position of the bird during the rest of the year, which placed the wintering site just 50 km to the north of where the bird was observed.

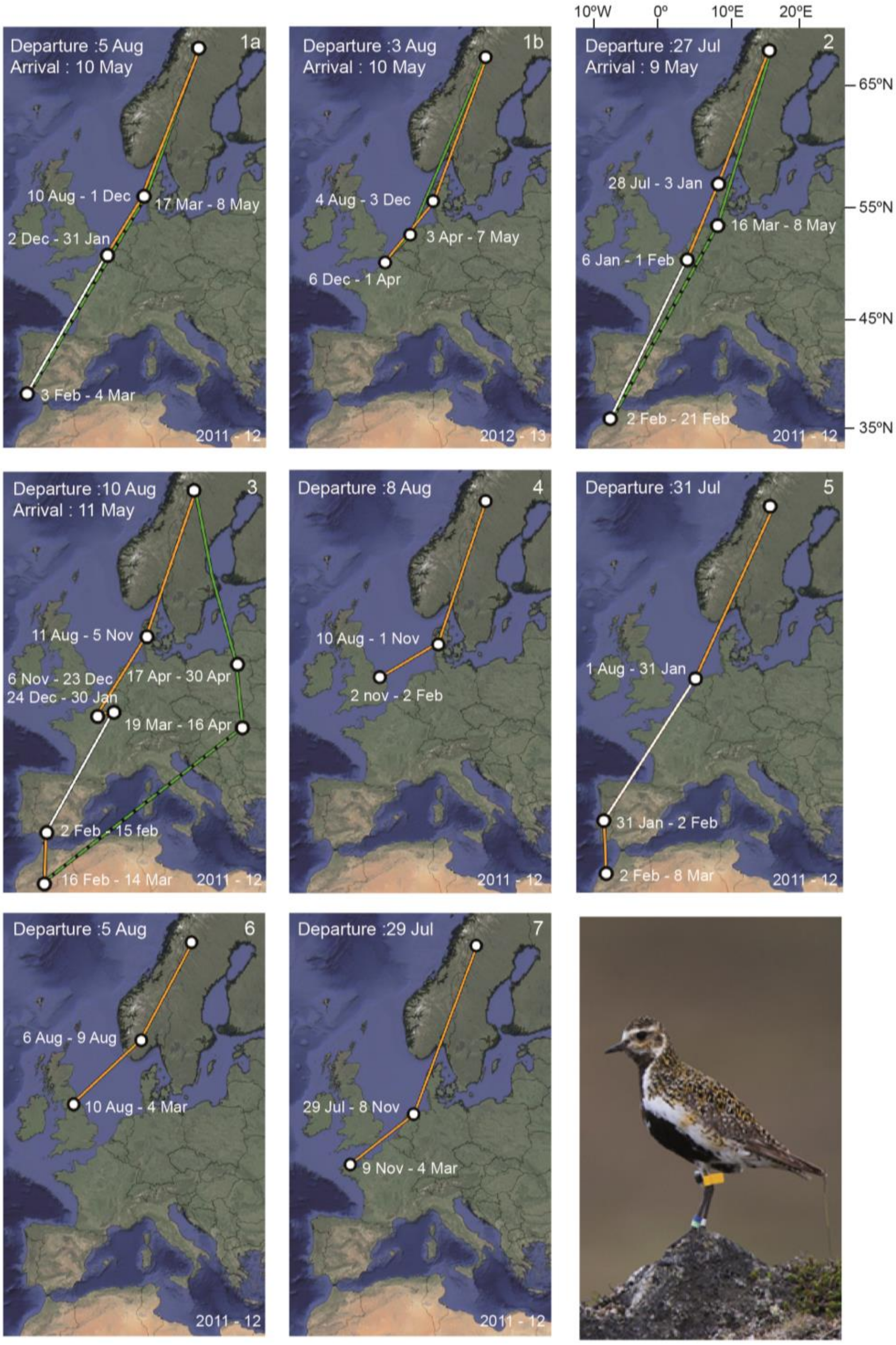

Figure 1. Migration routes of Golden Plovers deployed with geolocators. Orange lines refer to autumn migration, green lines to spring migration, and white lines to cold spell movements. Circles refer to stopovers and its duration is specified. Dashed lines refer to parts of the migratory movements that were uncertain due to interference by equinox. Question marks along dashed lines indicate that somewhere along this track stopovers were made, but the exact location is unknown (duration is specified). Each map correspond to a different

individual except map 1a and 1b, which refers to two subsequent migration of the same individual. Map source: QGIS open plugin Google Satellite.

Table 1. Summary of migration parameters for each individual. See main text for details about how different parameters were calculated. Values in Italic were not included in the calculation of averages.

ID	**1a**	**1b**	**2**	**3**	**4**	**5**	**6**	**7**	**average**
General information									
Ring number	-434	-434	-408	-419	-420	-430	-432	-433	
Sex	male	male	female	male	male	female	female	female	
Breeding success before migration	fail	-	success	success	fail	success	success	fail	
Date nest failed or hatched	2 Jul	-	1 Jul	30 Jun	27 Jun	10 Jul	10 Jul	2 Jul	
Tracking season	‘11-‘12	‘12-‘13	‘11-‘12	‘11-‘12	‘11-‘12	‘11-‘12	‘11-‘12	‘11-‘12	
Date logger failure	-	-	-	-	2 Feb	8 Mar	4 Mar	4 Mar	
Autumn migration (breeding ground until wintering site NW Europe, i.e. excluding cold spell movement)									
Departure from breeding area	10 Aug	4 Aug	28 Jul	11 Aug	7 Aug	1 Aug	6 Aug	28 Jul	4 Aug
Distance movement 1 (km)	1229	1265	1004	1180	1171	1519	813	1483	1208
Stopover Scandinavia	10 Aug- 1 Dec (113d)	5 Aug- 3 Dec (121d)	28 Jul – 6 Jan (161d)	11 Aug – 6 Nov (86d)	11 Aug – 1 Nov (82d)	-	6 Aug- 10 Aug (4d)	29 Jul – 8 Nov (101d)	100d
Distance movement 2 (km)	532	658	826	1067	617	-	822	773	756
Wintering site NW Europe	2 Dec- 1 Feb (61d)	6 Dec- 1 Apr (117d)	6 Jan- 1 Feb (26d)	6 Nov- 31 Jan (84d)[1]	2 Nov- *2 Feb* (-)[2]	1 Aug- 31 Jan (183d)	10 Aug- *4 Mar* (-)[2]	9 Nov- *4 Mar* (-)[2]	94d
Total duration (d)	114	124	162	87	87	(1)	(4)	104	85[3] / 113[4]
Total distance (km)	1761	1923	1830	2247	1788	(1519)	(1635)	2256	1870[3] / 1968[4]
Migration speed (km/d)	15.4	15.5	11.3	25.8	20.5	(1519)	(408.7)	21.7	255[3] /18.4[4]
Cold spell movement									
Departure date	1 Feb		1 Feb	31 Jan		31 Jan			31 Jan
Distance (km)	1834	-	2023	1569	-	2555	-	-	1995
Wintering site S Europe/N Africa	3 Feb- 4 Mar (30d)	-	2 Feb- 21 Feb (19d)	2 Feb- 13 Mar (39d)[5]	-	2 Feb- *8 Mar* (-)[6,2]	-	-	29
Duration (d)	2	-	1	2.5	-	1	-	-	1.3
Travel speed (km/d)	917.3	-	2023	628.1	-	2555	-	-	1531
Spring migration									
Departure from wintering area	4 Mar	1 Apr	7 Mar	13 Mar	-	-	-	-	3 Mar[8] /1 Apr[9]
Arrival at breeding area	10 May	10 May	9 May	11 May	-	-	-	-	10 May[8] /10 May[9]
Total duration (d)	67	39[7]	63	59	-	-	-	-	67.7[8] /39[9]
Total distance (km)	3597	1918[7]	3885	5087	-	-	-	-	4190[8] /1918[9]
Migration speed (km/d)	53.7	49.2[7]	61.66	86.2	-	-	-	-	67.2[8] /49.2[9]

Notes:
1. Actually two very nearby stationary periods: 6 Nov-23 Dec and 24 Dec-31 Jan
2. Logger failed
3. Average including two autumn migrations without longer stopover (i.e. including ind. 5&6), n=8
4. Average excluding two autumn migrations without longer stopover (i.e. excluding ind. 5&6), n=6
5. Consists of two parts: after cold spell movement the bird arrived in S Spain, where it stays from 2 Feb-15 Feb (13d). Final wintering area is in Morocco (16 Feb-13 Mar).

