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**Influence of environmental factors on nestling
growth of the white-winged snowfinch (*Montifringilla
nivalis nivalis*)**



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1 Abstract

High alpine bird species are thought to be particularly threatened by global warming. Among them, the snowfinch (*Montifringilla nivalis*) has received little attention. It is important to understand the basic biology to determine the conservation measures for future protection of this species. In this study we focussed on the nestling growth of the snowfinch at the Furka pass in the Swiss Alps. The nestlings were measured at least every third day. The measurements included the following body features: weight, wing length, the 8th primary feather length (P8), body length and tarsus. With the measurements the growth curves for mass gain and wing development of the nestlings could be drawn. To examine the food availability and the feeding rate every nest box was repeatedly observed for thirty minutes. We additionally measured the abundance of invertebrates at random points in a maximum distance of five hundred meters around the colony, which should give a reference value for the food availability in the landscape. In generalized additive mixed model the morphological data was combined with the weather data of a weather station. There is evidence that the growth rate of mass of the nestlings may be influenced by temperature. Furthermore, it seems that the impacts of night temperatures are more crucial for the growth rate of mass than the day temperatures. The temperatures seem to have less effect on wing development than on weight gain. However, due to the small sample size, these results should be treated as provisional. Our results provide insight on how environmental factors, such as temperature, may influence the nestling growth and can serve as basis for further research. With additional data the precision of the estimated effects can be enhanced to better understand how the snowfinch may react in times of global warming.

2 Introduction

The Snowfinch *Montifringilla nivalis* (Linnaeus, 1766) is a passerine bird living in high mountain habitats. This bird species is well adapted to the rough climate conditions of the alpine ecosystem. Such adaptations include the ability to increase the metabolic rate to keep body temperature, to decrease body temperature in adverse periods to save energy or building well insulated nests (Deng & Zhang, 1990; Glutz von Blotzheim, 1997). Furthermore, there are several morphological adaptations: Snowfinches have an efficient body insulation, due to elongated downy barbules and a high node density at the downy feathers, which traps a layer of air against the skin (Lei et al., 2002). Lu et al. (2008) found that snowfinch populations at higher elevations had longer wings and smaller body sizes compared to their conspecifics living at lower elevations, which they assumed to be an adaptation for flying in thinner air.

The alpine habitat belongs to the habitats, which are particular vulnerable to climate change (Schröter, 2005; Akademien der Wissenschaften Schweiz, 2016). The impacts of climate change on alpine bird species are especially high (Maggini, 2014). Therefore also the snowfinch is likely to be threatened by the proceeding global warming (Maggini, 2014; Brambilla et al., 2016). Alpine birds are often threatened due to indirect effects of climate change, such as changes in availability of insects for insectivorous birds (Hazeu et al., 2010), which may be a result of vegetational changes. There was a significant increase of forest cover in the Swiss Alps at an elevation of 1650 and 2450 meters above sea level and this is likely to continue with global warming (Gehrig-Fasel, 2007). The upward shift of the treeline could result in increasing fragmentation and isolation or even loss of high alpine habitat (Chamberlain, 2013). The reduction of the open alpine habitat could pose a severe threat for a number of high alpine bird species, including the snowfinch (Chamberlain, 2013). Brambilla et al. (2016) studied the contraction of the habitat for several alpine bird species (including snowfinch) in northern Italy and predicted a reduction up to 97% of the suitable area for the snowfinch due to climate change and conflict with ski pistes. Additionally, the food availability (e.g. nutritious arthropods provided to nestlings) may decrease or its seasonal occurrence may change if snow

patches are getting rarer or are melting earlier due to global warming. This may affect the snowfinch breeding performance, because Tipulidae larvae that are easily accessible at the edges of melting snow patches constitute a major food source for the nestlings (Heiniger, 1991).

There is a lack of knowledge of biology, status and trends of high alpine birds, due to the fact that studies in high alpine ecosystems are often challenging (Chamberlain, 2013). The breeding biology of the white-winged snowfinch is poorly studied till now and few references exist on the subspecies *Montifringilla nivalis nivalis* (e.g. Grangé, 2008; Strinella, 2011). It is crucial to understand even the basic biology of the snowfinch to determine the conservation measures to protect this bird species in the future (Chamberlain, 2013). The Swiss Alps host around 15% of the world population of the snowfinch subspecies *Montifringilla nivalis nivalis* (Keller et al., 2010) and thus has a high responsibility to protect this species. That's why the Swiss Ornithological Institute has launched a project to study the breeding biology of the snowfinch in the Swiss Alps.

In this project we studied the breeding biology of the species *Montifringilla nivalis nivalis*, which is a subspecies of *Montifringilla nivalis* (see chapter 3.1). The aim of my bachelor thesis was to understand how temperature and food availability influence the nestling growth rate. For this purpose we examined the nestling growth of the white-winged snowfinch (*Montifringilla nivalis nivalis*). An aim was to describe how the nestling development proceeds and how the growth curves for different morphological variables look like. Additionally, we wanted to figure out which factors influence the nestling growth. How do the ambient temperatures (day and night temperatures) and the food availability influence the nestling growth? Do they grow faster if temperatures are higher? Are night or day temperatures more crucial for the growth? What is more crucial for the nestling growth rate: the temperatures or the food availability? To answer these questions we studied the snowfinch population at the Furka Pass in the Swiss Alps (see chapter 3.2).

3 Methods

3.1 Study species

The study species of this project, the white-winged snowfinch *Montifringilla nivalis nivalis*, is a passerine bird living year-round in high mountain habitats. There are different subspecies with habitats extending from Iberia to Himalaya (Cramp & Perrins, 1994). The subspecies *Montifringilla nivalis nivalis* (white-winged snowfinch) breeds above the tree line in the Pyrenees, the Alps, Corsica, the Apennines, the Rhodope mountains and on the northern Peloponnese. The Swiss Alps host around 15% of the world population of this subspecies (Keller et al., 2010). The breeding habitat in the Alps ranges usually from 2000 to 2700 meters above sea and in a few cases even up to 3500 metres above sea. Their nesting sites have to satisfy several needs: they have to be sheltered from wind, precipitation and low temperatures. Last but not least they have to find enough food for their young and themselves in the surrounding of their nesting site. It is not unusual that there is a closed snow cover until mid-June in the breeding area of the snowfinch and there can be temperatures below zero degrees even during the breeding period. That's why it is essential that the breeding habitat includes some patches, which are snow free due to wind drift or because they are on steep slopes (Glutz von Blotzheim, 1997).

The snowfinches often use rock crevices or small holes in rocks to build their nest in. As an alternative they use anthropogenic nesting sites, such as buildings or ski lift poles. The nesting sites mostly have a narrow entrance and the nest is often placed in a distance of 40-80 cm from the entrance as a protection from the harsh climate conditions (Lang, 1939). The nest itself is thick-walled and is made mainly out of blades from *Carex* and *Poaceae* and can contain few lichens and mosses. Additionally, the hollow of the nest is well insulated with lots of feathers (particularly from the snow grouse) and mammalian hair (e.g. from sheep or chamois) (Aichhorn, 1989). The clutch size is normally between 2 and 5 eggs (Heiniger, 1991). The incubation period is approximately 13-14 days long, which is rather short for a habitat with such low ambient temperatures (Heiniger, 1991). The nestlings stay around 20-21 days in the nest before they fledge (Lang, 1939).

While outside of the breeding season the snowfinches eat almost entirely seeds from alpine plants, their main nourishment during the breeding season are thought to be arthropods (larvae, lepidoptera, arachnida etc.), which they collect from the ground (Heiniger, 1991). The main component of the nestling food is larvae from Tipulidae, because they are especially nutritious. The Tipulidae larvae live in the cavern between the snow blanket and the ground. In the evening they freeze in the melt water and are released when the snow melts on the following day. That's why there are many Tipulidae larvae at the edge of snow patches, which are easily accessible for the snowfinches (Heiniger, 1991).

3.2 Study area

The study took place from the beginning of June till the beginning of August 2016 at the Furka Pass in Switzerland (46°34'36.09"N, 8°25'16.60"E). The Furka Pass is a high mountain Pass in the Swiss Alps, connecting the two cantons of Valais and Uri. The Furka Pass is on an elevation of 2'427 metres. At the Furka Pass there are 12 buildings of a former military camp, which the snowfinches used to build their nests beneath the roof (Figure 1) In the year 2012 Heinz Bachmann from the Swiss Ornithological Institute Sempach installed twenty nest boxes for the snowfinch. The boxes were specially designed to meet all requirements of a snowfinch nesting site and are easy to detach to do research projects on breeding. The nest boxes were well accepted by the snowfinches in the following breeding seasons. In autumn 2015 ten additional nest boxes were installed.

