



universität
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MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

Frugivorous Noctuoidea in the Danube flood plain
east of Vienna – guild structure and reproductive biology

verfasst von / submitted by

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angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of
Master of Science (MSc)

Wien, 2017 / Vienna 2017

Studienkennzahl lt. Studienblatt /
degree programme code as it appears on
the student record sheet:

A 066 831

Studienrichtung lt. Studienblatt /
degree programme as it appears on
the student record sheet:

Masterstudium Zoologie

Betreut von / Supervisor:

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1 Acknowledgements

Thanks to the authorities at National Park Donauauen and the district government of Lower Austria for granting the permits to sample moths for this study. The staff of the park, especially Dr. Christian Baumgartner, also provided logistic support during field work. Various colleagues of the Division of Tropical Ecology & Animal Biodiversity helped with sampling and keeping moths.

2 Content

1	Acknowledgements	2
2	Content	3
3	Abstract	4
4	Introduction.....	5
5	Materials and methods	8
5.1	Moth sampling and identification	8
5.2	Biodiversity analysis.....	9
5.3	Fitness of adult moths in feeding trials	10
5.3.1	Longevity	11
5.3.2	Fecundity	12
6	Results	15
6.1	Biodiversity	15
6.1.1	Species richness.....	15
6.1.2	Species diversity	17
6.1.3	Species composition.....	19
6.2	Fitness.....	22
6.2.1	Longevity	22
6.2.2	Fecundity.....	26
6.2.3	3-way mixed model ANOVA to show influences of predictors.....	34
7	Discussion.....	46
7.1	Biodiversity	46
7.2	Fitness.....	48
8	Summary	55
9	References.....	56
10	List of tables	61
11	List of figures	65
12	Appendix.....	67

3 Abstract

The aim of this thesis was to investigate local biodiversity and reproductive biology of fruit feeding central European noctuid moths: firstly, if there are differences in species richness, diversity and composition between flooded and non-flooded areas of a riparian forest area in Eastern Austria, and secondly to determine possible fitness benefits that might accrue to these moths from feeding on rotting fruits. For tropical butterflies, it has been shown that feeding on rotting fruits, rather than nectar, is important to achieve high adult life expectancy and may have large positive effects on their reproductive output. Many European cold season noctuid moths also avidly feed on such resources.

Between September 2005 and November 2005, fruit-feeding noctuid moths were caught using sugar baits in flooded and non-flooded areas of the National Park Donau-Auen. This yielded a sample of 444 individuals from 34 species in 22 genera. Species richness showed no significant differences between flooded and non-flooded areas. Species composition showed significant phenological differences, but not between areas. Species diversity (measured as Shannon's exponential index) was higher in non-flooded habitats than in areas prone to annual inundation.

Field-caught individuals of 5 species were fed sucrose solution, sucrose solution enriched with vitamins, or banana slices plus sucrose solution, respectively, under identical greenhouse conditions. These moths represented three life cycle types (autumn species, adult hibernators, and early spring species). Benefits were expected to be especially pronounced in moths which overwinter as adults, in relation to their unusually long and thus nutrient-demanding imaginal lifespan (6–9 months). Indeed, adult food type significantly affected length of the oviposition period, mature oocytes remaining within the abdomen, potential fecundity and egg size. Some of these effects were contingent on species identity or life cycle type.

Keywords: Noctuoidea, adult nutrition, longevity, nectar, fruit feeding, species composition, flooded area, fecundity, feeding experiments

4 Introduction

Noctuoidea are the largest superfamily in the Lepidoptera. They are globally represented with over 70.000 described species (Lepidoptera Taxome Project, 2017). About 2.250 noctuid moth species and subspecies are found in Europe (Fauna Europaea, 2017), of which 685 species occur in Austria (Huemer and Tarmann, 2013). Moth communities typically vary among different habitats, thereby reflecting local ecological conditions, for example in varying types of forest or grassland (Truxa and Fiedler, 2012b; Greco *et al.*, 2016; Alonso-Rodríguez, Finegan and Fiedler, 2017). The “Donau-Auen National Park” is a protected riparian wetland area near a large city (Vienna) that harbours a species-rich fauna of nocturnal moths (Truxa, 2012). A long levee, the Hubertusdamm, separates the area into almost annually flooded and non-flooded regions, respectively. Accordingly, the forest in this reserve can be categorized in two main fractions: softwood riparian forest and hardwood riparian forest. The vegetation of softwood riparian forest is adapted to regular floods and includes White and Purple Willows, Alder, Silver Poplar and the rare Black Poplar (Gebhardt, Pohl and Vornam, 2001; Guilloy-Froget *et al.*, 2002). The hardwood riparian forest, in contrast, is located on the land side of the Hubertusdamm. It is seldom reached by flood waters and major tree species include elms, oaks, maples, or ash (Ward *et al.*, 2002). Multiple studies in recent years have confirmed that the fauna differs markedly between almost annually inundated areas and those fractions cut off from natural river dynamics (moths: (Truxa and Fiedler, 2012b); butterflies: (Fies *et al.*, 2016); grasshoppers: (Demetz *et al.*, 2013). One goal of my thesis was to determine whether communities of fruit-feeding noctuid moths in these rare flooded and non-flooded riparian areas also differ regarding species richness, species diversity or species composition.

Hypothesis:

There are significant differences in species richness, species diversity and species composition between flooded and non-flooded areas. In non-flooded areas, more species can be found than in flooded areas, since regular inundations act as mortality factor and thus as habitat filter for many moth species.

Income of nutrients during the adult stage frequently has important fitness consequences among representatives of the order Lepidoptera (Tammaru and Haukioja, 1996). Carbohydrates and amino acids taken up have shown to increase longevity as well as fecundity in a range of butterfly and moth species (Murphy, Launer and Ehrlich, 1983; Leather, 1984; Adler, 1989; Hill, 1989; Leahy and Andow, 1994). For income breeders among the Lepidoptera, floral nectar and similar carbohydrate solutions comprise the principal source of adult nutrients (Mevi-Schütz and Erhardt, 2005; Boggs, 2009; Javoiš, Molleman and Tammaru, 2011), and the lepidopteran proboscis is a versatile tool to especially utilize that type of resource (Krenn, Zulka and Gatschnegg, 2001; Krenn, 2010; Monaenkova *et al.*, 2011). Supplementing nectar carbohydrates with amino acids from pollen even results in record life expectancies (of 6–9 active months), but seems to be confined to a small fraction of Neotropical *Heliconius* butterfly species (Gilbert, 1972; Dunlap-Pianka, Boggs and Gilbert, 1977; O'Brien, Boggs and Fogel, 2003). In more recent years it has been shown that butterflies fed on rotting fruits rather than floral nectar may achieve particular fitness benefits from that mode of resource use (Braby and Jones, 1995; Beck, 2008; Molleman *et al.*, 2008, 2009). In particular, fruit-feeding in butterflies seems to be strongly linked to high physiological longevity (Molleman *et al.*, 2007).