6. Consists of two parts: after cold spell movement the bird arrived in Portugal, where it stays from 31 Jan-2 Feb (2d). Final wintering area is in Morocco (2 Feb-8 Mar).
7. This individual did not make a cold spell movement, so spring migration started from NW France
8. Average for individuals migrating from wintering site in S Europe/N Africa, n=3
9. Average for individual migrating from wintering site in NW Europe, n=1

General migration patterns

Golden Plovers left the breeding area between 28 July and 11 August (Table 1). Departure date differed between sexes (t=-3.46, df=6, P=0.01, females departing on average 6 days earlier than males), but not between successful and failed broods (t=0.35, df=6, P=0.74). From the breeding site, the plovers moved SSW to SW to stopover sites in Norway (n=1), Denmark (5) and the Netherlands (1) (Figure 1). The exception is a bird (ID #5) that travelled directly from the breeding site to its NW European wintering site in the Netherlands, without making an additional stopover in Scandinavia. Autumn stopover sites were used for on average 100 days (range 4-161 days). In November – beginning of January the plovers left the stopover sites and made relatively short movements (average 756 km) to wintering sites in NW Europe in the UK (n=2) and Belgium/NW France (n=4). In addition, the NW European wintering site of individual #5 was located in the Netherlands. Autumn migration to the wintering sites in NW Europe for the individuals that made a prolonged stopover (i.e. excluding individuals #5 and #6), took on average 113 days. Average migration distance was 1968 km, resulting in an average migration speed of 18.4 km/d (Table 1).

In four cases, plovers left NW European wintering sites as a response to a sudden decline in temperature (see below). Final wintering sites of the latter individuals were located in Portugal (n=1) and Morocco (n=3) (Figure 1). In two cases the cold spell-induced winter movements consisted of two stages including short additional stopovers in Portugal and S Spain (Figure 1). Cold spell movements were notably fast, on average 1531 km/d. Final winter location latitude did not differ between sexes (t=-0.006, df=6, P=0.49).

Only four spring migration tracks were obtained from three different individuals, which included three spring migrations from wintering sites in Iberia/Morocco and one spring migration from a NW European wintering site (Figure 1). In all cases, the birds made at least one stopover, located in Denmark (1), the Netherlands (1), NW Germany (1), Romania (1) and Poland (1). These stopovers lasted 14 to 54 days (on average 37 days). No reliable information was obtained from the first part of the spring migration journeys as the birds initiated migration very close to the spring equinox, although using longitude data it is known that both individuals #1a and #2 made two stopovers during that period (Figure 1). In three cases, the spring migration route was very similar to the autumn migration route. In contrast, one individual (ID #3) followed a much more eastern route, reaching a longitude as far east as 23° E. This was the only bird approaching the breeding area from the southeast, possibly crossing the Baltic Sea. Birds returned to the breeding site between 9 and 11 May.

Spring migration for the three travels from Iberia/Morocco took 59-67 days, which was longer than the travel from the wintering site in NW Europe (39d), but this individual travelled a considerably shorter distance (1918 versus 4190 km). Subsequently, spring migration speeds were similar for the birds travelling from Iberia/Morocco (67.2 km/d) and the bird travelling from NW Europe (49.2 km/d). Migration speeds were higher during spring compared to autumn ($t=-5.6$, $df=8$, $P<0.001$).

The individual male tracked during two subsequent years (Figure 1, individual 1a and 1b) varied in its migration pattern between years. It used the same initial stopover site in autumn, but only in 2011/2012 it was pushed out by a cold spell, and wintered, in the end, in Portugal. In 2012-2013 the bird left the stopover area before temperatures dropped (see below), and moved to a much closer wintering site in NW France.

Timing of movements in relation to temperature

When the birds left the breeding area in late summer, temperatures were still relatively high, not reaching zero degrees. During the prolonged stopovers in Scandinavia (n=5) and the Netherlands (n=1, individual 7), minimum temperatures occasionally dropped below freezing point, but not maximum temperatures (Figure 2), and these stopover sites were left before maximum temperatures went down. At the NW European wintering sites temperatures were very similar to the temperatures experienced at the stopover sites. At the first occasion of a cold spell, occurring at 30 January - 1 February 2012, when maximum temperatures dropped rapidly to freezing point, the birds wintering in the Netherlands (n=1), Belgium (n=2) and NW France (n=1), left the wintering site and made a long and fast cold spell movement (Figure 1,2).

