



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

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## Abstract

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 favourable 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* 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.

## Significance statement

Yearly variation in environmental conditions may influence the life histories of whole cohorts of offspring. Understanding these ‘cohort effects’ is important to ultimately understand life history evolution. We studied the growth of golden plover chicks, a sub-arctic breeding shorebird, during two breeding seasons, and found that chick growth lagged behind in 2013. In birds, food availability and weather have been identified to be the two main factors affecting chick growth, but the relative importance of these factors in explaining differences in growth between years is poorly understood. These examples are indeed needed to ultimately understand population dynamics and life history evolution in the field.

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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 1993; 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 (Sæther et al. 1996; Sæther 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 et al. 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. 2007; 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. 2007). Third, arthropods might be less active on colder days, negatively affecting growth (Meltofte et al. 2007).

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 2 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.

## Materials 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-km<sup>2</sup> 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 per square kilometre (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 amongst 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 pit-fall 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 (0.75 g 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 handling 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 4 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.

**Data availability** The datasets analysed during the current study are available from the corresponding author on reasonable request.

### 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 Gompertz 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 and Yalden 2002). For all measurements, we fitted three-parameter 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 the following:

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

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

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 1 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 analyse 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 analysed in two different ways. First, we modelled 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 modelled 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 2 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 9 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 9 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 and 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).

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  $Z = 0.64$ ,  $df = 1$ ,  $p = 0.42$ ) (Fig. 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  $Z = 1.61$ ,  $df = 1$ ,  $p = 0.20$ ).

### Biological and environmental conditions

Thirty-six 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-Elipé 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; Fig. 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).



**Table 1** Fate of individual golden plover chicks that were tracked by radio transmitters in 2011 and 2013

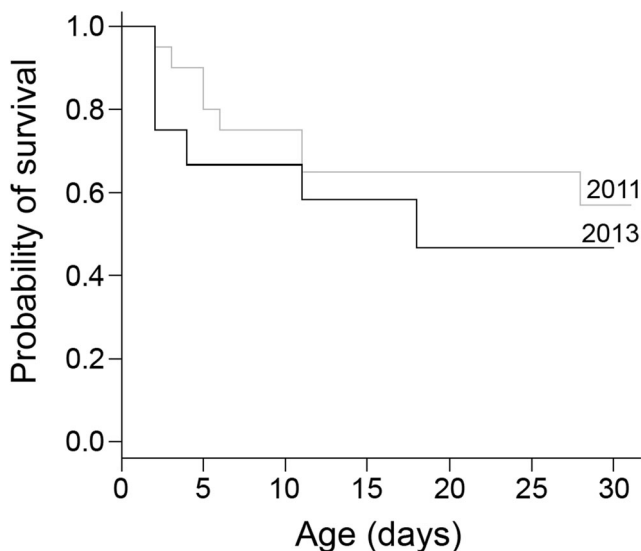
Year	Survived till fledging	Lost signal	Lost tag	Dead	
				Predated	Unknown
2011	6 (30%)	5 (25%)	2 (10%)	1 (5%)	6 (30%)
2013	3 (25%)	4 (33.3%)	2 (16.6%)	0	3 (25%)

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 14 July and 15 August, than in 2011, when cold weather only occurred on 13 July and 10 August (Fig. 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) (Fig. 2).

### Differences at hatching

Mean hatching dates of nests from which chicks were radio-tracked differed only 5 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<sup>3</sup>, 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



**Fig. 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)

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).

