

**Impact of weather conditions on food availability, feeding
behaviour, nestling growth and brood survival in a
Wryneck population in Valais (Switzerland)**

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Table of contents	Page
Abstract	4
1. Introduction	5
2. Methods	8
2.1. Study area	8
2.2 Data sampling	8
2.2.1 Ant nest census	8
2.2.2 Recording feeding frequency	9
2.2.3 Nestling growth	9
2.2.4 Brood success and daily nest survival during the nestling stage	9
2.2.5 Weather data	10
2.3 Statistical analyses	10
2.3.1 Ant nest density	10
2.3.2 Feeding frequency	10
2.3.3 Nestling development	11
2.3.4 Nestling change of body mass	12
2.3.5 Daily nest survival of Wryneck during the nestling stage	12

3. Results	14
3.1 Variation of food availability in relation to weather	14
3.2 Breeding success	14
3.3 Feeding frequency	14
3.4 Nestling development	15
3.4.1 Impact of short-term weather effects on nestling body mass, tarsus and 8 th primary lengths	15
3.4.2 Factors influencing the nestlings' change of body mass	16
3.5 Daily nest survival of Wryneck during the nestling stage	17
4. Discussion	19
5. Acknowledgements	26
6. References	27
Tables	33
Figure legends	41
Figures	43
Appendix	49

ABSTRACT

1. While habitat destructions are the most important reasons for the decline of the Wryneck (*Jynx torquilla*), it has been hypothesised that weather factors are also important for the population dynamics of this endangered species.
2. We studied the impact of short-term variations of weather conditions on food availability (ants), feeding behaviour, nestling growth and brood survival probabilities in a population from the Swiss Alps (Valais).
3. We recorded the feeding frequency of 17 breeding pairs in the breeding season 2004 during two days at different nestling ages, measured the growth of these nestlings at six days and monitored the fate of 166 nests in the years 2002 to 2004. We used linear mixed models and Mayfield methods to test the impact of temperature on feeding frequency, nestling growth and brood survival.
4. Weekly ant nest searches in fruit tree plantations revealed that ant availability was not dependent on daily temperature or duration of sunshine.
5. The feeding frequencies increased with increasing temperatures and this effect was stronger when nestlings were older. The higher feeding frequency during warmer days resulted in a faster body mass increase in older nestlings. Moreover, temperature had a positive effect on the length of the tarsus and the 8th primary when the nestlings were older.
6. At the older nestling stage, body mass increase was lower in heavy nestlings, indicating compensatory growth in lighter nestlings on one hand and sufficient available food on the other hand.
7. Daily brood survival probability declined strongly in the course of the season. It was positively affected by temperature and negatively by the amount of rainfall, yet these effects were not very strong.
8. We conclude that reproductive performance of Wrynecks was not strongly affected by the observed weather variations, because most effects were not very important or could be compensated. Therefore, ongoing climate change is likely to be less important for the decline of Wrynecks than other factors such as the reduction of food availability or number of nest sites.

1. INTRODUCTION

Global climatic changes (Easterling et al. 1997) have potentially strong impact on bird populations. For example arrival and departures in the breeding grounds can change in migratory birds (Gordo et al. 2005, Sparks et al. 2005, Jenni & Kéry 2003). Changes in the phenology of the bird's migration patterns or of its prey abundance can result in a mismatch between the time of highest food demand and the time of highest food availability, with negative consequences on the bird's population dynamics (Visser et al. 1998). The effect of global climatic change to bird populations is complex however, with marked regional differences (Saether et al. 2003, Sanz 2002, Sanz 2003). Moreover, not only the climate change on breeding grounds can have an impact on bird population dynamics, but also climate change at the wintering place (Gordo et al. 2005, Sillett et al. 2000). While climate change may have a negative effect on certain populations of birds, it may have a positive effect on other populations or species, even resulting in range expansions (Thomas & Lennon 1999).

While it has been demonstrated that climate changes can impact population dynamics through changes in reproductive output (Möller 2002, Mc Donald et al. 2004) or survival (Sillett et al. 2000), there are relatively few studies of the mechanisms involved in these changes. For example, to examine the mechanisms involved on reproductive output requires studying the impact of weather variation on food availability, parental behaviour, nestling growth and brood survival.

Change in food availability due to climate modification is likely to be one of the most important proximate factors impacting on reproductive output. Parents could increase foraging activity and provisioning effort in case of food shortage. However, this may not be beneficial, as the residual reproductive value could decrease (Dijkstra et al. 1990). If food provisioning to nestlings is significantly reduced, nestling mortality

could increase, nestling growth may be reduced, potentially resulting in reduced future survival chances after fledging (Naef-Daenzer & Keller 1999, Naef-Daenzer et al. 2001). All these factors affect population dynamics.

The food of Wrynecks *Jynx torquilla* during the breeding period almost entirely consists of broods of ground-dwelling ants (Menzel 1968, Bitz & Rohe 1993, Hölzinger 1992, Freitag 1996, Freitag 1998) with very limited possibilities to switch to other food types when ant availability is temporally reduced. Therefore it is an ideal species to study the relationships between weather variation and food availability, feeding frequency, nestling growth and nest survival. Climatic changes such as increased rainfall during the breeding season are supposed to have initiated the long-term decline of European Wrynecks in the first half of the 20th century (del Hoyo et al. 2002). More information about factors limiting breeding success is needed. Here I studied whether short-term weather changes result in changes in ant availability, feeding frequency, nestling growth and brood survival rates of Wrynecks in the Swiss Alps.

Ground-dwelling ants move their brood in response to temperature and humidity changes in the soil to ensure an optimal growth of progeny (Anderson & Munger 2003, Pranschke & Hooper-Büi 2003, Seifert 1996). We hypothesised that ant broods deeper in the soil were not or less easily accessible for Wrynecks. Given that birds should adjust their behaviour to variation in food availability, we supposed that feeding frequency would be highest when ant availability is highest, thus under warm temperature conditions. As a result, we hypothesised that nestling growth should be highest when feeding activity was highest, thus when warm temperatures prevailed. Because the food demand of the nestlings is higher when they are old compared to when they are young (Turner 1983), we hypothesised these relationships to be stronger at the later nestling stage. Besides studying behaviour

and physiological responses at individual level, we also wanted to know, whether these effects were relevant at the brood level. Using detailed brood survival data of 3 years, we tested whether daily brood survival was affected by short-term weather variations. We predicted daily brood survival to be higher when warm temperatures prevailed and to be reduced by extensive rainfall.

2. METHODS

2.1. Study area

The main part of the study was carried out in 2004 in the Upper Rhône Valley (Switzerland), between Vernayaz and Sierre, around Sion (46.2°N, 7.4°E; 482 m above sea level). Some additional data were sampled in the same area in 2002 and 2003. The study area was about 62 km² (1.6 x 40 km). Most of the intensively cultivated plain is covered by fruit tree plantations and vineyards. In earlier years, 712 nestboxes were installed for the Hoopoe *Upupa epops*, mostly in small agricultural cabins in the vicinity of fruit tree plantations. Wrynecks breed regularly in these nestboxes.