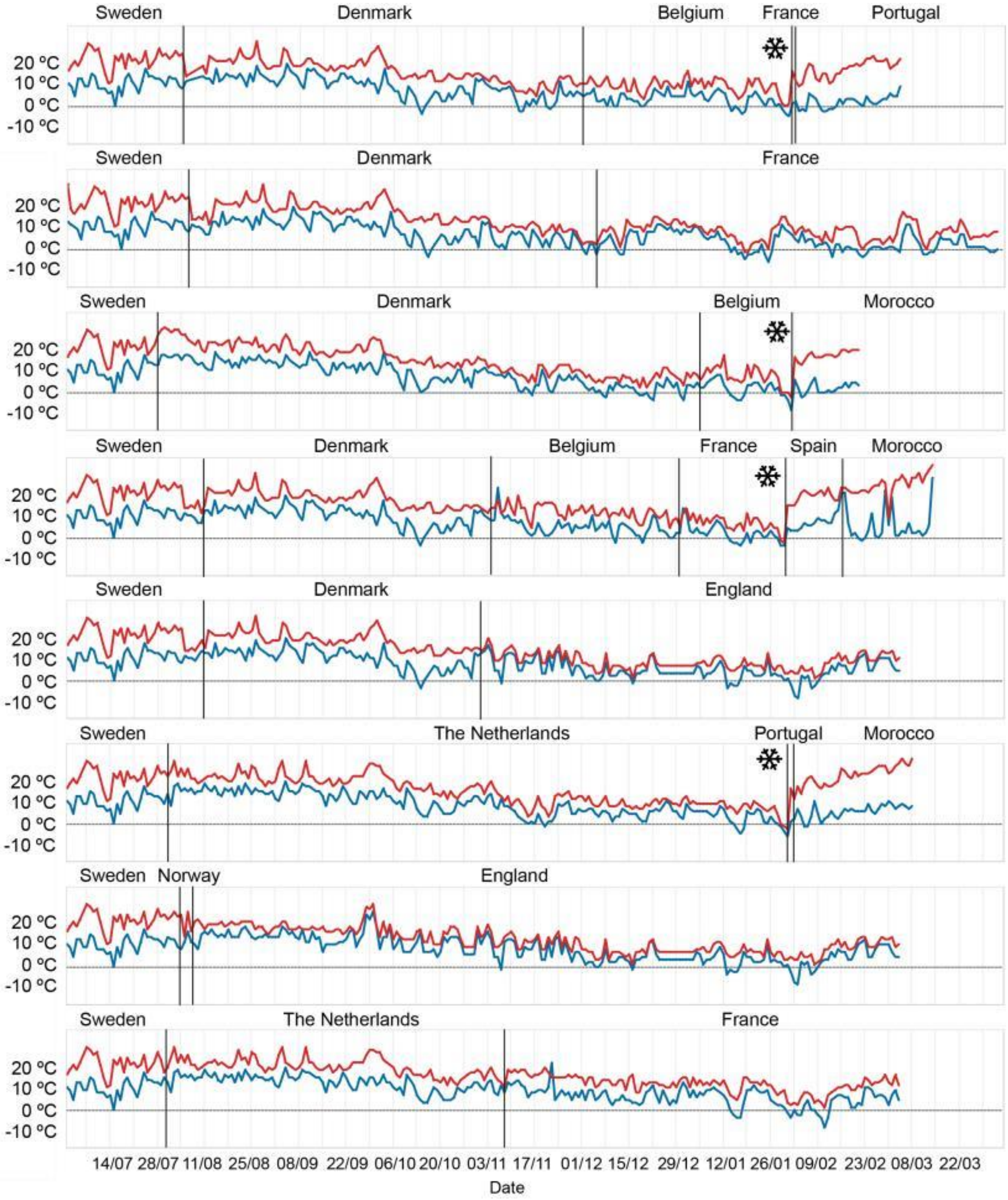

Figure 2. Minimum (blue) and maximum (red) temperatures as experienced by different individual Golden Plovers throughout their annual cycle, for autumn and winter. Vertical lines indicate the movement to the subsequent stationary site. Snow crystals mark the movements we considered to be cold spell-induced winter movements (see main text).

The birds wintering in England (n=2) and W France (n=1) experienced milder conditions during this period, in which maximum temperatures did not drop below zero degrees (Figure 2), and these individuals remained at their NW European wintering sites. For these individuals, temperatures remained relatively mild throughout the winter, i.e. never really dropping below freezing point. For 2013, data from only one individual was obtained (1b). During its stay at its NW European wintering site in NW France the individual experienced at least four cold spells in which maximum temperatures dropped to freezing. In two cases this appeared before the beginning of February, i.e. before the period the cold spell movements occurred in 2012. Despite these cold spells, the bird did not leave this wintering area.

Discussion

General migration patterns

The annual movements of the seven Golden Plovers we successfully tracked using geolocators confirmed ideas about general migration patterns of Scandinavian Golden Plovers as had been inferred from observations and ring recoveries (Jukema et al. 2001, Gillings et al. 2012). After the breeding season, the plovers fitted with geolocators moved to sites in NW-Europe for a stopover. Lindström et al. (2010) intensively studied Golden Plovers during their autumn stopover in S Sweden, which revealed that a main function of these stopovers is to moult flight feathers, suggesting that these are key high-quality stopover sites for plovers. Based on observations on individuals fitted with radio transmitters, they estimated that the plovers would stay for at least 80 days (i.e. mean for birds fitted with transmitters in August), which is slightly less than the average of 100 days as observed in this study. Importantly, Lindström et al. (2010) suggest that the plovers leave the stopover site in S Sweden in October-November in response to the first prolonged period of ground frost. Our results indicate that these stopover sites instead are left before the occurrence of cold spells. However, this might simply be an effect of the particular year as in winter 2011-2012 a real cold spell did not occur in NW Europe until the end of January (see below).

One of the novelties of the current study is that we mapped migration patterns of Golden Plovers at the level of the individual bird. This enabled us to get more reliable estimates of for example stopover durations (cf. above) and migration speeds, which is difficult if not impossible on the basis of observations of (colour) ringed birds (Strandberg et al. 2009a). Overall migration speed in spring and especially autumn was notably low, as expected for a short-distance migrant (see e.g. Strandberg et al. 2009b). In addition, tracks of individual birds provide an unbiased picture of migration patterns, in contrast to ring recoveries which are strongly biased due to variation in reporting probability (Strandberg et al. 2009a). This is especially true for Golden Plovers, which are studied extraordinary intensively in the Netherlands (see Jukema et al. 2001), meaning that the probability that a plover is reported from the Netherlands is relatively high. Thus, from ringing recoveries it appears that the Netherlands is the single most important non-breeding area for Golden Plovers, and although the Netherlands in fact is very important for plovers, its relative importance certainly is overestimated on the basis of ring recoveries. For example, ‘only’ three out of the seven plovers we tracked with geolocators actually visited the Netherlands, which is less than one might had expected on the basis of ring recoveries (Jukema et al. 2001). The unbiased picture of migration patterns of the Golden Plovers fitted with geolocators also revealed that some of the Scandinavian breeding birds use an eastern migration route in spring. This is new information as it hitherto was believed that birds returning via the eastern route were Russian breeding birds (Jukema et al. 2001). The downside of geolocator studies is that sample sizes typically are small, as in this study, making it difficult to judge how representative observed patterns really are for the whole population.

Weather-induced movements

In four out of eight cases, the plovers left their NW European wintering site in response to a notable sudden drop in temperature, in which also maximum temperatures dropped to freezing. These movements we considered to be “cold spell escape movements”. Thus part of the plovers seems to stay in northern continental Europe until they are pushed out by harsh winter weather, possibly because food availability is reduced when the soil freezes (Kirby and Lack 1993). Contrary to the suggestion by Fuller and Youngman (1979), i.e. that birds would return to the northern sites as soon as conditions improved again, plovers remained at southern sites throughout the rest of the winter. Individuals that stayed in locations with a milder winter climate (e.g. England), did not experience severe cold spells and remained in these relatively northern areas throughout the whole winter.

The interesting character of cold spell escape movements was that they were long. Final wintering sites of the individuals that made cold spell escape movements were located in Iberia and Morocco. Other movements, not induced by dropping temperatures, were much shorter, bringing the birds to more northern final wintering sites in England and N France. This difference is nicely illustrated by individual 1, for which we obtained tracks for two subsequent years. In 2011 the bird was pushed out by cold weather and it finally wintered in Morocco. In the subsequent year, it did not make a cold spell escape movement and wintered in NW France.

We want to stress that most of the movements between staging sites were not related to a drop in temperature. In other words, Golden Plovers frequently move for other reasons than escaping winter weather, and possible factors involved are for example competition, predation risk, and local changes in food availability (Alerstam and Lindström 1990; Newton 2008). Moreover, we would like to highlight that plovers did not always move when a cold spell occurred. For example individual #1 did not leave its wintering site in NW France in winter 2012/2013, despite the fact that four cold spells occurred during this period. It is unclear why the bird did not make a cold spell movement, but a possible explanation could be that local temperatures dropped too little to induce a movement. Alternatively, plovers might only respond to cold spells within a certain time window of the annual cycle, but this is an unlikely explanation in this particular case as the cold spells occurred around the time this individual made a cold spell movement in the previous winter.

Due to the fact that some individuals made long cold spell-induced escape movements whereas other did not, the spread in final wintering areas is remarkable. Clearly, the potential wintering range for this breeding population is large, leaving little room for strong migratory connectivity between breeding and wintering populations (Webster et al. 2002), thus we might expect that the winter distribution of breeding birds from the UK, Scandinavia and Russia strongly overlaps.