### Growth curves

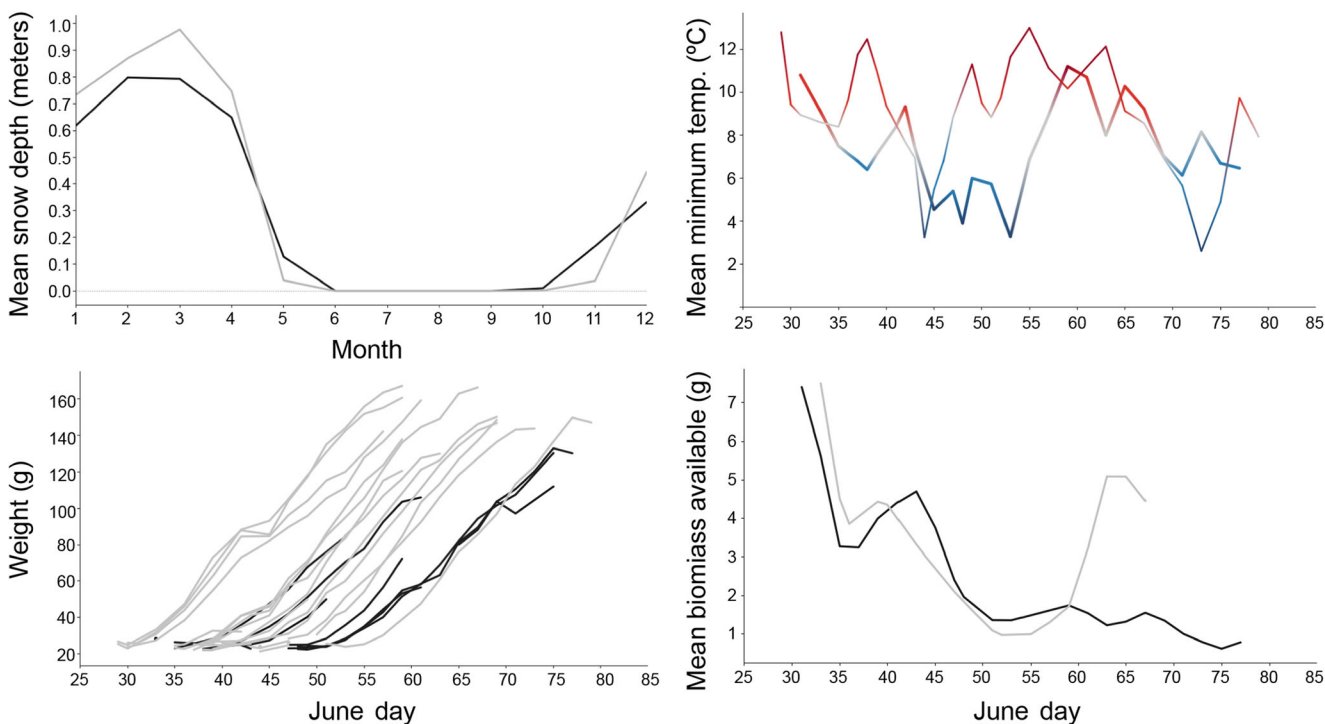
Growth decelerated from hatching for all structural measurements (tarsus, bill, and bill-head length), whereas growth initially accelerated for weight until the deflection point at an age of 16 days where the maximum weight gain was achieved (Fig. 3; Table 3; supplementary material 1). Hence, Gompertz growth curves with three parameters could describe growth of the structural measurements, whereas a Gompertz growth curve 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 (Fig. 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 (Fig. 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).

### 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 (significant interaction between year and age; Fig. 4; 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 (Fig. 4; supplementary material 2).



**Fig. 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

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; Fig. 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.

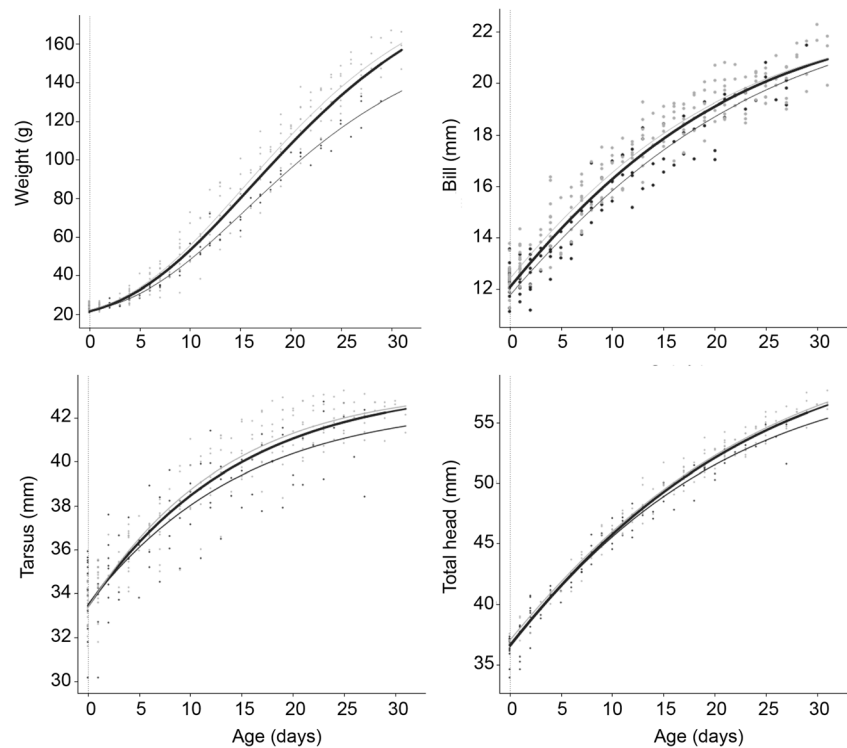
Another factor that turns out to affect residual growth is sex of the chick. In older chicks, males were heavier and had longer tarsus lengths (supplementary material 2).