2.2 Data sampling

2.2.1 Ant nest census

The aim was to study whether food availability for Wrynecks changed in relation to weather variation. The ants react to weather changes by moving the vertical position of their brood in the soil, which potentially modifies food availability for Wrynecks (Anderson & Munger 2003, Pranschke & Hooper-Bùi 2003, Seifert 1996).

We selected six fruit tree plantations and recorded weekly the density of ant nests in each plantation from 27 May to 2 August. Per plantation and week ten random patches were examined. Such a patch measured 0.5 m² and was defined by a wooden frame put on the ground between the tree trunks. The area within the frame was searched for ant nests by softly scraping the surface of the soil using a rack. The ground between the trunks was usually completely free of vegetation and it can be reasonably assumed that no ant nests were overlooked unless the ants retreated deep into the soil. For each found nest we noted the presence of larvae, pupae

and/or winged ants and determined species (*Lasius niger*, *Lasius flavus*, *Tetramorium caespitum* and *Formica spec.*).

We assumed that the overall ant nest density did not change between visits. Therefore, any variation in the observed nest density would have been due to vertical movements of the ants within the soil. We then tried to explain the variations of observed nest density with changes in the short-term weather conditions.

2.2.2 Recording feeding frequency

Using a miniature camera that was fixed into the roof of a nestbox we filmed feeding adult Wrynecks. A time lapse function enabled us to record up to eight hours of behaviour on a 240 minutes video tape. Video tapes were replaced around mid day to ensure continuous recording. Feeding frequency was recorded when the nestlings were 5 days old, and a second time when they were 14 days old. Hourly feeding rates were calculated after visioning the tapes.

2.2.3 Nestling growth

We recorded the growth of all nestlings of filmed broods when they were 3, 5, 7, 12, 14 and 16 days old. We measured body mass (± 0.1 g), tarsus length (± 0.1 mm) and the length of the eighth primary (± 0.5 mm). At the first measurement each nestling was marked on its claws with nail polish to allow individual identification. At the fourth or fifth measurement the nestlings were ringed.

2.2.4 Brood success and daily nest survival during the nestling stage

During the years 2002 to 2004 all nestboxes within the study area were controlled every fortnight. Nestboxes occupied by Wrynecks were then checked more frequently, about every third to fifth day. At each visit the number of eggs or nestlings

were counted and it was recorded whether the brood was still alive, had failed, or fledged successfully. Based on these data of all three study years both the annual brood success and the daily nest survival probability of the broods could be estimated.

2.2.5 Weather data

We used weather data recorded in Sion, (46.2°N, 7.4°E) by MeteoSwiss (Federal Office of Meteorology and Climatology). We considered temperature, amount of rainfall, relative humidity, and average hourly sunshine duration for the analyses. However, not all weather variables were used for all analyses. We had to exclude amount of rainfall from all analyses regarding ant nest density, feeding frequency and nestling growth. It hardly ever rained during the field season and the sample size of rainy days compared to days without rain was too small to ensure reliable results. Furthermore, the plantations were regularly irrigated. Without knowing the exact irrigation regime it would have been difficult to disentangle the effects of rain and irrigation, especially concerning the analyses of the ant nest densities.

2.3 Statistical analyses

2.3.1 Ant nest density

We summed up the number of ant nests found in the 10 plots within one plantation and day and tested whether this number depended on the temperature, hourly duration of sunshine, relative humidity and plantation identity by a linear model.

2.3.2 Feeding frequency

We analysed the feeding frequency with a linear mixed model. The dependent variable was the number of feedings at a given brood for each full hour. The brood

was considered as a random factor. The fixed factors were the number of nestlings per breeding pair, the age of the nestlings, the mean hourly temperature and its square. The latter was used to test for a possible curvilinear increase of the feeding frequency with temperature. Besides the factors themselves we tested the interactions of temperature with age, squared temperature with age and number of nestlings with age of nestlings.

2.3.3 Nestling development

To assess the development of three traits (body mass, tarsus length and 8th primary length) the nestlings have been measured six times. The different measurements from a nestling were not completely independent from each other (e.g. a nestling that is heavy at day x is likely to be heavy at day $x + t$). Therefore, we analysed them with a repeated measurement model. As the time gap between the six measurements varied, the correlation between two consecutive measurements was likely to decrease with increasing time gap between them. We therefore used a power model in which the correlation between two measurements t units of time apart is Φ^t . This model is a generalisation of an auto-regressive model. The nestling identity was nested with the brood, and both were considered as random factors. The fixed terms of the model were nestling age, brood size and mean ambient temperature. The mean ambient temperature (T_a) was calculated from 6:00 to 20:00 on the day before measurements took place, and from 6:00 to 12:00 on the day of measurements. Because the effects of both brood size and temperature on the nestling development may differ according to the age of the nestlings, we also considered their interactions with the factor 'nestling stage' (with levels "early" for nestlings being 3, 5 or 7 days old, and "late" for nestlings being 12, 14 or 16 days old).

2.3.4 Nestling body mass change

To analyse nestling mass change we calculated for each nestling the differences between measurements at 5 and 7 days and at 14 and 16 days of age. To analyse these data we considered a linear mixed model with brood as a random factor. T_a , mean number of hourly feedings per nestling on day 5 or 14, brood size and body mass measured at first measurement (day 3 or 12, respectively) were considered as fixed factors. Additionally, the interaction between the first mass measurement and T_a was tested. We performed two separate analyses for young and older nestlings.

For mixed models analyses we used the method of residual maximum likelihood estimation (REML; (Patterson & Thompson 1971)), because of unequal sample sizes among categories. All analyses were performed with Genstat 5.41 (Payne et al. 1993).

2.3.5 Daily brood survival at nestling stage

We estimated daily brood survival during the nestling stage by an extension of the Mayfield method allowing the estimation of temporally varying daily nest survival rates (Dinsmore et al. 2002). This advanced nest survival model allows modelling the variation of daily nest survival probabilities as a function of daily varying environmental covariates, such as weather. The needed data for this model are 1) the day the nest was detected, 2) the last day the nest was checked alive, 3) the last day the nest was checked, and 4) the fate of the nest (successful or not successful). We defined a priori a set of biological hypotheses that we used to develop specific models to explain variation in the nest survival of Wrynecks. We fitted these models and used information-theoretic approach to rank the models according to their support by the data by means of the Akaike Information Criterion (AIC) (Anderson et al. 2000). The hypotheses were as follows:

- 1) Year. Annual variation can be a common source of variation in nest survival, and can result from factors such as changes in predator density or regional weather.
- 2) Time. The assumption of constant nest survival across season seems unrealistic, early nests are often more successful than late nests (Dinsmore et al. 2002). Biological reasons may be the seasonal change of food availability. Besides a model with constant nest survival across season we also fitted a model in which the nest survival changed linearly across season.
- 3) Age of the nest. The probability that a nest survives is likely to depend on its age. As the feeding frequency increases with nestling age, the nest may be more easily detected by predators and hence nest survival may decline with nest age. On the other hand the readiness of the adults to give up a nest due to short-term food shortage is likely to decline as nest ages and nestlings become more robust to short-term food shortage as they age. If this is true, nest survival would increase with nest age. We fitted models in which the nest survival was a linear function of the nest age.
- 4) Daily temperature. We predict that daily nest survival rates increase with increasing mean daily temperature, because the provisioning of the nestling with food increases with increasing temperature.
- 5) Daily amount of rainfall. We predict that daily nest survival rates decrease with increasing amount of rainfall during the day, because access to ant brood is reduced during heavy rainfall.