The fact that the plovers responded instantly to a cold spell suggest that they are fully prepared to leave, i.e. carrying around sufficient fat stores during the winter to make these notably long and fast movements. Jukema et al. (2001) provided data on the body weights of Golden Plovers throughout the winter in the Netherlands and indeed showed that Golden Plovers are heavier in November-January (230-240g) compared to August-September (190g). Piersma et al. (2003) noted that mid-winter weights of plovers have decreased over time (maximum weights decreased about 30g), which were attributed to an increase in avian predators. This suggests that it possibly has become more difficult for Golden Plovers to make the long cold spell-induced winter movements.

Conclusions

Using geolocators, we successfully tracked a sample of Golden Plovers breeding in Swedish Lapland, providing some first data of the migration pattern of this short-distance migrant and on its cold spell-induced winter movements. Because of these long winter movements, the migration system of Scandinavian Golden Plovers includes both stopover and wintering sites in NW Europe, as well as wintering sites in S Europe and N Africa. These southern wintering areas must be important for this population, especially or even exclusively so in years when temperatures in NW Europe drop below freezing. This flexibility in the migratory behaviour of Golden Plovers and the apparent ease of the species to perform rapid movements to southern staging areas in relation to cold spells are important aspects of their migration strategy, and possibly of the migration strategy of short-distance migratory waders in general.

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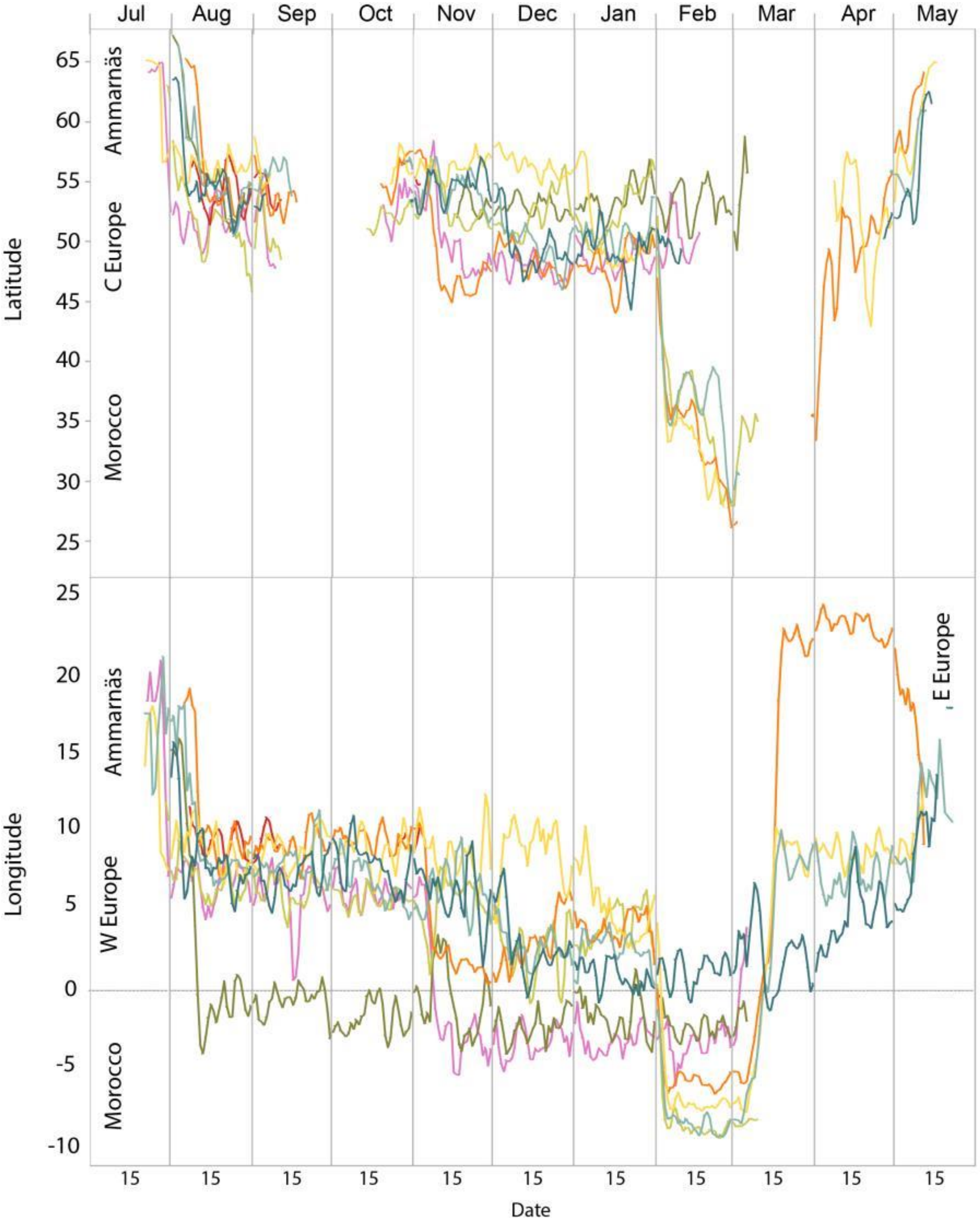
Supplementary material

Figure 1. Latitude and longitude of each migration route over time. Dark blue 5145434 (1b), light blue 5145434 (1a), yellow 5145408 (2), orange 5145419 (3), red 5145420 (4), light green 5245430 (5), dark green 5245432 (6), pink 514543 (7).



CHAPTER 7

General discussion

Paula Machín

Benefits and challenges of breeding in the *Subarctic*

Introduction

Waders occur everywhere on the globe, and breed in a variety of habitats from tropical areas to the poles. Wader species thus experience a high diversity in climate and seasonality, from warm climates with low seasonality in tropical areas to cold climates with high seasonality in the arctic. In the arctic, waders are the most dominant bird group of birds breeding (Järvinen and Väisänen 1978, Boyd and Madsen 1997, Lindström and Agrell 1999). They thus seem well adapted to cold weather conditions and short breeding seasons. By being so they face high energetic demands to cope with harsh weather conditions while produce eggs, incubate and rear the chicks, the already most energetically demanding efforts in a bird annual cycle (Piersma et al. 1996a, 2003, Newton 2008). On the other hand, in temperate and tropical areas they have more leeway in their breeding schedules.

I studied waders, and particularly the Golden Plover, in a subarctic breeding area. In this region, environmental conditions are intermediate to arctic and temperate areas. Weather is less extreme in comparison to the Arctic and the time constraint of a short breeding season is less rigid. However, seasonality is higher and the breeding season is shorter in comparison to temperate areas (Figure 1).

The reason I wanted to study waders in the Subarctic is that surprisingly little is known about their ecology, despite subarctic ecosystems are threatened by climate change (IPCC 2014). Snow cover upon arrival and predation of eggs and young are the two main factors that seem to dictate breeding success at subarctic latitudes. In the Subarctic, the amount of snowfall during winter is highly variable between years and under a climate change scenario it is predicted to become even more variable with more frequent springs with late snow melt (Callaghan et al 2011).

In this concluding chapter I aim to describe benefits and challenges of breeding in the Subarctic by comparing it with temperate and high arctic breeding sites. I discuss latitudinal variation in predation rate, chick growth rate, food availability, and flight feather moult. Finally, I summarize ideas about how climate change could affect the subarctic ecosystem.