Bearing this in mind, further experimental investigation whether similar benefits in terms of life expectancy and fitness accrue to nocturnal moths which also feed on rotting fruits is needed. In central Europe, few moths are specialist fruit feeders, but a large number of species are known to facultatively utilize such resources whenever available (Ebert, 1997). This behaviour has been exploited since over a century by entomologists to sample moth species using fruit baits (Süssenbach and Fiedler, 1999). In central Europe, the attitude of feeding on rotting fruits is especially prevalent amongst Noctuidae and Erebidae species whose adult flight period covers the cold season, i.e. from autumn to early spring. Many noctuid and some erebid species that fly between September and April may even be more effectively sampled at such fruit baits rather than by light-trapping. This fondness for rotting fruits might thus indicate that moth species which use this type of resource gain fitness advantages over mere nectar feeding. Mechanistic reasons for such benefits could be routed in a more balanced complement of nutrients in fruits as opposed to nectar. In particular, one may expect fruits to contain more vitamins and/or amino acids than standard floral nectars that are notoriously

dominated by a few mono- and disaccharides as nutrient compounds (González-Teuber and Heil, 2009; Heil, 2011).

In central Europe, cold season noctuoid species can be divided into three life cycle types. Autumn species emerge from the pupa between late August and October, and mate and lay their eggs until the onset of true winter weather (usually in November). Then, all adults die and only eggs hibernate. Typical representatives are genera such as *Agrochola*, *Allophyes*, *Mniotype*, or *Tiliacea*. Adult hibernators also emerge in autumn, but mating and egg-laying only take place in early spring, after hibernation. These moths frequently resume flight activity during spells of warm weather in winter, i.e. they show a dormancy behaviour that is equivalent to a quiescence syndrome rather than true diapause (Müller, 1992; Ebert, 1997). During activity periods in winter rotting fruits are usually the only available nutrient sources, since no moth-pollinated plants are in flower. Adult moths of these hibernator species survive through to April or May, i.e. reach life expectancies of 6–9 months. Major representatives are *Eupsilia*, *Conistra* and *Lithophane*. Early spring species hibernate in the pupal stage and emerge between February and April, depending on the onset of warm weather. *Orthosia* and *Anorthoa* are the most prevalent genera in Europe. These moths visit early flowering plants (such as *Salix* spp.), but are also frequently attracted to rotting fruits or fruit baits.

Representatives of all these three life cycle types were sampled from wild populations in the National Park Donau-Auen by attraction to fruit baits and were then subjected to a controlled feeding experiment in the laboratory.

Hypothesis:

When given access to a fruit resource of standardized quality, cold season noctuoid moths will profit by surviving for longer periods and enhancing their fecundity in laying more or/and larger eggs than individuals that are offered sucrose solutions only.

5 Materials and methods

5.1 Moth sampling and identification

Moths were attracted to baits composed of red wine and sucrose (1:1 weight relation). This bait mixture has proven to be highly attractive in many previous studies (Süssenbach and Fiedler, 1999). Pieces of cotton cloth (approx. 5 × 10 cm in size) were soaked with this bait and exposed 1.3–1.7 m above ground on shrubs or trees at forest edges. In addition, some moths used for experiments were also attracted to a light source (2 x 15 W tubes: F15W/350BL-T8 UVA & F15W/BL B-T8, Sylvania). Moths were sampled in various habitats in the Danube flood plain, about 30 km east of Vienna (near the village Orth at the Danube in the Danube National Park), Austria. Sampling sites were chosen at random to attract a representative range of cold season noctuid moths from flooded and non-flooded areas. There were 35 sampling evenings in the period from September 15th to November 15th in the year 2005 and 9 evenings from March 30th to May 2nd in 2006. In 2005 flooded and non-flooded areas were sampled alternately, whereas in 2006 only non-flooded areas were sampled, because of the inaccessibility of the flooded areas in spring. On the first 19 sampling evenings baiting was done at only one site, afterwards baits were exposed on two sampling sites in parallel, with 100 baits per site. Baits were exposed around sunset and moths were taken from the baits every 30 min for a period of 3–4 hours per evening. Sampling only took place when ambient temperature was above 0°C and when there was no rain.

Altogether, 695 moth-individuals belonging to the superfamily Noctuoidea were sampled, representing 53 species in 33 genera. 661 individuals (representing 43 species in 25 genera) were attracted to baits and 34 individuals (representing 20 species in 16 genera) to the light source (see Appendix).

Moths were identified to species using the following sources: (Skou, 1991; Ebert, 1997; Fajcik and Slamka, 1998; Nowacki, 1998). Nomenclature follows the Fauna Europaea project (Fauna Europaea, 2017).

5.2 Biodiversity analysis

Only moths which were captured at red wine / sucrose baits in 2005 were used for this analysis.

Total expected species richness in flooded and non-flooded areas, respectively, was estimated using the package EstimateS (Colwell and Elsensohn, 2014). Estimators were chosen according to the procedure suggested by Brose and Martinez (2004). The chosen estimators were S(est) (expected number of species in t pooled samples, given the reference sample (analytical)), ACE (abundance-based coverage estimator of species richness (mean among runs)) and Jack2 (second-order Jackknife richness estimator (mean among runs)). 100 randomisations were used to obtain these estimators.

Species diversity of fruit-feeding moths in the whole area and separately in flooded and non-flooded areas was also analysed using EstimateS. Estimators were chosen according to Fiedler and Truxa (2012). The chosen estimators were Fisher's alpha which is a parametric index of diversity that assumes that the abundance of species follows a log-series distribution, and Shannon's exponential measure which shows units of equivalent, equally abundant species. 100 randomisations were used for estimators.

Species composition was analysed through non-metric multidimensional scaling (NMDS) using Primer 5.0 (Clarke and Gorley, 2001), based on a Bray-Curtis similarity matrix calculated from square root transformed data to account for great variation of individuals caught per species. Results were visualized by an unconstrained ordination plot. To explore possible community shifts due to phenology, moth samples from flooded and non-flooded habitats were further split into two partitions, viz. early autumn from 15th of September to 15th of October 2005, and late autumn from 16th of October to 15th of November 2005. Samples with less than 5 moth individuals were excluded from data analysis. The significance of habitat and season effects was assessed by two-way ANOSIM (Analysis of Similarities) with 999 permutations of. The factor groups for analysis were habitat and season.

To further assess which moth species were responsible for the observed faunal dissimilarities relative to habitat and season, a SIMPER (Similarity Percentages) analysis was performed, again using square root transformed data. The cut-off for low contributions was set to 90%. Species which contributed less than 3% to the dissimilarities were excluded.

5.3 Fitness of adult moths in feeding trials

In total 5 species that were sufficiently common in the samples (two autumn species: *Agrochola circumcellaris*, *Allophytes oxyacanthae*; two hibernating species: *Conistra vaccinii*, *Eupsilia transversa*; one spring species: *Anorthoa munda*) were chosen for final analysis. Of these, *Conistra vaccinii* and *Eupsilia transversa* were further separated into two groups, viz. HL and HF (HL – hibernated in laboratory, i.e. collected before hibernation; HF – hibernated in field, i.e. collected after hibernation). This makes up a total of 7 experimental groups.

Right after capture, moths were put in glasses (50ml, lined with a piece of filter paper, with air holes in the plastic lid), transferred into a cool and dark bag, kept in a refrigerator overnight and transported into the laboratory on the next day. In the morning after capture, each moth was identified to species and placed into an individually marked rearing jar (transparent 500ml plastic cups) with a mosquito gauze on top. The bottom of each jar was lined with moist filter paper to maintain sufficient humidity. All moths had access to water ad libitum and to cut twigs of their larval host plants to induce them to deposit their eggs. The jars were positioned in three groups in a greenhouse on the roof of a university building. Temperature varied, with average temperature during daytime being 20°C (maximum: 26°C) and 12°C (minimum: 7°C) during the night.