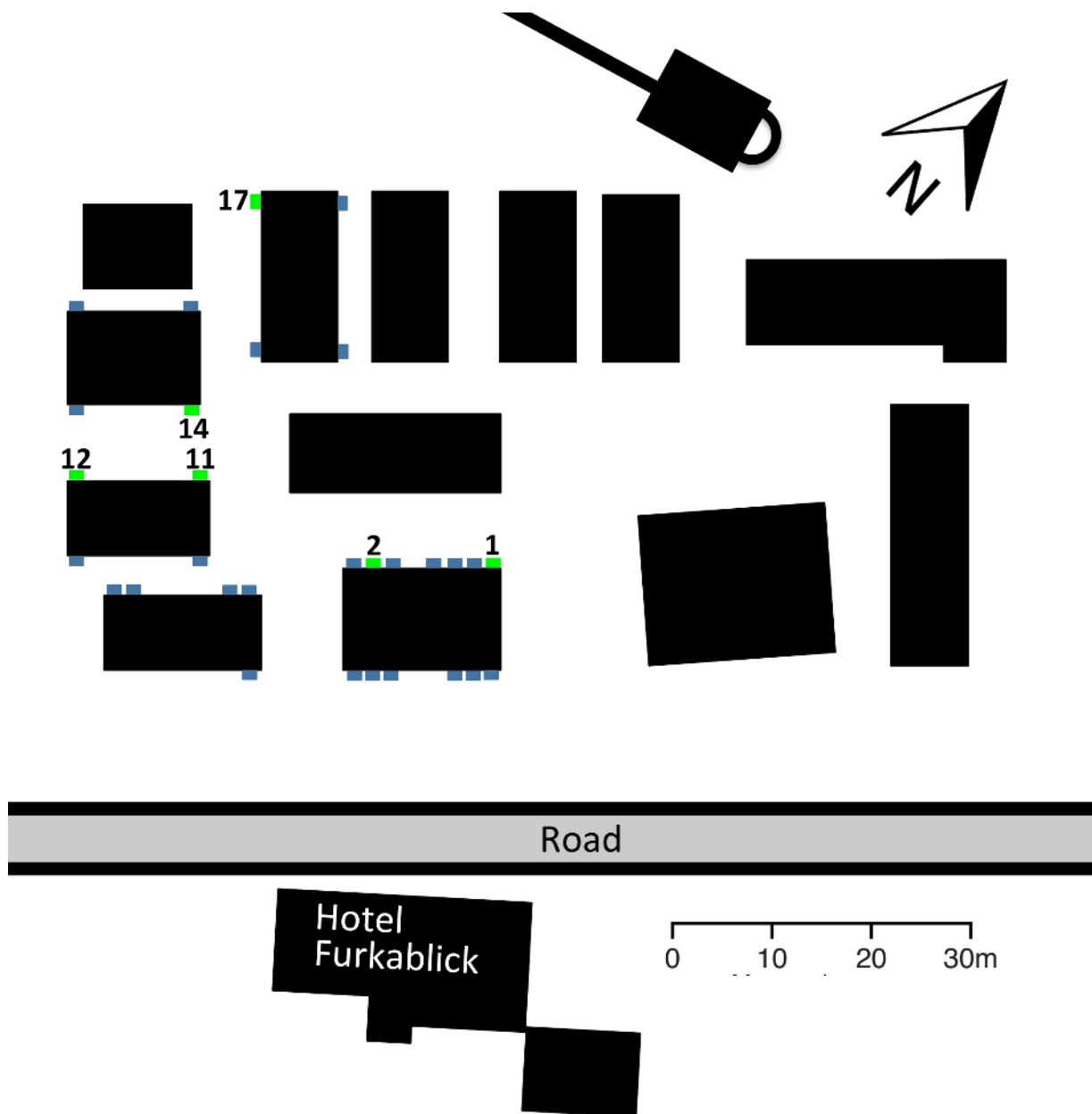


Figure 1: Map of the buildings on Furka pass based on a map of the Federal Office of Topography swisstopo (<https://map.geo.admin.ch/>). The nest boxes are drawn as rectangles. The colours of the nest boxes indicate if there were nestlings in the nest box in summer 2016. All the nest boxes with broods are green and with the nest box number, the others are blue.

3.3 Nestling measurements

After the hatching, we detached the nest boxes every third day to measure the nestling size and weight. We weighted the nestlings with a calibrated balance (Kern Emb 500-I, 0.1g) and took standardised pictures on a mm-grid paper. We took a picture from the dorsal side to see how the feathers grow and how the nestling appearance is changing with its age. The pictures from the ventral side would be used to see the fat deposition. You can recognize the fat as yellowish areas under the skin. Once the nestlings were a few days old we additionally took pictures in front of a white paper from the whole body with closed and with open wings. We used a small box with a cherrystone-pad, which we heated up in the microwave to prevent the nestlings from cooling off too much during the measurements. We further measured the tarsus, the wing-length, the 8th primary feather length (P8) (once they had feathers) and the body size from the head to the end of the tail. In the first measurements of a nestling we only determined the weight and we took the standardised pictures. I later used the pictures of the young chicks to measure the wing length in hindsight (see Figure 2). In four nestlings we directly measured the wing length from the beginning. I used this data to compare the two wing measurement methods to see if there is a systematic deviation. As you can see in Table 1 the two methods coincide very well, so we used all data for the analysis.

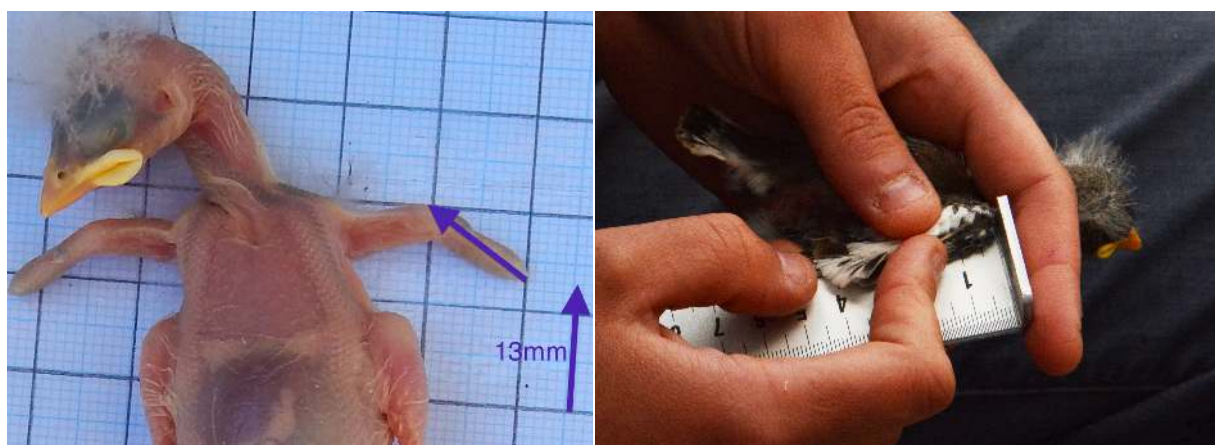


Figure 2: Pictures of the two methods for measuring the wing length. The left picture shows the measurement of the wing length based on a picture, which was taken on a mm-grid. The right picture shows the direct measuring in the field.

Table 1: Comparison of the direct and the picture-based method for measuring the wing length. The direct method was the measuring of the wings with a ruler directly in field. The picture method was the measuring of the wings based on the picture of the nestlings taken on the mm-grid (Figure 2)

Nestling (ringnr.)	Age [d]	Direct [mm]	Picture [mm]
N 566734	2.5	10	10
N 566735	2.5	6	7
N 566736	2.5	8	7.5
N 566737	2.5	6	7
N 566734	5.5	18	18.5
N 566735	5.5	10.5	11
N 566736	5.5	13	12.5
N 566737	5.5	14	13
N 566732	6	15	14.5
N 566733	6	18.5	18

After the weight and length of the nestling was determined, we put it back in the box and continued with its siblings. We did this work as fast as possible to minimize the disturbance of the birds. The nest box was put in place again after around 10 min.

For individual identification the nestlings were marked with red nail colour on different nails. Once the nestlings were around twelve days old, we ringed them with metallic rings from the Vogelwarte Sempach that contained a unique individual id number. And, when they were around 15 days old we additionally put a plastic ring with a 3 alphanumeric code on it (height 10mm, inner diameter 3.3mm, Interrex).

3.4 Food availability – feeding rate

To examine the food availability and the feeding rate, we repeatedly observed every nest box for thirty minutes. For this purpose a „hide“ (little, portable booth out of wooden rod and plastic sheets) was build that was put up in a distance of more than five meters from the nest box to minimize the disturbance of the feeding parents. For

the observation we used a scope (Optolyt TBG 80 80x30mm). On a prepared data-sheet we noted every movement at the nest box and, if possible, the kind and amount of food that the parents were provisioning. Furthermore, we noted the sex of the individual feeding the young.

We made so called “foraging walks” where we headed two points, which were randomly chose in the 500 meters surrounding of the colony. There we searched on one square meter for insects and other invertebrates (spiders, worms etc.) on the surface. For each invertebrate, we recorded the size (classes: 2-10 mm, 10-20 mm, > 20 mm), the state (larvae, adult) and the order or family (Tipulidae, other Diptera, Lepidoptera, Coleoptera, Arachnida, other). Afterward we used a small hand rake to scratch (1-2 cm deep) on the same square meter to search for invertebrates below the surface and recorded them similarly as described above. This should give a reference to the food availability in the landscape (Appendix).

We collected some of the found invertebrates for later biomass determination. However, as our collection did not cover all the food types that were observed, we used dry biomass data of invertebrates collected 2015 in the Valais by Nathan Horrenberger and Jaime Resano-Mayor (cf. Nathan Horrenberger Master Thesis, University of Berne – Conservation Biology, p20).

The data on feeding rates, amount of food brought and the biomass data were combined to estimate the received (dry) food (in g) for each nestling per day (see Appendix). Below, I call this estimate “food biomass index”. The food biomass index indicates an average amount of food biomass, which a single nestling received over the last two respectively three days (Appendix).

3.5 Weather data

The researchers from the alpine research station „ALPFOR“ (www.alpfor.ch) operate an own weather station. We received the mean air temperature [°C] for every ten-minute interval for the whole breeding season (1 min measurement interval).

3.6 Statistical analysis

All statistical analyses were performed in R version 3.2.1 (R Core Team, 2016) using the `mgcv` (Wood, 2006) and `lme4` (Bates et al., 2015) packages.

A generalized additive mixed model (GAMM) was used to assess relationships between environmental factors and the nestling growth rate of mass. Nestling growth rate of mass [g/d] was calculated as weight gain [g] divided by the period [d] since the last measurement. A normal distribution was assumed as error distribution in the model. As fixed factors were included average day and night temperatures, the age of the nestlings, the clutch size and the food biomass index. Thin plate regression splines (Wood, 2003) were used for modelling the non-linear relationship of growth and age of nestlings. In addition there were two random factors included: the nest and the individual to account for repeated measurements of the same individual and non-independence of nest mates. As day temperatures we defined the temperatures from 7 a.m. until 7 p.m. and as night temperatures the temperatures from 7 p.m. until 7 a.m. The explanatory variables (food biomass index, night and day temperature, clutch size) were averaged over the period [d].

For analysing the growth rate of wing length we used a same model structure as for growth rate of weight. The growth rate of the wing length was used as outcome variable for the GAMM. The growth rate of the wing describes the daily length gain of the wing in millimetre [mm]. All other factors were identical to the growth rate of mass model.