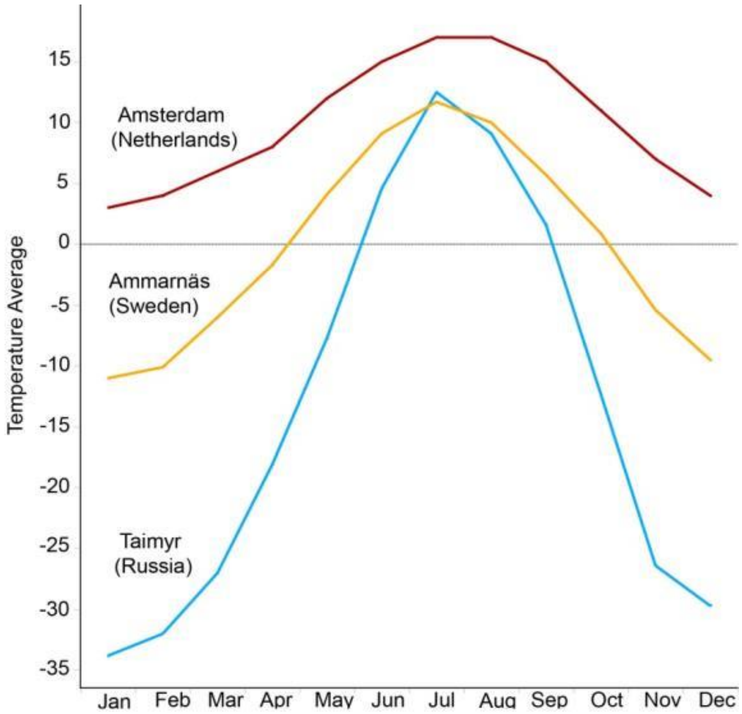


Figure 1. Average of temperature per month of three locations along a latitudinal gradient. Arctic region (Taimyr), subarctic region (Ammarnäs) and temperate region (Amsterdam).

Comparisons with other breeding areas

- latitudinal variation in predation rate.

In Europe, many breeding populations of waders have declined during the past decades (Donald et al. 2001, BirdLife International 2004, MacDonald & Bolton 2008a). One of the reasons suggested for the decline of European waders were increased levels of predation on eggs and chicks (Peach et al. 1994, Evans 2004, Langgemach & Bellebaum 2005, MacDonald & Bolton 2008a, Teunissen et al. 2008, Schekkerman et al. 2009, Roodbergen et al. 2012). Southern wader populations are tightly connected to wet grasslands, and both total area and quality of grasslands have declined throughout temperate Europe during the last centuries (Delaney et al. 2009, Jönsson 1991a, Newton 1998). This situation ‘forces’ waders to breed in high densities in smaller areas, increasing competition and possibly also predation risk (Newton 1998), the latter being one of the main factors influencing reproductive success of waders (Grant et al. 1999). At the same time most wader populations in subarctic northern Scandinavia have been stable in numbers and only a few have decreased (Delaney et al. 2009, Lindström 2009, Ottvall et al. 2009). This raises the question whether predation pressure on nests and young is lower in the Subarctic compared to temperate areas. So far, data on nest success and predation rates from the Subarctic are scarce. Most studies were conducted in the high Arctic (e.g. in Siberia, Greenland, and Svalbard). In these northern breeding areas, predation rates and subsequent breeding success of waders was tightly connected to rodent cycles with high predation rates and low breeding success in years when rodent numbers are low and vice versa (Alerstam& Jonsson 1999, Underhill et al. 1993). McKinnon et al. 2010 found a decreasing gradient of predation with latitude in an experimental study with artificial nests across 30 degrees in the American continent, suggesting that migratory birds that breed in Arctic regions compensate for their flying costs with a potentially lower predation risk.

In our study area the mean Daily Predation Rate (DPR) was similar to studies performed in the high Arctic (Mean DPR of main species was 0.022) (Schekkerman et al. 2004), but it was similar or somewhat higher than studies in southern latitudes, as in Groen and Hemerik 2002 in the Netherlands, Hötker and Segebade 2000 in Germany, Baines 1989, Ratcliffe et al 2005 in England and Kragten and de Snoo 2007 in The Netherlands (see Figure 2 and Figure 3). There is a negative relationship between DPR and latitude when including all European studies, but this relationship was not significant (t=-1.37, df=46, p=0.17 see figure 3 to see data sample). In our study area DPR for Golden Plover, Redshank and Dunlin were relatively low, except for 2012. This was a year with late snow melt and low lemming numbers, when DPR is much higher compared to southern areas. This annual variation in DPR must be taken into account when comparing sites and regions, which makes comparisons between climate zones more complex as long-term datasets would be required. Although in northern latitudes ecological foodwebs are in principle simpler (with less species involved), it seems clear that regional variations and local factors model predation rates of each particular location, more than simply latitude.

In conclusion, the relationship between DPR and latitude is at the best very weak. Species characteristics as antipredator behaviour of the species, nest crypsis, type of parental care or incubation rhythms (Bulla et al. 2016) could explain the variation of nest predation among species, but also specific regional factors as abundance of predator in the area, nest density and field type could also be important, as suggested by MacDonald & Bolton (2008a).

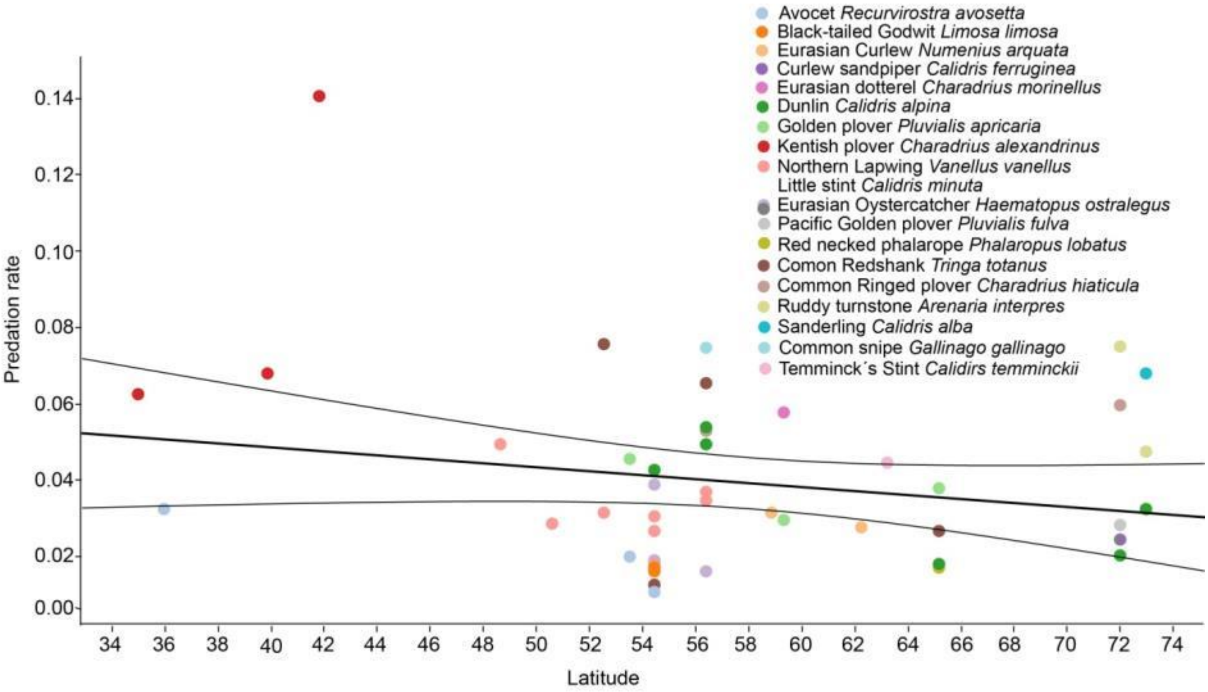


Figure 2. Daily predation rate for studies from MacDonalnd and Bolton 2008, Schekkerman 2004, data from Greenland Ecosystem Monitoring Programme, unpublished (provided by the Department of Bioscience, Aarhus University, Denmark), data from Jeroen Reneerkens, unpublished, and own study (filled circle) in relation to latitude. All the DPR values in this figure were calculated using Mayfield 1975.