Moths were randomly assigned to one of three feeding treatments:

- (1) Banana: sucrose solution (150 g sucrose in 1000 ml distilled water) supplemented with slices of banana.
- (2) Vitamins: sucrose solution (150 g sucrose in 1000 ml distilled water), enriched with 7.5 g modified Vanderzant vitamin mixture (vitamin mix for insects no. 300100, Dyets Inc., for composition see: <http://dyets.com/vitamin-mixes>; last accessed: 16 Mar 2017).
- (3) Sugar: only sucrose solution (150 g sucrose in 1000 ml distilled water)

Nutrient solutions were offered in 1 ml tubes, while banana slices were placed on top of the gauze lid. Banana was chosen because this fruit can be obtained in standardized quality all the year round. Fruit slices were kept moist by spraying them with water regularly. Sugar solutions and banana slices were replaced every 2–6 days, as required.

Moths were inspected every 1–2 days, and it was noted if they were still alive. It was also recorded whether they had laid eggs or not. Eggs were collected every 1–2 days and conserved for further data acquisition. All eggs were counted and measured in blocks up to 50 eggs per day with the circumference of the eggs as parameter, using the program Cell-ID (Gordon *et al.*, 2007). Each individual moth was followed until its death. After death wingspan of some moths was measured as a proxy for body size. Moths were dissected to confirm if they were fertilized or not and remaining eggs in the abdomen were counted.

5.3.1 Longevity

The time span between day of capture and death in captivity was taken as measure of the moth's minimum physiological life expectancy (the time since eclosion from the pupa was of course unknown in field-caught moths). Only moth individuals that lived at least 5 days in captivity were included. If moths died earlier in the laboratory, this was considered as an artefact of the transport and maintenance conditions. For sample sizes see Table 1.

Table 1 Sample sizes for longevity experiment. A – autumn species; HF – hibernated in field; HL – hibernated in laboratory; S – spring species.

Species	Banana			Vitamins			Sugar			Total
	Female	Male	Total	Female	Male	Total	Female	Male	Total	Total
<i>Agrochola circumcellaris</i> A	1	38	39	4	34	38	8	31	39	116
<i>Allophytes oxyacanthae</i> A	25	13	38	20	19	39	26	12	38	115
<i>Conistra vaccinii</i> HF	17	11	28	22	7	29	22	6	28	85
<i>Conistra vaccinii</i> HL	6	1	7	5	3	8	5	4	9	24
<i>Eupsilia transversa</i> HF	14	8	22	13	7	20	18	4	22	64
<i>Eupsilia transversa</i> HL	3	5	8	8	1	9	5	4	9	26
<i>Anorthoa munda</i> S	3	3	6	2	5	7	2	5	7	20
Total	69	79	149	74	76	150	86	66	152	450

To assess possible differences in longevity among different sexes t-tests were performed. For further investigation of significant results ANOVAs with Welch correction were performed. As no significant differences in longevity with varying food treatment on males and females could be found, sexes were put together for continuing research. To explore differences of food treatment per species Welch corrected ANOVAs were performed.

5.3.2 Fecundity

Fecundity was assessed for 187 female individuals. Table 2 shows the exact number of moths per treatment and their food source. Only female moths that laid eggs and lived more than 5 days after transfer into the laboratory were included (HL – hibernated in lab, HF – hibernated in field). In *Agrochola* and *Anorthoa* not enough females laid eggs, so these species had to be excluded from further data analysis.

Table 2 Sample sizes for fecundity assessment. A – autumn species; HF – hibernated in field; HL – hibernated in laboratory; S – spring species.

Species	Banana	Vitamins	Sugar	Total
<i>Allophytes oxyacanthae</i> A	24	19	26	69
<i>Conistra vaccinii</i> HF	13	17	17	47
<i>Conistra vaccinii</i> HL	3	5	3	11
<i>Eupsilia transversa</i> HF	14	13	17	45
<i>Eupsilia transversa</i> HL	3	8	5	16
Total	57	68	62	188

To determine the global impact of food on fecundity, oviposition period (time span between the first to the last egg laying day), potential fecundity (total number of eggs), remaining eggs within the abdomen and realised fecundity (laid eggs), ANOVAs were performed (moths had an unaccounted oviposition period and number of eggs laid in the field prior to capture).

For egg size analysis one individual of *Conistra vaccinii* HL had to be discarded because of erratic egg sizes over the course of its lifetime.

Table 3 Sample sizes for egg size assessment – *Conistra vaccinii* HL

Species	Banana	Vitamins	Sugar	Total
<i>Conistra vaccinii</i> HL	3	5	2	10

For the research on differences among egg-size a sample of eggs on each oviposition day was measured and summarised to a mean for each individual. An ANOVA on the mean egg surface size was performed to show potential differences among eggs laid by one single individual. A Games-Howell post hoc Test was performed to show further differences on the significant results.

A 3-way mixed model ANOVA was used for two hibernating species *Conistra vaccinii* and *Eupsilia transversa* as they could be caught in sufficient numbers both as HL and HF, leading to a total of 119 individuals (see Table 4). Due to hibernation in the adult stage these two species were the ones which lived longest. Accordingly, food treatment effects were expected to be strongest here. The individuals considered for analysis all lived for at least 5 days in the laboratory.

Response variables in the analysis of the experiments on reproductive traits were duration of the oviposition period, realised fecundity, oviposition rate (laid eggs per oviposition period), mature oocytes remaining within the abdomen after a female's death, potential fecundity (viz. sum of realised fecundity plus oocytes remaining), and mean egg size.

Table 4 Sample sizes for the 3-way mixed model ANOVA comparison in two noctuid species that hibernate as adults.

Species and Group	Banana	Vitamins	Sugar	Total
<i>Conistra vaccinii</i>	16	22	20	58
HF	13	17	17	47
HL	3	5	3	11
<i>Eupsilia transversa</i>	17	21	22	61
HF	14	13	17	45
HL	3	8	5	16
Total	33	43	42	119

As before, for egg size analysis one individual of *Conistra vaccinii* HL fed with sugar had to be discarded because of erratic egg sizes.

Table 5 shows the factors and their interactions considered (with species as a random factor, and food and life cycle as fixed factors).

Table 5 Factors and their interactions included in ANOVA model with species as random factor and food and life cycle as fixed factors

Species
Life cycle
Food
Species x Life cycle
Species x Food
Life cycle x Food
Species x Life cycle x Food

For data management and analysis, Microsoft Excel® in the release 2016 and SPSS in the release 24 (IBM Corp.) was used. In all calculations, a confidence interval of 95% was used.

6 Results

6.1 Biodiversity

6.1.1 Species richness

Table 6 lists all noctuid and erebid moth species which were captured at red wine and sucrose baits in the autumn of 2005, separately for non-flooded and flooded habitats.

Table 6 Noctuid and erebid moths captured in autumn 2005 near Orth/Donau according to time and location of capture.