These factors could operate in conjunction. To reduce model space, we first modelled the factors that were not in first interest of our study (year, time, age). Then we used the structure of the best of these models (time and age in our case) and added the mean daily temperature and daily amount of rainfall (Table 7). All calculations were done with program MARK (White & Burnham 1999).

3. RESULTS

3.1 Variation of food availability in relation to weather

Throughout the breeding season we found 132 ant nests in 600 examined patches. Progeny was found in 109 nests (82.6%). Worker ant larvae were present in 17 nests, worker ant pupae in 82 nests, sexual ant larvae were in 5 and pupae in 45 nests. In 21 nests winged ants were discovered. Most of the nests belonged to *Lasius niger* (n = 124), and only few were from other species (*Lasius flavus* (6), *Tetramorium caespitum* (1), *Formica spec.* (1)).

We found no effect of temperature, duration of sunshine and relative humidity on nest detection probability (Table 1), indicating that the availability of ants was independent on these weather factors. Yet there was a significant difference between plantations, most likely reflecting true differences in ant nest densities and not differences in detection probabilities.

3.2 Breeding success

In 2004 we detected 71 broods in our nestboxes, of which 38 (53.5%) were successful (≥ 1 fledgling) (Table 2). There was no significant difference in the number of fledged nestlings per brood among the three years ($F = 0.1877$; d.f. = 2, 231; $p = 0.8290$; $n = 234$), and thus the breeding year 2004 can be considered to reflect a normal situation.

3.3 Feeding frequency

We filmed in total 17 different broods aged either 5 or 14 days, with 12 of them that could be filmed twice. Three broods failed between day 5 and 14. Two broods were only filmed when the nestlings were 14 days old. (Table I, Appendix). Feeding behaviour was observed during 353.6 h, totalling 2615 feeding events. After

excluding incomplete hours at the beginning and at the end of the filming, 306 full hours including 2381 feeding events could be considered for the analyses.

The mean (\pm SD) feeding frequency was 7.85 (\pm 6.1) feedings per hour (range: 0 - 34). The feeding frequency was not constant in the course of the day (Table 3). The frequency distribution had two peaks at 10 - 12h and about 16h, the former being higher (Fig. 1). The mean hourly T_a recorded on the filming days had one peak at about 12-13h (Fig. 2).

We tested whether the feeding frequency depended on temperature, age and brood size as well as their interactions (mixed model). All factors apart from brood size had a significant impact on feeding frequency (Table 4). The interactions temperature * age of nestlings, and squared temperature * age of nestlings were also significant. Higher T_a led to increased feeding frequencies in both age classes, but the effect was stronger in the older nestlings (Fig. 3), where feeding frequencies increased steadily with T_a up to about 25°C. Further increases of the T_a resulted in a slight decrease of the feeding frequency. The feeding frequency increased on average (\pm SE) by 3.2 (\pm 0.831) feeding events per hour from 5 days old to 14 days old nestlings. Despite not being statistically significant, the effect of the brood size on feeding frequency followed our expectation: with each additional nestling in the brood the hourly feeding frequency increased, on average (\pm SE), by 0.8 (\pm 0.245).

3.4 Nestling development

3.4.1 Impact of short-term weather effects on nestling body mass, tarsus and 8th primary lengths

The development of the three different morphological traits of the nestlings depended on the same factors (Table 5). Not surprisingly, the age of the nestlings had a highly significant impact on all traits, yet the pattern differed among traits. The body mass

increased fast until about day 12, thereafter the increase was much slower (Fig. 4 a). The tarsus length was almost fully grown at an age of about 12 days already (Fig. 4 b). The 8th primary appeared at an age of 5 to 7 days, increased fast thereafter and was not fully grown when the nestlings were 16 days old (Fig. 4 c).

Brood size didn't have an impact on the development of the traits, irrespective of whether the nestlings were in their early or late stage (Table 5). Apparently, adults are adjusting their feeding activity in such a way that the development of the nestlings is independent from brood size.

Mean hourly T_a had an impact on the development of all traits, and this impact differed between the two nestling stages (Table 5). T_a had a slight negative impact on nestling body mass during the first nestling stage (age 3, 5 and 7 days), with lower mass after warmer temperatures. From age 12 onwards, in contrast, the temperature had a clearly positive influence on nestling's body mass. An increase of 5°C T_a resulted in an increase of the expected body mass of 1.06 g.

Similarly, tarsus length was also negatively affected by temperature during the early nestling stage. Shorter tarsi were observed after days with warmer temperatures. Again, the effect changed into a positive one in the later nestling stage, but differences in tarsus length remained small at different temperatures because asymptotic growth was almost completed at that age.

The length of 8th primary was positively affected by the temperature at all six measurement events (Table 5), but the effect was stronger at the later nestling stage.

3.4.2 Factors influencing the change of the nestling's body mass

We wanted to know, whether the gain of body mass during two days was a function of the total number of feedings per nestling during one day, of the number of nestlings, of the body mass at the first day, of the temperature and of the interaction

temperature * first body mass measurement. At the early nestling stage none of these factors were significant (Table 6). At the late nestling stage the body mass at day 14 had a significant impact on the change of the body mass. Nestlings which were light when 14 days old had a larger increase of body mass during the next two days than nestlings which were heavy at day 14. Furthermore, the number of feedings per nestling at day 14 positively influenced the increase of body mass during the next two days.

3.5 Daily nest survival of Wryneck during the nestling stage

During the three years we monitored 166 nests during the nestling stage (altogether 2459 days). The first nestling hatched on 26 May and the last nestling fledged on 14 August. Thus, we modelled in total 80 daily survival rates in each year.

Modelling the main effects (year, nest age, linear time trend) revealed that nest survival changed linearly with nest age and within season, and that there were no important differences among the three years (Table 8). Daily nest survival decreased within season and increased with increasing nest age (Fig. 5). The estimated probability of nest success was 0.89 for the early nest, 0.72 for the mid-season nest, and 0.41 for the late nest.