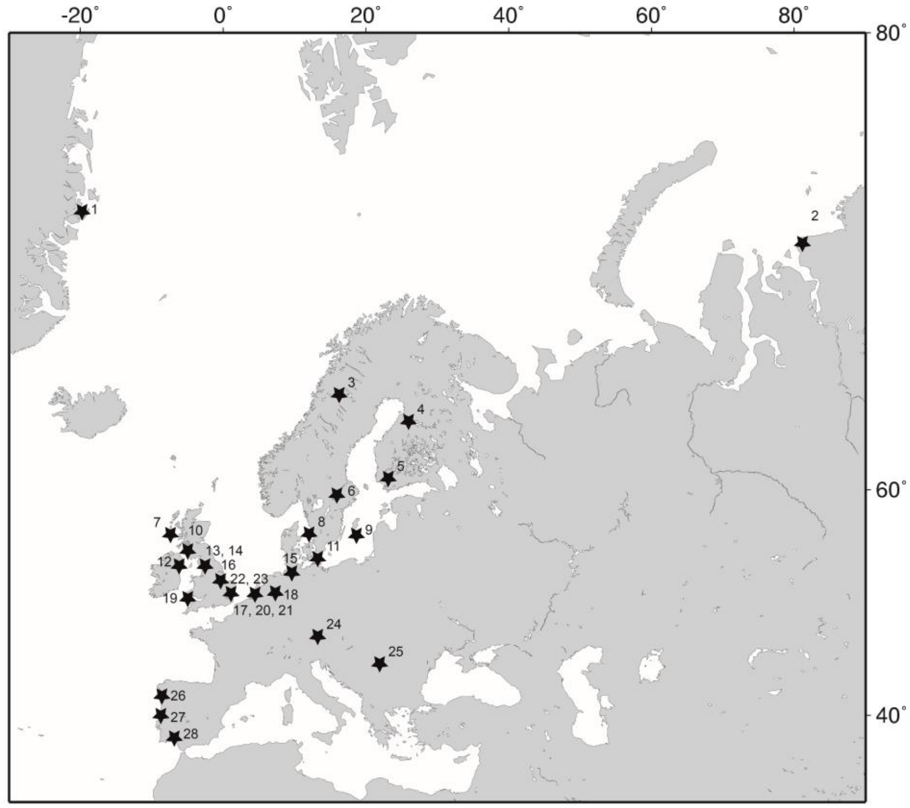


Figure 3. Latitudinal gradient of studies in Eurasia that has analyse DPR of waders using Mayfield 1975. Data was collected from MacDonald and Bolton 2008, Schekkerman 2004 and own study. Studies were selected according to the following criteria: more than 20 nests, natural conditions of study and calculation of DPR from Mayfield 1975.1. Greenland Ecosystem Monitoring Programme, unpublished. 2. Schekkerman et al 2004, 3.Ammarnäs (this study), 4. Rönka et al 2006, 5. Valkama et al 1999, 6. Berg 1992, 7. Jackson 2001 and Jackson & Green 2000, 8. Wallander & Andersson 2003, 9. Ottvall 2005, 10. Galbraith 1988, 11. Jönsson 1991, 12. Grant et al 1999, 13. Whittingham et al 2001, 14. Baines 1989, 15a.Hötker & Segebade 2000, 15b Cervencl et al 2011, 16. Seymour et al 2009, 17. Verboven et al 2001 18. Thyen & Exo 2005, 19. MacDonald & Bolton 2008b, 20. Kragten & de Snoo 2007, 21. Groen & Hemerik 2002, 22. Ratcliffe et al 2005, 23. Hart et al 2002, 24. Sálek & Smilauer 2002, 25. Székely 1992, 26. Dominguez & Vidal 2003, 27. Norte & Ramos 2004, 28. Cuervo 2005. Map generated in seaturtle.com/maptool

- latitudinal variation in chick growth rate.

Different studies already described that in arctic regions growth rates of wader chicks are higher than in temperate areas (Ricklefs 1968, 1976, Beintema & Visser 1989, Schekkerman et al. 1998, Tjorve 2007). Schekkerman et al. 1998 suggested that in cold temperatures chicks need to be brooded more often and for longer time periods and when they get older spend more energy maintaining their body temperature, so they suffer a feeding time constraint. The diminishing of feeding time could be balance with a faster growth rate. Contrary, in temperate and tropic areas, birds have lower metabolic rates to compensate with the higher environment temperatures (Brown & Downs 2002) and thus will require lower intake rate.

Tjorve (2007) compared the K parameter from the growth curves of several species, corrected for adult body mass, and related this with latitude. She found that both adult body mass and latitude were highly correlated with growth, the first being negative (bigger birds grow slower) and the second being positive (chicks grow faster at higher latitudes). Our results (Chapter 4) fit perfectly with these findings. The (relative) growth rate of Golden Plovers in our study area is intermediate to chick growth rates of species breeding in temperate and arctic areas (Figure 4)when comparing it with data from precocial species from Tjorve 2007 and with a study from England (Pearce-Higgins and Yalden 2002). The overall correlation between growth rate and latitude was significant (t=3.099, df=15, p<0.01).

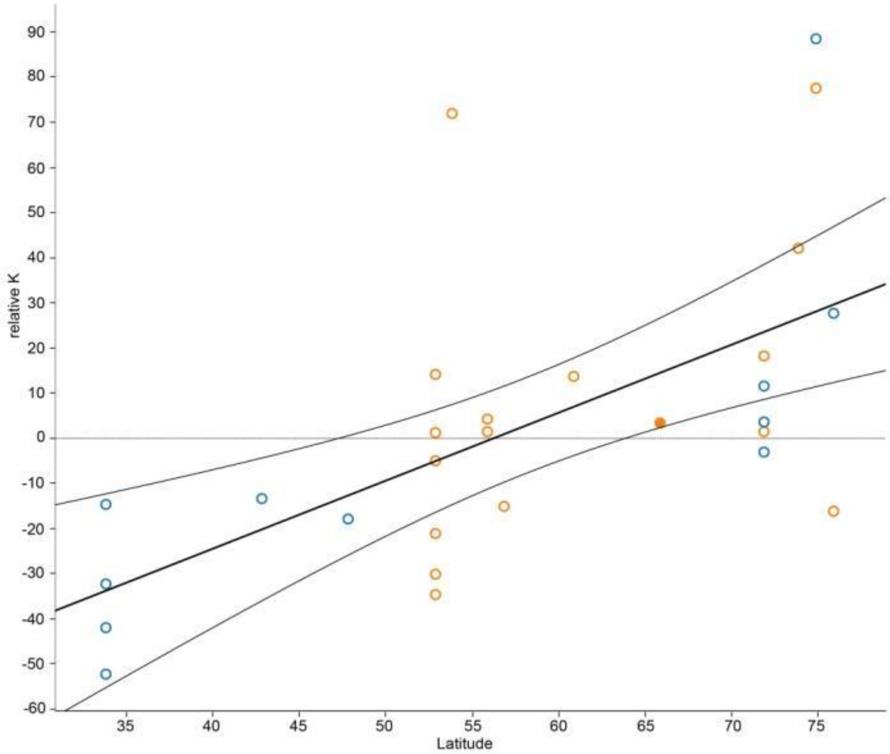


Figure 4. K values extracted from Table 1 from Tjorve 2007, Pearce-Higgins and Yalden 2002 and own study (filled circle) in relation to latitude. Orange corresponds to values from Palearctic species and blue to non-Palearctic species.