Species	Non-flooded		Flooded	
	Early autumn	Late autumn	Early autumn	Late autumn
<i>Abrostola triplasia</i>	2		2	
<i>Agrochola (Anchoscelis) helvola</i>			2	
<i>Agrochola (Anchoscelis) litura</i>			1	
<i>Agrochola (Anchoscelis) nitida</i>			1	
<i>Agrochola (Leptologia) lota</i>		2		
<i>Agrochola (Leptologia) macilenta</i>	1	10		1
<i>Agrochola (Sunira) circellaris</i>	4	61	12	46
<i>Agrotis ipsilon</i>	5			1
<i>Allophytes oxyacanthae</i>	25	39	28	30
<i>Ammoconia caecimacula</i>	3	2		
<i>Amphipyra (Amphipyra) berbera</i>	1			
<i>Amphipyra (Amphipyra) livida</i>	1		1	
<i>Amphipyra (Amphipyra) tragopoginis</i>			1	1
<i>Autographa gamma</i>	23	1	15	2
<i>Catocala nupta</i>	2		1	
<i>Conistra (Conistra) rubiginosa</i>		13		6
<i>Conistra (Conistra) vaccinii</i>	13	5	4	1
<i>Conistra (Dasycampa) erythrocephala</i>		1		1
<i>Eupsilia transversa</i>	2	16	4	8
<i>Hypena rostralis</i>				1
<i>Lacanobia (Diataraxia) oleracea</i>	2			
<i>Lithophane (Lithophane) ornitopus</i>		1	1	
<i>Meganephria bimaculosa</i>	1			
<i>Mniotype satura</i>	1			
<i>Mythimna (Mythimna) conigera</i>	1			
<i>Mythimna (Mythimna) vitellina</i>	2			1
<i>Phlogophora meticulosa</i>	1		1	
<i>Rhizedra lutosa</i>		1		
<i>Scoliopteryx libatrix</i>	4	2	4	9
<i>Tiliacea aurago</i>	1			
<i>Tiliacea citrargo</i>	1			
<i>Xestia (Megasema) c-nigrum</i>	1			
<i>Xestia (Xestia) castanea</i>	1			
<i>Xylena (Xylena) exoleta</i>	1	3	1	1
	99	157	79	109
		256		188
				444

Altogether 34 species were found at the baits: 29 species at sampling sites in the non-flooded area and 22 species in near-annually flooded area. In total, these amounted to 444 individuals, 256 at non-flooded sites and 188 at flooded sites.

A species accumulation curve indicates that species richness of the two areas did not differ significantly, since confidence intervals of the accumulation curves overlap (Figure 1). Yet, observed species richness was slightly larger if summed across sites in the non-flooded part. At the flooded sites, not on every sample night moths were caught, so the non-flooded areas show more sample nights.

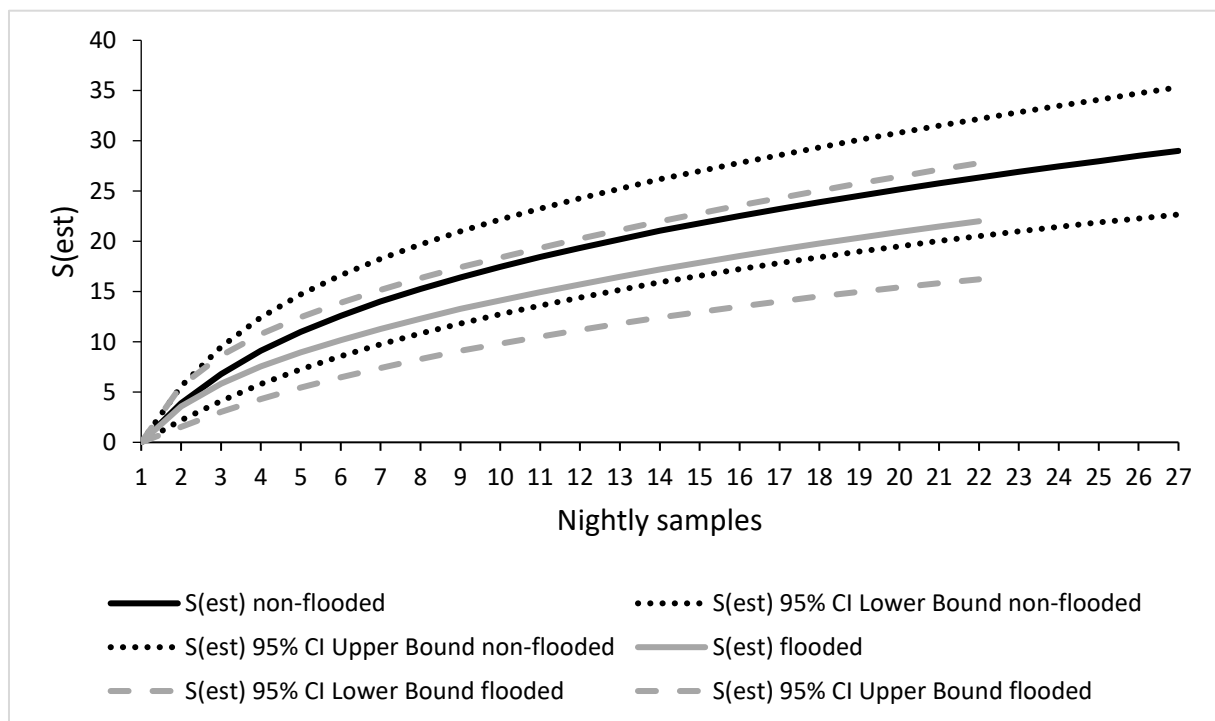


Figure 1 Randomized sample-based species accumulation curves (with 95% confidence intervals) for noctuid and erebid moths attracted to fruit baits in the two areas in the National Park Donau-Auen.

Table 7 shows the estimates of total species richness in both sampling areas in comparison with observed richness. According to these estimates, almost 50 noctuoid moths could have been expected to visit fruit baits in the non-flooded areas, compared to about 40–45 in the flooded areas. Fruit-feeding moths were under sampled in both parts of the sampling region, but in flooded parts completeness was slightly higher (64–74%, depending on estimator) than in non-flooded ones (58–59%).

Table 7 Estimates of total species richness of fruit-feeding noctuid and erebid moths in autumn 2005, according to the two flood regimes at sampling sites, in the National Park Donau-Auen. ACE – Abundance-based coverage estimator; Jack2 – second-order Jackknife estimator. 'Completeness' indicates the ratio of observed to expected species richness.

	non-flooded	completeness	flooded	completeness
Observed	29.00		22.00	
ACE	49.83 (43.72...55.94)	58%	45.55 (39.04...52.06)	64%
Jack2	49.07 (43.06...55.08)	59%	38.99 (33.42...44.56)	74%

6.1.2 Species diversity

Both indices of species diversity suggest that fruit-feeding moth diversity was slightly higher in the non-flooded than the flooded area (Table 8).

Table 8 Species diversity measures (\pm 95% confidence intervals) for fruit-feeding noctuid and erebid moths, segregated for sample sites in the two flood regimes.

	non-flooded	flooded
Fisher's alpha	8.41 (\pm 1.03)	6.46 (\pm 0.92)
Shannon's Exponential Diversity	10.53 (\pm 1.29)	7.46 (\pm 1.07)

If values of Fisher's alpha are explored as a function of sample number (Figure 2), it is obvious that no asymptote was reached in either inundation regime, but values for moths in flood-prone areas were consistently lower than for moths from non-flooded habitats. The first samples were cut out, since erratic estimator values at these low sample sizes would have distorted the graph.