The models including the weather variables had slightly less support than the best model without weather variables (Table 8). Because of this small difference we cannot reject the hypotheses that daily nest survival was independent from weather factors. The daily mean temperature had a positive (slope on the logit scale: 0.0769 [SE: 0.0662]; $\text{logit } x = \log [x/(1 - x)]$) and amount of rainfall a negative effect on daily nest survival rate (slope on the logit scale: -0.0061 [SE: 0.0031]). In order to understand better whether these effects were biologically significant, we calculated the success of nests where the brood hatched on 1 June for different daily mean

temperatures and amounts of rainfall. The date was chosen because it falls into the peak period of hatching events. For these calculations we assumed a nestling period of 21 days and that the weather variables remained constant during the complete nestling period. If T_a was 10°C during the whole nestling period the probability that the nest succeeds would be 20% less than if T_a were 30°C (Fig. 6). Likewise, if there were no rainfall during the complete nestling period, the probability that the nest succeeds would be 20% higher than if there were 15 mm of daily rainfall (Fig. 6). Although the weather scenarios considered are extreme the estimated difference of nest success remained moderate.

4. DISCUSSION

Although large scale climatic conditions influence a species' demography and phenology (Rodriguez & Bustamante 2003), short-term weather conditions can also have a considerable impact on nestling growth (Naef-Daenzer & Keller 1999) and survival (Siikamäki 1996, Veistola et al. 1997, Sillett et al. 2000) and, ultimately, on the seasonal reproductive success of a population. However, besides weather, a lot of other factors may have an impact on traits like growth and survival in birds: year and season, habitat quality, brood size (Dijkstra et al. 1990), food availability (Freitag et al. 2001), food quality (Johnston 1993), ectoparasite load (Fitze et al. 2004) or risk of predation. This variety of effects acting together obviously makes it difficult to quantify the influence of single factors. Though, as it is impossible to investigate a problem in a comprehensive way in just one field season, we mainly concentrated on the links between weather and food availability, feeding activity, nestling development and brood survival in Wrynecks.

Ant availability was neither temperature nor humidity dependent. To obtain information about the availability of ant brood especially, we wanted to measure the depth of the brood in the ant nest in order to evaluate whether the brood was really transported up and down according to temperature as reported in the literature (Seifert 1996). When the ant brood is stored deep down in the soil the foraging success of Wrynecks is supposed to be reduced, as the profitable prey gets harder to be detected and is more difficult to reach. Food shortages may therefore occur (Bitz & Rohe 1992). But as measuring the depth of the ant brood in the soil is difficult (they aren't clear-shaped and distinctive) we chose another approach to gain information on ant availability. We checked if the number of found ant nests within six fruit tree plantations changed with variation of the weather conditions. Because we only surveyed the soil near the surface we supposed to detect more nests under

favourable temperatures, if ants really move their brood as a reaction to temperature changes. This phenomenon couldn't be observed in our study. Maybe the weather was not variable enough to force the ants to adjust the depth of the brood chambers. As plantations were regularly irrigated, the soil probably kept some moisture even during hot weather leading to equable conditions throughout the season. As our procedure was rather rough and based on several assumptions (e.g. constant detection probability across time) we cannot exclude small temperature effects on ant behaviour and thus on temporal variation of food availability for Wrynecks.

The number of found ant nests strongly differed between the plantations. The apple plantations had far less ant nests than pear plantations. Fruit tree plantations may all look very similar to us. Still, some seem to be better habitats for ants than others. It would be interesting to have a closer look at these plantations. Maybe they differed in soil cultivation, irrigation rhythm or herbicide and pesticide use. Another explanation may be that pear plantations offer more food resources (aphids) than apple plantations. But to be sure about the consistency of these differences larger sample sizes (more study plots) and further investigations would be needed.

Lasius niger was the most abundant species. It is often mentioned as an important prey species for Wrynecks (Glutz von Blotzheim & Bauer 1980, Hölzinger 1992, Hölzinger 2001, Freitag 1998, Freitag 2000) and was the species most frequently found in food pellets of Wrynecks in the study area (Ehrenbold 2004). Future work on ants and their availability for Wrynecks could therefore be limited to *Lasius niger*, at least in this region.

Although there was no correlation between temperatures and ant availability, we showed that higher temperatures increased feeding frequency and led to higher mean values of body mass and 8th primary length in the later nestling stage. The

increase of feeding frequencies resulted in higher gains of body mass during the later nestling stage.

On average (\pm SD), adult Wrynecks fed their young 7.85 (\pm 6.1) times per hour. Another study of two broods on the Rhône plain using an autonomous monitoring system in 1998 reported a mean feeding frequency of 11.7 (\pm 6.2) (Freitag et al. 2001). While we studied a larger number of nests but just for two days, Freitag et al. (2001) uninterruptedly monitored two nests for fourteen days. Therefore their higher mean estimate might be the result of including one brood with a relatively large number of nestlings (9). Additionally, our video recordings enabled us to clearly separate real feeding events from parents entering the nestbox without food. Relying on counting nestbox entries one probably overestimates the feeding frequency. But some broods in our study had high feeding frequencies as well: the highest number of feedings ($n = 235$) per day was reached by brood A 105 (10 nestlings) on 22 June. A similar maximum number of daily feeding events ($n = 230$) was reported from a brood in Hitzkirch (Switzerland) in 1938 (Bussmann 1941).

The feeding frequency was not constant in the course of the day, but had two peaks. The reduction in the early afternoon coincides with the hottest hours of the day. Similar patterns were found in other studies (Freitag et al. 2001, Glutz von Blotzheim & Bauer 1980). As ant availability was not reduced as response to T_a , it can be assumed that the reduction of feeding activity was not due to a temporal lack of ants. Maybe the nestlings needed time to digest or the parents had to feed for themselves. The feeding frequency increased with increasing T_a and reached a maximum at ca. 25°C. In the early morning and in the evening ants are probably less active than during the day and nests may be more difficult to be detected. For Wrynecks it is possibly not worth to forage in the early and late hours of the day. The

reduction of provisioning in the evening could also mean that parental feeding effort was optimized as early as possible.

Feeding frequency was age-dependent with the older nestlings fed more often. This is what we had expected, because older nestlings have higher food demand. Wrynecks fledge at an age of about 20 – 21 days, and they have reached their fledging mass until about day 14 – 16. Yet, although their body mass increase at day 14 is slow, their energy demand is likely to be high, because energy is needed for feather growth, thermoregulation and increased activity (Turner 1983). Nevertheless, it is likely that feeding activity would decrease between day 14 and 21 because energy demand is decreasing (Turner 1983). Interestingly, feeding frequency did increase only slightly (not significantly) with brood size, which is different from other studies where brood enlargements resulted in clearly higher rates of food provisioning (Sanz & Tinbergen 1999, Dijkstra et al. 1990, Naef-Daenzer & Keller 1999). Despite this, average nestling body mass was not less in larger broods as is elsewhere reported (Siikamäki 1996, Tinbergen & Boerlijst 1990). Instead of increasing the feeding frequency parents might have brought more food per feeding event.

We could show an effect of the number of feedings per nestling on the gain of body mass during the following two days, but only at the older nestling stage. Since nestlings need less food in the first few days of the growth period, the amount of needed food is not likely to be limited by the temperature. With ongoing growth the food requirement increases. Parents need to exploit more food, perhaps as much as is currently available. The reduction in growth of the nestlings will be higher when the difference between the food requirements of the nestlings and their food supply becomes larger (Keller & van Noordwijk 1993).