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 (Fig. 5; supplementary material 3).

**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

		Weight	Measurements at hatching		
			Tarsus	Bill	Total head
Year	Estimate ± SD	-0.86 ± 0.49	-0.43 ± 0.44	-0.08 ± 0.22	-0.69 ± 0.48
	<i>t</i>	-1.73	0.96	-0.37	-1.43
	<i>p</i>	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
	<i>t</i>	-1.11	-1.99	1.61	2.41
	<i>p</i>	0.27	0.05	0.11	0.03

**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 and thick black lines to both years combined



### Differences at fledging

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,  $N=6$ ). Plover 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 g at that moment, which is the weight expected for a 24-day-old chick.

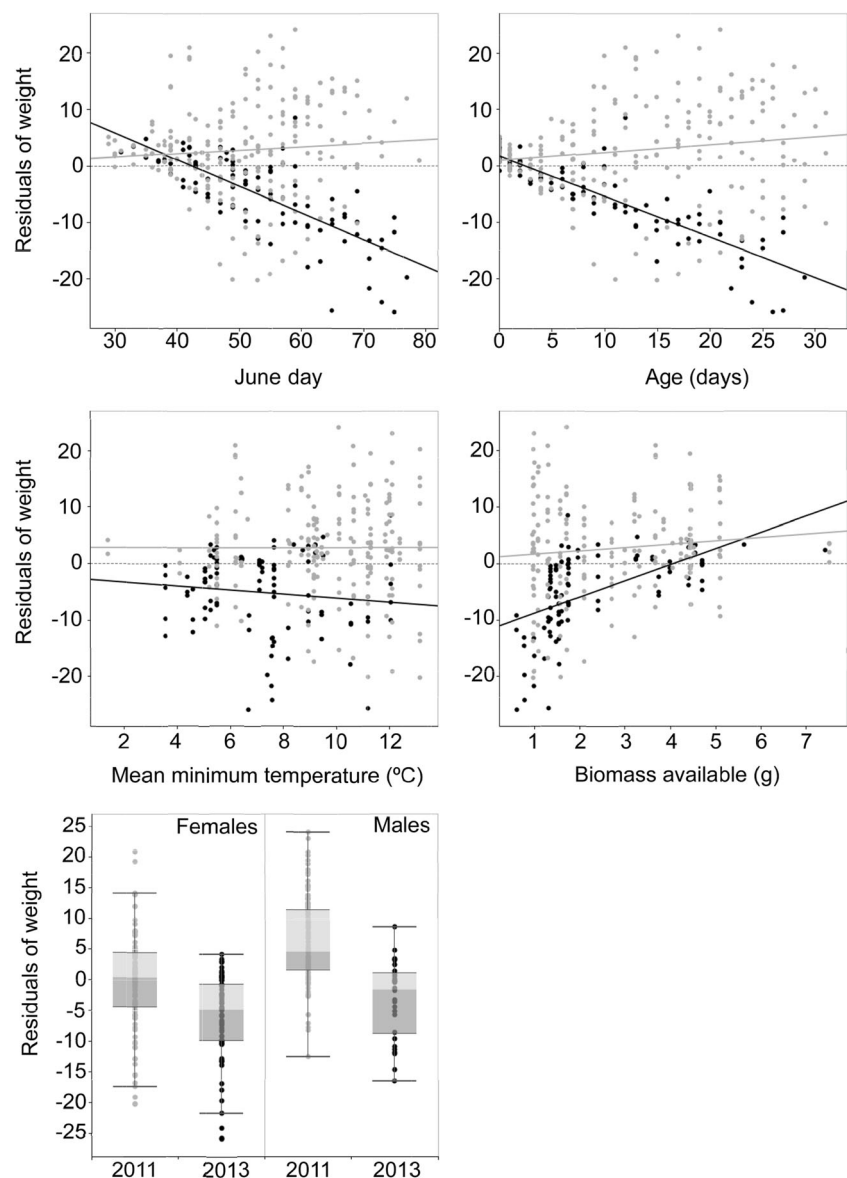
### Discussion

The growth of the golden plover chicks in our study area in Swedish Lapland differed markedly between years. 2011 appeared to be a favourable season in which the chicks achieved