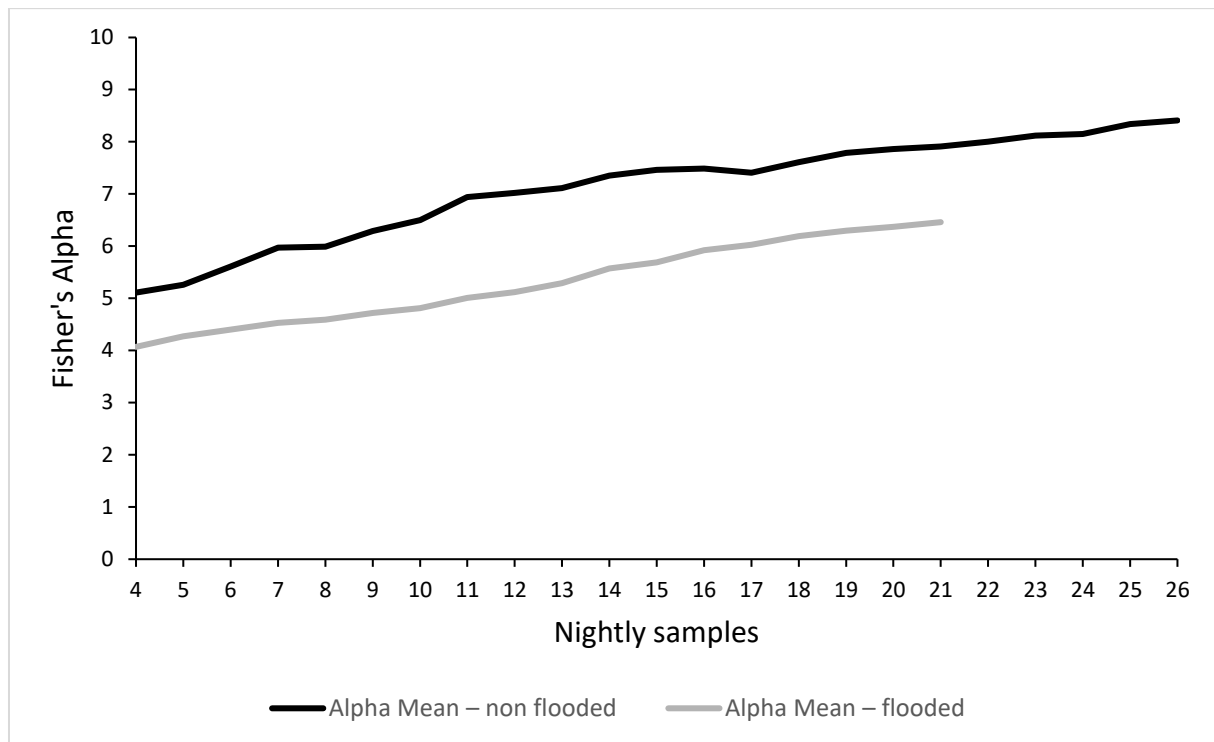


Figure 2 Species diversity of fruit-feeding moths, expressed as cumulative values of Fisher's alpha, as a function of the number of nightly samples.

In contrast, Shannon's exponential diversity revealed an almost asymptotic behaviour, especially in the flooded area. Since the 95% confidence intervals did not overlap, differences between flooded and non-flooded habitats can be deemed as statistically significant here. Again, the first few samples were cut out, because the erratic estimator values would have distorted the graph (Figure 3).

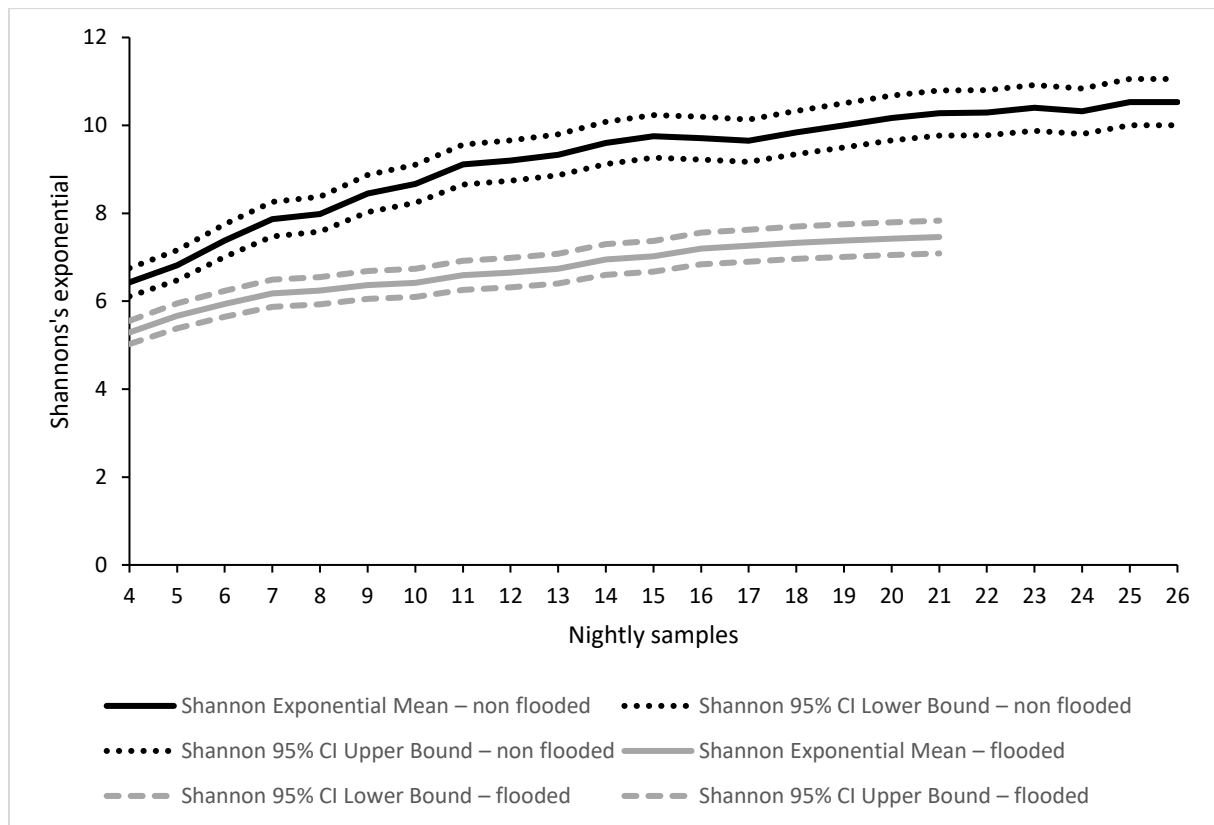


Figure 3 Species diversity of fruit-feeding moths, expressed as cumulative values of Shannon's exponential index, as a function of the number of nightly samples.

6.1.3 Species composition

In the non-flooded area 10 sites were sampled in early and 8 sites in late autumn. In the flooded area, 4 sites in early and 8 sites in late autumn (see Appendix for further details) were sampled. Species composition of these samples differed between early and late autumn, whereas no segregation was apparent between sites under different flood regimes (see Table 9).

Table 9 Results of a two-way ANOSIM on moth species composition (expressed as Bray-Curtis similarities; 999 permutations). Significant results printed in **bold**.

	Sampling time	Flood regime
<i>R</i>	0.316	0.316
<i>p</i>	0.010	0.288

The non-metric multidimensional scaling (NMDS) plot (Figure 4) confirms that there were differences in species composition of fruit-feeding moths relative to the progression of the season, but not in relation to the flood regimes of the sampling sites.

