A golden life
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CHAPTER 1

Introduction

Paula Machín
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 northern 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 influenced by a plethora of factors (Figure 1.1). 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).

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
Figure 1.1: Environmental and biotic factors that influence on the performance of each stage of the life cycle of a Golden Plover.
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 Arctic 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 grounds, 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, according to 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 retrac-
tion 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 snow 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 1.2). 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).

**Aims and approach**

Three main threats of climate change for migrant waders have been identified (Lindström & Agrell 1999, 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.

I, together with my co-authors 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 sub-arctic breeding site, in 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 high 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 us the opportunity to study moult and migration of the Golden Plover. When study-ing 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 lit-erature, extracting information about nesting success, chick growth, and moult.

**Study area**

Ammarnäs is a small village located in southern Lapland, Sweden (65°57’N; 16°13’E) (Figure 1.3, 1.4), 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 km2. 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) accord-ing to Birdlife International (BirdLife International 2017).

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 1.4). 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 we started to observe snow free patches 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° in 2012 and
Figure 1.3: Image from the study area.

Figure 1.4: 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).
10.7° in 2013. The study area is notably wet during the breeding season. Mean rainfall (May–August) 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 myrtillus and Salix herbacea. 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.lu.se). In total, 12 species of waders breed regularly in the area. Population trends are stable to positive (Svensson & Andersson 2013, Table 1.1). The species with highest densities are Dunlin Calidris alpina, Golden Plover Pluvialis apricaria, Red-necked Phalarope Phalaropus lobatus and Redshank Tringa totanus. Species present in lower densities are Temminck’s Stint Calidris temminckii, Ruff Calidris pugnax, Ringed plover Charadrius hiaticula, Common snipe Gallinago gallinago, Dotterel Charadrius morinellus, and then there are species present in very low numbers, with only a few pairs, such as Whimbrel Numenius phaeopus, Wood sandpiper Tringa glareola, Purple sandpiper Calidris maritima, Broad-billed sandpiper Limicola falcinellus and Common sandpiper Actitis hypoleucos.

During our own studies (2008–2013) a total of 664 wader nests of 14 species were located (Table 1.1). 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 massive 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.

**Table 1.1:** Number of nests found in each species during all years of study together with population trends in breeding waders in the Vindelfjällen Nature Reserve (recorded in at least 20 of the 40 years 1972–2011, data from Svensson & Andersson 2013).

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of nests</th>
<th>Population trend 1972–2011</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2008 2009 2010 2011 2012 2013 Total</td>
<td>Trend P</td>
</tr>
<tr>
<td>Broad-billed Sandpiper <em>Limicola falcinellus</em></td>
<td>1 2 1 4</td>
<td></td>
</tr>
<tr>
<td>Common Sandpiper <em>Actitis hypoleucus</em></td>
<td>1 1 2</td>
<td></td>
</tr>
<tr>
<td>Common Snipe <em>Gallinago gallinago</em></td>
<td>3 4 3 1 1 12</td>
<td>0.9909 ns</td>
</tr>
<tr>
<td>Eurasian Dotterel <em>Charadrius morinellus</em></td>
<td>1 1 1 2</td>
<td>1.0112 ns</td>
</tr>
<tr>
<td>Dunlin <em>Calidris alpina</em></td>
<td>29 39 49 50 26 28 221</td>
<td>1.0292 &lt;0.01</td>
</tr>
<tr>
<td>Golden Plover <em>Pluvialis apricaria</em></td>
<td>19 35 43 60 36 37 230</td>
<td>1.0181 &lt;0.01</td>
</tr>
<tr>
<td>Purple Sandpiper <em>Calidris maritima</em></td>
<td>1 1</td>
<td></td>
</tr>
<tr>
<td>Red-necked Phalarope <em>Phalaropus lobatus</em></td>
<td>2 10 9 11 11 12 55</td>
<td>1.0189 ns</td>
</tr>
<tr>
<td>Redshank <em>Tringa totanus</em></td>
<td>3 11 10 16 13 8 61</td>
<td>1.0532 &lt;0.01</td>
</tr>
<tr>
<td>Common Ringed Plover <em>Charadrius hiaticula</em></td>
<td>1 2 2 1 2 3 11</td>
<td>1.0384 &lt;0.01</td>
</tr>
<tr>
<td>Ruff <em>Philomachus pugnax</em></td>
<td>1 7 4 11 5 7 35</td>
<td>0.9934 ns</td>
</tr>
<tr>
<td>Temminck's Stint <em>Calidris temminckii</em></td>
<td>1 3 8 3 7 4 26</td>
<td>0.9926 ns</td>
</tr>
<tr>
<td>Whimbrel <em>Numenius phaeopus</em></td>
<td>1 1</td>
<td></td>
</tr>
<tr>
<td>Wood Sandpiper <em>Tringa glareola</em></td>
<td>1 1 2</td>
<td></td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>60 116 128 156 103 101 664</strong></td>
<td></td>
</tr>
</tbody>
</table>
**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 such as the Netherlands and UK, and in southern Europe or 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.

Table 1.2: Biometry of adult Golden Plovers trapped in Ammarnäs. Table provides mean values (in mm) and standard deviation.

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

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 1.2).

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 the Subarctic. 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 notable exceptions as Tulp 2007, Tjørve 2007, Tjørve 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.