Maybe the parents adjusted their feeding behaviour to the nestlings' needs in order to support their optimal growth rather than feeding them at maximal rates (Masman et al. 1989). 90% of the nestlings that were filmed twice were growing normally and finally fledged; feeding can therefore be assumed to have been sufficient, and food abundance wasn't a limiting factor for nestling growth. This conclusion is confirmed also by the compensatory growth; nestlings that were light at day 14 showed a higher gain of body mass until day 16 than heavier nestlings. If food would have been scarce and competition among the siblings strong we would have expected the heavier nestlings to have outcompeted the lighter ones. A high fledging body mass is normally correlated with a higher chance of post-fledging survival (Naef-Daenzer et al. 2001, Tinbergen & Boerlijst 1990). But as the heavier nestlings didn't grow much between day 14 and 16 (the body mass difference could even get negative) there could be an optimal fledging body mass which is below maximum body mass. Still, there might be further body mass changes until fledging (Becker & Wink 2003), so that body mass measured at day 16 might not be strongly correlated with fledging mass.

The impact of temperature on feeding behaviour of the adults led to differential nestling development. Body mass and tarsus length were negatively correlated with temperature during the early nestling stage and positively during the later stage. The reason for increasing body mass and tarsus at the later nestling stage with increasing temperatures is likely the higher feeding activity. In the early nestling stage there was just a slight increase of feeding frequency with higher temperatures (Fig. 3). The increasing feeding activity could have reduced the brooding behaviour. The small nestlings without plumage suffered from cooling and higher energy expenditure maybe more than they profited from the extra food.

Growth of 8th primary was positively correlated with T_a over all six measurement events, even if the time interval of 1.5 days (used for the calculation of average T_a before the measurement event) was probably rather short to explain well the growth pattern of a trait needing not only the accumulation of biomass but also the formation of a complex structure (McCarty & Winkler 1999).

Although T_a did influence nestling growth, its effect was limited in our study. As temperatures were never below 13°C before measurement days we cannot reliably tell what would have happened after longer periods of cold or even rainy conditions. Other studies about insectivorous bird species showed that rain is a detrimental factor, reducing food availability on one hand and increasing energy demands of nestlings on the other (Veistola et al. 1997, Keller & van Noordwijk 1994, Radford et al. 2001). Two days of very cold and rainy weather reduced the body mass of young Wrynecks by several grams according to data of one brood in Basel (Sutter 1941). Unfortunately, it hardly ever rained on filming days, so we had to exclude precipitation as explanatory variable from the analyses. Since the Rhône valley usually has warm and dry weather during the breeding period of Wrynecks, a comparative study from an area with harsher weather conditions would be of particular interest.

As now shown, ambient weather conditions do influence parental feeding behaviour as well as nestling development. But how do these factors affect Wrynecks on a broader scale, namely on the population level?

The average number of fledged nestlings per brood was slightly lower in 2004 compared to 2003, although the clutch size was slightly larger. As the year 2003 was extremely warm and dry, the higher breeding success might have been the result of a higher brood survival. Still to cause a considerable reduction of the brood survival weather conditions must be remarkably bad (mean T_a of 10°C - 15°C compared to

25°C - 30°C, 15 - 20 mm of daily rainfall compared to 0 - 5 mm during the whole breeding season). With normally changing temperatures in a range of 15°C to 30°C and moderate rainfall, as observed, weather is of rather little importance in reducing brood survival, especially when compared to other factors such as predation. Moreover, the distribution of Wrynecks in Valais and in Switzerland was not dependent on mean spring and summer temperatures as well as on the amount of rainfall (Ehrenbold 2004). Thus, we conclude that variation of weather effects during the breeding period are of minor importance for long-term population trends and the distribution at our latitudes.

As our study showed, the short-term weather conditions had some impact on the development of the nestlings and the survival probability of nests, but this impact was of limited importance at the population level. Therefore, it can be hypothesized that other factors, such as habitat destruction, have been more important for the decline of the Wryneck in Switzerland than climatic changes. Further studies should concentrate on the general availability of food and nest sites, which may be low in regions abandoned by Wrynecks during the last decades.

We conclude that Wrynecks in Valais would not be negatively affected by the expected temperature and precipitation changes due to global change per se. However, there might be indirect influences such as denser vegetation through higher amounts of rainfall which might reduce access to food and therefore have a negative impact.

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TABLES

Table 1. Analysis of covariance to test the impact of different weather factors on the ant nest density in six fruit tree plantations (n = 60: total number of nests per plantation and searching day).

	Mean squares	F-Ratio	d.f.	p
Temperature	0.038	0.006	1	0.9379
Sunshine	3.034	0.495	1	0.4847
Relative Humidity	8.068	1.317	1	0.2564
Plantation	275.680	8.999	5	< 0.0001
Error	318.574		52	

Table 2. Determinants of the breeding success of the Wryneck in Valais (Switzerland) in all three years of the study.

	2002	2003	2004
# broods	72	90	71
# successful	43 (60%)	58 (64%)	38 (54%)
# failed	29 (40%)	32 (36%)	33 (46%)
# eggs	589	712	577
mean per brood	8.2	7.9	8.1
# hatchlings	345	476	354
mean per brood	4.8	5.3	4.9
hatching success	58%	67%	61%
# fledglings	271	364	266
mean per brood	3.8	4	3.7
fledging success	79%	76%	75%

Table 3. Impact of time of day (h), nestling age and their interaction on feeding frequency evaluated by a mixed model. Shown are the test statistics (Wald χ^2 , degrees of freedom [d.f.], p) of the fixed effects. The random factor of the model was the brood (n = 17 broods).

Factor	d.f.	Wald statistic	p
Time of day (h)	13	103.6	< 0.001
Age of nestlings	1	39.7	< 0.001
Age of nestlings* Time of day (h)	13	25.7	0.019

Table 4. Impact of temperature, age and number of nestlings on feeding frequency (number of feedings per hour) evaluated by a mixed model. Shown are the test statistics (Wald χ^2 , degrees of freedom [d.f.], P) and the effect sizes of the fixed terms in the model. The random factor of the model was the brood (n = 306 hours from 17 broods).

Factor	Wald statistic	d.f.	p	Effect (SE)
Temperature	12.5	1	< 0.001	0.279 (1.356)
Temperature ²	8.3	1	0.004	- 0.003 (0.034)
Age of nestlings	31.4	1	< 0.001	2.745 (0.900)
Brood size	3.3	1	0.069	0.613 (0.509)
Temperature*Age of nestlings	8.6	1	0.003	4.799 (1.640)
Temperature ² *Age of nestlings	5.2	1	0.023	-0.092 (0.038)
Brood size* Age of nestlings	0.2	1	0.655	0.163 (0.388)

Table 5. Impact of number of nestlings, age of nestlings (3, 5, 7, 12, 14 or 16 days), nestling stage (≤ 7 vs. ≥ 12 days), temperature and interactions on body mass, tarsus length and length of the eighth primary, evaluated by a repeated measurement mixed model. Shown are the test statistics (Wald χ^2 , degrees of freedom [d.f.], P) and the effect sizes of the fixed terms in the model. The effect sizes of the main effect refer to the early nestling stage, the effect size of the interactions are the differences between the early and the late nestling stage. The random factors of the models were the brood and the nestling identity nested with brood (n = 72 nestlings from 12 broods).