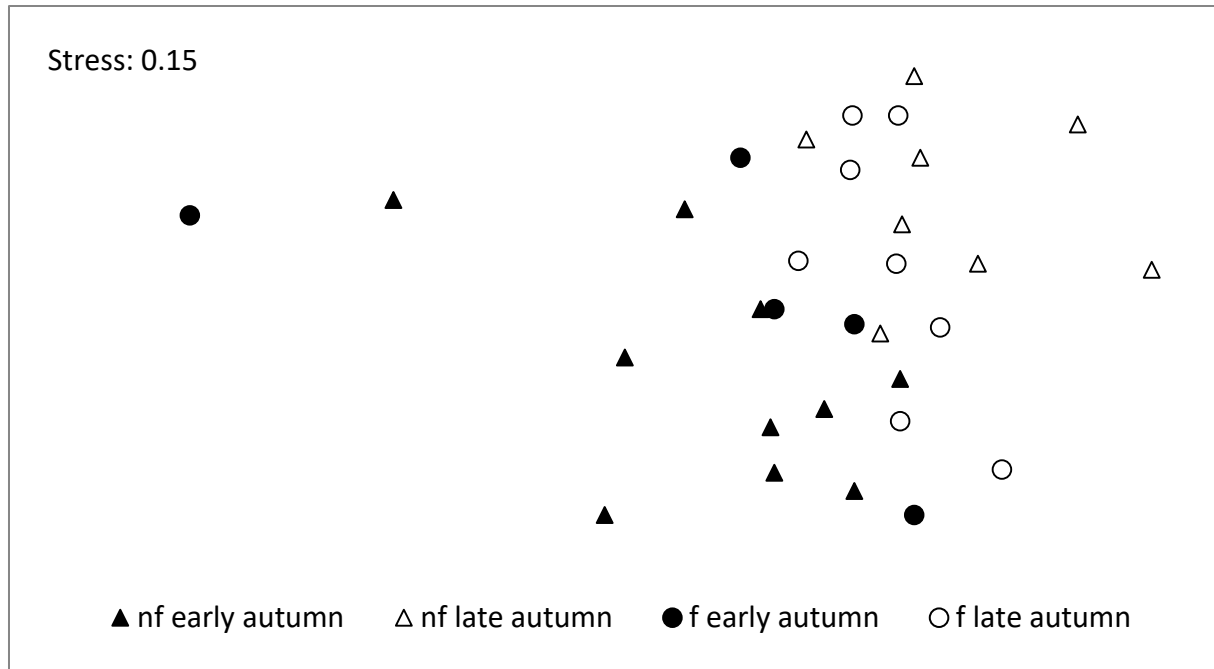


Figure 4 Non-metric multidimensional scaling (NMDS) plot of samples of fruit-feeding noctuid and erebid moth species in autumn 2005 in the National Park Donau-Auen. Filled symbols – early autumn; empty symbols – late autumn. Circles – flood-prone sites; triangles – non-flooded sites. Early samples (to the left) are segregated from late ones (to the right).

A SIMPER analysis revealed which species are mostly responsible for the phenological shift in species composition of fruit-feeding moths. Nine moth species contributed more than 2% each to overall dissimilarity. Taken together these accounted for 78% of the observed dissimilarity between the two phenological groups of samples (Table 10). *A. circellaris*, *A. oxyacanthae*, *E. transversa*, *A. macilenta* and *C. rubiginosa* were more prevalent in late autumn samples, whereas *A. gamma*, *A. triplasia* and *C. vaccinii* were more frequent in early autumn samples.

Table 10 Results of a SIMPER analysis: Contribution of the 9 most diagnostic noctuid and erebid species to phenological dissimilarity of fruit-feeding moth species assemblages. Reported are mean numbers per nightly samples, mean and standard deviation of contribution to dissimilarity between groups; and individual as well as cumulative contribution of the 9 species. SD – standard deviation; EA – early autumn samples; LA – late autumn samples.

Average dissimilarity: 72.45%						
Species	Mean number EA	Mean number LA	Mean dissimi- larity	SD dissimi- larity	Contribu- tion (%)	Cumulative (%)
<i>Agrochola circellaris</i>	1.00	6.50	12.79	1.25	17.65	17.65
<i>Allophyes oxyacanthae</i>	3.07	4.06	9.62	1.19	13.28	30.93
<i>Autographa gamma</i>	2.07	0.19	8.31	1.30	11.47	42.39
<i>Eupsilia transversa</i>	0.33	1.31	6.74	0.96	9.30	51.70
<i>Conistra vaccinii</i>	1.13	0.38	4.73	0.84	6.52	58.22
<i>Conistra rubiginosa</i>	0.00	0.94	4.70	0.58	6.48	64.70
<i>Scoliopteryx libatrix</i>	0.53	0.63	4.43	0.88	6.12	70.82
<i>Agrochola macilenta</i>	0.07	0.69	3.05	0.66	4.22	75.04
<i>Abrostola triplasia</i>	0.27	0.00	2.19	0.51	3.03	78.07

6.2 Fitness

Results are split into a first section aiming to detect effects of adult resource access in univariate tests, separately for all species (or hibernation types within species), and a second section based on a 3-way mixed model ANOVA that looked in detail only at the two adult hibernators, viz. *Conistra vaccinii* and *Eupsilia transversa*.

6.2.1 Longevity

Sex differences in longevity

Only in two cases (*Agrochola circumcellaris*; *Eupsilia transversa* collected after hibernation) females lived significantly longer in captivity than males (Table 11). In all other groups under study, life expectancy was not contingent on sex (Table 11, Table 12).

Table 11 Outcome of t-tests with Welsh correction for sex differences in longevity of captive moths.

Species	Life cycle	t	p
<i>Agrochola circumcellaris</i>	A	-2.745	0.017
<i>Allophyes oxyacanthae</i>	A	0.874	0.385
<i>Anorthoa munda</i>	S	1.323	0.206
<i>Conistra vaccinii</i>	HF	-1.367	0.179
	HL	0.509	0.618
<i>Eupsilia transversa</i>	HF	-4.497	<0.0001
	HL	-0.862	0.406

Table 12 Longevity (in days) of moths in the feeding experiment. Given are means and standard deviations (SD). Cases with significant sex difference are printed in bold.

Species	Life cycle	Sex	N	Mean (SD)
<i>Agrochola circellaris</i>	A	Female	13	31.38 (19.87)
		Male	103	16.05 (9.26)
<i>Allophyes oxyacanthae</i>	A	Female	71	10.93 (3.62)
		Male	44	11.61 (4.34)
<i>Anorthoa munda</i>	S	Female	7	11.00 (3.00)
		Male	13	13.00 (3.61)
<i>Conistra vaccinii</i>	HF	Female	61	18.23 (4.00)
		Male	24	16.83 (4.33)
<i>Conistra vaccinii</i>	HL	Female	16	138.19 (49.56)
		Male	8	148.50 (45.38)
<i>Eupsilia transversa</i>	HF	Female	45	19.42 (5.55)
		Male	19	14.16 (3.61)
<i>Eupsilia transversa</i>	HL	Female	16	135.38 (19.01)
		Male	10	123.70 (40.11)

Looking into detail among the two species that showed significant longevity differences among sexes shows only one significant difference on varying food treatments using a t-test with Welch correction (Table 13, Table 14)

Table 13 t-test on different food treatment on male and female individuals of species with significant sex differences on longevity with Welch correction.