In conclusion, Golden Plovers in our study location do have an intermediate growth rate in comparison to arctic and temperate areas.

- latitudinal variation in food availability

Some studies have suggested that food abundance (insect biomass) is higher in arctic regions than in temperate areas (Lack 1968, Salomonsen 1972, Andreev1999, Bolduc et al 2013), however others have shown that this is not the case (Schekkerman et al 2003). High annual variation in insect phenology and abundance seems to make it difficult to demonstrate such pattern (Schekkerman et al 2003, Reneerkens et al 2016). Pitfall data on insect abundance over time for three different locations is presented in Figure 5.

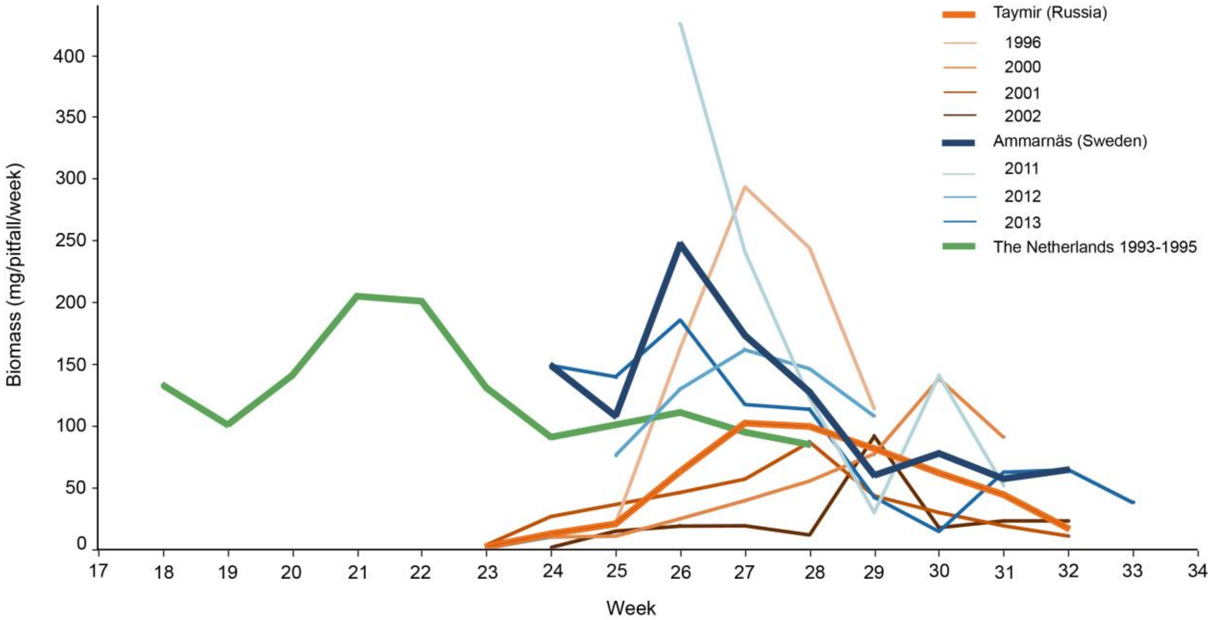


Figure 5. Total biomass per week in different latitudinal sites. Thick lines for Taymir and Ammarnäs represent the average of all years of sampling combined.

When comparing the biomass per week obtained from our results with other studies in temperate areas (Schekkerman 1997) and in higher Arctic areas (Tulp and Schekkerman 2009) I do not find strong differences in abundance. If anything, I find the opposite pattern, insect abundance decreases with latitude. In Taimyr, the most northern location (73 degrees latitude) the lowest biomass was recorded.

In the Netherlands biomass was high and relatively stable between years. In Ammarnäs, insect biomass varied considerably between years, and in one year (2011). Data presented in figure 5 were not always collected in exactly the same way. Schekkerman and Tulp used a modified version of the pitfall traps, although difference between methods seems to not be significant (Tulp and Schekkerman 2009). There are also differences on timing. High availability of food in temperate areas occur up to 5 weeks earlier than in the subarctic area and 6 weeks earlier than in the arctic region. The timing in food peak is as expected, being the earliest in temperate areas, intermediate in the Subarctic and latest in the Arctic. A thorough search was performed to find more data about phenology of ground insects studied with pitfalls, but the lack of this information is surprising, given the fact that insect abundance is such important and dominant ecological factor, that could even affect the distribution of waders around the globe.

The hypothesis that food abundance would be higher in arctic and subarctic areas seems not to be supported by field observations. However, as stated before, chicks grow at faster rates in arctic regions. Other factors than the abundance of prey might explain fast growth rates in the Arctic. Basically, chicks need to increase their food intake rates to achieve faster growth rates, as Schekkerman et al. 2003 indicate that they have higher energy demands. It actually might be easier to capture arthropods in low tundra vegetation, which might be the reason why these chicks can achieve higher intake rates despite relatively low food abundance.

In conclusion, there is not a clear positive latitudinal pattern of abundance of food, but the opposite might be true. Other factors related to the habitat the chicks forage in could explain how chicks in the Arctic achieve higher intake rates. However, data on intake rates is virtually lacking, and this is a formidable challenge for future research.

- latitudinal variation in moult.

waders show different patterns of flight feather moult. Some species moult at the breeding area before autumn migration, as Jack Snipe (*Lymnocryptes minimus*) and some populations of Purple sandpiper (*Calidris maritima*) and Dunlin (*Calidris alpina*), and others moult in temperate or tropical wintering areas after migration, as Red Knot (*Calidris canutus*) (Newton and Brockie 2008) (Figure 6). In some species moult is even split between breeding grounds, stopover areas and wintering areas (Little ringed plover *Charadrius dubius*). Primary moult duration is related to body mass and latitude in wader species that moult in the wintering grounds (Dietz et al 2015). However, in a broader overview represented in figure 6 moult strategy does not seem to be related to breeding latitude neither to wintering latitude. What is also known is that overlap between moult and breeding is rare in migratory birds (Newton 2009) as this would form a time and energetic bottleneck within the annual cycle. (Buehler and Piersma 2008). Golden Plover is the only wader species that is known to moult during breeding, both while incubating and chick rearing, during stopovers on autumn migration and during winter.