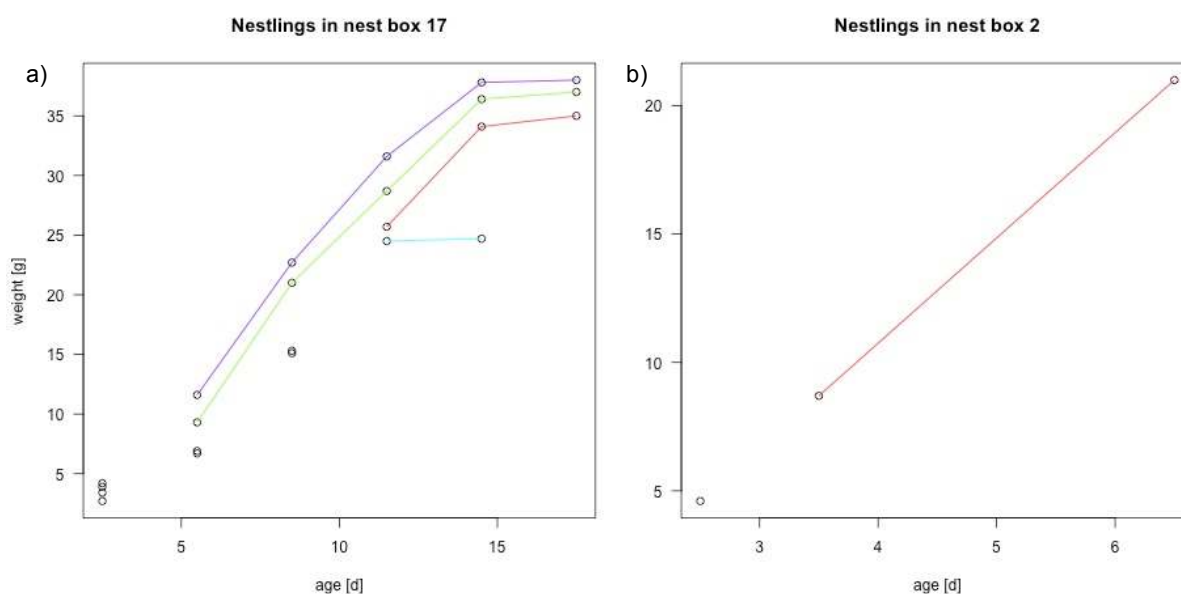
Standard diagnostic residual plots were used to assess model assumptions.

4 Results

4.1 Nestling growth curves

4.1.1 Weight

During the summer 2016 eighteen nestlings (six broods) hatched in the nest boxes. The measured weights plotted against the age of the nestlings for each of the six broods are represented below (Figure 3 a-f). The plots are ordered chronologically according to hatching date (cf. legend Figure 3). The youngest nestling we measured was $2.5 (\pm 0.5)$ days old and the oldest $18 (\pm 0.5)$ days old. The growth curves of the nestlings do not differ essentially. The growth curves show that the nestlings gain weight nearly linearly up to an age of approximately 13-14 days and that the weight gain decreases henceforth till they fledge. In some nestlings, the weight is reduced during the last days at the nest (e.g. Figure 3c). In nest box 17 we couldn't distinguish the nestlings in the first few measurements, because they lost the nail colour, therefore the data points in Figure 2a are not connected for the first measurements. The lightest nestling in nest box 17 (turquoise line) did not gain weight from the age of 12 days to 15 days and died afterwards (cf. Figure 3a) The two nestlings in nest box 2 died at an age under 10 days (cf. Figure 3b).



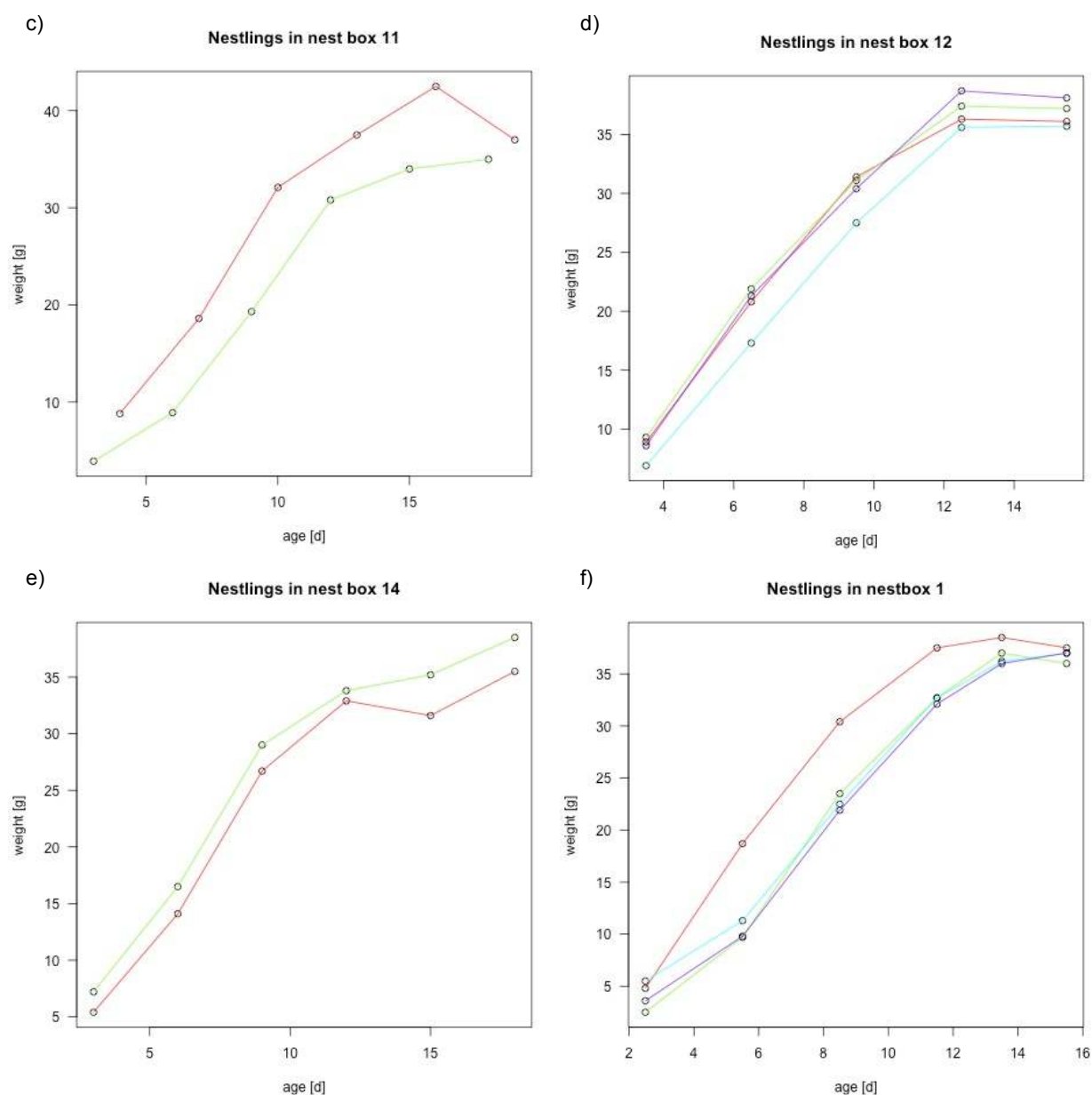


Figure 3 a-f: Growth curves of the 18 snowfinch nestlings - weight of nestlings [g] plotted against their age. The plots are ordered chronologically according to the hatching date. Hatching dates: a) 17.06.2016 ($\pm 2d$); b) 18.06.2016 ($\pm 1d$); c) 22.06.2016 ($\pm 1d$); d) 28.06.2016 ($\pm 1d$); e) 02.07.2016 ($\pm 1d$); f) 14.07.2016 ($\pm 1d$).

In Figure 4 all the weight measurements are plotted together. The nestlings from the same nest are indicated with the same colour of the data points. A generalized additive mixed model was used to draw the regression line in the plot. The solid line illustrates how an average snowfinch nestling grows. The dashed lines indicate the 95% confidence interval of this average growth curve. This growth curve over all our data illustrates even better how the weight gain of a snowfinch nestling looks like: a

almost linear weight gain up to an age of 13-14 days and afterwards a flattening of the growth curve in the last third of the nestlings period.

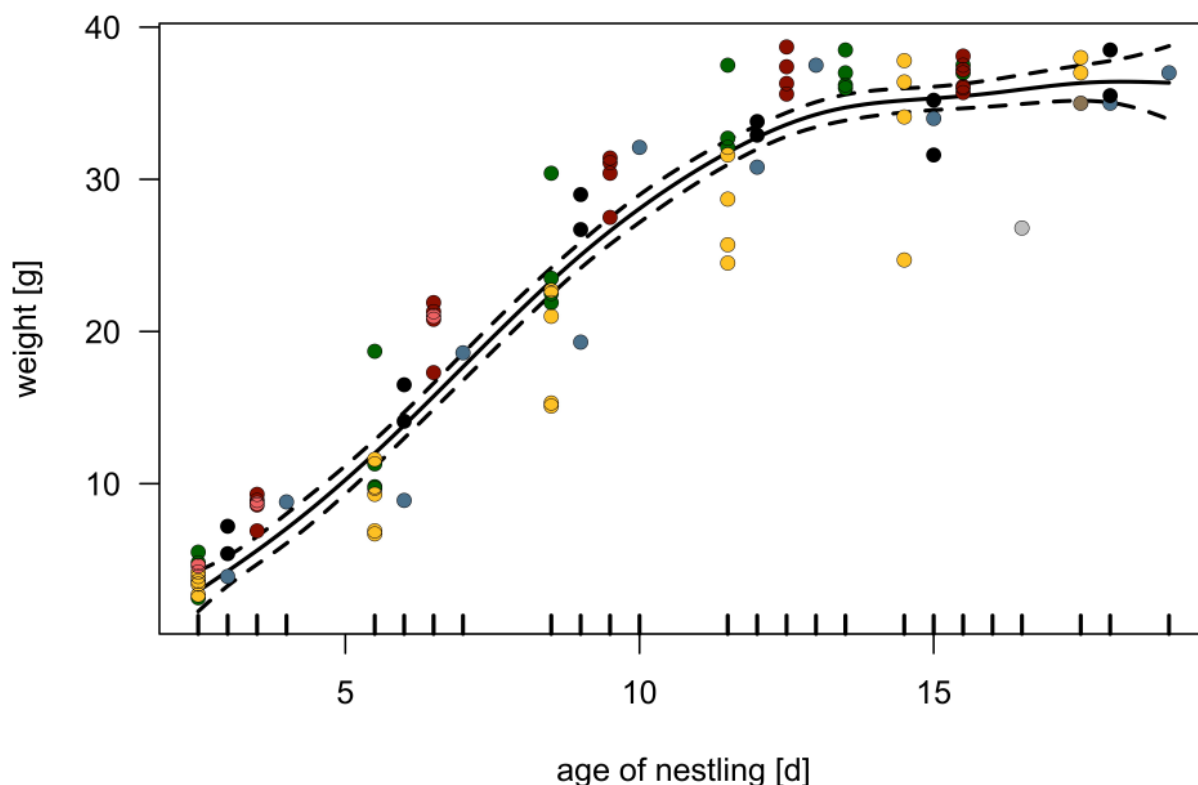


Figure 4: The growth curve of an average snowfinch nestling: the weight [g] plotted against the age [d]. A generalized additive mixed model (GAMM) was used to fit the regression line. The dashed lines show the 95% confidence interval of the growth curve. The colours of the data points indicate the nestlings from the same broods.

