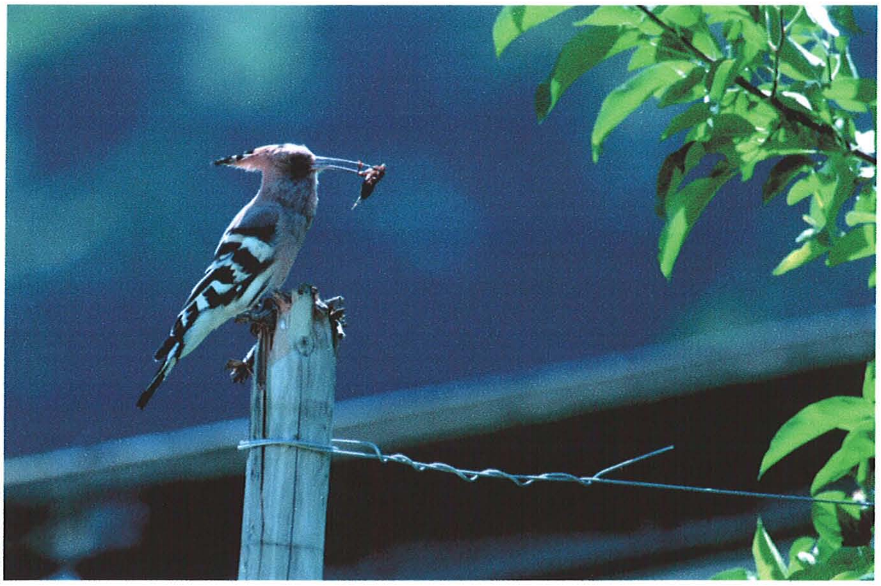
Influence of weather conditions on chick provisioning activity in the Hoopoe (*Upupa e. epops*)



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1. Abstract

Bird population status strongly depends on overall breeding performance. The latter may be affected by limited food provisioning to chicks due to adverse weather conditions. Prey availability may decrease when the weather becomes cold and wet, which could subsequently reduce chick survival. In insectivorous species showing principally a Mediterranean distribution, the climatic context can be the ultimate factor determining population size at range edge. A small Hoopoe (*Upupa e. epops*) population inhabiting the upper Rhone Valley (Valais, Switzerland) characterised by a relatively dry and warm climate is known for its strong dependence upon Molecrickets (*Gryllotalpa gryllotalpa*) for chick provisioning. Although providing an unlimiting number of nestboxes to the endangered local Hoopoe population drastically improved its average breeding success, the among-year variance in productivity remained large. We therefore tested whether Hoopoes' food provisioning activity to chicks was influenced by weather conditions. Fewer food items, less biomass (one third) and a smaller proportion of Molecrickets were provisioned on days with unfavourable weather conditions; additionally, food diversity was greater on bad days, apparently as a consequence of a lower availability of the most profitable prey, Molecrickets. This suggests that the fate of this threatened population may eventually depend in first place on weather fluctuations and / or possible long-term climate changes.

2. Introduction

One of the most important parameters on bird population dynamics is overall breeding success, which strongly depends on the number of successful breeding attempts and on the number of fledglings (Crick et al., 1993). Limited access to optimal nesting sites, intraspecific conflicts, limited food resources, brood losses due to predation or unfavourable weather conditions are some of the problems that breeding birds are facing. What remains largely unpredictable for breeding birds is food availability and weather conditions during the forthcoming breeding period. Food availability is determined by the abundance of food items and by their accessibility to the predator. If food provisioning is reduced for only two or three days during a crucial stage in the chicks' development this can have a strong influence on nestling survival, on breeding success and, ultimately, on population size (Newton, 1998). Unfavourable weather can appear at different temporal scales ranging from some hours to periods lasting up to several days, affecting foraging activity. Cold weather can in addition diminish nestling survival if thermoregulation ability is altered (Newton, 1998).

2.1. Mediterranean bird species in Middle Europe

Most European birds of the temperate zones are well adapted to changing weather conditions so that they do not seem to suffer too much under unfavourable weather conditions. Within these zones, there exist areas with warmer and drier climate in which bird species with a principally Mediterranean distribution occur such as the Eurasian Scops Owl (*Otus scops*), the Hoopoe (*Upupa epops*), the European Bee-eater (*Merops apiaster*), the Rock Thrush (*Monticola saxatilis*) or the Woodchat Shrike (*Lanius senator*). Because these birds are well adapted to warm and dry climate, they are more sensitive to weather factors and usually face great problems under wet and cold conditions (Cramp, 1985). Populations in these warm and dry enclaves often form the northern border of these species' distribution. Most of them feed mainly on big insects whose activity is negatively influenced by cold and wet weather due to their endothermic physiology (Begon, 1991; Newton, 1998). This has practical consequences such as limitation in food availability for these bird species.

2.2. Conservational aspects

A question concerning the conservation of these birds' marginal populations inhabiting northern warm and dry climatic enclaves is whether it makes sense to protect birds when they are especially rare, whereas they are still numerous in more southern locations with better climatic conditions. Yet, marginal populations often have a great conservation value because of potential local genetic adaptations, which drastically increases overall genetic diversity within a species. As a consequence, conserving marginal populations is one of the goals of Conservation Biology.

2.3. The Hoopoe in Europe

The Hoopoe (*Upupa e. epops*) is a secondary cavity breeder, which feeds mainly on large invertebrates. Usual foraging places are vineyards, fields, orchards, gardens and pastures, as long as ground vegetation lacks on the ground (Schmid et al., 1998). The Hoopoe is presently one of the most endangered species in Western and Central Europe (Hustings, 1997). In the middle of the 19th century it was still common in most parts of Middle Europe as far north as southern Scandinavia. At the end of the 19th century, however, there was a remarkable decline of the Middle

European population; its distribution area shrunk, especially in the northern and northwestern parts. In the middle of the 20th century a small recovery was perceptible but it obviously did not last long enough to enable a total population and distribution recovery. Populations declined further (Glutz, 1980; Cramp, 1985).

2.4. Problematic

The reasons suggested for this decrease of the Hoopoe have been manifold: As a secondary cavity-nester, the Hoopoe suffers from the loss of suitable nesting sites due to the removal of old rotting trees and the decline of excavators, mainly woodpeckers. Moreover, in alternative breeding sites, such as in stone walls, broods are often threatened by predation (Martín-Vivaldi et al., 1999). Habitat changes seem to influence the abundance of Hoopoe's optimal prey (Glutz, 1980), what might mainly be due to the increasingly intensifying agriculture (Schmid et al., 2001). The Molecricket (*Gryllotalpa gryllotalpa*) is an important prey for the Hoopoe (Bussmann, 1950; Glutz, 1980; Fournier & Arlettaz, 2001). This up to 5 cm long Saltatoria lives in humid and loose soil in pastures, marshes and humid ditches, and also in anthropogenic landscapes such as orchards or vineyards. It apparently suffers habitat loss where the soil is treated mechanically (Hahn, 1958; Detzel, 1998). The use of pesticides could further affect Molecrickets that are considered to be a major pest in agricultural landscapes (Harz, 1957; Detzel, 1998). Some scientists state that Molecrickets are locally rare and therefore play only a marginal role in Hoopoe's diet (Hirschfeld & Hirschfeld, 1973). Alternative prey to Molecrickets are Cockchafer larvae (*Melolontha melolontha*), Lepidoptera larvae or Vertebrates as Wall Lizards (*Podarcis muralis*) (Fournier &

Arlettaz, 2001) or Sand Lizards (*Lacerta agilis*) (Hirschfeld & Hirschfeld, 1973), but the latter remain anecdotal in diet composition. Molecrickets therefore probably represent the most profitable prey for Hoopoes in Central Europe (Fournier & Arlettaz, 2001).

Population fluctuations during the last two centuries have often been attributed to climatic changes. There exists a correlation between the decrease of the Hoopoe population and cold and wet weather (Hirschfeld & Hirschfeld, 1973; Glutz, 1980; Cramp, 1985; Rehsteiner, 1996). This is particularly clear when the situation in Middle Europe is compared to that in a Mediterranean country such as Spain (Rehsteiner, 1996). The fluctuations seem to be more pronounced in Middle European than in Mediterranean populations (Cramp, 1985). As climate is warmer and rain is usually less frequent in Mediterranean countries, with shorter showers (Rehsteiner, 1996), differences in population fluctuations could be largely explained by differences in weather conditions. Hoopoes could either loose clutches through strong rain floating their nest site, or they could face major problems in accessing food during a rainy season (Bussmann, 1934; Bussmann, 1950).

2.5. The Hoopoe in Valais

In Switzerland the Hoopoe is classified as an endangered species (Keller et al., 2001). During the last two centuries, the Swiss population has faced similar fluctuations as those in other Middle European countries. Whilst the bird was widely distributed in the Swiss lowlands before 1950, it is now mainly restricted to the canton of Valais. This last population in Switzerland has been intensively monitored since 1979 (Arlettaz, 1984; Arlettaz et al., 1998; Arlettaz et al., 2000a; Arlettaz et al., 2000b;

Schaad et al., 2001). Since 1998, the Hoopoe is subject to a conservation program lead by the Valais Field Station of the Swiss Ornithological Institute (Sempach). A milestone in this study was the discovery of the negative impact of a large distance between nesting sites on the foothill slope and foraging sites on the plain upon the Hoopoes' reproductive success (Fournier & Arlettaz, 2001). As a result, nestboxes were systematically installed closer to the food resources on the plain (Arlettaz et al., 1998). This suddenly provided an unlimiting number of suitable, predator-safe nesting sites to the local Hoopoe population.

Although population increased steadily after this nestbox campaign, the annual breeding success continued to fluctuate greatly. Breeding success (ratio of fledglings on laid eggs) was 65% in 1998, 18% in 1999, 57% in 2000 and 47% in 2001 (Arlettaz et al., 1998; Arlettaz et al., 2000a; Arlettaz et al., 2000b; Schaad et al., 2001). The main reason for these breeding success fluctuations was suspected to be inter-annual weather fluctuations.

In the study area most of the Hoopoes breed in nestboxes that are installed on the inner side of cottage walls, with the hole through the building wall, which ensures brood protection. Brood loss due to direct weather impact can therefore be excluded. Yet, an indirect influence of weather may be linked to a limited access to food resources in adverse conditions. First, Hoopoes may face difficulties when attempting to forage in wet grass vegetation. Second, Hoopoe's prey may be less accessible under adverse weather conditions (Bussmann, 1934; Bussmann, 1950). Evidence for this stems from 1999 when breeding success was low (18%), with many broods abandoned, presumably due to unfavourable weather conditions, in particular frequent, heavy rainfall (Arlettaz et al., 2000a).

The Molecricket (*Gryllotalpa gryllotalpa*) appears to be the most important prey in our study area (Fournier & Arlettaz, 2001). The latter authors have shown that 68% of the biomass provided to chicks by adult Hoopoes consisted of Molecrickets. Investigations with "Barber"-traps have shown a seasonal coincidence between the peak in Hoopoe feeding investment and the peak of Molecrickets phenology (Arlettaz et al., 2000b; Schaad et al., 2001). Also, Hoopoe distribution strongly coincides with the distribution of Molecrickets (Arlettaz et al., 2000b), and it seems that Hoopoe breeding success strongly depends on the percentage of provisioned Molecrickets (Fournier & Arlettaz, 2001). As Hoopoes bring only one prey item per feeding event (Fournier & Arlettaz, 2001) provisioning of a single item with high biomass is energetically more advantageous than the provisioning of several small items. In order to compensate for low prey profitability, adults have to spend more time and energy to provide small prey items than large ones. Therefore, as long as Molecrickets are abundant, Hoopoes should ignore smaller prey items. As soon as the former become rare, it may be worth taking smaller prey items instead of looking unsuccessfully for larger prey as described in the optimal foraging model (Krebs et al., 1977). If Hoopoes have access to Molecrickets, overall food diversity should thus remain low. If cold and wet weather has an impact on food provisioning, this may be due to a low Molecricket availability. As a consequence, food diversity would be higher on days with unfavourable weather conditions.

2.6. Hypothesis testing

We looked first at the proportion of Molecrickets in the present-day diet. Because Hoopoes have left the foothill slopes after the installation of nestboxes on the plain (Arlettaz et al., 1998), we predicted a greater proportion of this prey in the diet today than in the past (Fournier & Arlettaz, 2001). We tested whether parents fed fewer prey items, less biomass and a smaller proportion of Molecrickets on rainy and cold days than on nice days. We predicted that food diversity would be lower on warm and dry days. As Hoopoes have evolved a polygynous breeding system (Martín-Vivaldi et al., 2002), we predicted a greater investment in provisioning by fathers than by mothers. We further tested whether chick development stages and brood itself had an influence on provisioning activity, predicting a significant among-brood variance. Finally, we tested whether there was a relationship between food provisioned to nestlings and adult status, as well as chick fitness and the amount of provisioned food.

3. Material and Methods

3.1. Study area and Hoopoe population

This study was carried out in 2001 in the canton of Valais, in the Upper Rhône Valley, between Granges and Martigny (Southwestern Swiss Alps; 46°07'N, 07°08'E). The landscape is described in Arlettaz (1984) and in Fournier & Arlettaz (2001). The plain (460-468 m asl) is almost exclusively occupied by industrial farming. Dense orchards with small trees cover most of the area and only some spots with woodland remain. The lower part of the south-exposed slope on the right side of the Rhône river forms the northern border of the study area. The latter is mostly cultivated with vineyards between which few patches of natural habitats still exist. Humans inhabit the contact zone between the slope and the plain.

Since 1998 several hundred nestboxes were installed on the plain. Although Hoopoes tend to breed in nestboxes almost exclusively since their installation on the plain, the area was searched for calling males in April – early May in order to locate possible broods in natural breeding sites.

3.2. General field procedures

All nestboxes were controlled every second week during the breeding season from early April to early August 2001. Those containing broods were additionally checked every two to three days. The controls were done from the outside of the nestbox in order to avoid disturbance of the female. It was not attempted to count the number of eggs or chicks if the female covered them, too. The investigation was made with a little mirror fixed to a stick and with a 4.5V bulb, which were put through the entrance of the nestbox to check content visually (Fournier & Arlettaz, 2001). Later on in the breeding season the nestboxes were opened to assess the number of chicks and estimate their age. Parents don't leave a brood following such an examination. All dead birds and unhatched eggs that were found in the nestboxes during these controls were collected and stored at –20°C.

Hatching success was calculated as the ratio of hatched eggs onto laid eggs. Fledgling success is the ratio of fledged chicks onto hatched eggs and breeding success is the ratio of fledged chicks onto laid eggs. The number of laid eggs was calculated as the sum of live and dead birds and the number of unhatched eggs that were found in a nestbox. As some Hoopoe females sometimes remove dead young and even eggs, these figures represent minimum clutch sizes.

Adult Hoopoes were captured with mist-nets during the feeding season when the chicks were five to ten days of age. Capture was done in front of the entrance hole to the nestbox. The birds were stored in cotton sacks until manipulation, which took place almost immediately. Body measurements were taken and the birds were marked with numbered aluminium rings of the Swiss Ornithological Station (Sempach) and coloured rings. Every adult bird was marked individually with a code of black spots on the side of the head (Fig. 1). Additionally, males and females were differently marked by colouring in black a white stripe of their wings with a waterproof marker. Marking was necessary for the latter identification of a bird's sex on the videotape recordings. The Hoopoes were phenotypically sexed by checking the size of the uropygial gland. A large gland and a well-filled reservoir, in addition to an intensive smell, indicates a female bird (Nitzsch in Sutter, 1946). For latter genetical sexing blood was taken from each adult Hoopoe by venipuncture, and the sample was stored in EDTA buffer (10 mM Tris, 100 mM EDTA, 0.1 % SDS, pH 8.5). After the manipulation, birds regarded as males were released directly, whereas those sexed as females were put back into the nestbox through the entrance hole.

The chicks were ringed at the age of about 20 days. Because Hoopoes hatch asynchronously, a "brood's age" corresponded to that of the eldest nestling whose age was known with an accuracy of more or less 1-2 days. Chicks were each taken from the nestbox and kept in a cotton sack until manipulation. To obtain DNA for later sexing, one growing feather was taken from each chick's tail and stored in a separate envelope. Each chick was immediately put back into the nestbox after the manipulation so that the parents would not consider their nest as empty. The chicks were marked with colour and numbered aluminium rings. The colour ring enabled us to identify the year of birth of a bird. The following measurements were taken: tarsus and bill length (±0.01 mm), wing and 3rd feather length (±0.5 mm). The chicks were also weighed (±1 g).