Factor	d.f.	Body mass			Tarsus length			8. Primary length		
		Wald statistic	p	Effect (SE)	Wald statistic	P	Effect (SE)	Wald statistic	p	Effect (SE)
Age of nestlings	5	2863.6	<0.001		3482.1	<0.001		7609.4	<0.001	
Brood size	1	1.7	0.192	-0.151 (0.190)	2.1	0.147	0.138 (0.108)	0.1	0.752	-0.267 (0.300)
Temperature	1	4.9	0.027	-0.051 (0.046)	7.0	0.008	-0.077 (0.022)	28.5	<0.001	0.109 (0.049)
Stage*Brood size	1	0.6	0.439	-0.101 (0.134)	0.9	0.343	0.061 (0.064)	2.6	0.107	0.229 (0.141)
Stage*Temperature	1	12.6	<0.001	0.263 (0.074)	6.1	0.014	0.087 (0.035)	9.3	0.002	0.242 (0.079)

Table 6. Impact of body mass, number of feedings, number of nestlings and temperature on gain of body mass during the early and late nestling stage evaluated with a mixed model. Shown are the test statistics (Wald χ^2 , degrees of freedom [d.f.], P) and the effect size of the fixed terms in the model. The random factor of the models was the brood (5 – 7 days: n = 92 nestlings from 12 broods; 14 – 16 days: n = 83 nestlings from 10 broods).

Factor	5 – 7 days				14 – 16 days			
	Wald statistic	d.f.	p	Effect (SE)	Wald statistic	d.f.	p	Effect (SE)
Number of feedings								
per nestling	0.3	1	0.584	0.129 (0.242)	7.8	1	0.005	0.182 (0.065)
Brood size	0.5	1	0.480	0.234 (0.337)	1.1	1	0.294	0.153 (0.148)
Body mass at day 5 or 14	0.0	1	1.000	0.014 (0.065)	34.5	1	<0.001	-0.363 (0.065)
Temperature	0.3	1	0.584	0.077 (0.174)	0.1	1	0.257	0.152 (0.130)
Temperature*Body mass	1.1	1	0.294	0.033 (0.031)	0.4	1	0.527	0.019 (0.031)

Table 7. Models that were considered for testing hypotheses about variation of daily nest survival.

Model	Notation
Single estimate of nest survival	$S_{(.)}$
Effect of year only	S_{year}
Effect of nest age only	S_{age}
Linear time trend only	S_T
Effect of year plus linear time trend	$S_{year + T}$
Effect of nest age plus linear time trend	$S_{age + T}$
Effects of year and nest age	$S_{year + age}$
Effects of year and nest age plus linear time trend	$S_{year + age + T}$
Effect of nest age plus linear time trend plus daily mean temperature	$S_{age + T + temp}$
Effect of nest age plus linear time trend plus daily amount of rainfall	$S_{age + T + rain}$

Table 8. Summary of model selection results for nest survival of Wrynecks during the nestling stage in central Valais, 2002 – 2004. For each model we show the deviance, the number of estimated parameters (K), the difference of the AIC_c of the current model and the best one (ΔAIC_c), and the Akaike weight (w_i). For the model notations see Table 7.

Model	Deviance	K	ΔAIC_c	w_i
$S_{T + age}$	234.69	3	0.00	0.33
$S_{T + age + rain}$	233.09	4	0.41	0.27
$S_{T + age + temp}$	233.35	4	0.67	0.23
$S_{year + T + age}$	232.14	5	1.47	0.16
S_{age}	244.93	2	8.23	0.01
S_T	245.37	2	8.67	0.00
$S_{year + age}$	242.09	4	9.40	0.00
$S_{year + T}$	242.81	4	10.12	0.00
$S_{(.)}$	250.82	1	12.13	0.00
S_{year}	247.79	3	13.10	0.00

Figure legends

Fig. 1. Mean feeding frequency (number of feedings per hour) in the course of the day when nestlings were 5 and 14 days old. Vertical lines show standard errors.

Fig. 2. Mean hourly temperatures on the days when feeding frequency was recorded (n = 20 days). Vertical lines show standard errors.

Fig. 3. Predicted mean number of feedings per hour at different temperatures and nestling ages based on the model in Table 4. Vertical lines show standard error.

Fig. 4. Mean nestling body mass (a), tarsus length (b) and length of 8th primary (c) at different nestling ages. Vertical lines show standard deviations. Sample sizes (number of nestlings / number of broods) are indicated in (a).

Fig. 5. Predicted daily nest survival rates and 95% confidence limits for three Wryneck nests at different dates. In the early season nest the nestlings hatched on day 1 (26 May), in the mid-season nest the nestling hatched on day 30 (24 June), and in the late season nest the hatching occurred on day 60 (24 July).

Fig. 6. Predicted success of Wryneck nests (nestlings hatched on 1 June) in relation to daily mean temperature and daily amount of rainfall. For the predictions it was assumed that the weather variables remained constant during the complete nestling period of 21 days. Values of the whole indicated range of temperature and amount of rainfall have been observed at single days during the breeding season 2004.