The growth rate for each time period between two measurements was calculated for each nestling. These growth rates are plotted in Figure 5 against the mean age of the period between two measurements. The plot shows that there is a maximum in the weight gain at an age of 4 to 8 days and that the daily weight gain decreases linearly until it reaches zero. When the nestlings are around 16 days old, some of them even loose weight (negative growth rate).

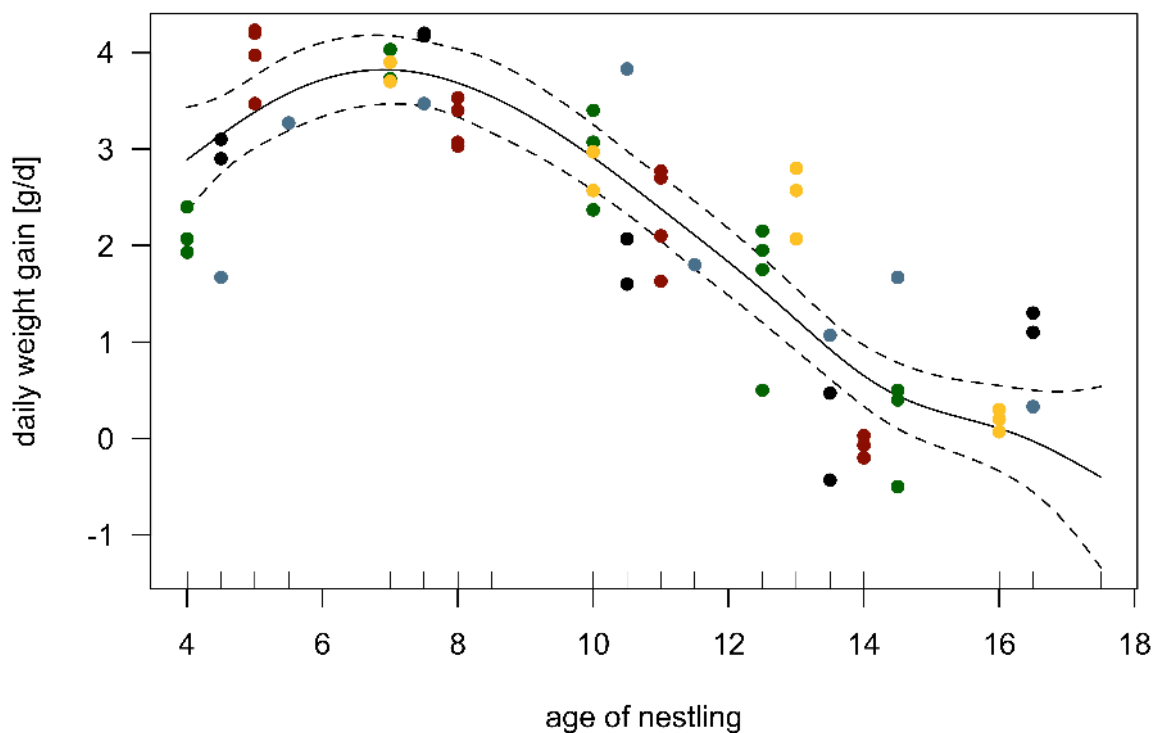


Figure 5: Daily weight gain of an average snowfinch nestling in grams [g]. As the age the mean age between two measurements was used. The colours indicate the broods. A generalized additive mixed model (GAMM) was used to fit the regression line. The dashed lines show the 95% confidence interval of the daily weight gain.

As the same absolute weight gain in grams is something different for a small nestling compared to a big nestling, the percentage weight gain compared to the lastly measured weight was calculated. Figure 6 shows this percentage growth rate.

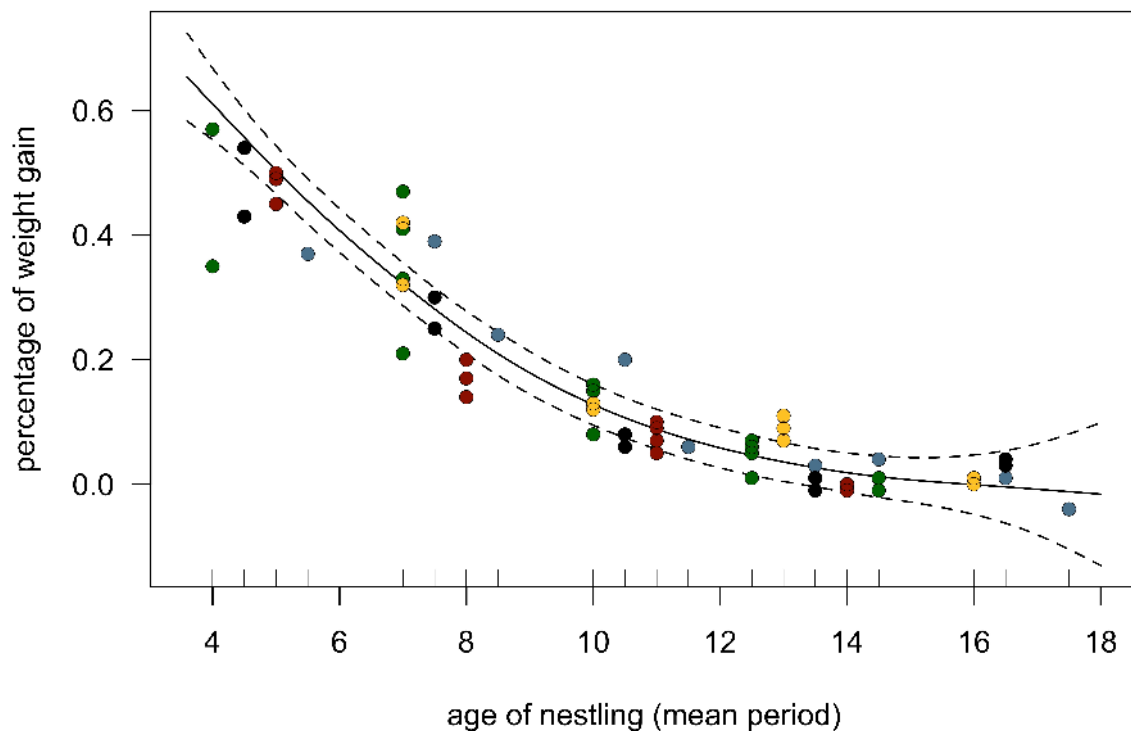


Figure 6: The daily weight gain in percentage [%/d] plotted against the age of the nestlings. It was calculated based on the weight from the last measurement. A generalized additive mixed model (GAMM) was used to fit the data. The dashed lines show the 95% confidence interval of the daily weight gain.

4.1.2 Wing length

The following plots (Figure 7 a-e) show the development of the wing length over the nestling period. The plots are in chronological order according to hatching date. The wing length changes linearly with the age of the nestlings. There is no visible flattening of the curves. This means that the wings grow linearly until almost the end of the nestling period. Nest box 2 is missing, as we didn't measure the wings of those nestlings (they died early; cf. Figure 3b).

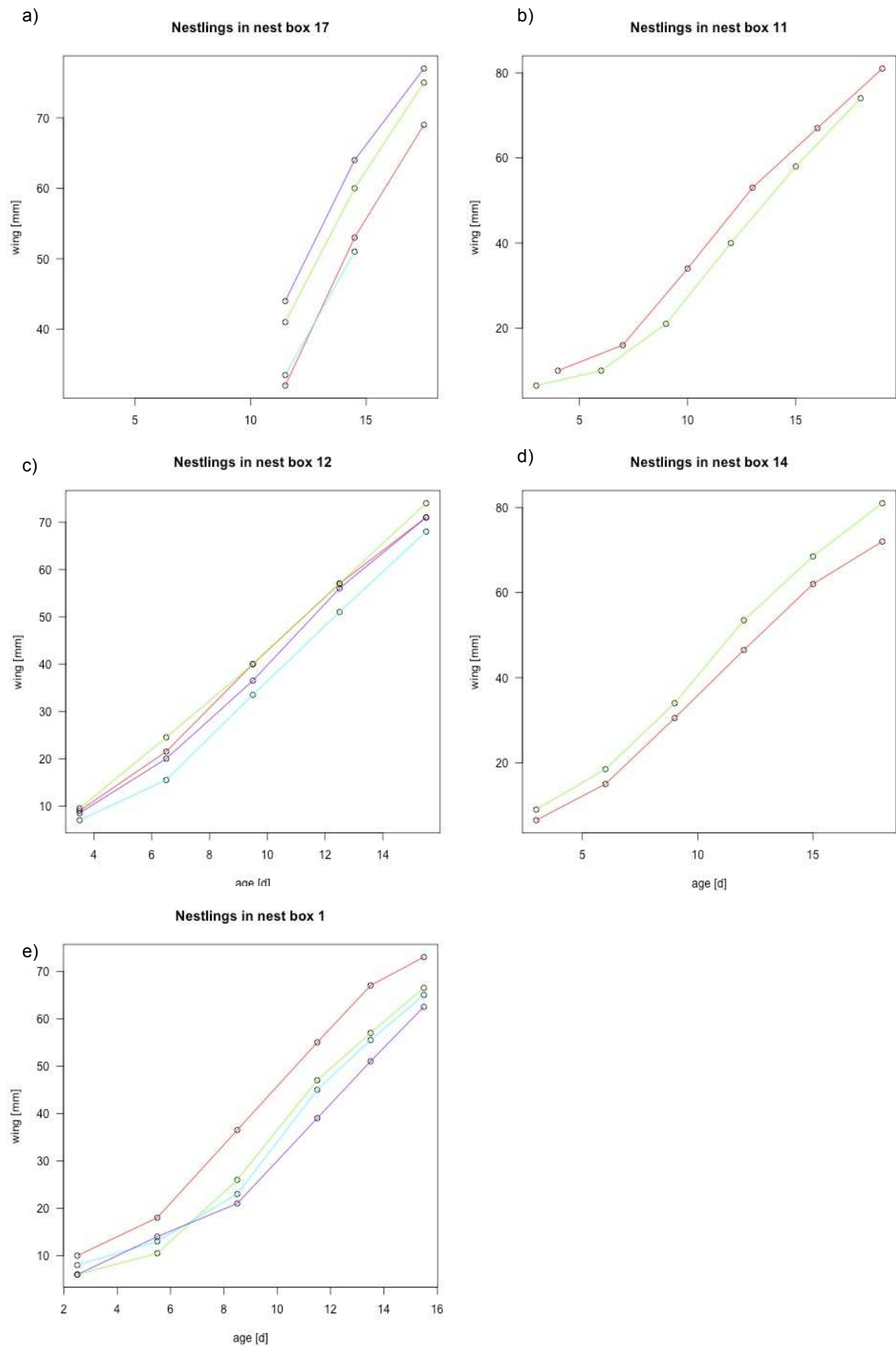


Figure 7 a-e: Wing length of the 16 nestlings against their age. (Nestling of the Nest Box 2 are not represented, because their wings weren't measured). Hatching dates: a) 17.06.2016 ($\pm 2d$); b) 22.06.2016 ($\pm 1d$); c) 28.06.2016 ($\pm 1d$); d) 02.07.2016 ($\pm 1d$); e) 14.07.2016 ($\pm 1d$).