3.3. Genetical sexing

Although some authors state that sexing adult Hoopoes in the field is possible, they rely only on slightly phenotypic differences such as breast and chin coloration, extension of streaking on sides of belly and breast (Baker, 1993; Glutz, 1980) or size of the uropygial gland (Nitzsch in Sutter, 1946). To avoid mistakes in this study, sex was determined genetically with the CHD-Gene-Method described by Griffiths et al. (1998). This further enabled us to see whether our method of phenotypical determination was reliable. Results of phenotypic sexing in the field were compared to genetical sexing in the laboratory.

DNA extraction was done with a Promega DNA extraction kit. 20µl of Hoopoe blood was added to a tube containing 300µl of Nuclei Lysis Solution; Then it was vortexed before adding 100µl of Protein Precipitation Solution. After vortexing for 20 s the mix was put on ice for 5 min before centrifuging for 5 min at 14'000 RPM. The supernatant was transferred to a new tube containing 300µl Isopropanol and mixed by invertion 50 times before centrifuging again for 20-40 min at 14'000 RPM. After this procedure, the Isopropanol was carefully removed by a vacuum pump in order not to destroy the pellet of DNA. The DNA was washed with 300µl Ethanol (70%) and dried for 15 min before adding 20µl of DNA Rehydration Solution. The DNA was stored at –20°C. PCR was done according to the method described by Griffiths et al. (1998). The PCR solution per sample consisted of: 1µl 1XBuffer, 1µl 0.02mM dNTP, 1µl 2.5mM $MgCl_2$, 0.5µl 1µM P2, 0.5µl 1µM P8, 0.05µl Hot Star Taq and 4.95µl H_2O HPLC. Each PCR tube was filled with 9µl of this mix and 1µl of DNA solution. The PCR reaction was as follows: A single step of 15 min at 95°C, 40 times 30 s at 95°C, 15 s at 52°C and 75 s at 72°C, followed by a single step of 7 min at 72°C before ending the PCR at 4°C. The resulting PCR products were analysed with electrophoresis (2 h at 60V) on a 3.5% MetaPhor-Agarose gel.

3.4. Video filming of food provisioning

Every brood was filmed three times during the chick feeding period. The first filming took place when the chicks were 11-15 days of age, the second one when they were 16-20 days of age and the third one when they were 21-25 days of age. Two video systems were used, each of them consisting a time lapse video recorder (Sanyo, SRT-7168P, Osaka, Japan), which allowed us to record over 16 hours of continuos activity on a normal 180 min VHS video cassette and a camera (Videotronic, CCD–7012P, Neumünster, Germany) with an automatic iris. Both devices were protected in specially designed cases (e.g. Videotronic, vitect–260W, Neumünster, Germany). The focus and sharpness of the images were controlled with a small portable monitor (Sony, GV-D800, Tokyo, Japan). The systems were secured with chains and hidden with camouflage nets. In addition, plastic foils were used if weather was bad. A generator (Honda EU 10I, Tokyo, Japan) was used for power supply. At midday the generator had to be refilled with petrol. Both filming systems were simultaneously running at two different nest locations during complete days (6 AM – 9 PM). The complete daily activity of the adults was recorded in that way. The distance from the camera to the nestbox was between one and five meters depending on the environment and level of human activity in the surroundings. The focus of the camera was set on the entrance of the nestbox so that the adult Hoopoes could be identified as well as the prey item they brought. The chicks were counted at the beginning and/or at the end of the filming period.

3.5. Analysis of videotapes

For each feeding event the following variables were taken: time, sex of the feeding adult, type of prey, Molecrickets (*Gryllotalpa gryllotalpa*) size. We distinguished four categories of prey: 1) Molecrickets (*Gryllotalpa gryllotalpa*), 2) Lepidoptera larvae, 3) Other prey and 4) unknown prey. Three visible sizes were distinguished in Molecrickets, including larval stages and imagoes. Except as regards Molecrickets, the type of prey was determined to order. Determination of prey was achieved using several identification keys (Zettel, 1999; Bellmann, 1993).

3.6. Estimation of frequency and prey biomass

Frequency data were obtained directly from videotapes. For each prey type and size, respectively, dry biomass was estimated following Arlettaz & Perrin (1995). For Molecrickets, values corresponded to 0.36g (stage 1), 0.46g (stage 2) and 0.68g (stage 3). Lepidoptera larvae, other prey items and unidentified prey types each represented 0.08g per item. Average hourly frequency and biomass data were obtained by division the total values for one given day by the number of complete minutes filmed multiplied by 60.

3.7. Prey diversity

The Shannon-Index was used to calculate the prey item diversity:

$$H_s = -\sum_{i=1}^{S} p_i \ln p_i \quad \text{with} \quad p_i = \frac{n_i}{N} \quad \text{and} \quad \sum_{i=1}^{S} p_i = 1$$

H_s = diversity related to the categories

S = sum of the categories

p_i = probability of the occurrence of a category i (0-1)

N = sum of prey items

n_i = sum of items of category i

A high Shannon-Index value indicates a high diversity.

3.8. Weather data

Weather data were collected at Sion, VS (46.2°N, 7.4°E); (Federal Office of Meteorology and Climatology; MeteoSwiss). Using four weather variables 1) hours of sun per day, 2) mean daily temperature, 3) daily rainfall and 4) mean daily relative humidity a Principal Component Analysis (PCA) was conducted. This produced a model whose first factor explained 63% of the overall variance. After invertion of its sign, this factor was correlated positively with the weather variables 1 and 2 and negatively with 3 and 4. A trend to a positive value indicates thus good weather conditions, a trend to a negative value indicates bad weather conditions.

3.9. Hoopoe fitness

3.9.1. Chick fitness

The correlation between chick fitness and mean provided biomass per hour in a given brood was tested. As an indicator for chick fitness, the mean value of the two tarsus length was used. The median of these means was then taken for each brood, the brood being the sampling unit.

3.9.2. Adult fitness

A Body-Condition-Index (BCI) was calculated for each adult Hoopoe as:

$$BCI = \frac{m}{l}$$

BCI: Body-Condition-Index
m: mass [g]
l: mean tarsus length [mm]

We then tested whether variables describing provisioning activity correlated with the BCI.

3.10. Statistical analyses

Data analyses were performed using the program JMP4 (SAS Institute Inc. 2001, Cary, NC, USA).

All feeding variables were tested for homoscedasticity before running ANOVAs. Most of them were transformed into normality using the box-cox transformation (Krebs, 1989) with the following function:

$$x' = \frac{x^{\lambda} - 1}{\lambda} \quad \text{if } \lambda \neq 0$$

$$x' = \ln x \quad \text{if } \lambda = 0,$$

where λ is the provisional estimate of power transformation parameter.

In addition, percentages were arcsine-transformed to achieve normality. Two different approaches were used to test for the influence of the different factors on feeding variables. In the first approach all data of the three chick stages were pooled and the chick stage was taken into the analysis as a factor. Accordingly, every brood was measured three times under different weather conditions and at different chick stages. In the second approach the three chick stages were looked at separately to avoid what may to some extent be considered as pseudoreplication in the first analysis.

4. Results

4.1. Population

More than 90% (n=56) of the known breeding adult Hoopoes were captured in 2001 whereof 31 (55%) were caught for the first time (twelve males and 19 females) and 25 (45%) were recaptured from among previous years ringed birds (16 males and nine females). None of the recaptured birds had been ringed outside our study area nor was any Hoopoe that was ringed in Valais controlled in another place (Swiss

Ornithological Station Sempach). The oldest controlled female was born and ringed in 1999 and already bred successfully in 2000. The oldest controlled male was born and ringed in 1998 but not controlled in 1999, whereas it bred successfully in 2000. In one nestbox a male nested with a female to whom he was social father in 2000. Five cases of partner changing between first and second brood, and two ascertained cases of polygamy were observed. One male had a second female on four eggs 700 m apart from his first female with whom he already had at that time seven chicks between 15 and 20 days of age. This second brood was not successful and, in a third breeding attempt, the male raised another four chicks with the first female. One female who had two successive broods with the same male was furthermore observed feeding in a third nestbox four km SW. At this time it should have covered the eggs of its second brood.

In our study area 43 broods were observed in 2001, of which in 9 (20%) no young fledged. Except for four broods all of them took place in nestboxes. Of the successful 34 broods, three (9%) were second broods. A total of ≥139 chicks fledged. The overall hatching success was 71%, fledging success was 73% and breeding success was 47% (see Methods 3.2. for definitions). On average, four chicks fledged per brood, taking in account only successful broods. There was a change of clutch size over time. With the advancement of season, clutch sizes became smaller (r_s=-0.326, n=29 p=0.047) (Fig. 2), whereas the number of fledglings did not decrease significantly (r_s=-0.365, n=29, n.s.). Five broods were abandoned for unknown reasons; in one case it could have been caused by observer manipulation. Chicks of an abandoned brood were taken into a cage and raised by hand. Most of them could be released in late summer.

4.2. Nestling diet

81 videotapes (n=27 broods with 3 days of observation each) totalling 73'078 min (1'217 h 58 min) were evaluated. A total of 5'601 prey items were counted whereof 3'366 (60%) were Molecrickets (*Gryllotalpa gryllotalpa*), 1'112 (20%) were Lepidoptera larvae, 270 (4.8%) were other prey items and 853 (15.2%) items could not be identified (Appendix 1 & 2) (Fig. 3). 93% of the biomass provisioned consisted of Molecrickets, 3% Lepidoptera larvae and 3% unidentified prey. Other prey items made up 1% of biomass (Fig. 3). The category “other prey items” consisted mainly of the following taxa: Aranaeidea, Coleoptera, Formicidae and Diptera larvae (mostly Tipulidae). A high variance was visible among different pairs regarding provisioning. In some, almost exclusively Molecrickets were fed, while in others provisioning consisted mostly of small caterpillars. Variation among the broods regarding the investment of males and females was also high. At some nests only one partner fed during the day of video filming. It happened that adults that were initially identified as a parent of a brood were in fact simple visitors, which were never seen later at the site. Visitors normally investigated cavities from the entrance of the nestbox without entering it. Only in one case, the visitor did almost enter the nestbox and it attempted to peck at the chicks. Visitors never provisioned any food so that behavioural evidence indicates that no helping took place. Other bird species also visited nestboxes, mainly Tree Sparrows (*Passer montanus*), Great Tits (*Parus*

major) and Wrynecks (*Jynx torquilla*). They never entered the nestbox nor did they bring food.

4.3. Sexing

The results of the genetical sexing were compared to the phenotypical sexing achieved in the field. The two sexing methods yielded similar results in all but one case where only one parent of a brood was captured; we identified it as a male whereas it was actually a female. Unlike in most other birds for which the CHD-Method was used, the product from the female CHD-W gene was smaller than the one from the male (CHD-Z gene) (Fig. 4).

4.4. Food provisioning

Two series of analyses (see methods 3.4.) were run, one with the three development stages pooled and a second one with them considered separately: Chick stage I (11-15 days of age), Chick stage II (16-20 days), Chick stage III (21-25 days).

4.4.1. Three chick stages pooled

4.4.1.1. Factors influencing biomass provisioned per hour

A multiway ANOVA was used to test whether factors weather, brood size and chick stage had an influence on the biomass delivered per hour in a given day. Less biomass per hour was fed under unfavourable weather conditions (F_1=18.17, $p<0.0001$) (Fig. 5); also, more biomass was fed when more chicks were present (F_7=13.04, $p<0.0001$) (Fig. 9), but there was no significant influence of the chick stage (F_2=1.30, n.s.) (Fig. 9).

4.4.1.2. *Factors influencing the biomass provisioned per hour and chick*

As brood size had an influence on biomass provisioned per hour, hourly biomass values were divided by the number of young present at the day of video filming before running the subsequent analyses. Then we tested again for the effect of brood size on the average biomass provisioned to an average chick. Brood size had no effect. On average, parents did not feed more food biomass to a chick in a small brood than in a large brood (Kruskal-Wallis-test, $X^2_6=4.19$, n.s.) (Fig. 10). Brood size was thus no longer considered in the subsequent analyses.

Then, a multiway ANOVA was used to test whether factors weather, brood or chick stage had an influence on the provided biomass per hour and chick. Less biomass per hour and chick was actually brought on days with unfavourable weather conditions ($F_1=15.71$, $p=0.0002$) (Fig. 6). In addition, there was a major brood effect ($F_{26}=2.28$, $p=0.006$). Chick stages, however, did not show any significant influence ($F_2=0.64$, n.s.) (Fig. 10).

4.4.1.3. *Factors influencing the number of prey items delivered per hour and chick*

A multiway ANOVA was used to test if factors weather, brood and chick stage influenced the number of provided prey items per hour and chick. Fewer prey items per hour and chick were brought under unfavourable weather conditions ($F_1=14.80$, $p=0.0003$) (Fig. 8). There was also a significant brood effect ($F_{26}=9.59$, $p<0.0001$), whereas chick stage did not affect the frequency of prey item delivery ($F_2=0.30$, n.s.) (Fig. 12).

4.4.1.4. *Factors affecting the proportion of provisioned Molecrickets*

A multiway ANOVA was used to test for the influence of factors brood, chick stage and weather on the proportion of provisioned Molecrickets.

Brood had an effect (F_{26}=6.51, p<0.0001), whereas no effect of chick stage was found (F_2=2.13, n.s.). There was a noticeable trend towards a smaller proportion of Molecrickets provisioned in adverse weather conditions (F_1=3.31, p=0.07).

4.4.1.5. Prey diversity vs. weather

A negative correlation was found between diet diversity and the weather factor (r_s=-0.34, n=80, p=0.0019). Diversity was reduced on good days suggesting a greater Molecricket availability on days with favourable weather conditions (Fig. 13).

4.4.2. Chick stages treated separately

The effects of factors brood size and weather on the following four feeding activity variables (biomass/hour, biomass/hour*chick, number of prey items/hour, number of prey items/hour*chick) were tested using ANOVAs.

4.4.2.1. Chick stage I

As regards chick stage I no effect of brood size on one of the feeding activity variables was found. In contrast weather had an influence on both the provisioned biomass per hour and on the provided biomass per hour and chick. On the contrary, no effect was detected on the number of prey items per hour and on the number of prey items per hour and chick. Less biomass was provided under unfavourable weather conditions, whereas equal numbers of prey items were fed under different weather circumstances (Tab. 1).

4.4.2.2. Chick stage II

As regards chick stage II an effect of brood size on the biomass provisioned per hour and on the number of provided prey items per hour was found. No effect of brood size was detected on the biomass provisioned per hour and chick nor on the number of prey items delivered per hour and chick. More biomass per hour was provisioned to larger broods but not more food was fed to a chick in a smaller brood than in a larger brood. No effect of weather on one of the four feeding activity variables was detected (Tab. 2).

4.4.2.3. Chick stage III

As regards chick stage III an effect of brood size was detected on the biomass provisioned per hour but not on the three other feeding activity variables. More biomass per hour was provided when more chicks were present. No effect of weather was detected on one of the four feeding activity variables (Tab. 3).

4.4.2.4. Proportion of Molecrickets in nestling diet

In chick stage I a correlation between the proportion of Molecrickets provisioned and the weather factor was detected. A higher proportion of Molecrickets in the total biomass and a higher proportion of Molecrickets in the number of provided prey items was seen on warm and dry days. No effect was shown for chick stage II and III (Tab. 4).

4.4.2.5. Diet diversity

A negative correlation between the prey item diversity and weather factor was detected in chick stage I. Prey item diversity was significantly higher on days with unfavourable weather conditions (Tab. 5). No correlation was seen in chick stage I and II, however.

4.5. Differences between the sexes

Males provided more than females in all chick stages regarding biomass provisioning per hour (Fig. 14) and the number of prey items per hour

(Fig. 15). Whereas in stage I only tendencies are visible, the difference is strongly significant in chick stage III (Tab. 6).

The mean values of the three chick stages were used to test for differences between the sexes regarding the proportion of Molecrickets in overall biomass and in the number of prey items. Males fed a higher proportion of Molecrickets regarding biomass and a greater number of prey items than females (Tab. 7).