Species	Life cycle	t	p
<i>Agrochola circellaris</i> A	Banana	0.286	0.776
	Vitamins	-2.041	0.073
	Sugar	-1.617	0.203
<i>Eupsilia transversa</i> HF	Banana	-1.058	0.303
	Vitamins	-5.105	<0.0001
	Sugar	-3.197	0.005

Table 14 Descriptive figures on different food treatment on male and female individuals of species with significant sex differences on longevity with Welch correction.

Species	Sex	Banana	Vitamins	Sugar
<i>Agrochola circumcellaris</i> A	Female	19.00 (0.00)	37.50 (27.05)	29.88 (17.82)
	Male	16.24 (9.53)	15.56 (6.65)	16.35 (11.42)
<i>Eupsilia transversa</i> HF	Female	17.86 (5.33)	21.08 (6.47)	19.44 (4.93)
	Male	15.88 (3.44)	13.86 (3.63)	11.25 (2.22)

So, for further longevity investigation female and male moths of the same species were put together into one group.

Overall longevity

Considering female and male individuals together the Welch corrected ANOVA on different food treatment shows only significant differences at *Conistra* HF regarding longevity.

Table 15 Welch corrected ANOVA on longevity with different food treatment per species.

Species	Banana	Vitamins	Sugar	F	p
<i>Agrochola circumcellaris</i> A	16.31 (9.42)	17.87 (12.05)	19.13 (13.86)	0.589	0.558
<i>Allophytes oxyacanthae</i> A	11.03 (3.39)	11.74 (5.00)	10.79 (3.05)	0.509	0.603
<i>Anorthoa munda</i> S	11.17 (2.86)	12.29 (3.86)	13.29 (3.73)	0.644	0.543
<i>Conistra vaccinii</i> HF	15.00 (3.03)	19.62 (3.90)	18.82 (3.87)	15.159	<0.0001
<i>Conistra vaccinii</i> HL	108.71 (45.29)	157.63 (21.31)	153.00 (56.51)	3.247	0.076
<i>Eupsilia transversa</i> HF	17.14 (4.74)	18.55 (6.57)	17.95 (5.55)	0.340	0.714
<i>Eupsilia transversa</i> HL	117.50 (39.70)	134.78 (23.36)	138.89 (19.98)	0.905	0.427

Most noctuid moths survived for about 2–3 weeks in captivity (Figure 5, Figure 6). The only notable exception were individuals of the two species *Eupsilia transversa* and *Conistra vaccinii*, which lived for 9–198 days if hibernated in the laboratory. No major effects of adult food resources on moth longevity were observed. Individuals of the species *Agrochola*, *Allophytes*, *Anorthoa* and *Eupsilia* showed no significant differences in longevity within the species when they were fed with different food. Whereas individuals of *Conistra* show significant differences, but only when they hibernated in the field (Table 15). Banana fed *Conistra* moths seem to live shortest and vitamin fed longest.

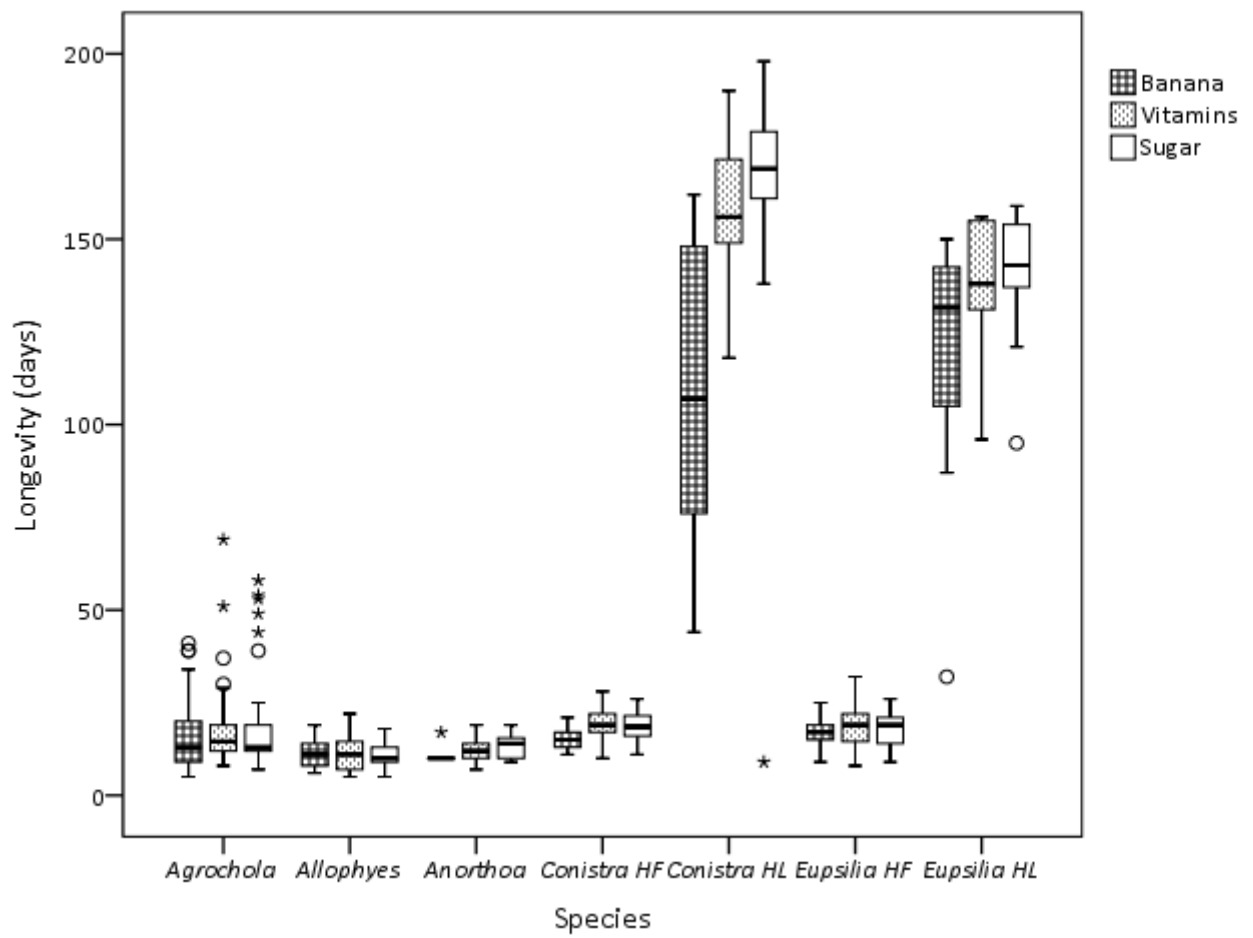


Figure 5 Box plot of moth longevity in captivity for the seven different moth groups, according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").