All the data of the wing measurements are represented in Figure 8. It is visible that the development of the wings is linear and does not flatten much at the end of the nestling period.

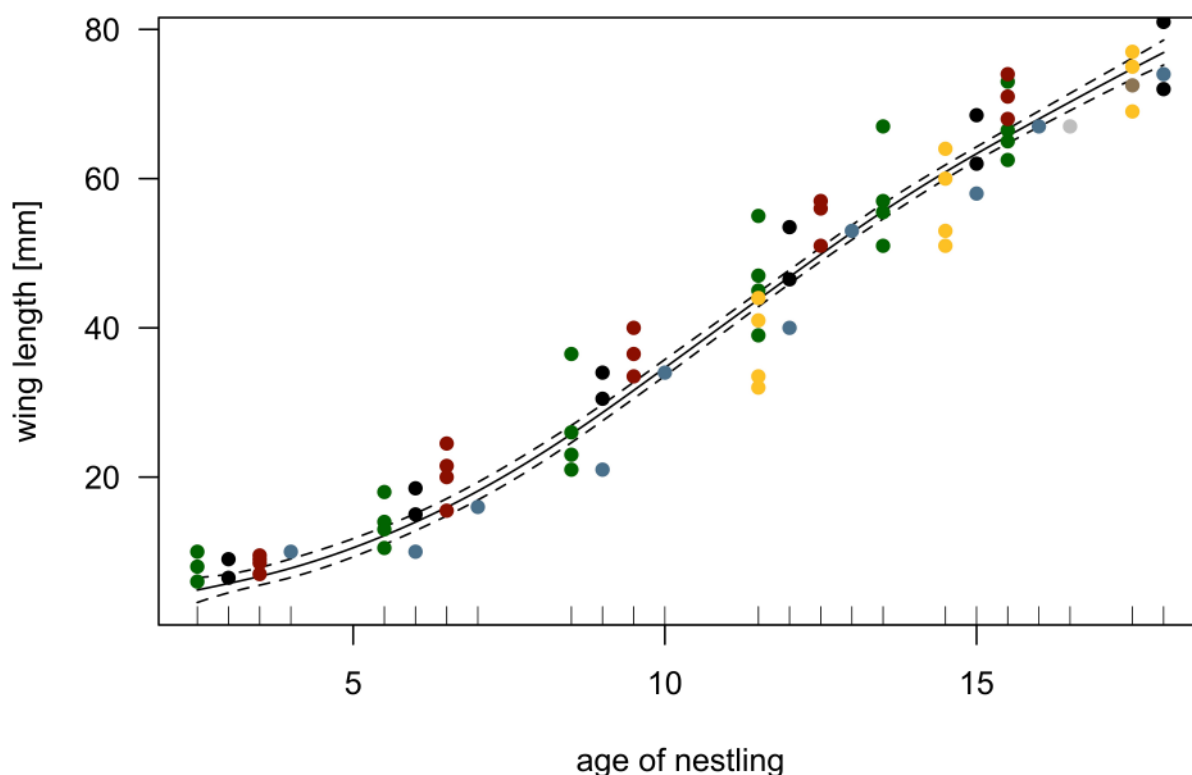


Figure 8: Wing length development over the age of the nestlings. A generalized additive mixed model (GAMM) was used to fit the regression line. The dashed lines show the 95% confidence interval of the wing length development.

4.2 Influences of temperatures and food availability on nestling growth

4.2.1 Influences on growth rate of mass

Due to the small sample size, the standard errors of the estimated correlations between daily mass gain and environmental factors are large (Table 2). Hence we cannot show clear influences of the environmental factors on daily mass gain. However, the night temperature may have a greater influence on the daily weight gain of the nestlings than the day temperatures (Figure 9). The night temperatures ranged from 0.7 – 10.5 °C and the average night temperature was 7.4°C. A 1°C warmer night was associated with in average around 0.19g (95% CI: -0.11 – 0.48g)

higher daily mass gain. Whereas the clutch size does not seem to have a big influence on the nestling weight, with an average of -0.06g (95% CI: -0.29 – 0.16g) in a 1°C warmer night.

Table 2: Parameter estimates of the GAMM with daily weight gain as outcome variable and environmental factors as explanatory variables.

	Value	Standard error SE
Intercept	1.477	0.543
Day temperatures	-0.094	0.160
Night temperatures	0.185	0.146
Food biomass index	0.481	0.726
Clutch size	-0.061	0.108

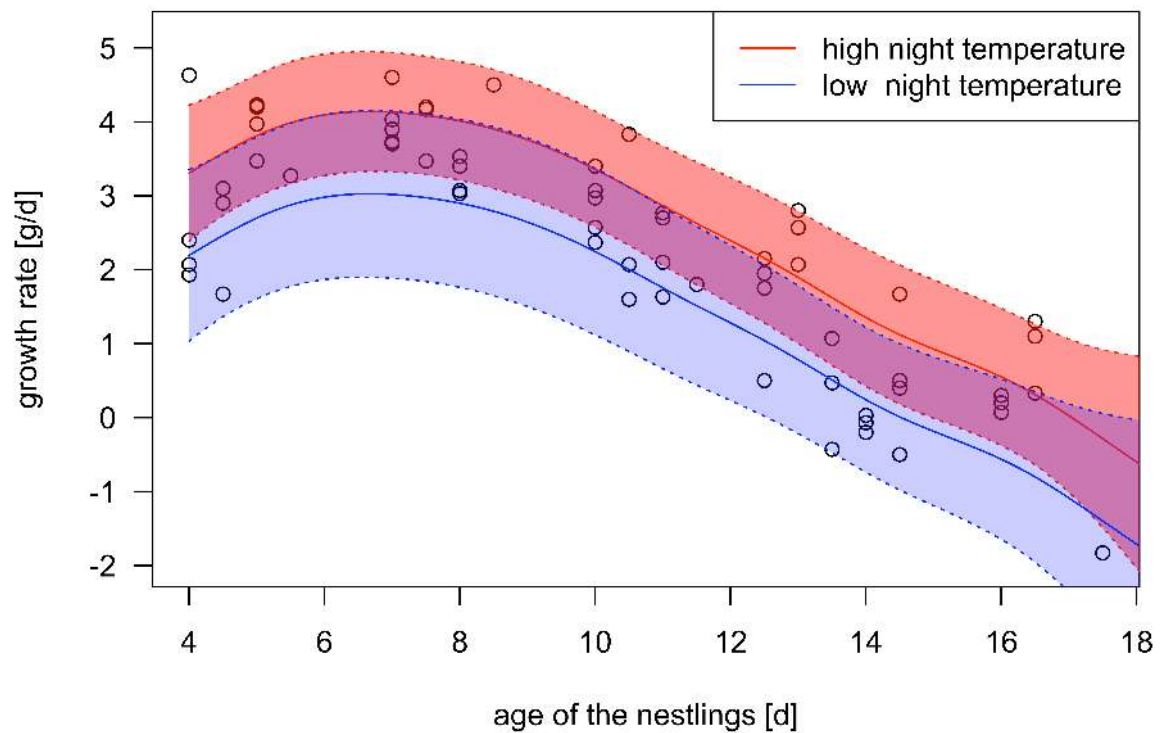


Figure 9: The growth rate of mass (daily mass gain, [g/d]) plotted against the age of the nestlings for cold and warm nights. The curves were fitted with the generalized additive mixed model (GAMM). The two curves indicate low respectively high night temperatures. They were defined as 3°C lower than respectively larger than the mean temperature (7.4°C): 4.4 °C and 10.4 °C. The dashed lines indicate the 95% confidence interval of the two curves.

4.2.2 Influences on wing growth

A 1°C warmer night was associated with in average around 0.10 mm (95% CI: -0.45 – 0.24g) lower daily wing length growth.

Table 3: Parameter estimates of the GAMM with daily wing growth [mm/d] as outcome variable and environmental factors as explanatory variables.

	Value	Standard error SE
Intercept	3.942	0.673
Day temperatures	0.051	0.196
Night temperatures	-0.104	0.171
Food biomass index	0.657	0.986
Clutch size	0.172	0.129

Again standard errors were large due to the small sample size. But none of the included environmental factors seems to have a severe influence on the wing development. As the average wing length growth per day is 4.9 mm/d the influences of the environmental factors seem to be quite small. Compared to the results of the growth rate of mass model, the results seem to be even less clear because the standard errors are high. For a conclusion additional data collection is required.

5 Discussion

The nestling measurements showed that the growth curve of weight of the snowfinch nestlings is quite similar to growth curves of other altricial bird species (e.g. Ricklefs, 1984). The highest daily mass gains were measured in nestlings of age 4-8 days. For older nestlings, daily mass gain decreased with age and reached even negative values towards the end of the nestling periods. Therefore, it may be possible that young nestlings have larger energy demands than old nestlings (as predicted by Ricklefs, 1984) even though the older nestlings have a higher basal metabolic rate due to their larger body size. In two of the six nests, the food provided by parents clearly showed a peak for young nestlings (see Appendix). At all nest, the food provided per day and nestling decreased towards the end of the nestling period. This reflects that young nestlings have a higher energy demand than older nestlings and the parents react to this energy demand by providing more food for young nestlings. As a consequence, food availability during the first few days after hatching may be the most crucial for development and survival of snowfinch nestlings. Lower temperatures in the beginning of the field season and probably also the lower food availability may be the reason why some of the first hatched nestlings died (Figure 2a, 2b; Appendix).