4.6. Chick fitness

Neither a correlation between mean tarsus length of the chicks and the mean provisioned biomass per hour (Spearman's r_s=0.06, n=27, n.s.) nor between mean tarsus length and the number of provisioned prey items per hour and chick (Spearman's r_s =0.02, n=27, n.s.) was detected.

4.7. Influence of the parents' fitness

Males with a low BCI brought a smaller proportion of Molecricket biomass (r_s=0.46, n=25, p=0.02) (Fig. 16) and a smaller proportion of Molecricket individuals (r_s =0.46, n=25, p=0.02) than males with a high BCI (Fig. 17). No correlation was detected between the other four provisioning activity variables (biomass/hour, biomass/hour*chick, number of prey items/hour, number of prey items/hour*chick) and BCI or a body measurement in males. No correlation was detected between one of the six provisioning activity variables and the BCI or a body measurement for females.

5. Discussion

5.1. Population

It seems that male Hoopoes are more philopatric than females. It is not known whether the unringed adults possibly come from another population outside the study area (ringing effort started in 1998) or whether these birds might have been born in Valais before 1998.

Two cases of polygamy and five cases of partner change between the first and the second brood were found. Yet, these data are purely observational. It is possible that a higher degree of polygamy actually exists. Additionally, it is supposed that extrapair paternity occurs in our Hoopoe population as in Spain (Martín-Vivaldi et al., 2002).

Clutch size decreased significantly during the season. Fitter Hoopoes, which lay large clutches, may return from the wintering quarters earlier in the season than less fit Hoopoes that have smaller clutches, returning later (Christians et al., 2001). Hoopoes that return early in the season could additionally have access to better breeding sites. Alternatively, a decrease in food availability over the season could lead Hoopoes to lay smaller clutches later on.

5.2. Videotape evaluation

On some videotapes the prey items were hardly recognisable and they could not always be determined. Additionally, the different size classes of Molecrickets were not always easily distinguishable. Errors in calculating prey biomass can thus not be excluded. Although none of the unidentified prey items was a Molecricket the estimated mean biomass of 0.08g for the former prey category remain rough. This could especially influence data from one brood (A-60b) where the parents fed up to 238 small unidentified prey items (out of 331) in a given day.

In most feeding events the identity of the adult Hoopoe was clear. Nevertheless, in cases where the distance of the entrance of the nestbox to the camera was great, the identification of the adult was difficult. Moreover, the markings on head sides disappeared after a while probably due to rain, abrasion or bleaching. Four times (out of 27) as regards chick stage III it occurred that chicks left the nestbox during the day of videomonitoring. Food was then brought to the chicks out of video, leading to an underestimation of provisioning. Also, it sometimes happened that females took food items from males' bill at nestbox entrance. Such prey was recorded as delivered by the male. It can not be excluded, that such a food transfer took place out of sight. Again this may have lead to biases in provisioning quantification.

5.3. Sexing

All except one adult Hoopoe were sexed correctly in the field, in particular from the size of the uropygial gland, which additionally produces a terrible smell in females in which the reservoir is always inflated. Phenotypic sexing is thus feasible in the field during the breeding season. Little difference exists in the length between the male-specific (CHD-Z) and the female-specific (CHD-W) gene. This could be solved by using an 8% denaturing acrylamid gel for analyses (Griffiths et al., 1998). A smaller specific product from the CHD-W gene in females is also observed in other Coraciiformes such as the European Bee-Eater (*Merops apiaster*) and in the Rock Pigeon (*Columba livia*) (Griffiths et al., 1998).

5.4. Food provisioning

With 60% of the provided prey items and 93% of the biomass supplied, Molecrickets (*Gryllotalpa gryllotalpa*) were dominant in nestling diet. This is a higher proportion than in any other study. In our study area, Fournier & Arlettaz (2001) reported, in the 80's, that 68% of the provided biomass and 26% of the provided prey items were Molecrickets. Whereas in that study Hoopoes were still mainly breeding on foothill slope of the valley they bred exclusively in the plain in 2001 as a clear consequence of the installation of numerous nestboxes there (Arlettaz et al., 1998). Not only more Molecrickets are fed when Hoopoes breed on the plain (this study), but their proportion in nestling diet also had a positive influence on breeding success as suggested by Fournier & Arlettaz (2001), who showed that the breeding success decreased with nest site altitude.

We can not rule out that Molecricket availability has recently improved, but the main reason for the increased proportion of Molecrickets in nestling diet is supposed to be due to shorter distances between breeding sites and foraging areas, which minimises energy expenditures during prey transport, favouring breeding success.

5.5. Factors affecting food provisioning

The fact that every brood was videomonitored three times (chick stages I, II, III) during breeding has to be looked at more closely. Because these three data sets are not independent from each other (same brood), this can be seen as a typical case of pseudoreplication. Given the small size of the local Hoopoe population (n=43 breeding pairs in 2001) we could not afford to replicate measurements on independent broods as regards these three chick stages. As a result, we ran two series of analyses, first on the overall data obtained from the three chick stages pooled, second on the three chick stages considered separately; the outcome of the two series was then compared to see whether major discrepancies appeared between the two approaches. In this respect, we have first to notice that chick stage was a non-significant factor in the first analysis. Without removing inherent theoretical biases due to pseudoreplication, this renders the grouping of all data (n=81 videomonitoring days collected from 27 broods) a biologically (if not statistically) sound approach. Also, the results of the two approaches do not differ much with respect to the influence of weather on the food provisioning, which was the main issue we wanted to address in this study.

In the first series, brood was a significant factor pointing out to a major among brood variation in provisioning efficiency. This may relate either to parents' quality or habitat suitability. At the study site, Molecrickets are actually not evenly distributed (Arlettaz et al., 2000b) and habitat selection by Hoopoes may be a crucial reproductive decision. Because basic trophic resources appear relatively clumped, we predict strong intraspecific competition for breeding habitat selection.

Food provisioning efficiency did not vary with respect to chick stage, at least between eleven and 25 days of age, which was the age when we made the videos. The asynchronous hatching of Hoopoe broods, combined with a relatively large brood size, could explain the even distribution of effort over breeding time.

When considering chick stages separately, some statistical effects could only be detected in a particular chick stage but not in others. This can be explained, at least partly, by the fact that weather conditions were less contrasted in some chick stages than in others (chick stage II and III vs. I, see Fig. 18).

Overall, rainy and cold weather had a negative influence on biomass provisioning. About three times less biomass and fewer prey items were provisioned on colder and/or wetter days than in hot and/or sunny days. Clearly, periods of several successive unfavourable days caused brood reduction, which was sometimes drastical. Indirect evidence for the effect of climate is given by breeding success. This was slightly smaller in 2001 (47%) than in 1998 (65%) and in 2000 (57%), but higher than in 1999 (18%). This supports the theory of climatic influence. In 2001, the weather conditions were mediocre compared to former years. The conditions were not so unfavourable as in 1998, but there were still several periods with heavy rain, whereas 2000 had been mainly hot and dry (Arlettaz et al., 1998; Arlettaz et al., 2000a; Arlettaz et al., 2000b; Schaad et al., 2001). Moreover, limited food provisioning can have additionally hampered the development of surviving chicks. Chicks originating from several broods abandoned during cold and rainy spells that were brought to captivity exhibited neural developmental problems although they were well fed in the cage and growth continued normally.

Hoopoes' sensitivity to limited food availability is discussed in relation to the brood reduction hypothesis in Martín-Vivaldi et al. (1999), which states that it is unpredictable food availability during the feeding season which determines the breeding investment of parents. This author reported that sometimes parents do not feed smaller chicks as long as the larger beg (Martín-Vivaldi et al., 1999), with the younger, less fed chicks having lower survival probability. According to the brood reduction hypothesis, Hoopoes which cannot predict food conditions for the forthcoming during breeding season, lay optimistic clutch sizes in order to raise as many chicks as possible. Because fewer Molecrickets are fed in unfavourable weather conditions, weather appears to be the ultimate factor responsible for a brood reduction strategy in the Hoopoe.

Yet, our results point to an apparent contradiction to the brood reduction hypothesis in the Hoopoe. Seemingly, Hoopoe parents could feed more than they actually do given that the average biomass provisioned to a single chick does not vary among broods of different sizes (Fig. 9). It is maybe simply the begging activity of the chicks which sets a limit to provisioning by parents.

In the second approach weather did not affect the number of prey items delivered although provisioned biomass was greatly affected. This means that prey of smaller size was provisioned on bad days more frequently than on nice days. Indeed, a smaller proportion of Molecrickets, the most profitable prey, was fed under unfavourable weather conditions. Optimal foraging theory predicts that Hoopoes should concentrate predation on the most profitable prey (Molecrickets) when feasible (Krebs et al., 1977). Yet, under low Molecricket availability, Hoopoes would be constrained to add less profitable prey to their diet. Dietary niche should then be more diverse on bad days because of this prey switch. We actually observed a more diverse diet under adverse meteorological circumstances.

The apparent Molecrickets' sensitivity to unfavourable weather conditions remains unclear. This insect species prefers humid soil. It even swims quite well (Harz, 1957). How then to explain its lesser proportion in diet on bad days? Maybe, higher ambient temperatures favour activity of Molecrickets (Detzel, 1998); in this case Molecrickets would be more difficult to detect by Hoopoes on bad days. Microhabitat selection by this underground prey may also change according to weather conditions (e.g. deeper location in soil on rainy days). Last but not least, Hoopoes possibly avoid foraging in Molecricket's habitats on rainy days. Molecrickets are partly vegetarian and colonise in first place grassland zones. But wet grass is clearly detrimental to terrestrial foraging birds such as the Hoopoe. It might then be Hoopoes, which are reluctant to search for their favourite prey in wet weather conditions. Indeed, it was observed that Hoopoes' plumage is very wet on rainy days, what might be due to walking through wet vegetation during foraging.

5.6. Sex-related investment in food provisioning

Males provisioned more food to chicks than females more than females. In chick stage I this was maybe partly due to the fact that the female was still covering the chicks, which would have resulted in an underestimation of female provisioning activity. However, the low level of provisioning by males better indicates that this scenario is irrealistic.

It is not clear whether the two sexes have evolved different basic investment strategies in food provisioning. To some extent, this difference may also be due to an adjustment of feeding in the absence of the partner. According to our data, four females had a second clutch with another partner after a successful first brood, whereas only one male was reported having a second clutch with a different partner. This suggests that it is females that leave the brood first because they are seeking a new partner for initiating a second brood. Males may thus be constrained to stay. Such a strategy could result from a biased operational sex ratio with more males than females present in the population, which still ought to be demonstrated. A similar pattern has been described in the Florida Snail Kite (*Rosthramus sociabilis*) (Beissinger & Snyder, 1987).

5.7. Chick fitness

Although no correlation between chick fitness and provided biomass was found it is still supposed that the amount of provided biomass has an influence on chick fitness. Possibly, the tarsus length is not an appropriate measure to describe chick fitness. As all chicks within one brood were ringed and measured on the same day, it may be that the tarsus of the smaller chicks were not fully grown at that time. Body mass would possibly be a better estimator of chick fitness. Due to high daily variations in chick mass because few feeding events per chick (Molecrickets), we renounced to measure body weight.

5.8. Influence of parents' fitness

High Body-Condition-Index (BCI) correlated with individual's fitness. Males with a high BCI are heavier than other males, of comparable body size (mean tarsus and wing length). Fitter males provided a higher proportion of Molecrickets. Males of higher quality may simply bring more Molecrickets because they are better in finding these insects. Also, high quality males were presumably occupying areas with a high density of Molecrickets, which in turn could explain a higher proportion of Molecrickets in food provisioning. Additionally, males living in good Molecricket habitats may consume more of this prey, which could result in a higher BCI.

No correlation between any feeding variable and fitness was found for females. Possibly female quality is not well described by BCI. As males deliver more food than females, it is possible that males' fitness depends upon effort in chick provisioning, whereas females' investment may concern primarily egg production.

5.9. Conservation aspects

As we showed here, weather has a strong influence on Hoopoes' food provisioning. It thus regulates the reproductive success in one year, and ultimately determines population dynamics. Climatic changes over decades could therefore largely influence Hoopoe population trends as suggested earlier (Hirschfeld & Hirschfeld, 1973; Glutz, 1980; Cramp, 1985; Rehsteiner, 1996).

The aim of this study was to improve the understanding of Hoopoe ecology in Valais, a climatic enclave at the northern border of this bird of southern origin. Marginal populations have a high adaptive value potential and their contribution to the overall genetic variance within a species might be of prime importance. It remains to be shown, yet, whether weather and/or climate are the main factors responsible for the survival of local Hoopoe populations. Other factors of anthropogenic origin can also play an important role. This was clearly assessed as regards the lack of natural cavities in our study area. Trees with natural cavities having been eradicated by agriculture intensification. Corrective measures applied on a wide scale (nestboxes) have solved this problem. Further cryptic factors may still act, such as for instance the use of pesticides against Molecrickets, which are considered as pest.

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8. Tables

Table 1: Effect of factors brood size and weather on the feeding activity variables (rows) (ANOVAs) at chick stage I.

Feeding activity variable	Brood size	Weather
Biomass/hour	F_6=2.14 p=0.10	**F_1=6.49** **p=0.02**
Biomass/hour*chick	F_6=0.81 p=0.58	**F_1=7.70** **p=0.01**
Number of prey items/hour	F_6=1.25 p=0.33	F_1=0.04 p=0.84
Number of prey items/hour*chick	F_6=0.63 p=0.70	F_1=0.09 p=0.77

Table 2: Effect of factors brood size and weather on the feeding activity variables (rows) (ANOVAs) at chick stage II.

Feeding activity variable	Brood size	Weather
Biomass/hour	**F_7=7.64** **p=0.0002**	F_1=2.22 p=0.15
Biomass/hour*chick	F_7=0.75 p=0.63	F_1=1.56 p=0.23
Number of prey items/hour	**F_7=2.55** **p=0.05**	F_1=2.00 p=0.17
Number of prey items/hour*chick	F_7=0.49 p=0.83	F_1=1.68 p=0.21

Table 3: Effect of factors brood size and weather on the feeding activity variables (rows) (ANOVAs) at chick stage III.

Feeding activity variable	Brood size	Weather
Biomass/hour	**F_7=4.07** **P=0.01**	F_1=1.26 p=0.28
Biomass/hour*chick	F_7=1.50 p=0.23	F_1=1.18 p=0.29
Number of prey items/hour	F_7=2.23 p=0.08	F_1=0.46 p=0.51
Number of prey items/hour*chick	F_7=1.32 p=0.30	F_1=0.54 p=0.47

Table 4: Correlation between the proportion of Molecrickets in provided biomass and the number of prey items provisioned vs. the weather factor at each chick stage, (Spearman's Rank correlation).

	Weather		
	Chick stage I	Chick stage II	Chick stage III
Proportion of Molecrickets in biomass	**r_s=0.51** **n=27** **p=0.007**	r_s=0.20 n=27 p=0.31	r_s=0.33 n=27 p=0.09
Proportion of Molecrickets in the number of prey items	**r_s=0.52** **n=27** **p=0.005**	r_s=0.21 n=27 p=0.30	r_s=0.33 n=27 p=0.09

Table 5: Correlation between the Shannon-Index and the weather factor at each of the three chick stages, (Spearman's Rank correlation).

	Weather		
	Chick stage I	Chick stage II	Chick stage III
Shannon-Index	**r_s=-0.48** **n=27** **p=0.01**	r_s=-0.19 n=27 p=0.35	r_s=-0.33 n=27 p=0.10

Table 6: Influence of factor sex as regards biomass and the number of prey items provisioned by hour. Non parametric ANOVA (Kruskal-Wallis).

	Sex		
	Chick stage I	Chick stage II	Chick stage III
Biomass/hour	X^2_1=3.03 p=0.08	**X^2_1=5.87** **p=0.015**	**X^2_1=14.35** **p=0.0002**
Number of prey items/hour	X^2_1=1.10 p=0.29	X^2_1=3.30 p=0.07	**X^2_1=10.29** **p=0.0013**

Table 7: Influence of factor sex as regards proportion of provided Molecrickets in biomass and in number of prey items provisioned. Non parametric ANOVA (Kruskal-Wallis).