**Table 3** Estimates  $\pm$  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 $\pm$ SD		
		All chicks	2011	2013
Weight	$K$	$-0.08 \pm 0.01$	$-0.08 \pm 0.01$	$-0.09 \pm 0.02$
	$t$	$15.95 \pm 4.06$	$15.22 \pm 0.62$	$15.53 \pm 1.57$
	$A$	$203.05 \pm 15.22$	$200.89 \pm 11.67$	$169.36 \pm 23.20$
	$c$	$17.45 \pm 0.83$	$18.20 \pm 4.05$	$19.06 \pm 4.84$
Tarsus	$K$	$-0.08 \pm 0.01$	$-0.08 \pm 0.01$	$-0.07 \pm 0.02$
	$t$	$-17.52 \pm 1.68$	$-16.06 \pm 1.78$	$-19.15 \pm 3.60$
	$A$	$43.47 \pm 0.48$	$43.39 \pm 0.46$	$42.65 \pm 1.03$
Bill	$K$	$-0.06 \pm 0.00$	$-0.06 \pm 0.01$	$-0.06 \pm 0.01$
	$t$	$-7.07 \pm 0.42$	$-7.77 \pm 0.60$	$-6.75 \pm 0.58$
	$A$	$22.97 \pm 0.56$	$22.85 \pm 0.58$	$23.23 \pm 1.23$
Total head	$K$	$-0.05 \pm 0.00$	$-0.05 \pm 0.00$	$-0.06 \pm 0.00$
	$t$	$-11.56 \pm 0.41$	$-12.01 \pm 0.70$	$-11.69 \pm 0.60$
	$A$	$62.28 \pm 0.86$	$62.91 \pm 1.13$	$59.86 \pm 1.26$

**Fig. 4** Factors affecting growth. Absolute residuals of weight in relation to June day, age, temperature, arthropod biomass and sex of the chick. Light grey represents 2011 and dark grey represents 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