The growth curves of the snowfinch were similar to the related house sparrow (*Passer domesticus*) (Weaver, 1942). Both species, snowfinches and house sparrows, show almost linear weight gain until an age of around 13-14 days. Due to the fact that the nestling period of the snowfinch, with 20-21 days, is around 4-5 days longer than the nestling period of the house sparrow, the time where the nestling stays in nest but does not gain weight is longer in snowfinches than in house sparrows. Since adult house sparrows are smaller (22-32g) than snowfinches (~32-47g) the snowfinch nestlings show a higher daily mass gain [g/d].

The longer nestling period could be due to the larger body size of the snowfinch or a shorter nestling period in the house sparrow could be an adaptation to higher nest predation rates (Remes & Martin, 2002). Further research is needed to assess nest predation rates in snowfinches and house sparrow. Furthermore, the nestling growth and nestling period should be compared in a standardized manner. To do so, growth

of different body parts such as tarsus and skeletal measurements would help assessing the developmental state at fledging.

The nestling growth rate can be influenced by weather variables (temperature, precipitation) directly or indirectly (Bradbury et al., 2003). Lower temperatures can chill the nestlings and thus increase their energy demand for thermoregulation. The weather can influence the invertebrate availability and thus indirectly influence the received amount of food by the nestling (Bradbury et al., 2003). There are a variety of studies, focussing on the different energy allocation strategies in reproducing adult birds but rather few which study the energy allocation from nestlings (Dawson et al., 2005). Nestlings have to allocate their energy for their growth and for thermoregulation. It is likely, that the ambient temperature at the nest site influences thermoregulation and thus influences the energy allocation (Dawson et al., 2005). Dawson et al. (2005) studied the nestling growth of tree swallows (*Tachycineta bicolor*) and found that the temperature expedites growth of the primary feathers and that there is a trend for a positive correlation between the temperature and the growth rate of mass. They found no temperature dependency of the tarsus growth. Our study may also indicate that temperature has an influence on the growth rate of mass of the snowfinch nestlings. This temperature effect we found is corrected for food availability by including the food biomass index in the models. With this we reduced the risk for wrong conclusions, caused by the temperature dependency of food availability. But since we made an observational study and did not experimentally change the temperatures in the nest boxes, pseudo-correlations can not be completely excluded.

In our study we further distinguished between day and night temperatures and found that the night temperatures tend to be more crucial for the nestlings growth than the day temperatures. This may be explained with the fact that the snowfinch parents normally do not stay in the nests during nights. Thus the nestlings may use a lot of energy to keep their body temperatures during cold nights. It might be that the night temperatures have different impact on growth rate of mass and on wing development. Due to the small sample size (only 6 nests, 18 nestlings) all our results on temperature dependency should be treated with care and it should be confirmed with additional data. If further research show, that night temperature influences only

the mass gain of the nestling and does not influence the wing development this could be an evidence that the nestlings of the snowfinch do not do a torpor during cold nights. Because we expect that the wing development would also be slowed if they would do a torpor during cold nights.

Peréz et al. (2016) studied the nestling growth of two species of Arctic-breeding passerines, *Zonotrichia leucophrys gambelii* and *Calcarius lapponicus*. They used similar measuring methods of the nestlings, an electronic balance for weight and a caliper for tarsus. They found a negative correlation between precipitation and daily weight gain in both species and one species, *Calcarius lapponicus*, showed a positive correlation between temperature and daily weight gain. Precipitation probably had an important influence on the growth rate in these species, because they are ground breeding bird species and thus more direct vulnerable to precipitation than cavity-nesting birds like the snowfinch. However, there could be indirect effects of precipitation such as different feeding behaviour or changing food availability. In our model we included precipitation indirectly via the food biomass index. For the estimation of received food by the nestlings, rain was used as a predictor. However, the correlation between rain and food availability was not clear (Appendix).

It can be concluded that there is further research needed to clearly understand how environmental factors influence nestling growth of the snowfinch. Additional data collection is needed to test if the found tendencies about the influence of night temperature on growth rate of mass are reinforced. For full proof that the night temperatures influence the nestling growth one could experimentally warm and cool nest boxes during night (e.g. Dawson, 2005). To understand the influencing factors specific for the Swiss Alps it would be crucial to continue with the nestling measurements at the Furka pass and in other places. Datasets from several years would allow comparison between warm vs. cold breeding periods. Care has to be taken that the nestling measurements are started as soon as possible after hatching to get data of the freshly hatched nestlings and also to do measurements of nestlings close to fledging. Especially the measurements at the end of the nestlings period could be of high interest, because the growth is slowed in this period and it would be

interesting to understand which part of the body stops growing at what age of the nestling.

We showed and plotted the mass gain and the wing development of the snowfinch nestlings. The curve of the mass gain seems to be comparable to other sparrows, such as the house sparrow. The growth rate of mass of the nestlings may be influenced by temperature. There is a trend that night temperatures have a stronger effect on growth rate of mass than day temperatures. This shows that the microclimate in the nest (influenced by nest site and nest construction) may be an important factor for growth and survival of snowfinch nestlings. Therefore, the availability of suitable nest sites (rock crevices, buildings, nest boxes) seem to be an important measure for the protection of the snowfinch. It might be that the temperature has other or less impacts on the wing development than on weight gain. But due to the small sample size all of the found environmental effects on nestling development are not clear. Therefore further research and additional data collection is required to increase the sample size. For full prove of temperature influences experimental manipulation of the nest box temperature should be considered.

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8 Appendix

Estimating the daily biomass provisioning of Snowfinch nestlings

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Introduction

Daily parental provisioning rate is one of the most crucial factors that determine nestling growth rate and survival in altricial bird species (Ricklefs 1984). Therefore, daily provisioning rate largely influences reproduction and fledging success and is an important factor in determining population growth rate in short-lived species (Sæther and Bakke 2000).

How much food parents provide to their chicks depends on the availability of food and on the degree of parental investment mediated by their experience and number of siblings. Food availability is greatly influenced by environmental, biotic and abiotic factors such as habitat coverage, intra- or inter-specific competition, vegetation type and structure and weather variables like temperature and precipitation (e.g. Pérez et al. 2016).

In this study, we investigate the cascade from 1) biotic (vegetation) and abiotic (weather) environmental conditions to 2) food availability to 3) the biomass that is provided to the nestlings of White-winged Snowfinch (*Montifringilla nivalis nivalis*). To do so, we first describe correlations of environmental factors and food availability. Second, we correlate feeding rates and food types with food availability and environmental factors. We also quantify between-nest and between-day variances in feeding rate and food type.

As a result, we present an estimate of the biomass of food that was provided during each day to six broods of Snowfinches at Furkapass. These food-provisioning estimates serve for the investigation of nestling growth rates as we want to better understand the effects of food provisioning rates and biomass on nestling growth rates.

Methods

Data collection

Random and foraging points

Two random points included within a 500m radius around the Snowfinch Furka colony and spaced between 300m apart were randomly chosen. Then, while walking on the transect between the two random points, we opportunistically registered foraging points whereas Snowfinches were observed collecting food. Food availability and vegetation was measured at the last foraging point of the transect. Therefore, almost every day, at random time of the day, a pair (or triple) points were selected and both habitat measurements and food availability were recorded within a 1-meter square for each point.

A set of environmental variables was mapped at every point: Temperature at 10cm (°C), wind (m/s), solar radiation (W/m^2), relative habitat cover (%). Before habitat mapping, all the invertebrates detected within the 1-m square were visually recorded. For each invertebrate item, we estimated the size (classes: 2-10mm, 11-20mm, > 20mm), the development stage (larvae or adult) and the taxonomic order or family (Tipulidae, Other Diptera, Lepidoptera, Coleoptera, Hymenoptera, Heteroptera, Arachnida, Annelida, other). After recording all invertebrates on the ground, the ground was scratched to around 1-2cm depth using a small garden rake and all insects recorded similarly as described above. After 07.07.2016, we stopped scratching but only searched on the surface for prey items. As a consequence only around half of the numbers of items were found than if the original method would have been used.

Observation of feeding rates and food types

We observed repeatedly the number of times that parents provided food to each of six clutches during half an hour, at random times of the day, in order to determine feeding rates (n=68 half hours). When it was possible, we noted the sex of the parent, the time it stayed inside the nestbox as well as the number and category of food items it brought. Of 102 out of 340 feeding events, at least one food item could be identified and the total number of food items could be estimated.

Biomass measurements

The insects collected on our study site have been measured, identified to the level of the taxonomic categories defined above, dried and weighed (dry biomass).

In addition to our own data, we used dry biomass data of invertebrates collected in 2015 in the Valais by Nathan Horrenberger (Nathan Horrenberger Master Thesis, Universität Bern – Conservation Biology, p20).

Statistical analyses

All statistical analyses were done in R 3.3.1 (R Core Team 2016).

Food availability index

We first analyzed correlations between the number of available invertebrates, hereof called prey items, and weather, habitat variables, date and time of the day in order to understand what factors influence food availability. Second, we developed a model for estimating the food availability in a buffer of 500m around the colony at any time over the whole breeding season.

For the first analysis we used two multiple regressions. First we used only the number of large prey items, which were defined as larger than 1 cm in length. Second, we used the number of all prey items as outcome variable. Both outcome variables were increased by one and logarithm transformed prior to analysis. As predictors we used day of year, time during the day, an indicator variable of rain, an indicator variable of whether scratching has been used for searching for the prey items or not, vegetation height (log-transformed and z-transformed so that the mean

was zero and the standard deviation one), solar radiation (z-transformed), an indicator variable of whether the plot was completely covered by snow, distance to snow (log-transformed and z-transformed). Data of 130 points (13 foraging/117 random) were used for this analysis. Model assumptions, particularly linear relationships were assessed using standard residual plots, and by plotting the residuals against each of the predictor variable.

The aim of the second analysis was to find a model that allows for estimating food availability for all hours over the whole breeding season. Therefore, we could only use predictor variables of which continuous measurements over the season were available. Thus, we used time, date, temperature and rain as predictors. We further included an indicator of whether scratching was used or not. We used a generalized additive model (GAM) within which we allowed for non-linear relationship between prey abundance and time and date. Such a non-linear relationship may account for temporally variable effects, like the one of solar radiation, which were not included in the model. These effects were not included because they were measured specifically on the points and therefore not available for interpolating. As outcome variable we used the total number of all prey items that was increased by one and logarithm transformed. A normal error distribution was assumed. We used two dimensional penalized cubic regression splines for date and time to model the temporal pattern of food availability.

Data of 133 points were used for this analysis. The model was fitted to the data using the function `gam` from the package `mgcv` (Wood 2006). Model assumptions were assessed using standard residual plots, particularly by plotting the residuals against each of the predictor variable.