	Sex
Proportion of Molecrickets in biomass	**X^2_1=10.78, p=0.001**
Proportion of Molecrickets in the number of provided prey items	**X^2_1=8.76, p=0.003**

9. Figure legends

Figure 1: Example of distinctive individual head marking in one adult male Hoopoe.

Figure 2: Relationship between clutch size and absolute time (date) (r_s=-0.326, n=30, p=0.047). Crosses correspond to the date of hatching.

Figure 3: Proportion of the different prey categories in overall provisioned prey frequency (n=5'601) and biomass.

Figure 4: Genetic sexing. Gel showing four samples (2 males and 2 females). In females (marked f) two bands can be seen, whereas in males (marked m) only one. Note that the female-specific product is smaller (ran farther).

Figure 5: Correlation between biomass provisioned per hour and weather factor. Each letter represents a different brood (3 replicates each).

Figure 6: Correlation between biomass provisioned per hour and chick and weather factor. Each letter represents a different brood (3 replicates each).

Figure 7: Correlation between the number of provisioned prey items per hour and weather factor. Each letter represents a different brood (3 replicates each).

Figure 8: Correlation between the number of provisioned prey items per hour and weather factor. Each letter represents a different brood (3 replicates each).

Figure 9: Biomass provisioned per hour shown for different brood sizes and chick stages (mean+sem). Sample sizes $[x_{I}, x_{II}, x_{III}]$ were, for the various brood sizes (first figure before brackets): 1[0,1,3], 2[3,4,4], 3[3,2,2], 4[5,6,8], 5[7,5,3], 6[5,5,4], 7[3,3,2], 8[0,0,0], 9[1,1,1]).

Figure 10: Biomass provisioned per hour and chick shown for different brood sizes and chick stages (mean+sem). Sample sizes $[x_{I}, x_{II}, x_{III}]$ were, for the various brood sizes (first figure before brackets): 1[0,1,3], 2[3,4,4], 3[3,2,2], 4[5,6,8], 5[7,5,3], 6[5,5,4], 7[3,3,2], 8[0,0,0], 9[1,1,1]).

Figure 11: Number of provisioned prey items per hour shown for different brood sizes and chick stages (mean+sem). Sample sizes $[x_{I}, x_{II}, x_{III}]$ were, for the various brood sizes (first figure before brackets): 1[0,1,3], 2[3,4,4], 3[3,2,2], 4[5,6,8], 5[7,5,3], 6[5,5,4], 7[3,3,2], 8[0,0,0], 9[1,1,1]).

Figure 12: Number of provisioned prey items per hour and chick shown for different brood sizes and chick stages (mean+sem). Sample sizes $[x_{I}, x_{II}, x_{III}]$ were, for the various brood sizes (first figure before brackets): 1[0,1,3], 2[3,4,4], 3[3,2,2], 4[5,6,8], 5[7,5,3], 6[5,5,4], 7[3,3,2], 8[0,0,0], 9[1,1,1]).

Figure 13: Correlation between the Shannon-Index for diet diversity and weather factor (r_s=-0.34, n=81, p=0.0019).

Figure 14: Total biomass provisioned per hour presented separately for each chick stage and sex (n=27 broods, 10th and 25th percentiles, median, 75th and 90th percentiles are shown. Crosses indicate means.)

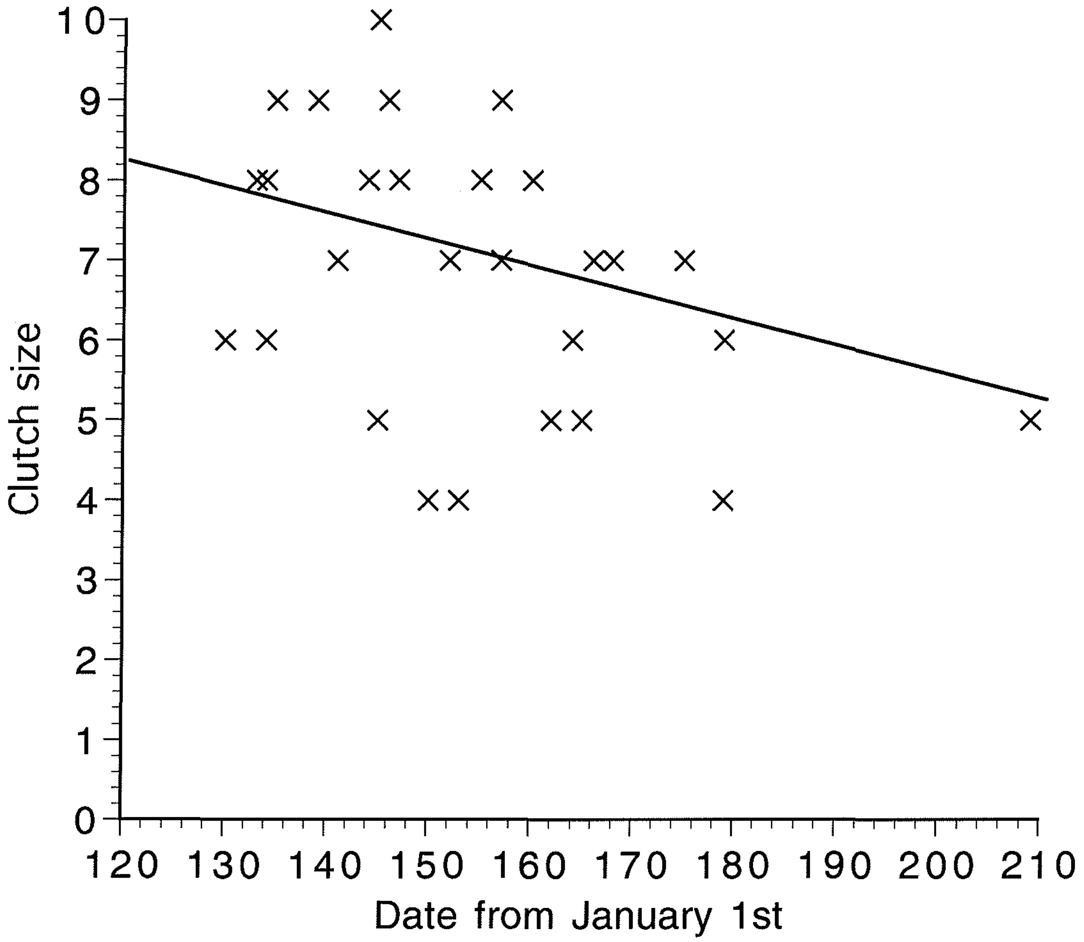
Figure 15: Total number of provisioned prey items per hour presented separately for each chick stage and sex (n=27 broods, 10th and 25th percentiles, median, 75th and 90th percentiles are shown. Crosses indicate means.)

Figure 16: Correlation between proportion of Molecricket in provisioned biomass and the Body-Condition-Index in males and females (r_s=0.46, n=27, p=0.02).

Figure 17: Correlation between proportion of Molecricket in the number of provisioned prey items and the Body-Condition-Index in males and females (r_s=0.46, n=27, p=0.02).

Figure 18: Distribution of the weather conditions in the three chick stages regarding biomass provisioned per hour. Note that in chick stage II the weather conditions are clumped, whereas in chick stage I they are well distributed (n=27 broods).

Figure 1



10
9
8
7
6
5
4
3
2
1
0
Clutch size
120
130
140
150
160
170
180
190
200
210
Date from January 1st

Figure 2

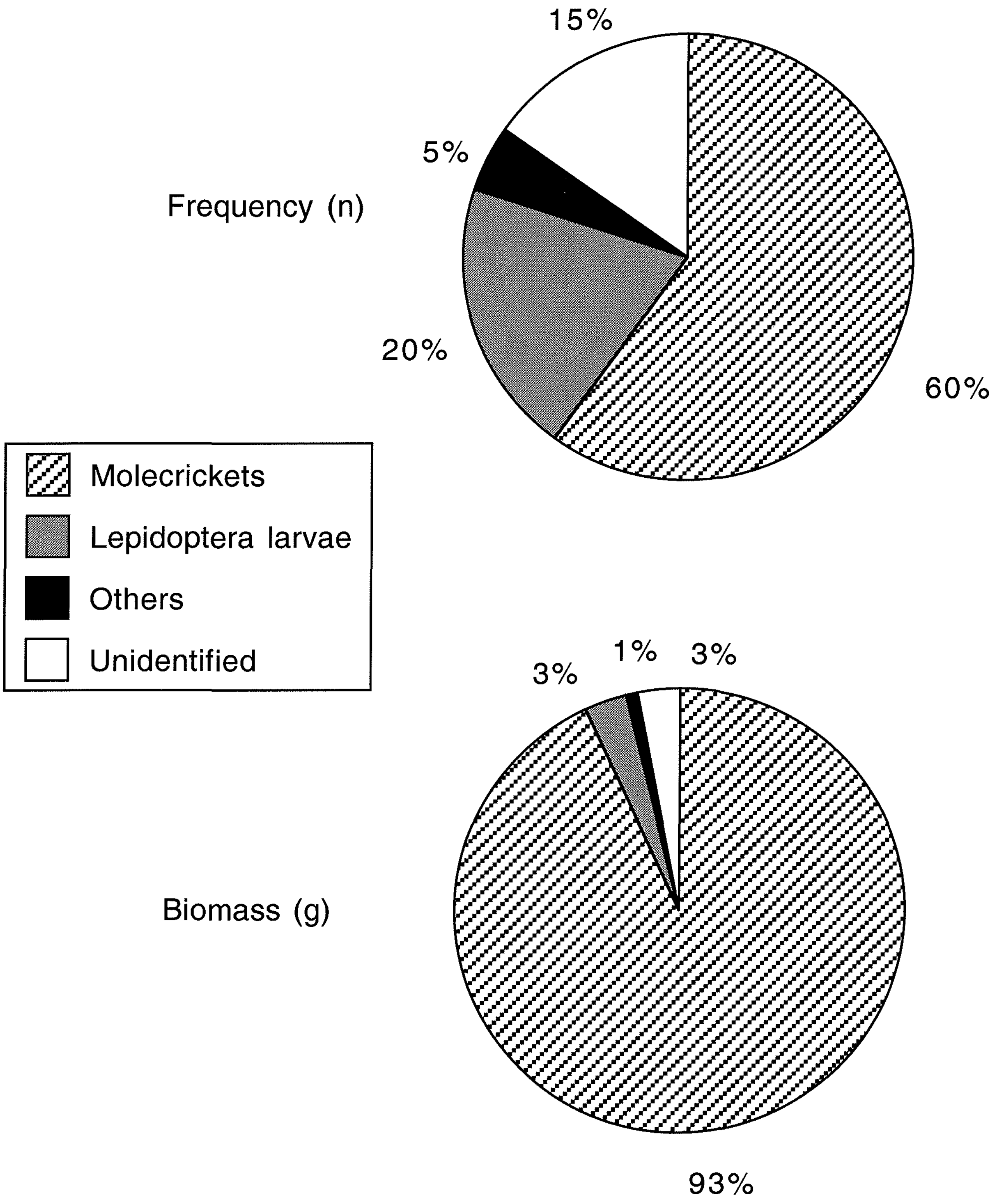

15%
5%
Frequency (n)
20%
60%
Molecrickets
Lepidoptera larvae
Others
Unidentified
3%
1%
3%
Biomass (g)
93%