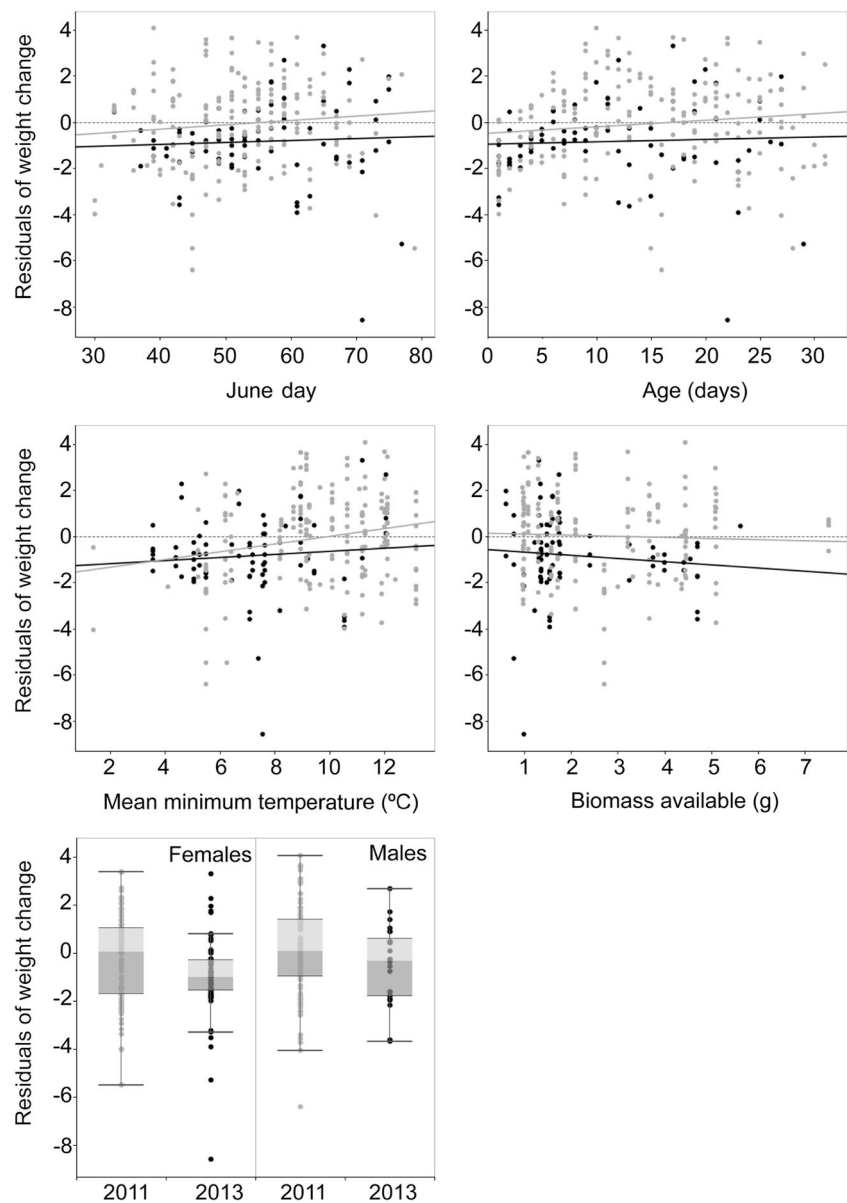
fast growth rates (see below for a comparison with other studies). This strongly contrasted with 2013, when residuals for weight decreased with age, suggesting that the condition of the chicks steadily deteriorated throughout the season. In addition, residuals for structural measurements (tarsus, bill, 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 be 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 2 years suggests 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 Monaghan 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.

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 2 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



**Fig. 5** Factors affecting growth rate. Residuals of weight change in relation to June day, age, temperature, arthropod biomass and sex of the chick. Light grey represents 2011 and dark grey represents 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



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. 2007; Tjørve et al. 2009) on the growth of shorebird chicks. However, how general our notion, in which 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 (Melfo et al. 2007). 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 3 to 4 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.

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### Compliance with ethical standards