From the model, we calculated the expected number of prey items for each hour of the season based on temperature, rain and the smoother function of prey item on time and date. This expected number of prey items can be interpreted as an index of general food availability in the vicinity of the Snowfinch colony. It is used for the analyses of biomass per feeding event and feeding rate (see below).

Biomass per feeding event

For 102 feeding events, we could identify at least one item that was brought). For these 102 feeding events, we calculated the biomass brought by multiplying the number of items per type with their specific dry weight and summed this weight over all prey types brought at one feeding event. For non-identified items, we inserted average weights of 0.016 g for larvae, 0.004 g for imagos and 0.01 g for the others.

We used a linear mixed model to predict biomass per feeding event from date, temperature, food availability index, age of the nestlings and brood size. The outcome variable biomass was logarithm transformed. The brood was used as random factor to account for between-parents variance in biomass brought per feeding event. The model was fitted to the data using the function `lmer` from the package `lme4` (Bates et al. 2015).

Model assumptions were assessed using standard residual plots.

From the model we obtained an expected average biomass fed per feeding event for each brood and day.

Feeding rates

In total for the six broods, we observed adult feeding rates 68 times during a 30min interval. These feeding rates were correlated with weather factors, food availability, date, time and with age of the nestlings and brood size. To this end, we used a generalized linear mixed model. The number of feeding events per 30min was used as outcome variable and a Poisson error distribution was assumed. Temperature, food availability index, time, day of year, nestling age and the square of nestling age (as nestling age has a clear quadratic effect) and brood size were used as predictors. The brood and the date were included as random factors. The model was fitted to the data using the function `glmer` from the package `lme4` (Bates et al. 2015).

Model assumptions were assessed using standard residual plots. Particularly, residuals were plotted against each of the numeric predictor variables to assess linear relationships. The dispersion was 1.04, thus no correction for over dispersion was necessary.

From this model, we interpolated feeding rates for all day hours (5 to 21) during the nestling period of each of the six broods.

Total biomass fed to the nestlings

To obtain an estimate of the total biomass the nestlings of each brood received per day, we first multiplied the estimated feeding rates per 30min with the corresponding estimates for the biomass per feeding event. Second, we multiplied the resulting number by two to get the biomass fed per hour. Finally, the estimates for the hours 5 to 21 were summed for each day and brood.

Results

Food availability

Prey abundance and prey size increased over the breeding season (Figure 2).

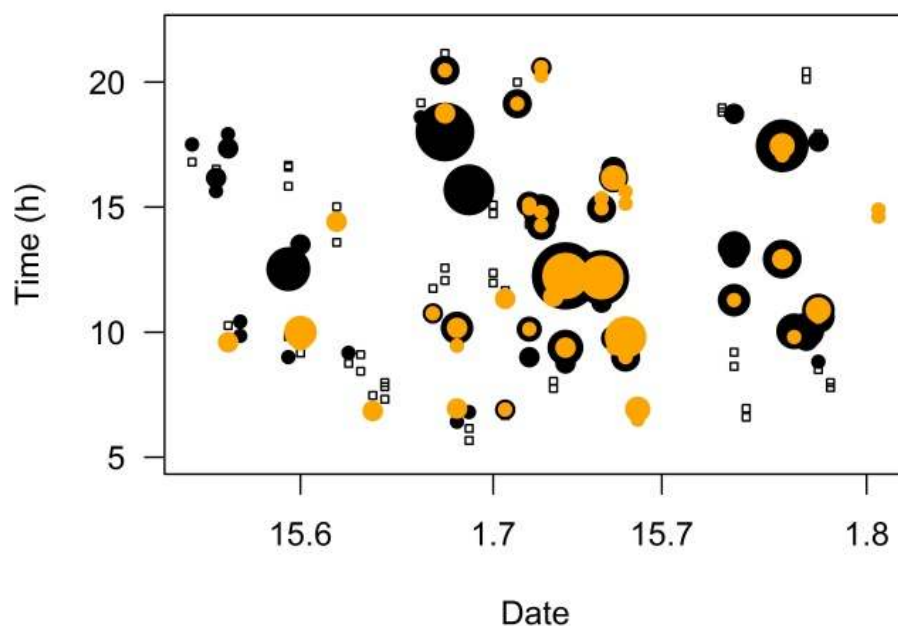


Figure 2. Temporal (daily) and seasonal distribution of the number of prey items found in 1m² plots within 500m of the breeding colony at Furka. Open squares = no prey found; the size of the filled circles corresponds to the number of prey items found, black = all prey types, orange = prey types larger than 1 cm. After 7.7.2016 we stopped scratching but only searched on the surface for prey items. As a consequence only around half of the numbers of items were found than if the original method would have been used.

Day of year and scratching showed the strongest correlation with the number of (all and large) prey items found (Table 2). Number of large prey items (and also indicated, though with large uncertainty, for all prey items) decreased with distance to snow patches (

Figure 3). The average number of prey items found increased by 2% every day over the season for both prey types. When the 1m² plot was scratched, we found 65-72% more prey items. Solar radiation was positively correlated with all prey abundance.

Table 2. Parameter estimates of the multiple regression with the number of prey items per 1m² plot (transformation: $\log(x+1)$) as outcome variable. Sample size was 130 plots. Large prey items are prey larger than 1 cm length.

Parameter	large prey		all prey	
	Estimate	SE	Estimate	SE
Intercept	-3.22	1.11	-3.00	1.65
Date (day of the year)	0.02	0.01	0.02	0.01
Time (hour)	0.00	0.01	0.02	0.02
Temperature (°C)	-0.01	0.02	0.00	0.03
Indicator of rain	0.03	0.13	0.12	0.19
Indicator of scratching	0.54	0.17	0.50	0.26
Vegetation height (log, z-transformed)	0.12	0.08	0.10	0.12
Solar radiation (z-transformed)	0.04	0.05	0.17	0.08
Indicator of complete snow cover	-0.15	0.18	-0.24	0.27
Distance to snow (log, z-transformed)	-0.15	0.07	-0.09	0.10

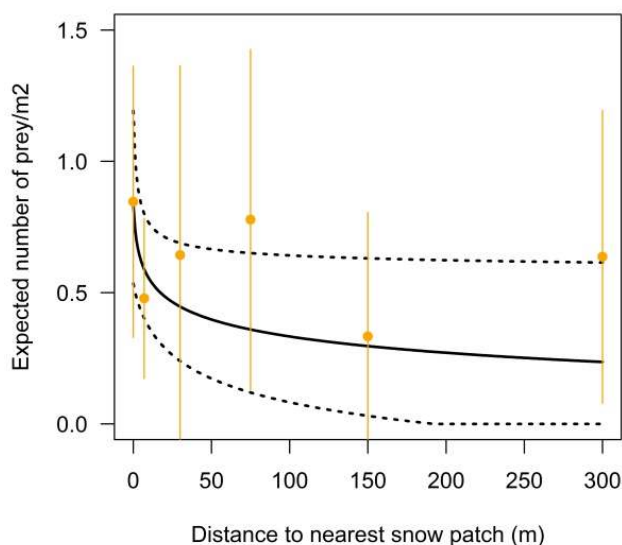


Figure 3. Effect of distance to nearest snow patch on the number of large prey items/m². Bold line is partial regression line (all other predictors held constant on their means), dotted lines show the 95% confidence interval. Orange dots are means of the data with 95% credible intervals.

The generalized additive model showed a clear increase of food availability over the season as well as a distinct effect of time (hour) of the day (Figure 4). Food availability peaked in the early afternoon. The correlation of food availability and rain or temperature was not as clear as it was in the first model where we included more predictor variables (Table 3). The interpolation of the expected number of prey items for each hour in the season showed the following food availability patterns: food availability was very low until the end of June. In the last third of June food availability moderately increased but decreased again at the end of June. During the first half of July, food availability increased until a second decrease in mid July. This second decrease coincided with a snowfall on the 14th July. After that snow fall, food availability continuously increased again until the end of the Snowfinch breeding season in early August.

If we included only the large prey items, the effect of time was less pronounced, i.e. the large prey items are more evenly distributed along the day, but otherwise the seasonal pattern looked similar.

Table 3. Parameter estimates of the generalized additive model (GAM) designed for estimating a food availability index for the whole season.

Parameter	Estimate	SE
Intercept	0.17	0.17
Temperature (°C)	0.01	0.02
Indicator of rain	0.06	0.19
Indicator of scratching	0.62	0.27
Smoother time x date (degrees of freedom)	6.11	-

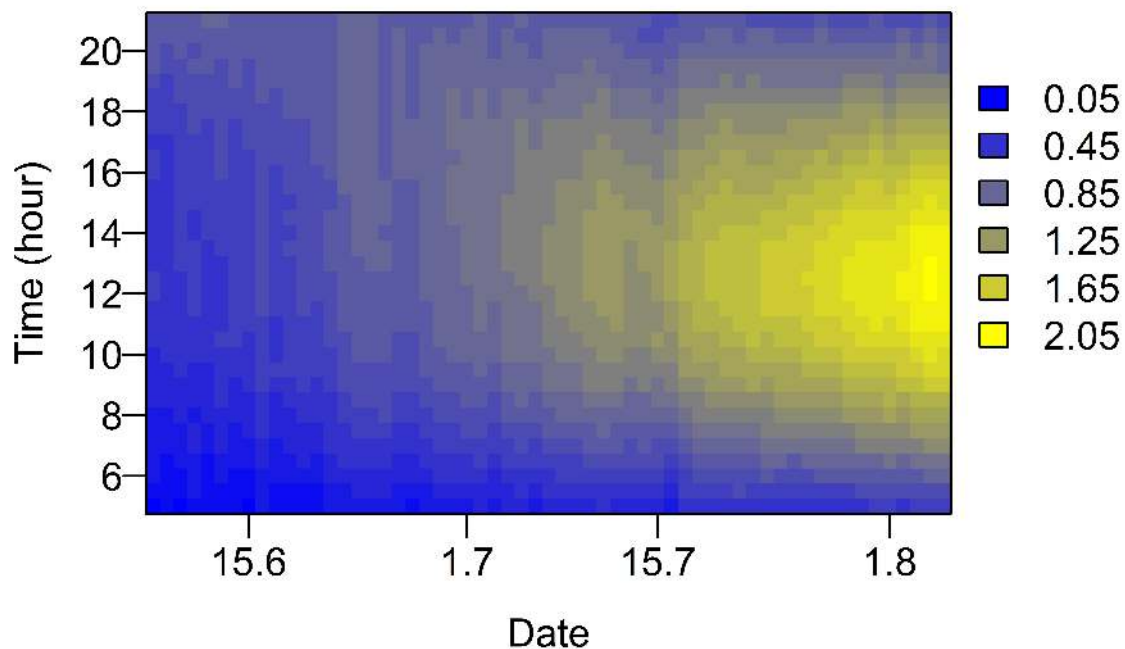


Figure 4. Food availability index for the whole season based on daily time (hour), date, rain and temperature.