Figure 3

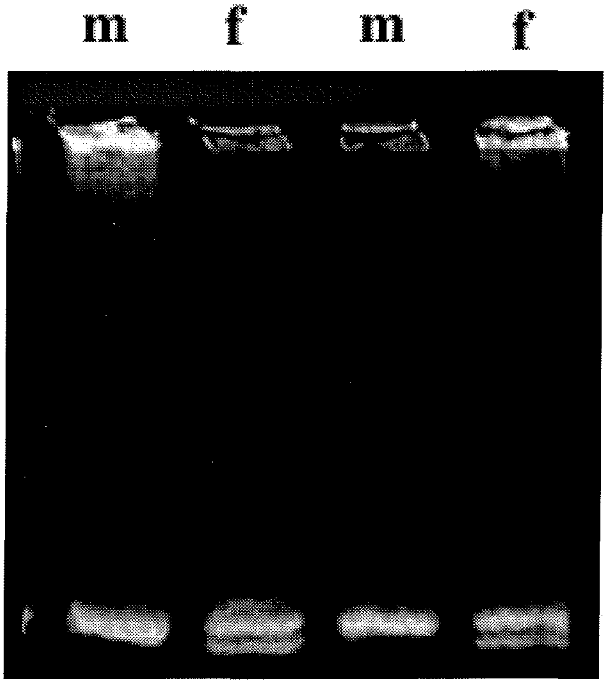


Figure 4

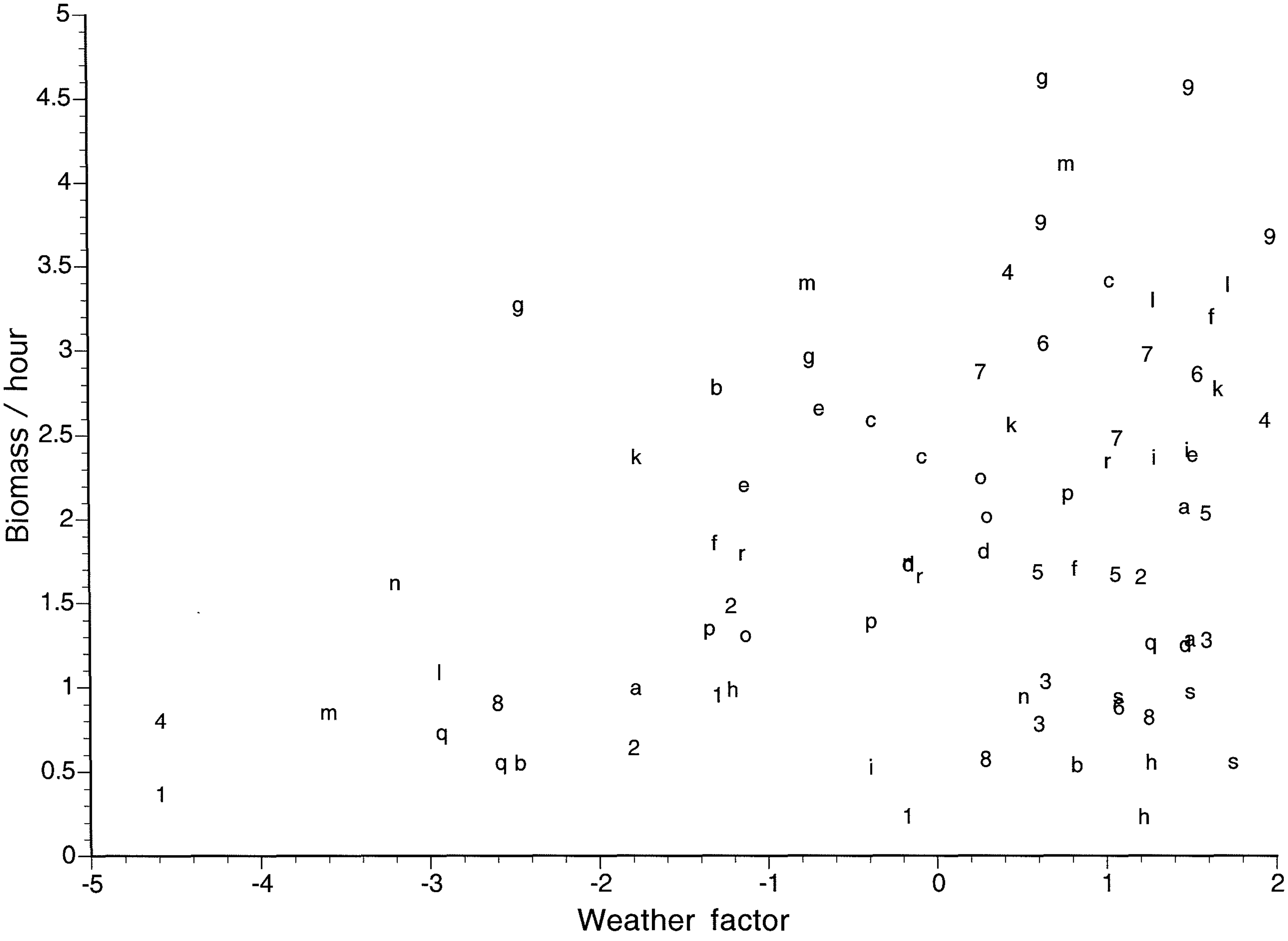
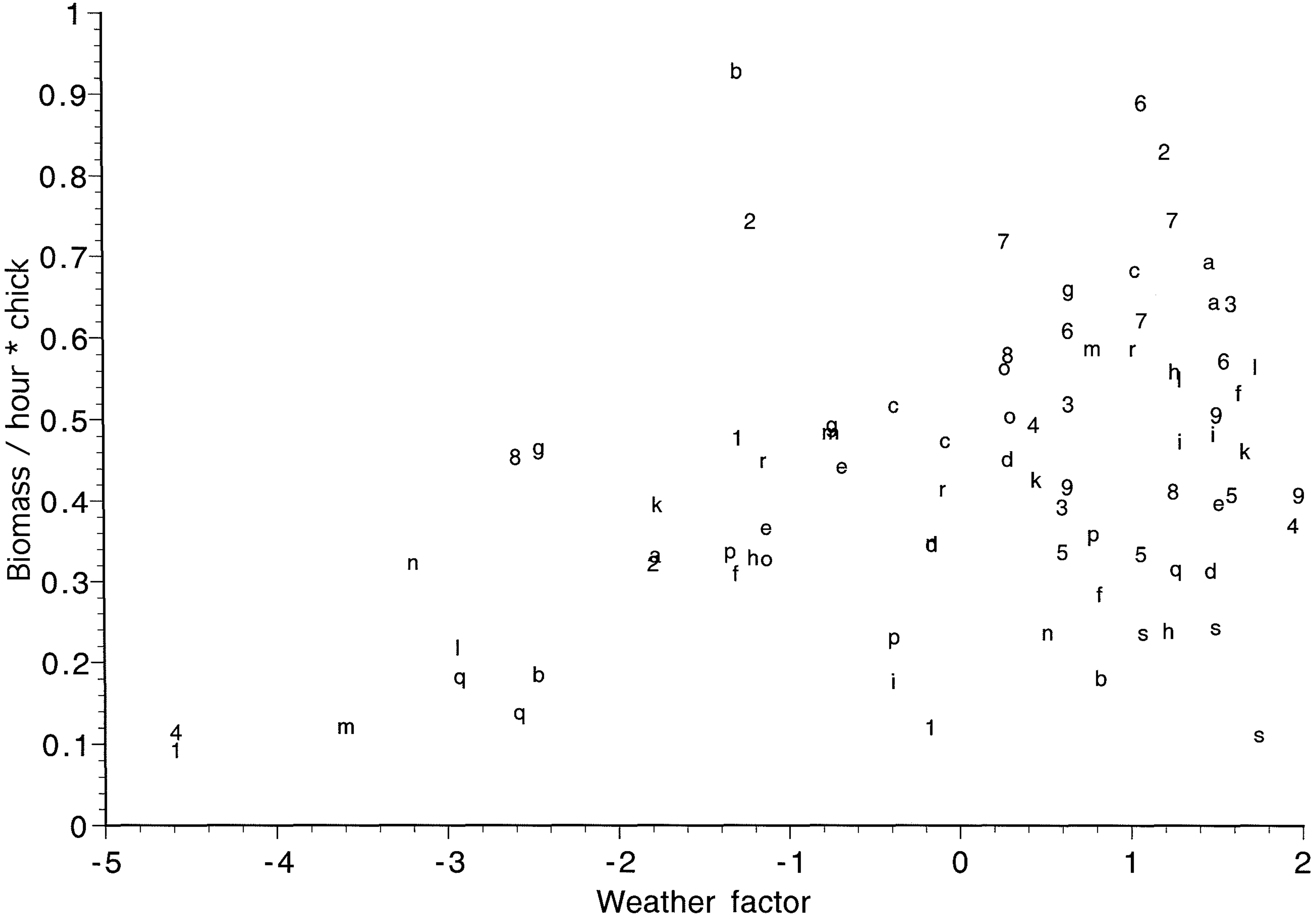


Figure 5



Biomass / hour * chick
Weather factor
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
-5
-4
-3
-2
-1
0
1
2

Figure 6

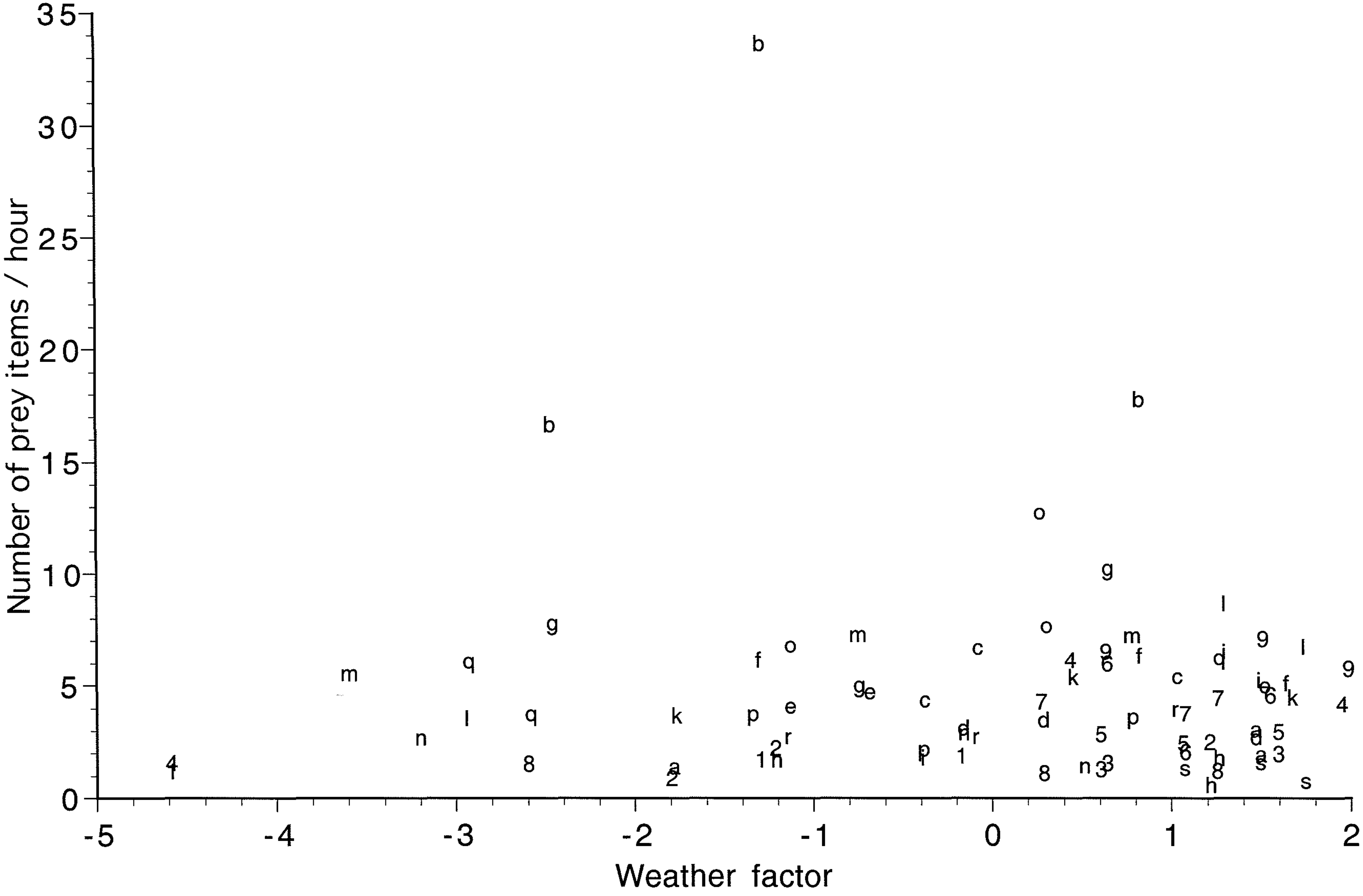

Number of prey items / hour
35
30
25
20
15
10
5
0
-5
-4
-3
-2
-1
0
1
2
Weather factor

Figure 7

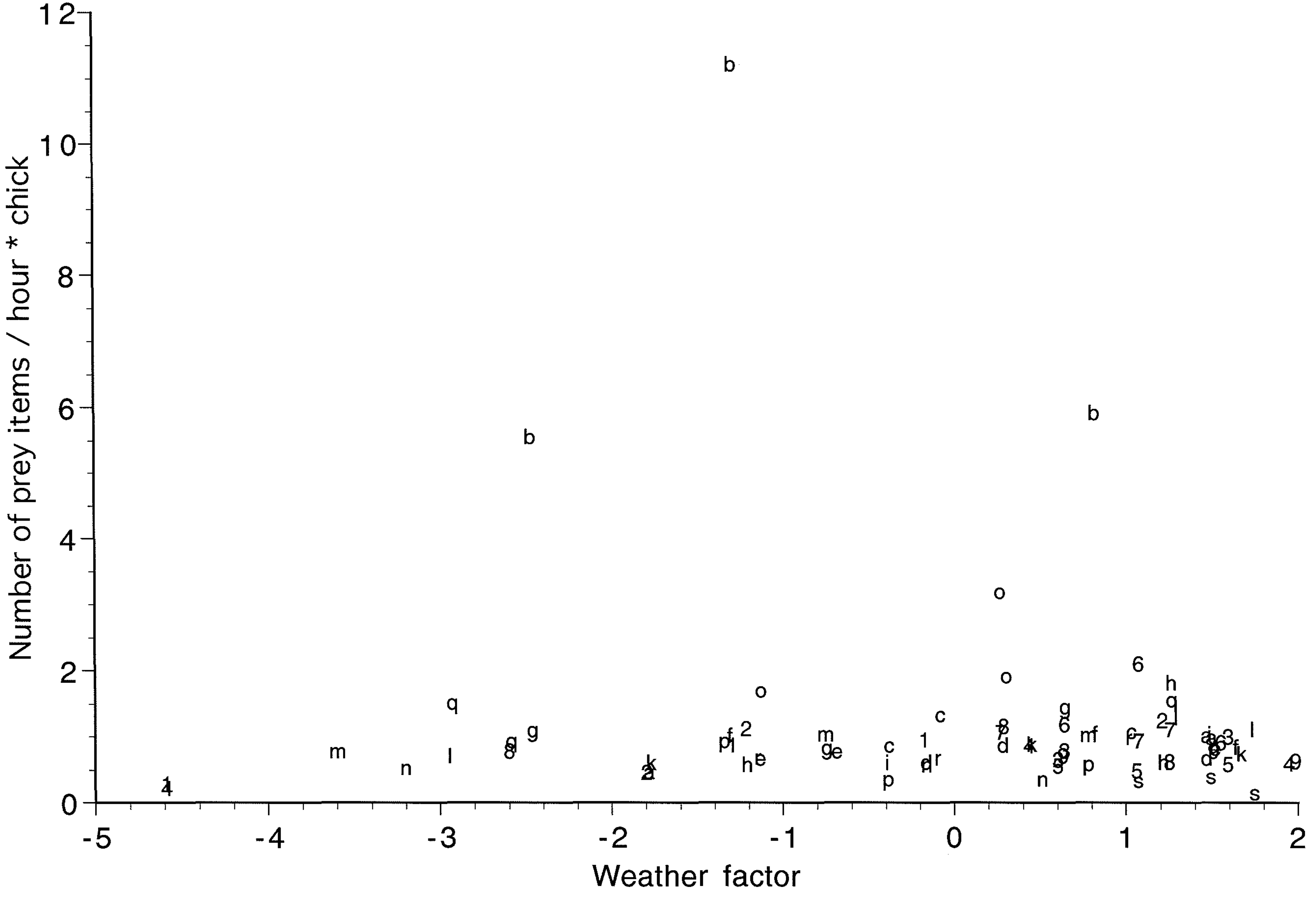

Number of prey items / hour * chick
Weather factor
0
2
4
6
8
10
12
-5
-4
-3
-2
-1
0
1
2

Figure 8

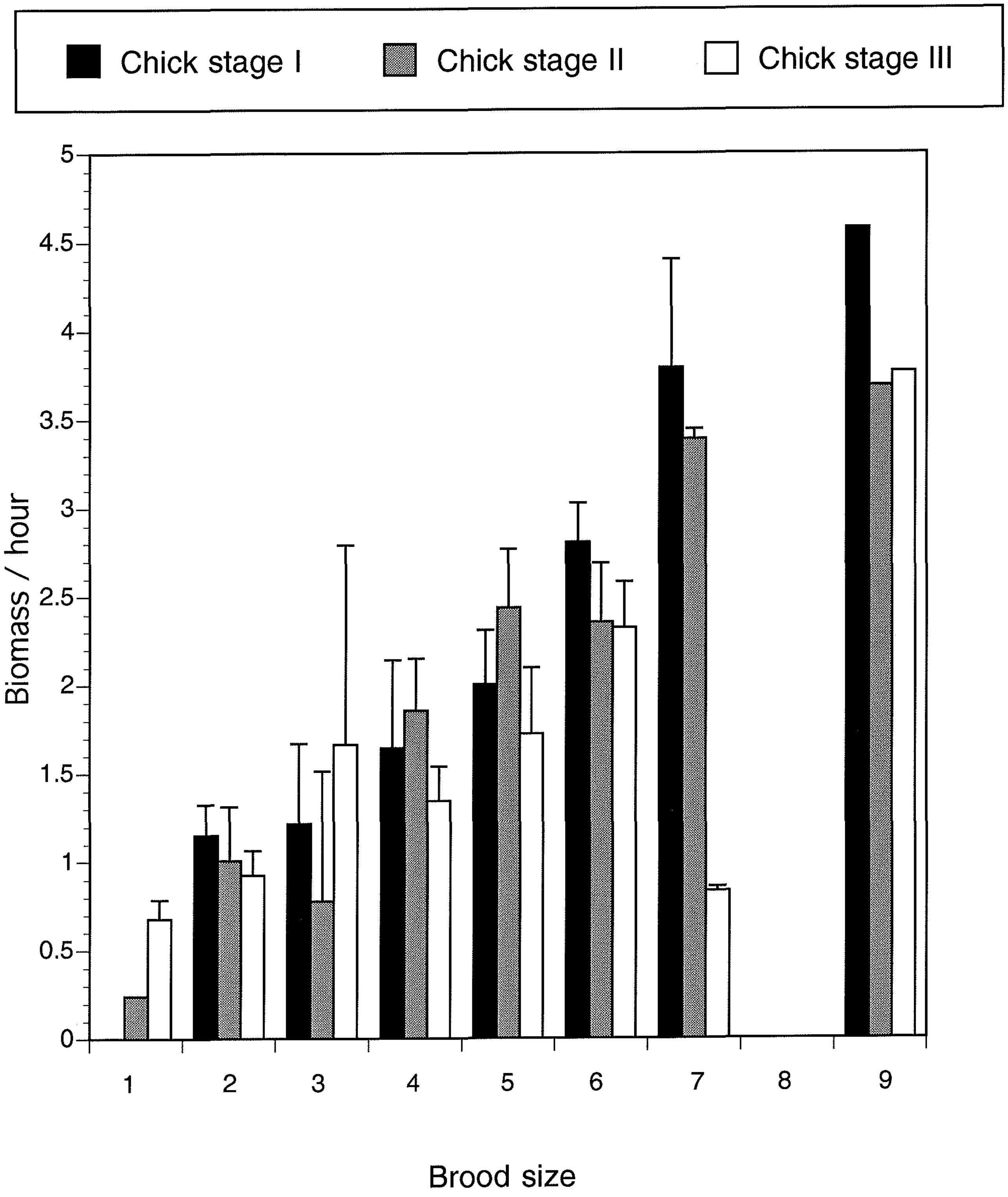

Chick stage I
Chick stage II
Chick stage III
Biomass / hour
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
1
2
3
4
5
6
7
8
9
Brood size