**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).

## References

- Andersen PK, Gill RD (1982) Cox's regression model for counting processes: a large sample study. *Ann Stat* 10(4):1100–1120. <https://doi.org/10.1214/aos/1176345976>
- Beintema AJ, Visser GH (1989) Growth parameters in chicks of charadriiform birds. *Ardea* 77:169–180
- Byrkjedal I, Thompson DBA (1998) Tundra plovers: the Eurasian, Pacific and American golden plovers, and grey plover. T. & A.D. Poyser
- Callaghan TV, Björn LO, Chapin FS, Chernov Y, Christensen TR, Huntley B, Ims R, Johansson M (2005) Arctic tundra and polar desert ecosystems. In: Symon C, Arris L, Heal B (eds) Arctic climate impact assessment: scientific report. Cambridge University Press, Cambridge, pp 243–352
- Cam E, Aubry L (2011) Early development, recruitment and life history trajectory in long-lived birds. *J Ornithol* 152(Suppl 1):187–201. <https://doi.org/10.1007/s10336-011-0707-0>
- Dunn JC, Hamer KC, Benton TG (2010) Fear for the family has negative consequences: indirect effects of nest predators on chick growth in a farmland bird. *J Appl Ecol* 47(5):994–1002. <https://doi.org/10.1111/j.1365-2664.2010.01856.x>
- Fridolfsson AK, Ellegren H (1999) A simple and universal method for molecular sexing of non-ratite birds. *J Avian Biol* 30(1):116–121. <https://doi.org/10.2307/3677252>
- Giner G, Smyth GK (2016) Statmod: probability calculations for the inverse Gaussian distribution. *R J* 8:339–351
- Grafen A (1988) On the uses of data on lifetime reproductive success. In: Clutton-Brock TH (ed) Reproductive success. Studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, pp 454–471
- Handel CM, Gill RE (2001) Black turnstone (*Arenaria melanocephala*), no. 585. In: Poole A, Gill F (eds) The birds of North America. The birds of North America, Inc., Philadelphia
- Kentie R, Hooijmeijer JCEW, Trimbos KB, Groen NM, Piersma T (2013) Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *J Appl Ecol* 50(1):243–251. <https://doi.org/10.1111/1365-2664.12028>
- Krijgsveld KL, Reneerkens JWH, McNett GD, Ricklefs RE (2003) Time budgets and body temperatures of American golden-plover chicks in relation to ambient temperature. *Condor* 105(2):268–278. [https://doi.org/10.1650/0010-5422\(2003\)105\[0268:TBABTO\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2003)105[0268:TBABTO]2.0.CO;2)
- Liebezeit JR, Smith PA, Lancot RB et al (2007) Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* 109(1):32–47. [https://doi.org/10.1650/0010-5422\(2007\)109\[32:ATDOSE\]2.0.CO;2](https://doi.org/10.1650/0010-5422(2007)109[32:ATDOSE]2.0.CO;2)
- Lindström J (1999) Early development and fitness in birds and mammals. *Trends Ecol Evol* 14:343–348
- Machin P, Fernández-Elipe J (2012) The role of snow after a lemming peak year in Lapland. Poster presented at: International Wader Study Group Conference, Séné, [https://www.researchgate.net/publication/312936860\\_The\\_role\\_of\\_snow\\_after\\_a\\_lemming\\_peak\\_year\\_in\\_Lapland](https://www.researchgate.net/publication/312936860_The_role_of_snow_after_a_lemming_peak_year_in_Lapland)
- Machin P, Fernández-Elipe J, Flinks H, Laso M, Aguirre JI, Klaassen RHG (2017) Habitat selection, diet and food availability of European golden plover *Pluvialis apricaria* chicks in Swedish Lapland. *Ibis* 159(3):657–672. <https://doi.org/10.1111/ibi.12479>
- Machin P, Fernández-Elipe J, Flores M, Fox JW, Aguirre JI, Klaassen RHG (2012) Individual migration patterns of Eurasian golden plovers *Pluvialis apricaria* breeding in Swedish Lapland; examples of cold spell induced winter movements. *J Avian Biol* 46:634–642
- McKinnon L, Nol E, Juillet C (2013) Arctic-nesting birds find physiological relief in the face of trophic constraints. *Sci Rep* 3(1):1816. <https://doi.org/10.1038/srep01816>
- Meltofte H, Piersma T, Boyd H et al (2007) Effects of climate variation on the breeding ecology of Arctic shorebirds. *Bioscience* 59:1–48
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260
- Newton I (1989) Lifetime reproduction in birds. Academic Press, London
- Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Glob Chang Biol* 13(9):1860–1872. <https://doi.org/10.1111/j.1365-2486.2007.01404.x>
- Pearce-Higgins JW, Yalden DW (2002) Variation in the growth and survival of golden plover *Pluvialis apricaria* chicks. *Ibis* 144(2):200–209. <https://doi.org/10.1046/j.1474-919X.2002.00048.x>
- Pearce-Higgins JW, Yalden DW (2004) Habitat selection, diet, arthropod availability and growth of a moorland wader: the ecology of European golden plover *Pluvialis apricaria* chicks. *Ibis* 146(2):335–346. <https://doi.org/10.1111/j.1474-919X.2004.00278.x>
- Pearce-Higgins JW, Yalden DW, Whittingham MJ (2005) Warmer springs advance the breeding phenology of golden plovers *Pluvialis apricaria* and their prey (Tipulidae). *Oecologia* 143(3):470–476. <https://doi.org/10.1007/s00442-004-1820-z>
- Pearce-Higgins JW, Dennis P, Whittingham MJ, Yalden DW (2010) Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Glob Chang Biol* 16(1):12–23. <https://doi.org/10.1111/j.1365-2486.2009.01883.x>
- Piersma T, Lindström A, Drent RH, Tulp I, Jukema J, Morrison RIG, Reneerkens J, Schekkerman H, Visser GH, Lindström Å (2003) High daily energy expenditure of incubating shorebirds on high Arctic tundra: a circumpolar study. *Funct Ecol* 17(3):356–362. <https://doi.org/10.1046/j.1365-2435.2003.00741.x>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Core Team R (2017) nlme: linear and nonlinear mixed effects models. *R Package Version 3:1–131* <https://cran.r-project.org/web/packages/nlme/nlme.pdf>
- Qvenild T, Rognerud S (2017) Mass aggregations of *Bibio pomonae* (Insecta: Diptera: Bibionidae), an indication of climate change? *Fauna Norv* 37:1–12. <https://doi.org/10.5324/fn.v37i0.2194>
- Development Core Team R (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna <http://www.R-project.org>
- Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P (2003) Environmental variability, life-history covariation and cohort effects in the red-billed chough *Pyrrhonorax pyrrhonorax*. *J Anim Ecol* 72(1):36–46. <https://doi.org/10.1046/j.1365-2656.2003.00673.x>
- Ricklefs RE (1973) Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:177–201
- Ritz C, Streibig JC (2005) Bioassay analysis using R. *J Stat Softw* 12:1–22
- Roff D (1993) The evolution of life histories. Chapman and Hall, New York
- Rogers LE, Hinds WT, Buschbom RL (1976) A general weight vs length relationship for insects. *Ann Entomol Soc Am* 69(2):387–389. <https://doi.org/10.1093/aesa/69.2.387>
- Saether B, Bakke O (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81(3):642–653. [https://doi.org/10.1890/0012-9658\(2000\)081\[0642:ALHVAC\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[0642:ALHVAC]2.0.CO;2)