Dry biomass per feeding event

Relationships between average dry biomass brought per feeding event were unclear. Brood size may be the most important factor in determining the amount of food the parents bring in one feeding event (Table 4). The between-brood variance was very small.

Table 4. Parameter estimates of the linear mixed model of logarithm transformed biomass fed per feeding event. Between brood standard deviation was close to zero ($7.1e-8$), residual standard deviation was 1.21.

Parameter	Estimate	SE
Intercept	0.46	3.78
Temperature (°C)	0.10	0.07
Food availability index	0.22	0.86
Date (day of the year)	-0.03	0.02
Nestling age (day)	-0.02	0.03
Number of nestlings (Brood size)	0.27	0.16

Based on the mixed model we interpolated the average biomass per feeding event for all nestling ages for the six broods (Figure 5). Differences in biomass brought per feeding event differed between the broods.

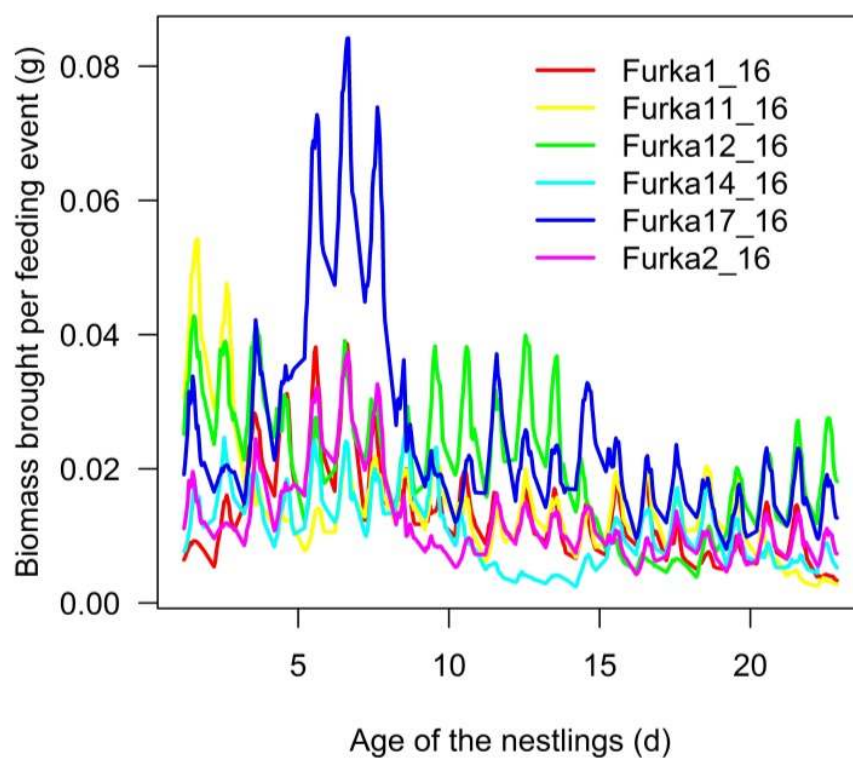


Figure 5. Estimated dry biomass brought per feeding event depending on nestling age for the six broods.

Feeding rates

Feeding rates increased by 20% with each additional nestling (Table 5). It also increased with the age of the nestlings until they were around 15 days old. After 15 days the feeding rates decreased (Figure 6).

Table 5. Parameter estimates of the generalized linear mixed model for feeding rates. Between brood standard deviation and between-day standard deviations were close to zero (0).

Parameter	Estimate	SE
Intercept	0.46	0.31
Temperature (°C)	-0.01	0.01
Food availability index	0.41	0.30
Date (z-transformed, sd=11.5 days)	0.14	0.02

Time (hour)	-0.04	0.02
Nestling age (z-transformed, sd=6.0 days)	0.15	0.08
Nestling age ² (z-transformed, sd=6.0 days)	-0.24	0.07
Number of nestlings	0.18	0.06

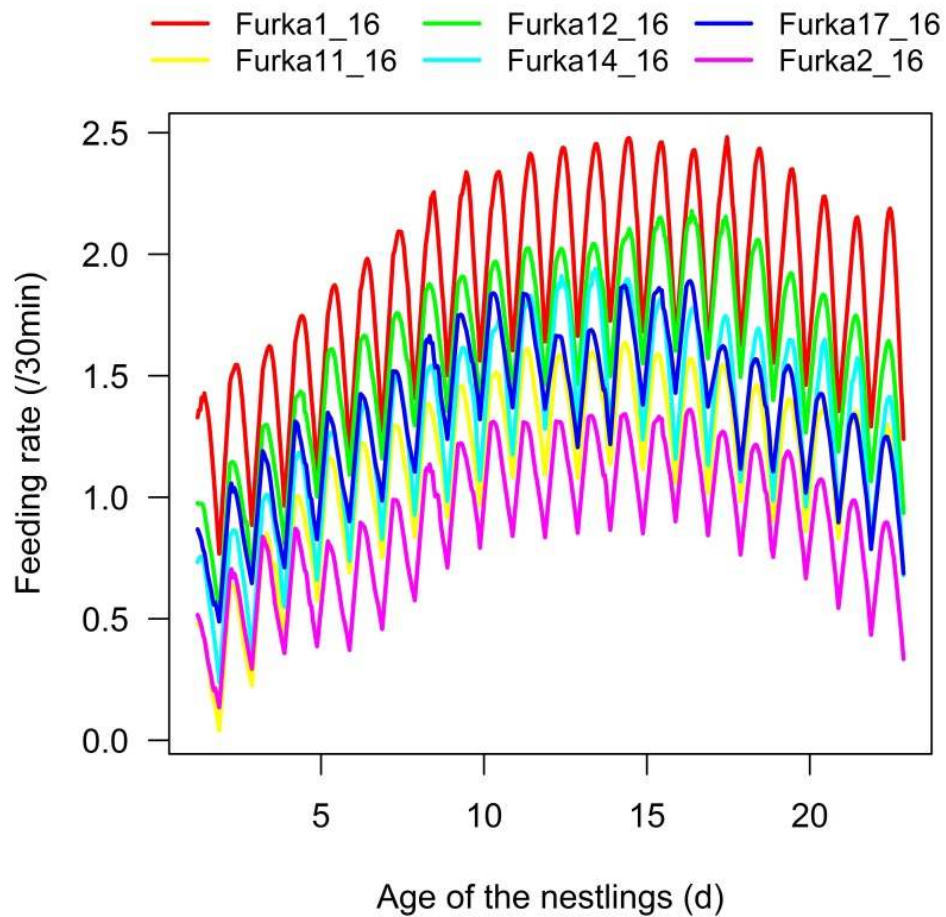


Figure 6. Estimated feeding rates for each brood over the nestling period.

Total dry biomass fed per day and brood

From the biomass and feeding rate models we inferred the total dry biomass that was fed to each of the broods every day along the chick rearing period (Figure 7). The biomass fed per day seemed to be twice as high in broods with four chicks (Furka1_16, Furka12_16 and Furka17_16) compared to broods with only two nestlings (Furka11_16, Furka14_16 and Furka2_16). In all broods, the biomass fed decreased towards the end of the nestling period.

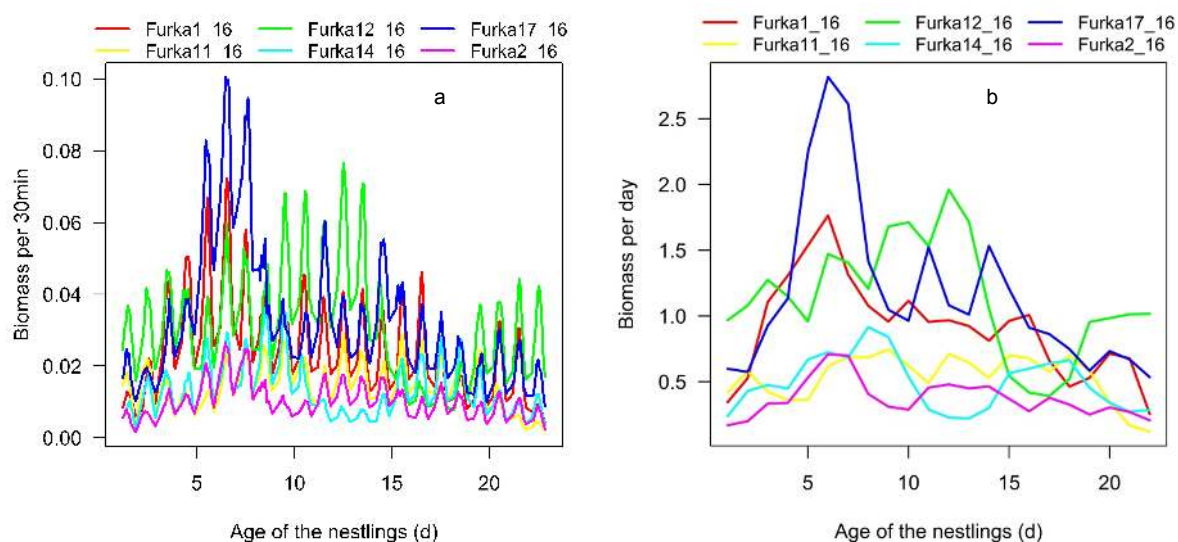


Figure 7. Estimated biomass fed per 30min (a) and per day (g) for each of the six broods.

Discussion

Methods

Absolute values of the estimates for the total biomass fed to the nestlings seem to be quite low. This could be either because we used dry biomass or because of numerical reasons. The sum of expected values of a variable that scatters in the upper tail may generally underestimate the mean of the sum of realizations of such a variable. Thus the estimates of the total biomass here may be used as an index of total biomass, but absolute values have to be treated with care.

Biology

Parents with more nestlings both increase the feeding rate and the amount of food brought at one feeding event. This increase in both feeding rate and food amount brought per feeding event results that in the end, the food provided per chick may be around equal in large and small broods.

Interestingly, feeding rates peaked around day 16 of the nestling period, whereas the biomass brought to the nestlings peaked much earlier (before day 10). This implies that the feeding behaviour and very likely also the composition of the nestlings diet changes with the age of the nestlings. Young nestlings receive a few times per day large biomasses (either larger or more prey items) and older nestlings are fed more often but with only little biomass. This observation deserves further analyses.

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