Figure 9

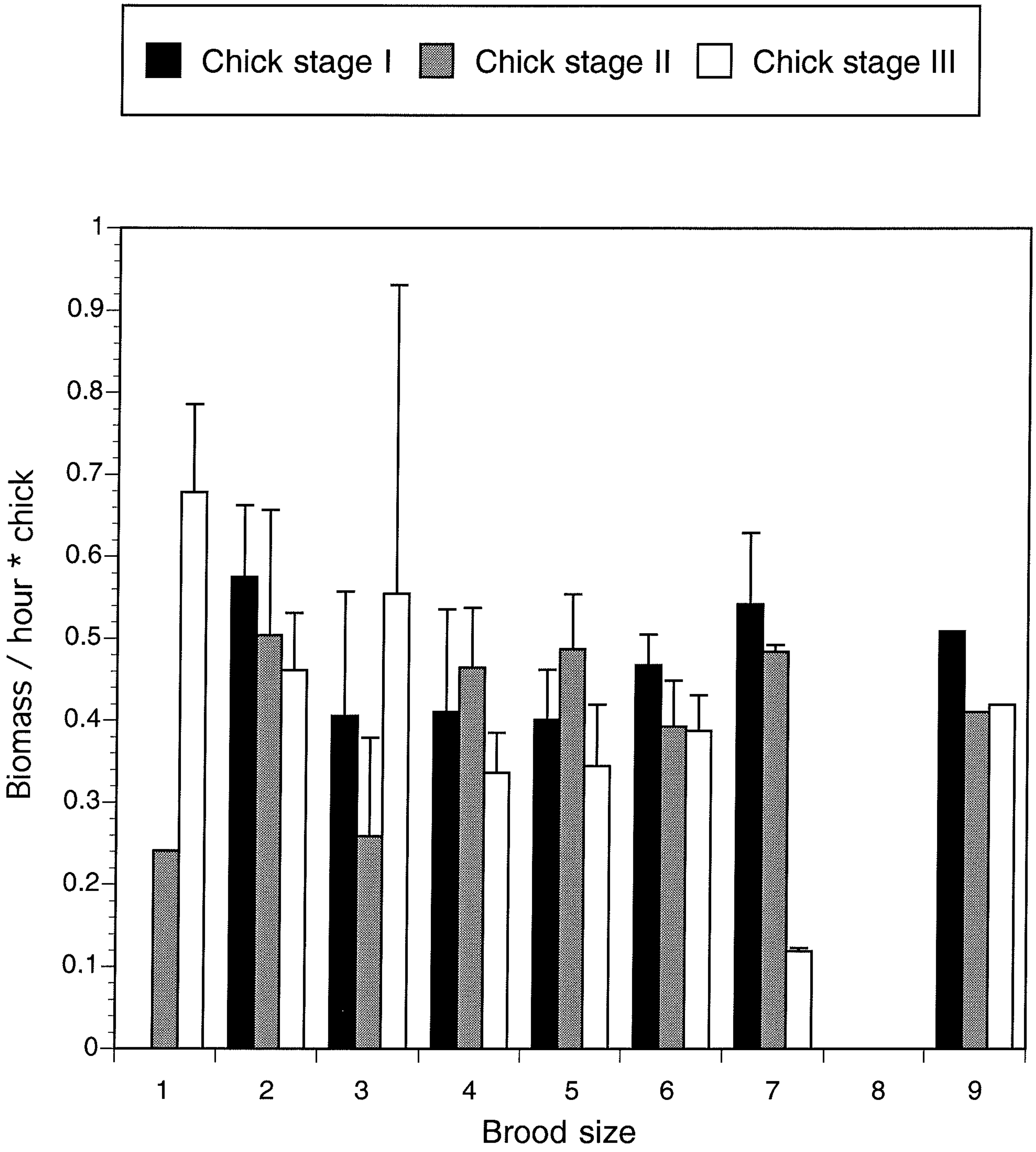

Chick stage I
Chick stage II
Chick stage III
Biomass / hour * chick
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1
2
3
4
5
6
7
8
9
Brood size

Figure 10

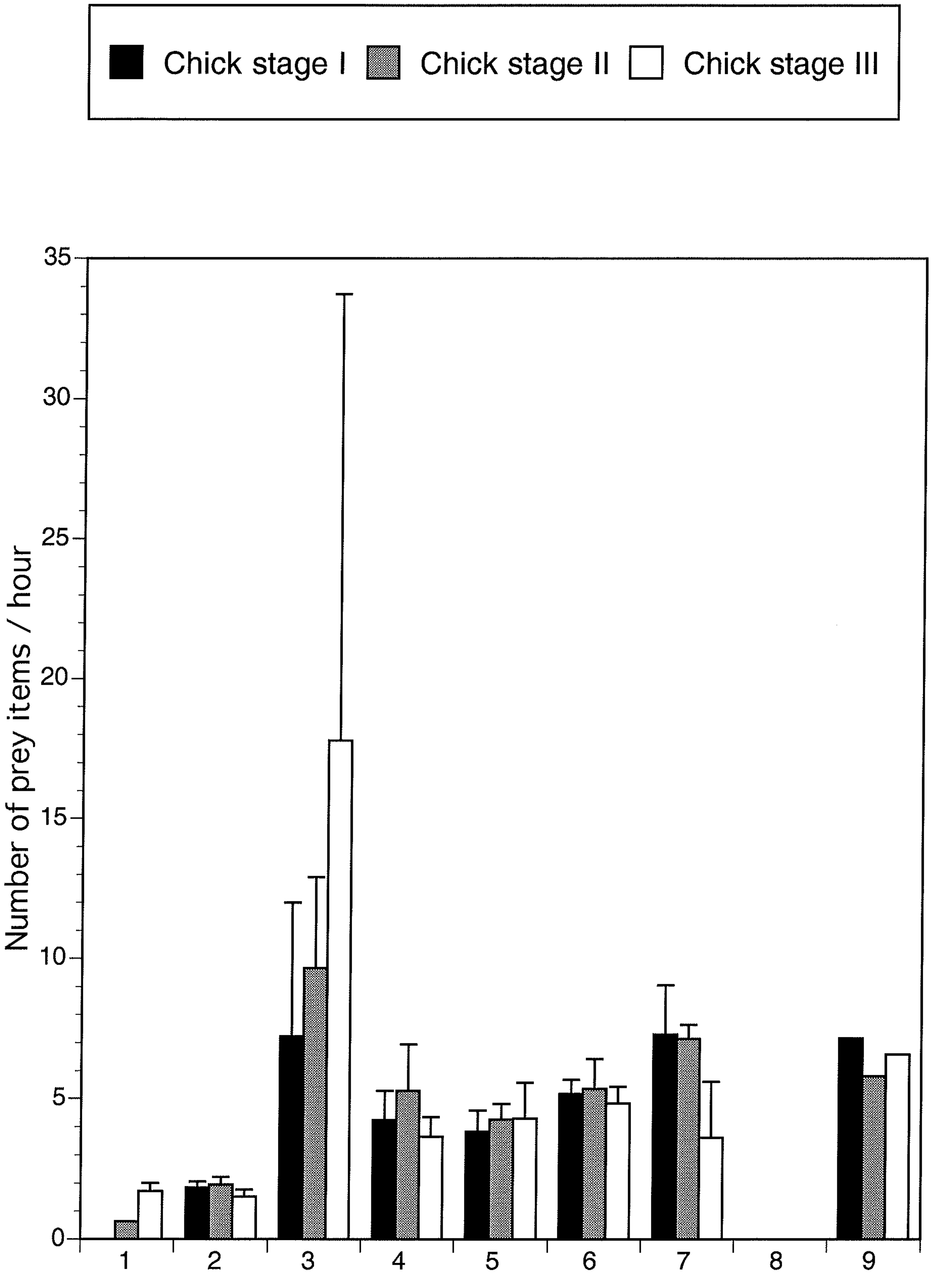
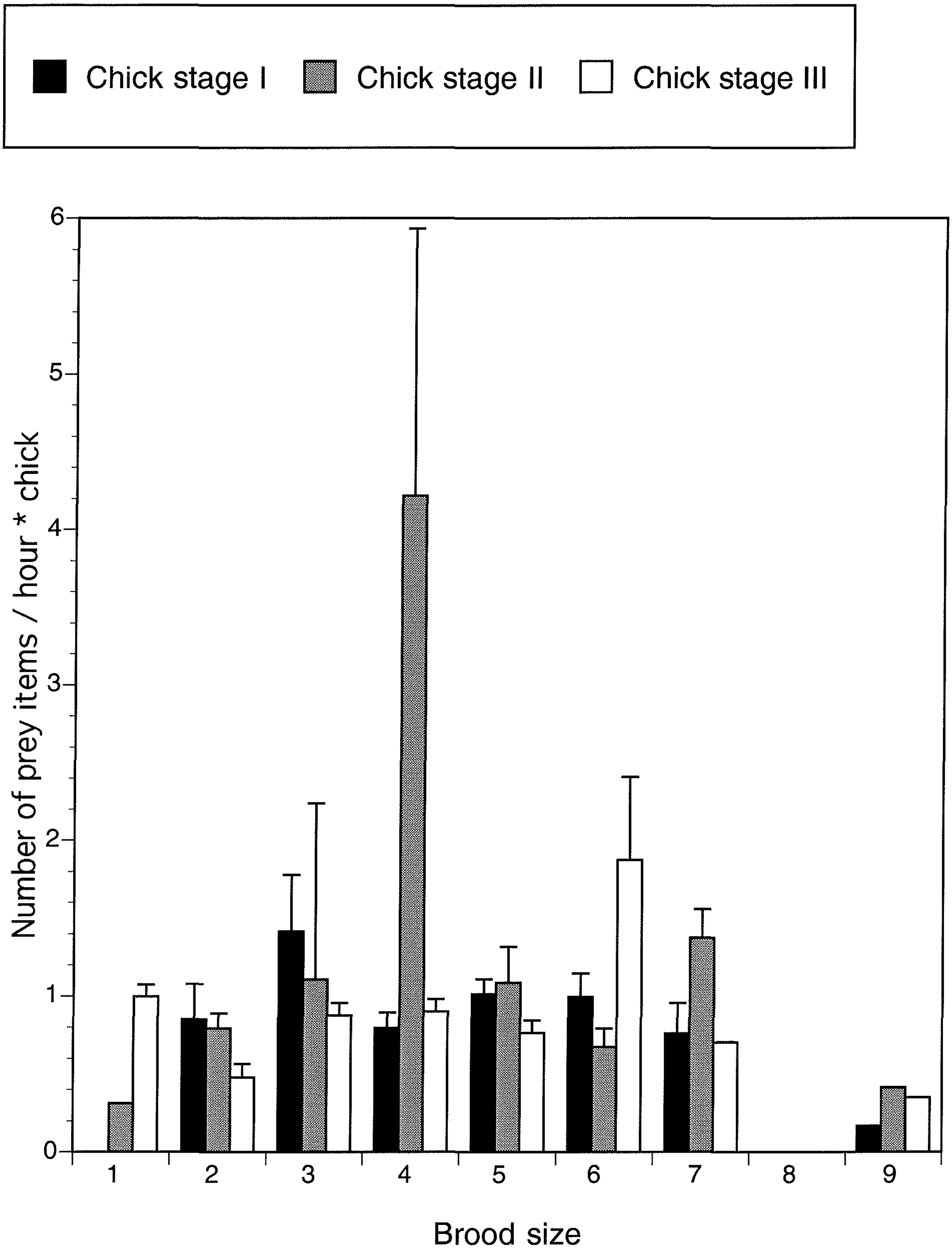
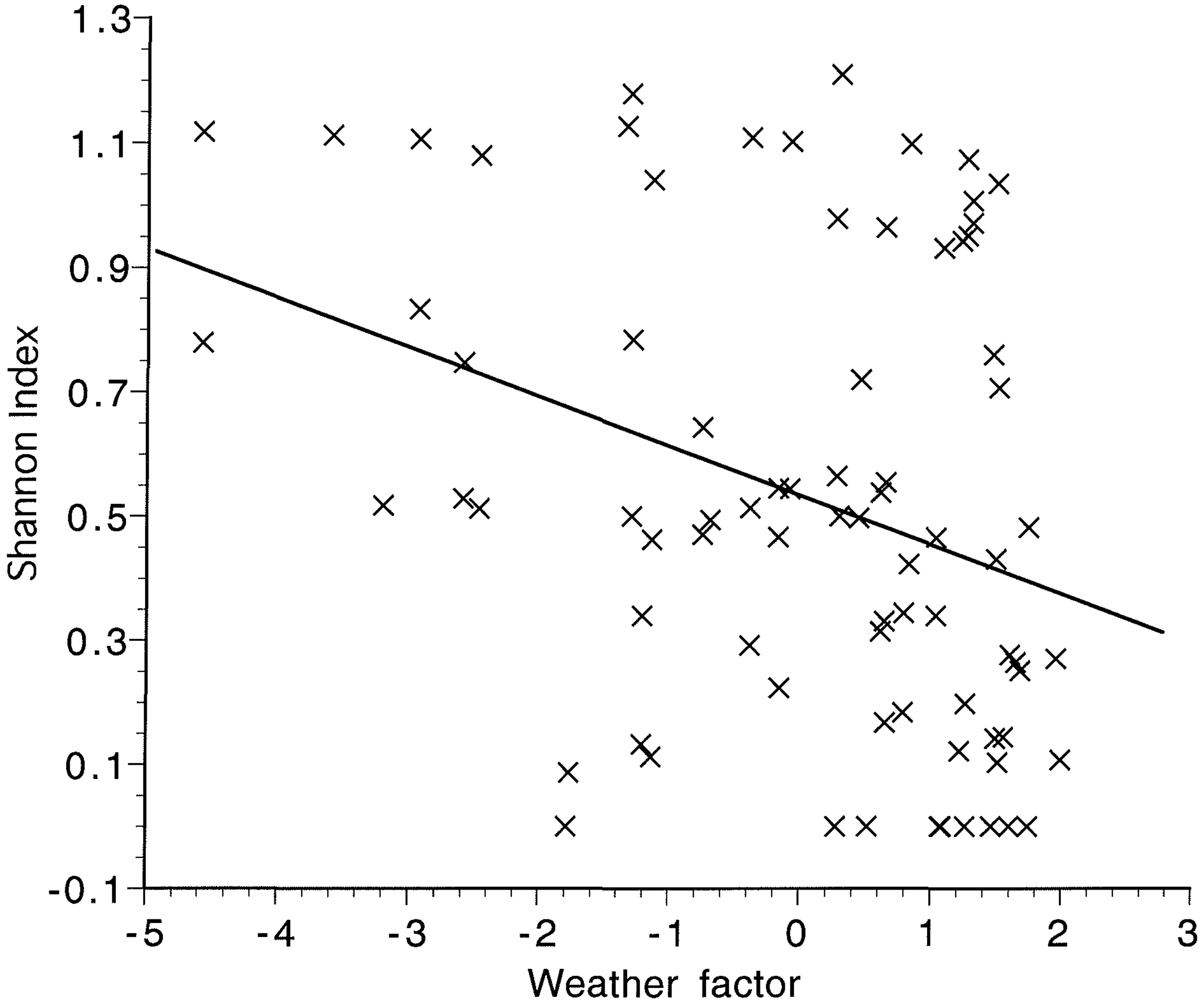

Chick stage I
Chick stage II
Chick stage III
Number of prey items / hour
35
30
25
20
15
10
5
0
1
2
3
4
5
6
7
8
9
Brood size

Figure 11



Chick stage I
Chick stage II
Chick stage III
Number of prey items / hour * chick
0
1
2
3
4
5
6
1
2
3
4
5
6
7
8
9
Brood size

Figure 12



1.3
1.1
0.9
0.7
0.5
0.3
0.1
-0.1
Shannon Index
-5
-4
-3
-2
-1
0
1
2
3
Weather factor