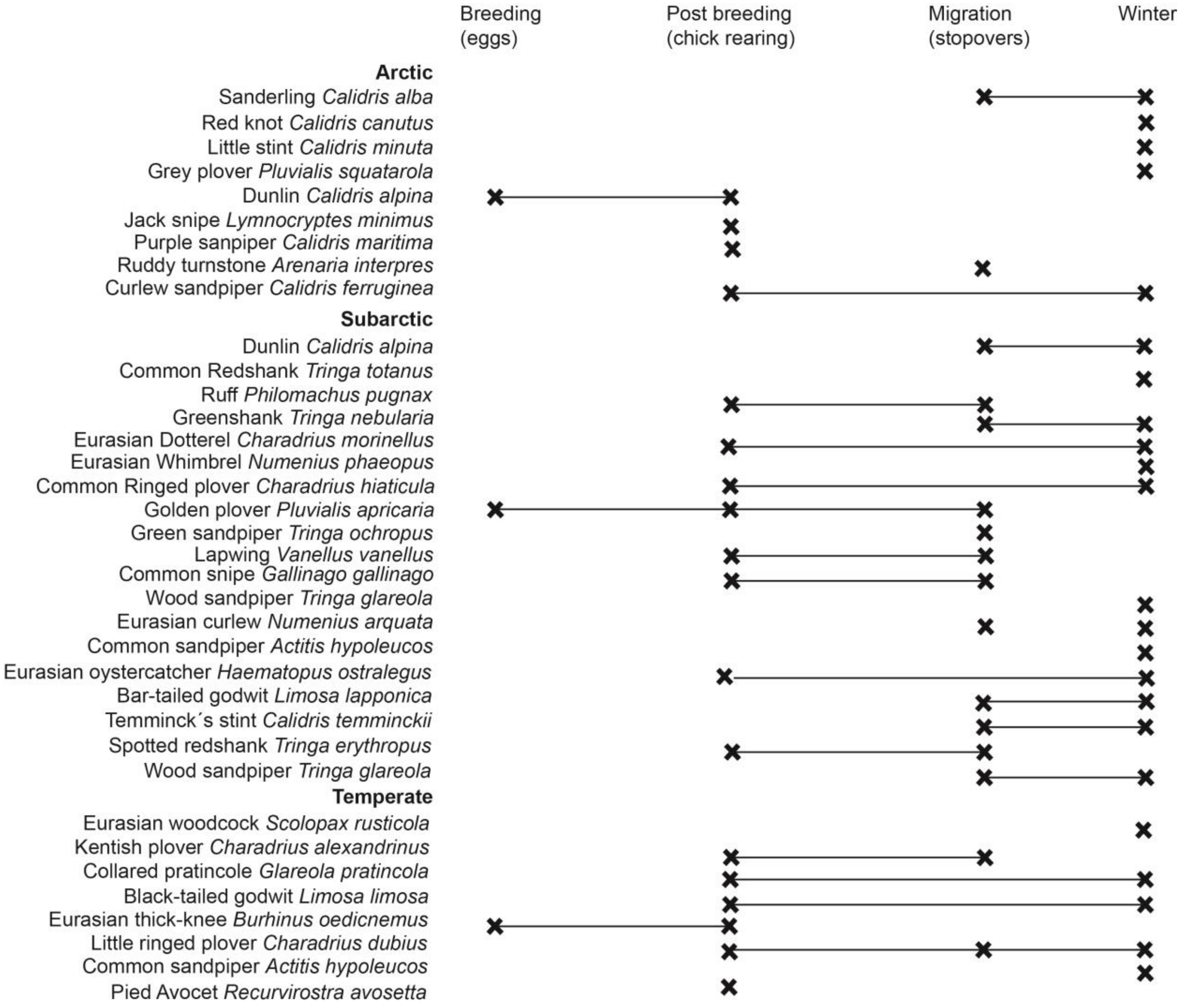


Figure 6. Moult strategy of different wader species from the Palearctic which information of their moult has been found in Newton and Brockie 2008 and Baker 2016.

I conclude that there are many other factors that influence the moult pattern of a migratory wader than latitude, as their migration strategy and the environmental conditions encountered at different sites throughout the year. The huge variation in moult patterns could be explained by the fact that it is the only key annual cycle stage that could be scheduled at different times of the year.

Climate change and the ecology of breeding waders in the Subarctic

The benefits and challenges that climate change supposes on ecological systems have been studied all over the world and have included many aspects of ecology. In this final synthesis I will sum up all the possible effects of climate change on the ecology of breeding waders in the Subarctic that have been discussed along the chapters of this thesis.

Timing

Time for breeding in the Subarctic is short. An increase of general temperature could lead to a longer breeding season and create leeway in their breeding schedules. It has been shown in many studies that birds advance laying dates when temperatures increase, and some species also have advanced their laying dates in the recent decades (Dunn 2004). If the Golden Plovers in the Subarctic would have a longer breeding season, they could stay longer and moult more flight feathers improving the quality of their plumage and therefore improving their migration flights, or they could decrease the overlap between breeding and moult. Changes in temperature would also affect the Golden Plovers' migration patterns; i.e. if less winter cold spells would occur they would less often make their long cold-spell movements to southern Spain and Morocco when temperatures in central Europe drop, wich might reduce their survival risk during migration.

However, another consequence of climate change in the Subarctic would be the increase of snowfall and the delay of snowmelt. More frequent years of late snowmelt, such as in 2012 in our study area, are predicted (Serreze et al. 2007, Popova 2004). Under these circumstances, as shown in Chapter 2, birds will be forced to delay their breeding and some pairs will forego breeding. At the same time, late snow melt will be detrimental for reproduction due to the increase in predation pressure. Predation rates would be especially high if late snowmelt would occur in a year when many predators are around and few alternative prey, i.e. after a lemming peak year, as predators find nests more easily in the few snow free patches that appear when snow is thawing.

Food availability

Effects on arthropod phenology, abundance or species assemblage are expected to happen in the near future due to climate change (Deutsch et al. 2008). Since arthropod in this regions are abundant for a limited period of time (MacLean and Pitelka 1971; Hodkinson et al. 1996; Schekkerman et al. 2004; Tulp 2007) chick growth will be directly influence by these changes (Tulp and Schekkerman 2001;

Schekkerman et al. 2003; Schekkerman et al. 2004, McKinnon et al. 2012). Breeding too late would create a mismatch between chick growth and arthropod availability. In our study area food availability declined throughout the season so species as the Golden Plover, with long breeding duration, will have to deal with dwindling food resources throughout the season, which is believed to have detrimental effects on chick growth. On the other hand, other arthropod species might increase with increasing temperatures and have higher and more common emergences, as seems the case with Bibionidae flies in our study area (Qvenild and Rognerud 2017). These changes could actually benefit chick growth and compensate for the effects of a potential mismatch. On the other hand, the increase of temperatures in southern Pennines, in England, have led to droughts, negatively affecting Cranefly larvae, resulting in a declining of emerging adults Craneflies in subsequent seasons. Golden Plovers, which highly depend on Craneflies in this area, suffer from this decline in Cranefly abundance (Pearce-Higgins et al 2010).

Habitat

Tundra habitat is decreasing in area, especially in alpine regions of the Subarctic. The boreal forest is expanding north and to higher altitudes (Kullman 2001, 2002, IPCC 2014). At the same time, Willow shrub habitat seems to expand. This could be beneficial for plover chicks, since its principal food intake is from Willow shrub habitat and it seems they could also benefit from a higher surface for shelter and avoid predation (see Chapter 3). On the other hand heathland and bare ground are the most common places for nesting and a reduction of its availability could also increase competition in some locations, and thus the plovers might no longer be able to complete their annual cycle in these areas.

Conclusion

Climate change is a reality that nobody can deny anymore (IPCC 2014). Researchers are urged to document the effects of climate change on organisms and ecosystems before it is too late. To properly determine the real effect of global warming, long-term studies are essential, but unfortunately historical data on wader ecology from subarctic and arctic areas is scarce. In the Arctic and Subarctic, global warming is more obvious than elsewhere, which makes it a perfect place to perform long-term studies on effects of climate change. In this thesis, by studying the basic ecology of a bird, it was possible to pinpoint some of the key factors that could lead to direct and indirect effects on the proper performance of the breeding ecology of this species and its survival. From my perspective, the continuation of field studies on the breeding ecology of waders is essential to identify the challenges and possible benefits of climate change on this characteristic species group.

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