- Sæther B, Ringsby T, Røskaft E (1996) Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms. *Oikos* 77(2):217–226. <https://doi.org/10.2307/3546060>
- Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Huppopp K, Huppopp O, Lehikoinen A, Lehikoinen E, Rainio K, Romano M, Sokolov L (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proc R Soc Lond B* 278(1707):835–842. <https://doi.org/10.1098/rspb.2010.1778>
- Schekkerman H, Tulp I, Piersma T, Visser GH (2003) Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. *Oecologia* 134(3):332–342. <https://doi.org/10.1007/s00442-002-1124-0>
- Schekkerman H, Tulp I, Calf K, de Leeuw JJ (2004) Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2002. Alterra report 922, Wageningen
- Schekkerman H, van Roomen MW, Underhill LG (1998) Growth, behaviour of broods, and weather-related variation in breeding productivity of curlew sandpipers *Calidris ferruginea*. *Ardea* 86:153–168
- Skartveit J (1995) Distribution and flight periods of *Bibio* Geoffroy, 1972 species (Diptera, Bibionidae) in Norway, with a key to the species. *Fauna Norv B* 42:83–112
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Therneau T, Grambsch P (2000) Modeling survival data: extending the Cox model. Springer-Verlag, Berlin. <https://doi.org/10.1007/978-1-4757-3294-8>
- Thomson DL (1994) Growth and development in dotterel chicks *Charadrius morinellus*. *Bird Study* 41(1):61–67. <https://doi.org/10.1080/00063659409477198>
- Tjørve KMC (2007) Does chick development relate to breeding latitude in waders and gulls? *Wader Study Group Bull* 112:12–23
- Tjørve KMC, Garcia-Peña GE, Szekely T (2009) Chick growth rates in Charadriiformes: comparative analyses of breeding climate, development mode and parental care. *J Avian Biol* 40:53–558
- Tjørve KMC, Schekkerman H, Tulp I, Underhill LG, De Leeuw JJ, Visser GH (2007) Growth and energetics of a small shorebird species in a cold environment: the little stint *Calidris minuta* on the Taimyr Peninsula, Siberia. *J Avian Biol* 38(5):552–563. <https://doi.org/10.1111/j.2007.0908-8857.04014.x>
- Tulp I, Schekkerman H (2001) Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2001. Alterra report 451, Wageningen
- Tulp I, Schekkerman H (2008) Has prey availability for arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. *Arctic* 61:48–60
- van Gils JA, Lisovski S, Lok T, Meissner W, Ożarowska A, de Fouw J, Rakhimberdiev E, Soloviev MY, Piersma T, Klaassen M (2016) Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science* 352(6287):819–821. <https://doi.org/10.1126/science.aad6351>
- van de Pol M, Bruinzeel LW, Heg D, van der Jeugd HP, Verhulst S (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*). *J Anim Ecol* 75(2):616–626. <https://doi.org/10.1111/j.1365-2656.2006.01079.x>
- van der Velde M, Haddrath O, Verkuil YI, Baker AJ, Piersma T (2017) New primers for molecular sex identification of waders. *Wader Study* 124 (published online, doi: <https://doi.org/10.18194/ws.00069>)