Figure 13

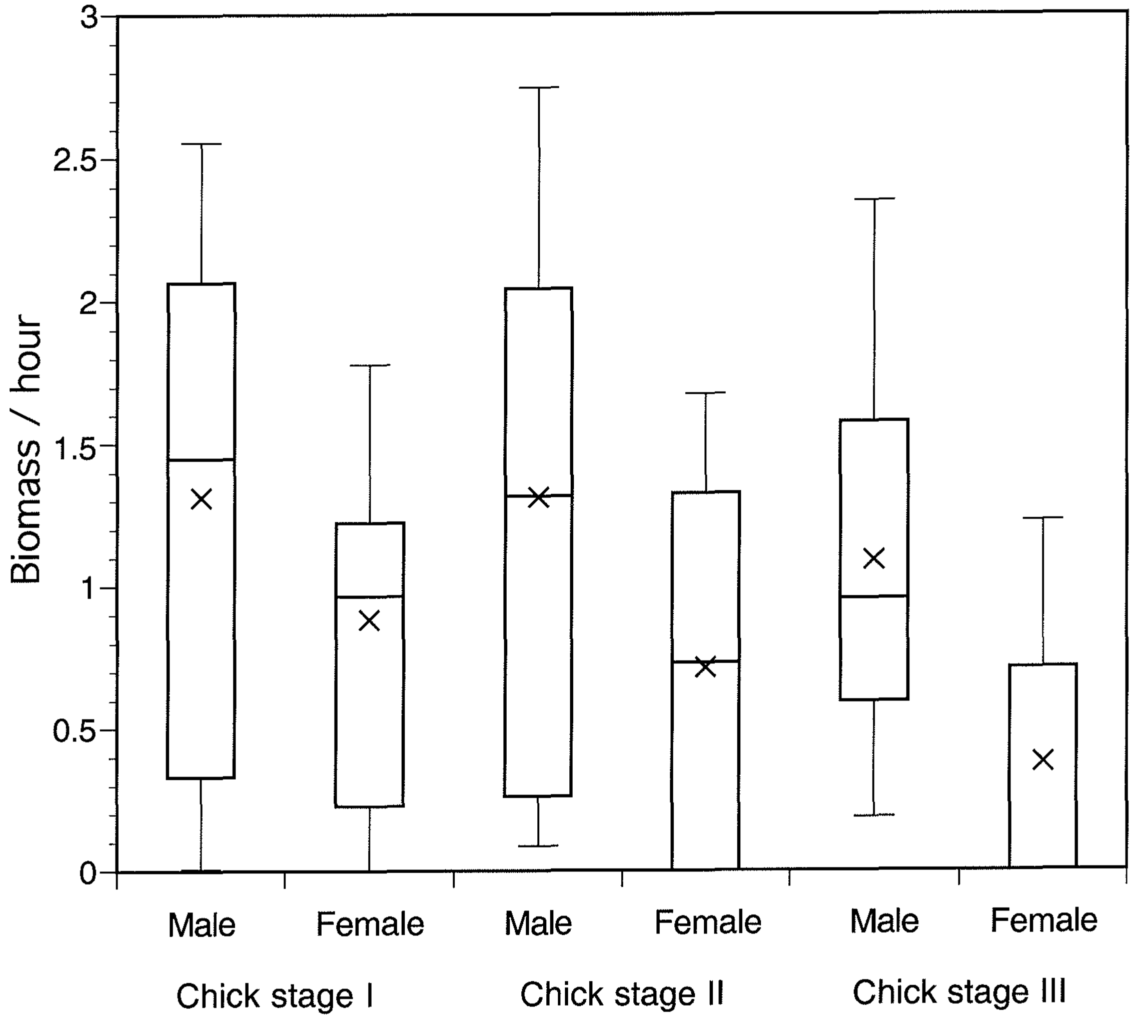

Biomass / hour
3
2.5
2
1.5
1
0.5
0
Male
Female
Male
Female
Male
Female
Chick stage I
Chick stage II
Chick stage III

Figure 14

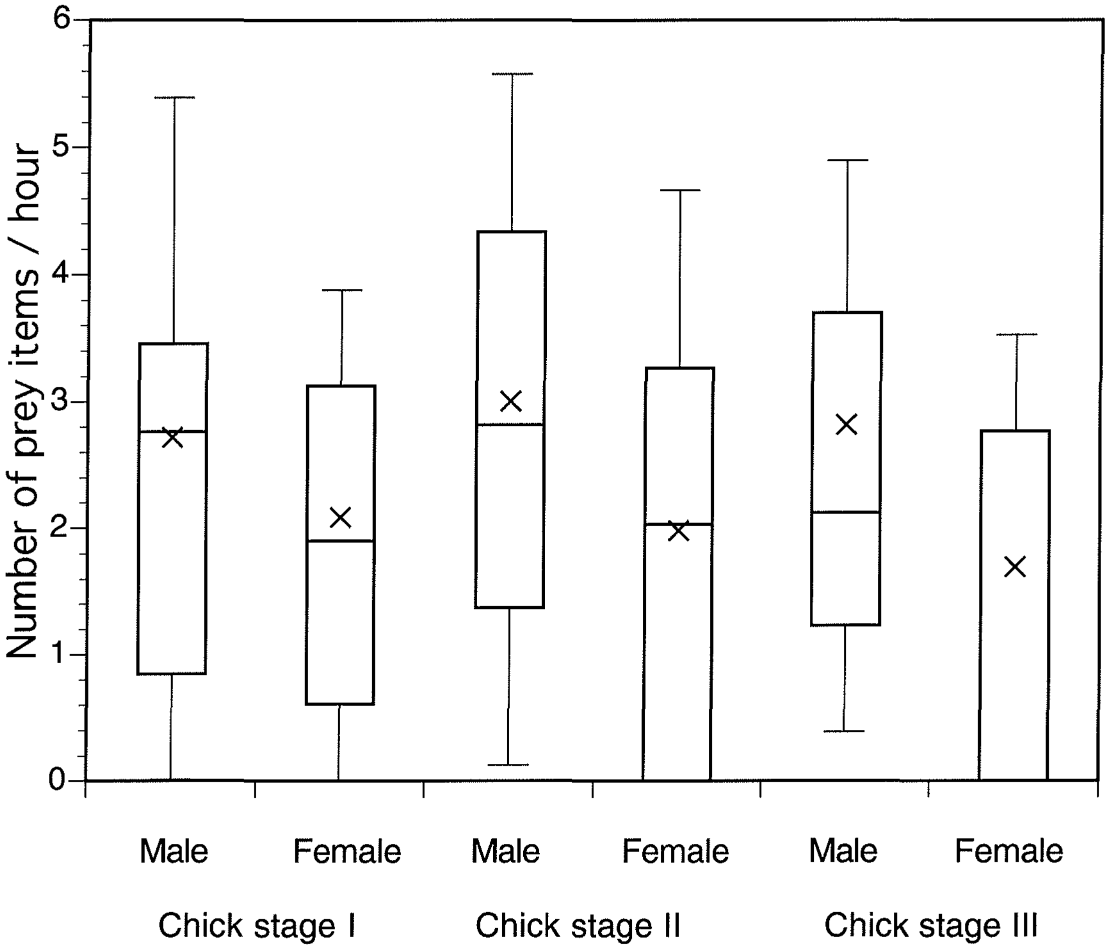

Number of prey items / hour
0
1
2
3
4
5
6
Male
Female
Male
Female
Male
Female
Chick stage I
Chick stage II
Chick stage III

Figure 15

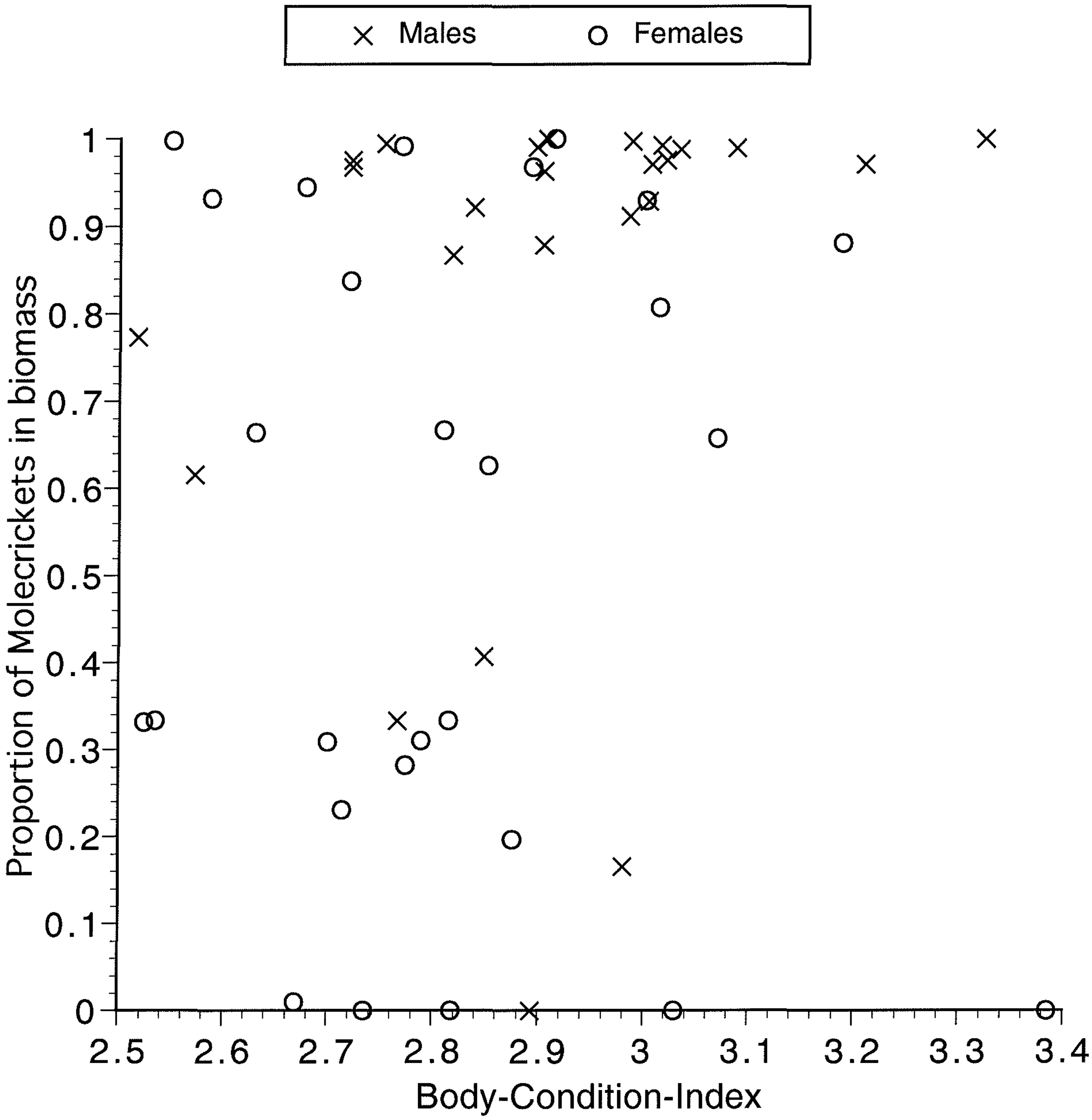

× Males
○ Females
Proportion of Molecrickets in biomass
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
2.5
2.6
2.7
2.8
2.9
3
3.1
3.2
3.3
3.4
Body-Condition-Index

Figure 16

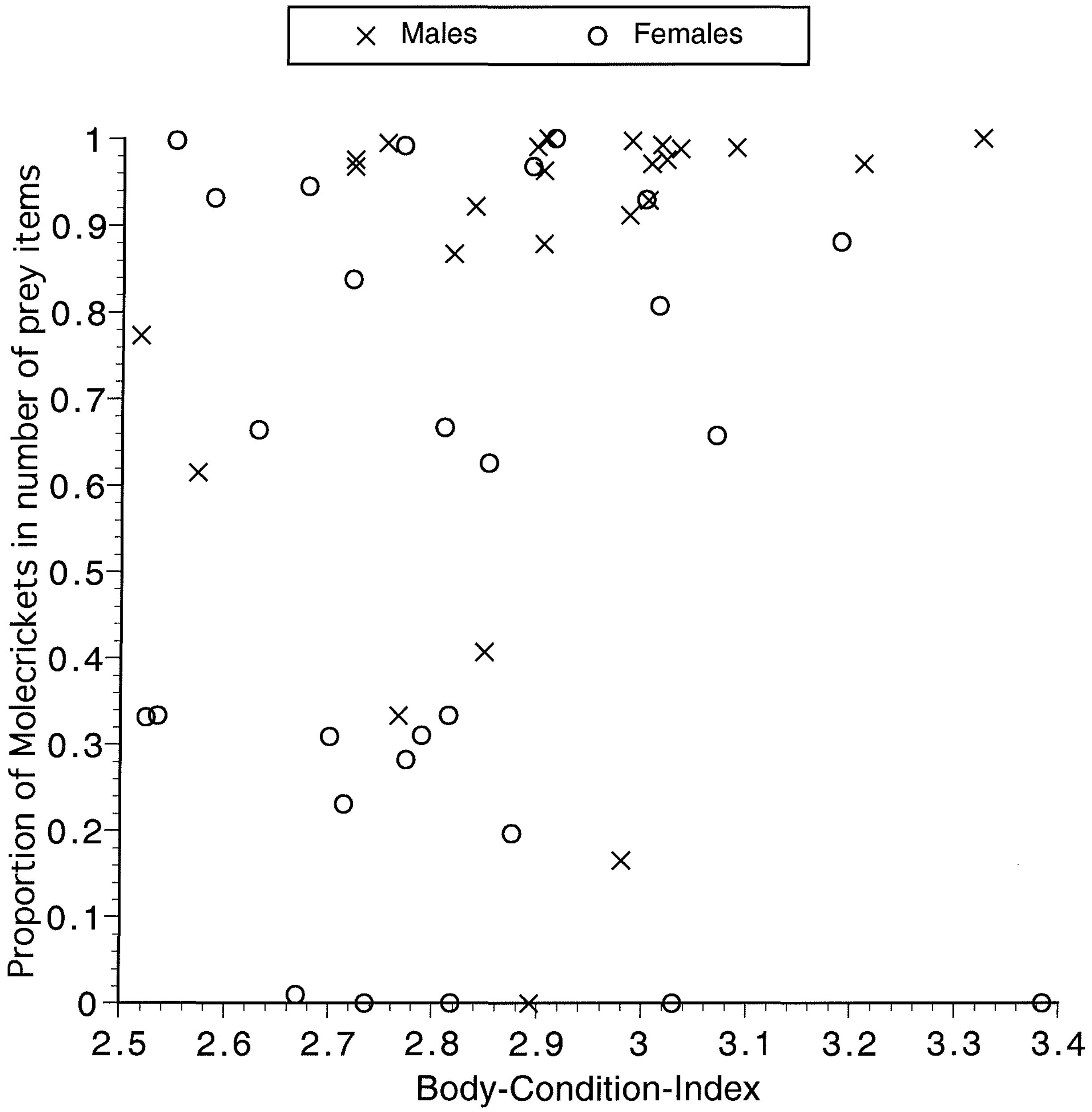

× Males
○ Females
Proportion of Molecrickets in number of prey items
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
2.5
2.6
2.7
2.8
2.9
3
3.1
3.2
3.3
3.4
Body-Condition-Index