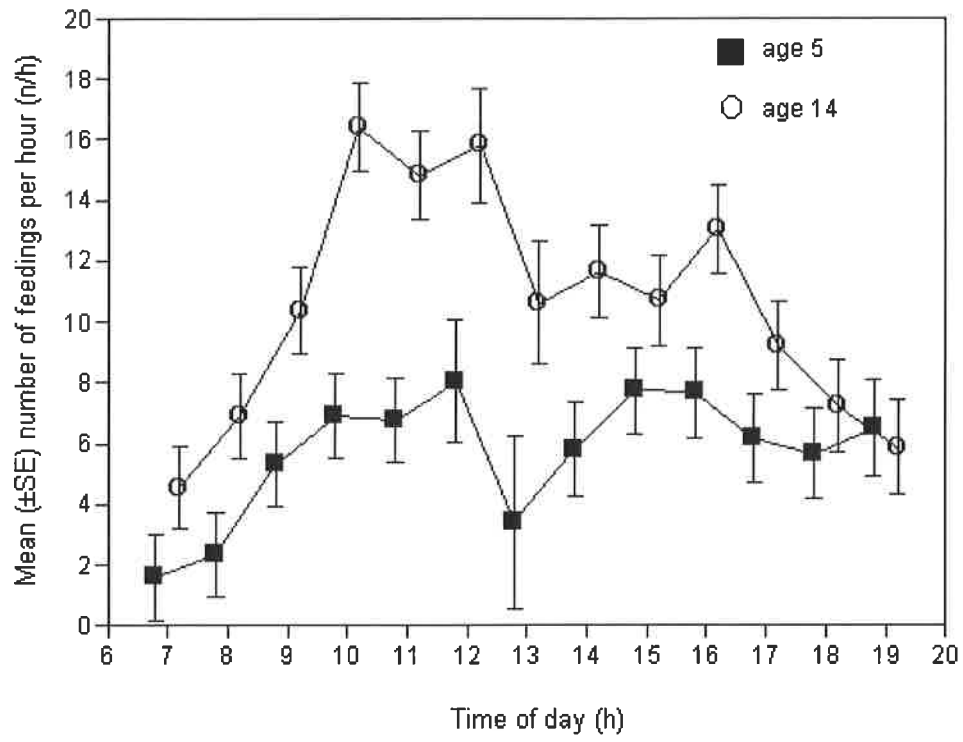


Fig.1

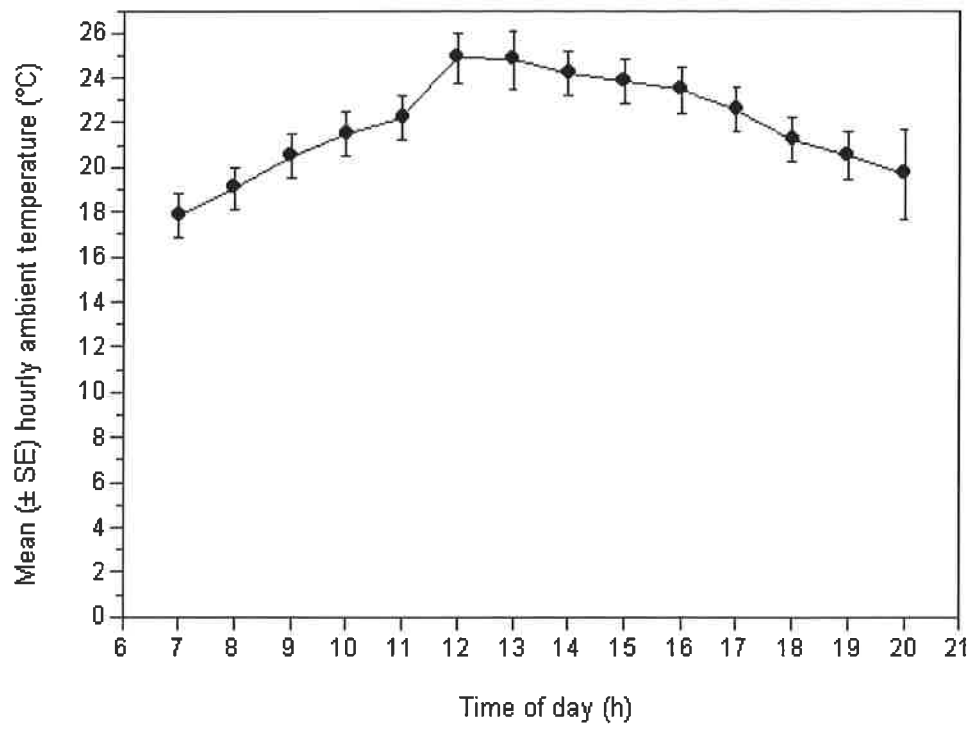


Fig. 2

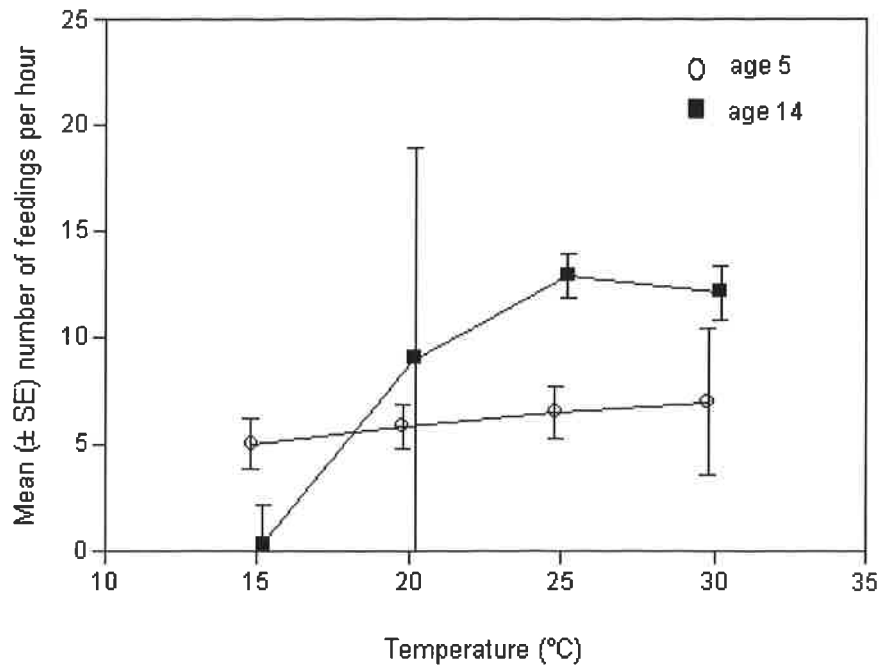


Fig. 3

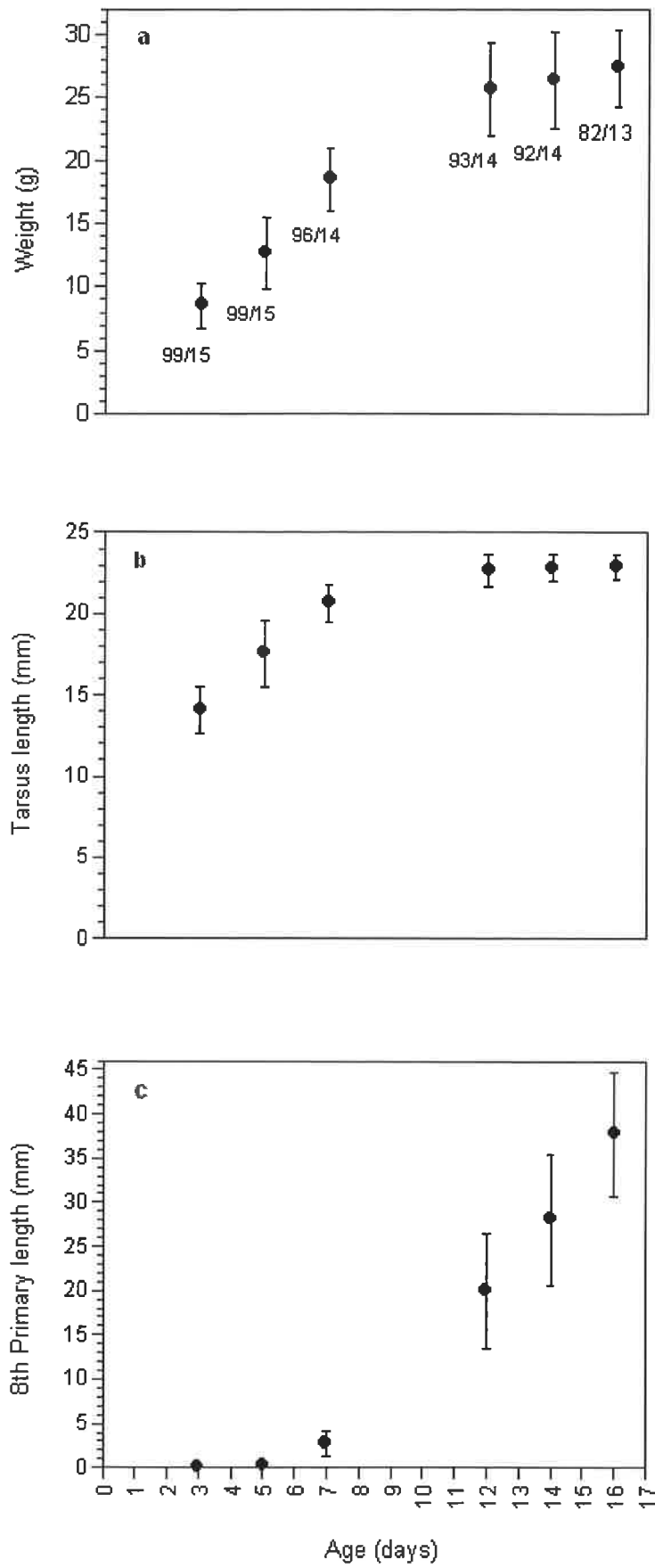


Fig. 4

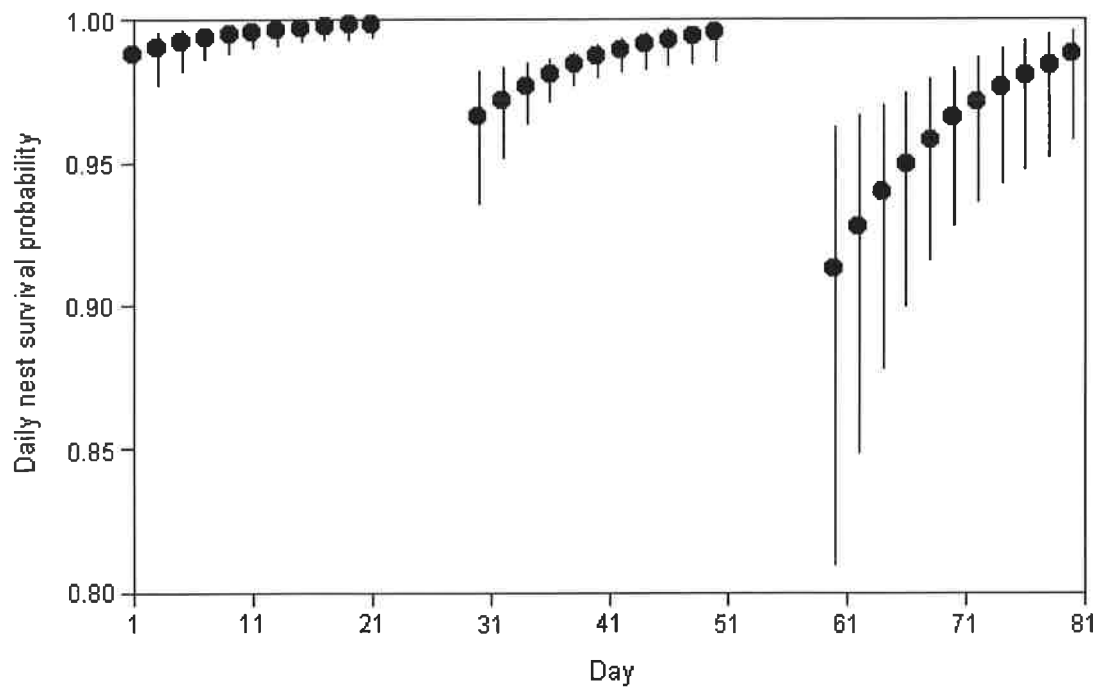


Fig. 5

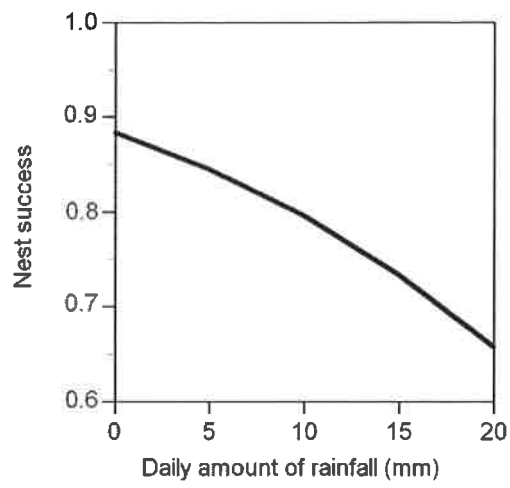
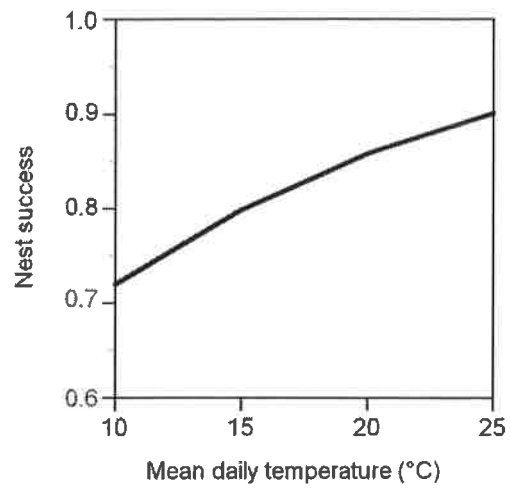


Fig. 6

APPENDIX

Table I. Dates and locations of the broods that have been filmed for recording feeding frequencies.

Nestbox*	Brood Nr.	Zone*	1 st Filming date	2 nd Filming date
B 37 w	1	B	28.5.2004	-
A 59 b	1	A	31.5.2004	10.6.2004
A 93 w	1	A	31.5.2004	10.6.2004
A 91 b	1	A	3.6.2004	12.6.2004
A 107 e	1	A	4.6.2004	-
A 89	1	A	13.6.2004	22.6.2004
A 105 e	1	A	13.6.2004	22.6.2004
B 45 w	1	B	16.6.2004	25.6.2004
B 23 w	1	B	23.6.2004	2.7.2004
A 49 e	1	A	27.6.2004	6.7.2004
A 58 b	1	A	27.6.2004	6.7.2004
B 21 w	1	B	2.7.2004	11.7.2004
A 93 w	2	A	9.7.2004	18.7.2004
A 77 b	1	A	14.7.2004	23.7.2004
B 8 s	1	B	23.7.2004	-
C 2 w	1	C	-	1.8.2004
A 84 s	1	A	-	1.8.2004

* Code of the Swiss Ornithological Institute