A golden life
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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

Abstract

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 where 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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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 change 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. 1999, 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 site
The study was performed in the breeding seasons of 2011 and 2013 at an area of 24 km² in the Vindelfjällen Nature Reserve, located next to a small village called Ammarnäs,
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 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 (10.0°C in 2011 and 10.3°C 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 km² (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 temminckii, 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).

**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.
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 3.1): 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 20× to 40× magnification and epidermal tissue of plants at 400× 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).

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**Table 3.1:** Characteristics of dominant habitats in the study area.

<table>
<thead>
<tr>
<th>HABITAT TYPE</th>
<th>Heathland</th>
<th>Willow shrub</th>
<th>Alpine meadow</th>
<th>Wet areas</th>
</tr>
</thead>
</table>
| Dominant plants | Several species of mosses and lichens. Mainly *Betula nana*, *Empertrum nigrum*, *Vaccinium myrtillus*, and *Salix herbacea* | 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 |
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 3.1 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: \( D = \frac{(r - p)}{(r + p - 2rp)} \), 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 (Calcagno & 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

Figure 3.1: Nest positions and home ranges (Minimum Convex Polygons) for chicks tracked by radio transmitters.
from 7 to 16, mean = 11.5, median = 11). Home ranges (minimum convex polygons) varied in size, ranging from 0.034 to 0.640 km$^2$ (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 3.1).

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 3.2A). 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 3.2A).

Figure 3.2: 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).
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 3.2). 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 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 3.2C).

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 3.2: 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.
**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 3.3 and 3.4). These two groups comprised about 70% of the diet of the chicks. Another relatively important order in the diet was Hymenoptera (Figure 3.3 and 3.4). The rest of the orders present in the diet were Araneae, Hemiptera, Homoptera, Lepidoptera and Opiliones. Acari (subclass) was also found in the faeces.

Chick diet varied between years (Table 3.3, Figure 3.3). 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 3.3, Figure 3.3). Coleoptera formed the most important prey for chicks at all ages, presenting between 32 and 49% of the diet at every age class (Figure 3.3). The proportion of Coleoptera in the diet differed significantly during the season, peaking at intermediate dates and increased with chick age (Table 3.3). Bibionidae imagoes was the second most important group, although

![Figure 3.3: Diet of Golden Plover chicks, as expressed as the proportion of different prey taxa in individual faeces (proportion of biomass), for different age classes.](image-url)
**Figure 3.4:** 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.

**Table 3.3:** 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 3.3 and 3.4 for corresponding graphs of age and habitat effects, respectively.

<table>
<thead>
<tr>
<th>Temporal</th>
<th>Habitat</th>
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<tbody>
<tr>
<td><strong>Coleoptera</strong></td>
<td>Date ●●●●</td>
</tr>
<tr>
<td></td>
<td>Age ++</td>
</tr>
<tr>
<td></td>
<td>Year 2013&gt;2011*</td>
</tr>
<tr>
<td><strong>Hymenoptera</strong></td>
<td>Age ----</td>
</tr>
<tr>
<td><strong>Hymenoptera larvae</strong></td>
<td>Age ----</td>
</tr>
<tr>
<td></td>
<td>Date ++++</td>
</tr>
<tr>
<td></td>
<td>Year 2013&gt;2011*</td>
</tr>
<tr>
<td><strong>Bibionidae (2011)</strong></td>
<td>Date ▲▲▲▲</td>
</tr>
<tr>
<td></td>
<td>Age ++</td>
</tr>
<tr>
<td><strong>Bibionidae larvae (2013)</strong></td>
<td>Date ▲</td>
</tr>
<tr>
<td></td>
<td>Age ▲</td>
</tr>
<tr>
<td><strong>Tipulidae</strong></td>
<td>Date ▼▼▼▼</td>
</tr>
<tr>
<td><strong>Nematocera</strong></td>
<td>Age --</td>
</tr>
<tr>
<td><strong>Lepidoptera larvae</strong></td>
<td>NS</td>
</tr>
</tbody>
</table>

Wet area a
Willow shrubs b
Heathland b
Alpine meadow b
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 3.3). Tipulidae imagoes were eaten relatively much by young chicks (up to 32% of the faeces content, Figure 3.3), but the proportion of Tipulid imagoes in the faeces strongly decreased with date (Table 3.3). 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 3.3). 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 3.4).

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.

**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, Ephmenoptera, Hemiptera and Plecoptera. Also Acari (subclass) and Ixodidea (family) were present in the pitfalls.

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 3.5). 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 3.6A). In both years, overall food availability decreased throughout the chick-rearing period (from 1st of July till 6th of August, Figure 3.6). Note that Tipulidae and Bibionidae larvae live in the ground, and thus pitfall trapping does not provide information about their abundance.

**Figure 3.5:** 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.

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
Figure 3.6: 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. Error 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.
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-Elpe, 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 3.3) whereas Tipulidae abundance was more or less constant over time (Figure 3.5). 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 3.6) 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.

**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 3.4). 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-Higgins & 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 3.4:** Comparison of habitat selection, diet and prey availability between three studies on the breeding ecology of Golden Plover chicks.

<table>
<thead>
<tr>
<th>Ammarnäs, Sweden</th>
<th>Northern Pennines, UK¹</th>
<th>South Pennines, UK²</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Selected habitat</strong></td>
<td>Willow shrub</td>
<td>Small patches of heather mixed with</td>
</tr>
<tr>
<td></td>
<td></td>
<td>grass, marshes, grasslands and</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Cotton grass</em> (Eriophorum vaginatum)*</td>
</tr>
<tr>
<td><strong>Avoided habitat</strong></td>
<td>Wet areas and Alpine meadows</td>
<td>Heather</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Prey availability</strong></td>
<td>Higher biomass and number in</td>
<td>Depends on the year, but always high</td>
</tr>
<tr>
<td></td>
<td>Willow shrub and Heathland</td>
<td>in <em>Cotton grass</em> mire and upland</td>
</tr>
<tr>
<td></td>
<td></td>
<td>grasslands</td>
</tr>
<tr>
<td><strong>Most selected prey items</strong></td>
<td><em>Coleoptera</em> and <em>Bibionidae</em></td>
<td><em>Tipulidae</em> and <em>Coleoptera</em></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Tipulidae</em>, <em>Lepidoptera</em>, <em>Coleoptera</em></td>
</tr>
</tbody>
</table>

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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