Figure 17

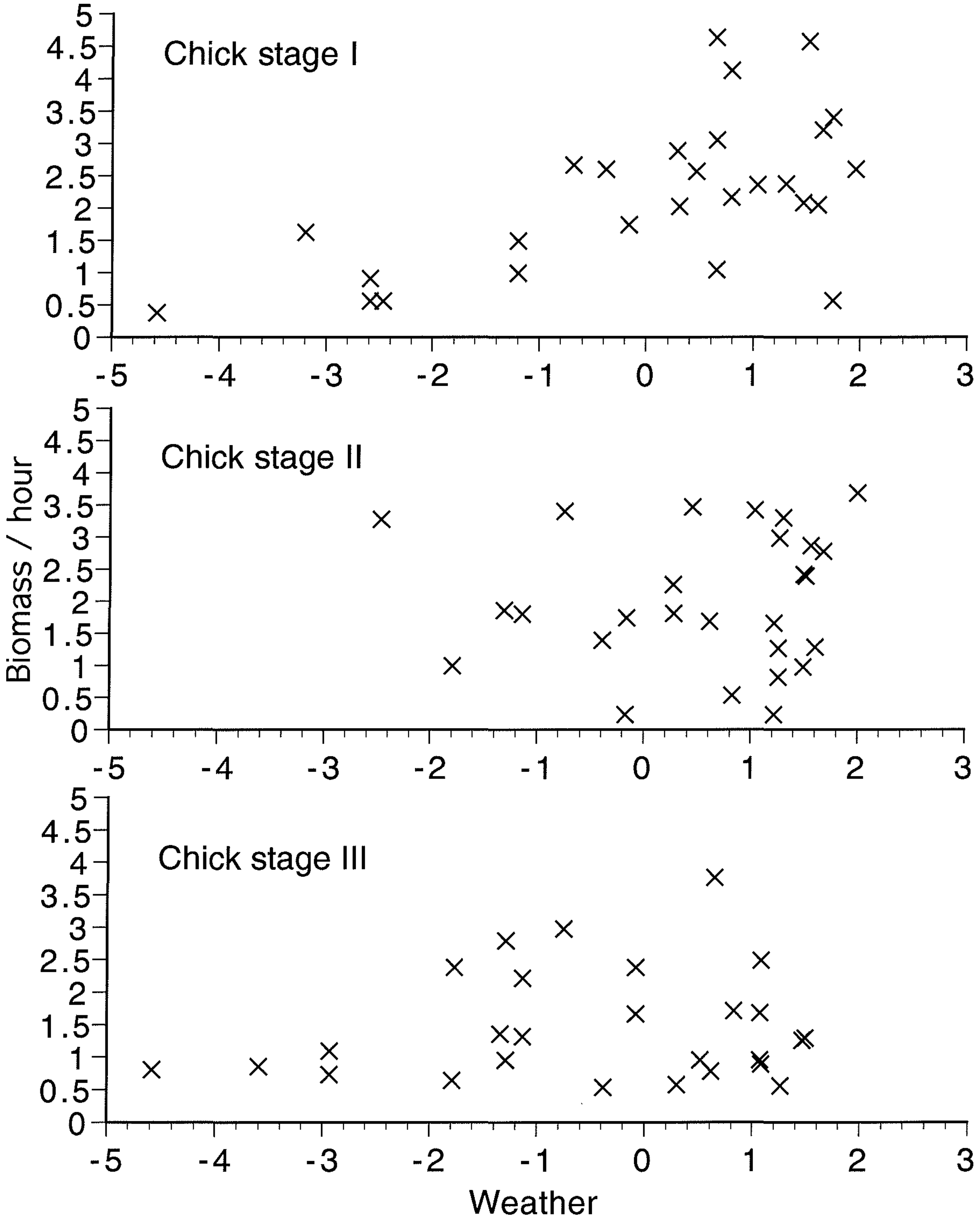

Chick stage I
Chick stage II
Chick stage III
Biomass / hour
Weather
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5
-5
-4
-3
-2
-1
0
1
2
3

Figure 18

Appendix 1: Provisioned biomass in one day

		Chick stage I										Chick stage II										Chick stage III										Total		Total
				Male				Female						Male				Female						Male				Female				Male	Female	
Brood code	1st / 2nd Brood	Brood size	Filmtime in min.	Molecrickets	Lepidoptera larvae	Others	Unidentified	Molecrickets	Lepidoptera larvae	Others	Unidentified	Brood size	Filmtime in min.	Molecrickets	Lepidoptera larvae	Others	Unidentified	Molecrickets	Lepidoptera larvae	Others	Unidentified	Brood size	Filmtime in min.	Molecrickets	Lepidoptera larvae	Others	Unidentified	Molecrickets	Lepidoptera larvae	Others	Unidentified			
A-11b	1	4	869	4.2	0.0	0.1	0.3	0.5	0.1	0.1	0.2	2	926	1.6	0.0	0.0	2.1	0.0	0.0	0.1	0.0	2	848	13.2	0.0	0.0	0.4	0.0	0.0	0.0	0.0	21.9	0.9	22.7
A-15pl	1	2	897	0.7	0.0	0.0	0.0	21.5	0.0	0.0	0.1	2	902	3.4	0.0	0.0	0.0	21.5	0.0	0.0	0.1	2	946	10.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.3	43.2	57.5
A-24pl	1	2	931	0.0	0.0	0.0	0.0	16.1	0.0	0.0	0.1	2	946	0.0	0.0	0.0	0.0	20.2	0.0	0.1	0.1	2	944	0.0	0.0	0.0	0.0	12.3	0.0	0.2	0.0	0.0	48.9	48.9
A-30b	1	7	919	39.5	0.0	0.0	0.4	0.0	0.0	0.0	0.0	7	922	52.2	0.2	0.0	1.0	0.0	0.0	0.0	0.0	7	896	11.6	0.1	0.3	0.1	0.0	0.0	0.0	0.0	105.3	0.0	105.3
A-35e	1	5	935	30.6	0.0	0.0	0.0	1.4	0.0	0.0	0.0	5	934	25.8	0.3	0.2	0.0	0.0	0.2	0.0	0.0	5	930	26.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	83.1	1.6	84.7
A-39b	1	5	947	35.8	0.1	0.1	0.2	11.2	0.1	0.0	0.8	5	947	45.2	0.0	0.1	0.1	0.0	0.1	0.0	0.0	1	905	12.5	0.1	0.7	0.2	0.0	0.0	0.0	0.0	95.0	12.1	107.1
A-42b	1	4	939	32.4	0.0	0.0	0.0	12.7	0.0	0.0	0.0	4	947	34.0	0.0	0.0	0.0	13.2	0.0	0.0	0.0	4	944	39.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	105.7	25.9	131.6
A-47b	2	2	945	9.3	0.2	0.0	0.1	4.8	0.0	0.0	0.0	2	941	12.9	0.1	0.0	0.0	0.0	0.0	0.0	0.0	1	256	2.4	0.0	0.1	0.0	0.0	0.0	0.0	0.0	25.1	4.8	29.9
A-52b	1	9	924	32.2	0.0	0.1	0.0	38.1	0.0	0.0	0.1	9	920	20.2	0.0	0.0	0.0	36.2	0.0	0.0	0.2	9	923	25.3	0.0	0.1	0.6	31.9	0.0	0.0	0.0	78.6	106.5	185.1
A-53pl	1	3	944	4.8	0.0	0.0	0.0	28.1	0.0	0.0	0.0	3	934	1.4	0.0	0.0	0.0	14.3	0.0	0.0	0.0	2	924	9.7	0.1	0.0	0.0	10.2	0.0	0.0	0.0	15.9	52.6	68.5
A-60b	1	3	570	1.0	1.7	0.2	0.5	0.0	1.0	0.7	0.2	3	931	0.7	1.6	0.0	2.9	0.0	0.0	0.0	0.2	3	589	0.7	3.7	0.2	7.2	0.5	4.3	0.6	10.2	20.4	17.7	38.1
A-68b	2*	5	933	23.8	0.1	0.2	0.0	15.9	0.3	0.2	0.0	5	930	31.7	0.2	0.2	0.0	20.9	0.2	0.0	0.0	5	922	18.1	1.3	0.4	0.1	14.1	2.0	0.2	0.6	76.1	54.3	130.4
A-93w	1	5	945	0.0	0.0	0.0	0.0	26.8	0.2	0.0	0.4	4	947	1.4	0.0	0.0	0.0	26.7	0.0	0.2	0.2	4	911	0.0	0.0	0.0	0.0	18.2	0.8	0.1	0.1	1.4	73.7	75.1
A-P	1	6	916	23.7	0.3	0.0	0.4	16.3	0.1	0.0	0.0	6	924	35.2	0.2	0.0	1.5	0.0	0.0	0.0	0.0	6	921	33.4	0.3	0.0	0.3	0.0	0.0	0.0	0.0	95.4	16.4	111.8
B-8n	1	6	932	30.9	0.2	0.0	0.0	18.6	0.2	0.0	0.1	6	939	11.1	0.9	0.1	0.2	13.4	0.1	1.4	0.1	6	913	14.1	1.6	0.0	1.1	6.8	0.9	0.0	1.6	60.1	43.1	103.2
B-10w	1	7	708	31.1	1.4	0.2	1.5	20.2	0.1	0.0	0.2	7	916	26.1	1.3	0.4	2.1	20.0	0.4	0.1	0.2	6	945	46.2	0.3	0.2	0.2	0.0	0.0	0.0	0.0	111.0	41.2	152.2
B-11e	1	3	946	0.5	0.0	0.0	0.0	15.0	0.2	0.0	0.0	1	947	0.0	0.0	0.0	0.0	3.4	0.0	0.1	0.3	1	947	7.5	0.2	0.0	1.1	0.0	0.0	0.0	0.0	9.3	19.0	28.3
B-15w	1	5	943	16.3	0.4	1.4	0.1	16.8	0.3	2.1	0.1	5	939	14.7	0.2	0.7	0.6	20.9	0.7	0.2	0.4	3	933	6.1	0.1	1.1	0.3	0.7	0.0	0.0	0.0	42.1	42.1	84.2
B-17w	1	6	916	21.4	0.2	0.0	0.4	16.1	0.2	0.0	1.0	6	926	42.7	0.1	0.0	0.2	0.0	0.0	0.0	0.0	6	934	37.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	102.0	17.3	119.4
B-35s	1	6	867	41.1	0.4	0.2	0.1	7.0	0.4	0.0	0.0	6	943	39.0	0.4	1.0	0.1	8.4	1.0	2.4	0.2	5	935	12.6	0.5	1.8	0.2	2.0	0.1	0.0	0.0	97.2	21.7	118.9
B-51e	1	7	732	24.8	0.0	0.1	0.1	25.3	0.1	0.0	0.0	7	939	24.7	0.0	0.0	0.0	26.5	0.0	0.2	0.1	7	921	1.8	0.1	0.1	0.0	5.6	3.7	0.2	1.7	51.6	63.4	115.0
B-51e	2	5	870	23.1	0.3	0.0	0.2	0.0	0.0	0.0	0.0	5	847	24.6	0.1	0.0	0.1	0.0	0.0	0.0	0.0	4	841	13.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	61.7	0.0	61.7
C-19w	1	4	928	21.7	0.1	0.6	0.0	3.2	1.4	0.1	4.3	4	932	18.1	1.0	0.5	1.0	3.9	0.5	0.1	9.4	4	923	12.5	2.6	0.0	0.7	1.0	1.4	0.0	2.1	58.7	27.4	86.1
C-37sw	1	6	898	17.7	0.0	0.0	0.0	14.3	0.0	0.0	0.5	6	933	1.4	0.0	0.0	0.0	20.2	0.0	0.0	0.0	4	928	6.6	0.0	0.0	0.0	12.0	1.4	0.2	0.8	25.6	49.4	75.0
C-45e	1	4	897	0.0	0.0	0.0	0.0	4.5	3.5	0.2	0.2	4	941	13.1	2.2	0.4	0.0	0.7	0.4	0.1	1.0	4	937	4.5	5.7	0.3	1.0	0.0	0.0	0.0	0.0	27.2	10.6	37.8
D-2	1	4	924	35.8	0.2	0.1	0.2	0.0	0.0	0.0	0.0	4	895	26.9	0.0	0.0	0.1	0.0	0.0	0.0	0.0	4	922	25.2	0.2	0.1	0.2	0.0	0.0	0.0	0.0	89.0	0.0	89.0
Pintset	1	5	935	8.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4	942	15.2	0.1	0.0	0.2	0.0	0.0	0.0	0.0	4	940	15.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	39.2	0.0	39.2

* second brood with different partner

Appendix 2: Number of provisioned prey items in one day

		Chick stage I										Chick stage II										Chick stage III										Total		Total
				Male				Female						Male				Female						Male				Female				Male	Female	
Brood code	1st / 2nd Brood	Brood size	Filmtime in min.	Molecrickets	Lepidoptera larvae	Others	Unidentified	Molecrickets	Lepidoptera larvae	Others	Unidentified	Brood size	Filmtime in min.	Molecrickets	Lepidoptera larvae	Others	Unidentified	Molecrickets	Lepidoptera larvae	Others	Unidentified	Brood size	Filmtime in min.	Molecrickets	Lepidoptera larvae	Others	Unidentified	Molecrickets	Lepidoptera larvae	Others	Unidentified			
A-11b	1	4	869	8	0	1	4	1	1	1	2	2	926	3	0	0	26	0	0	1	0	2	848	20	0	0	5	0	0	0	0	67	6	73
A-15pl	1	2	897	1	0	0	0	32	0	0	1	2	902	5	0	0	0	32	0	0	1	2	946	15	0	0	0	0	0	0	0	21	66	87
A-24pl	1	2	931	0	0	0	0	24	0	0	1	2	946	0	0	0	0	30	0	1	1	2	944	0	0	0	0	19	0	2	0	0	78	78
A-30b	1	7	919	60	0	0	5	0	0	0	0	7	922	80	2	0	13	0	0	0	0	7	896	18	1	4	1	0	0	0	0	184	0	184
A-35e	1	5	935	45	0	0	0	2	0	0	0	5	934	38	4	3	0	0	0	0	0	5	930	39	0	0	0	0	0	0	0	129	2	131
A-39b	1	5	947	60	1	1	3	19	1	0	10	5	947	71	0	1	1	0	0	0	0	1	905	20	1	9	2	0	0	0	0	170	30	200
A-42b	1	4	939	48	0	0	0	20	0	0	0	4	947	51	0	0	0	20	0	0	0	4	944	60	0	0	0	0	0	0	0	159	40	199
A-47b	2	2	945	14	3	0	1	7	0	0	0	2	941	19	1	0	0	0	0	0	0	1	256	4	0	1	0	0	0	0	0	43	7	50
A-52b	1	9	924	49	0	1	0	59	0	0	1	9	920	31	0	0	0	56	0	0	2	9	923	41	0	1	8	51	0	0	0	131	169	300
A-53pl	1	3	944	7	0	0	0	42	0	0	0	3	934	2	0	0	0	21	0	0	0	2	924	15	1	0	0	15	0	0	0	25	78	103
A-60b	1	3	570	2	86	2	6	0	52	9	2	3	931	1	157	0	36	0	81	0	2	3	589	2	46	3	90	1	54	7	128	431	336	767
A-68b	2*	5	933	35	1	2	0	24	4	3	0	5	930	47	2	3	0	31	2	0	0	5	922	27	16	5	1	21	25	2	7	139	119	258
A-93w	1	5	945	0	0	0	0	42	3	0	5	4	947	2	0	0	0	46	3	2	3	4	911	0	0	0	0	30	10	1	1	2	146	148
A-P	1	6	916	39	4	0	5	24	1	0	0	6	924	56	3	0	19	0	0	0	0	6	921	56	4	0	4	0	0	0	0	190	25	215
B-8n	1	6	932	47	2	0	0	28	2	0	1	6	939	17	11	1	3	21	26	17	1	6	913	21	20	0	14	11	11	0	20	136	138	274
B-10w	1	7	708	47	18	3	19	32	1	0	2	7	916	39	16	5	26	30	0	1	3	6	945	71	4	2	3	0	0	0	0	253	69	322
B-11e	1	3	946	1	0	0	0	24	3	0	0	1	947	0	0	0	0	5	0	1	4	1	947	12	3	0	14	0	0	0	0	30	37	67
B-15w	1	5	943	24	5	17	1	25	4	26	1	5	939	22	3	9	8	31	3	2	5	3	933	9	1	14	4	1	0	0	0	117	98	215
B-17w	1	6	916	35	2	0	5	26	3	0	12	6	926	66	1	0	3	0	0	0	0	6	934	57	0	0	1	0	0	0	0	170	41	211
B-35s	1	6	867	74	5	2	1	11	5	0	0	6	943	65	5	13	1	15	5	30	3	5	935	22	6	22	2	3	1	0	0	218	73	291
B-51e	1	7	732	41	0	1	1	45	1	0	0	7	939	40	0	0	0	48	24	2	1	7	921	3	1	1	0	11	46	3	21	88	202	290
B-51e	2	5	870	34	4	0	2	0	0	0	0	5	847	40	1	0	1	0	0	0	0	4	841	21	0	0	0	0	0	0	0	103	0	103
C-19w	1	4	928	33	1	8	0	5	18	1	54	4	932	28	12	6	12	6	17	1	118	4	923	19	33	0	9	2	17	0	26	161	265	426
C-37sw	1	6	898	27	0	0	0	22	0	0	6	6	933	2	0	0	0	30	3	0	0	4	928	10	0	0	0	19	18	2	10	39	110	149
C-45e	1	4	897	0	0	0	0	8	44	2	3	4	941	20	28	5	0	1	31	1	13	4	937	8	71	4	13	0	0	0	0	149	103	252
D-2	1	4	924	55	3	1	3	0	0	0	0	4	895	41	0	0	1	0	0	0	0	4	922	37	2	1	3	0	0	0	0	147	0	147
Pintset	1	5	935	13	0	0	0	0	0	0	0	4	942	23	1	0	2	0	0	0	0	4	940	22	0	0	0	0	0	0	0	61	0	61

* second brood with different partner