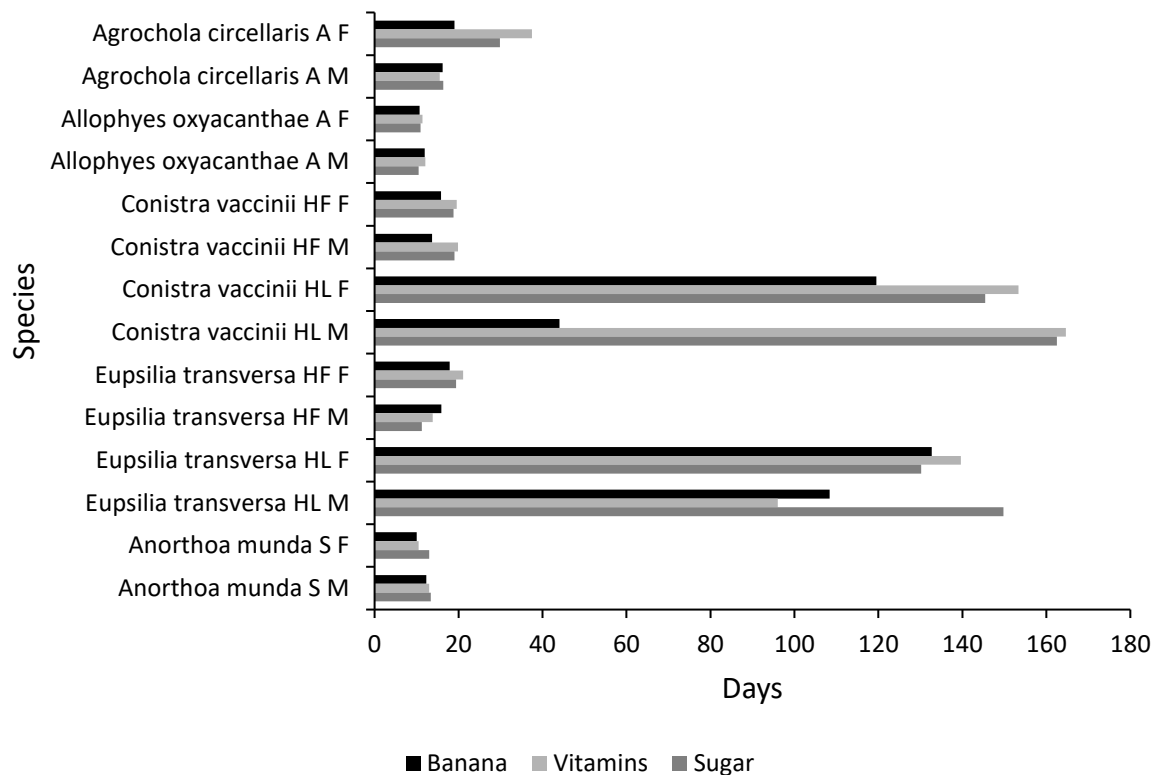


Figure 6 Average longevity with different food treatment of all species, split in females and males.

6.2.2 Fecundity

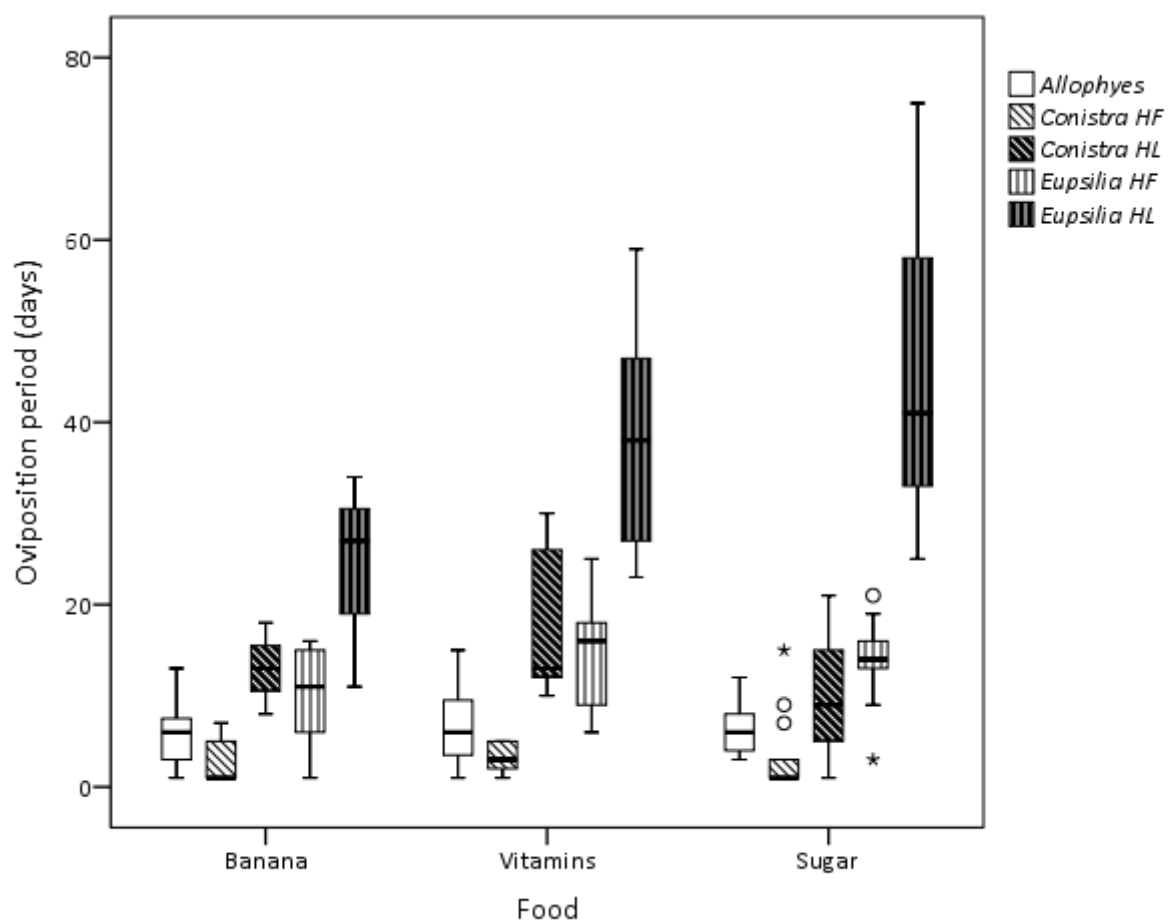
To determine the impact of adult food resources offered, I compared, within each of the 5 groups of females with sufficient sample sizes (*Allophyes*, *Conistra* HF, *Conistra* HL, *Eupsilia* HF and *Eupsilia* HL), the length of the oviposition period, realised fecundity, mature oocytes retained within the abdomen, potential fecundity, and egg size across the three feeding treatments. A Welch corrected ANOVA was used to show an overall effect of different food.

6.2.2.1 Duration of oviposition period

The mean length of the oviposition period in captivity of the different moth groups lasted from 3 (*Conistra* HF) to 38 days (*Eupsilia* HL). No significant differences in the length of the oviposition period in captivity could be found when moths had access to different food sources.

Table 16 Oviposition period (in days) of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of ANOVAs (with Welch correction).

Species	Banana	Vitamins	Sugar	F	p
<i>Allophyes oxyacanthae</i>	5.67 (2.84)	7.00 (4.53)	6.38 (2.68)	0.765	0.472
<i>Conistra vaccinii</i> HF	2.85 (2.23)	3.41 (1.70)	3.24 (3.80)	0.282	0.756
<i>Conistra vaccinii</i> HL	13.00 (5.00)	18.20 (9.12)	10.33 (10.07)	0.678	0.549
<i>Eupsilia transversa</i> HF	10.71 (4.80)	14.46 (6.50)	13.33 (5.05)	2.409	0.111
<i>Eupsilia transversa</i> HL	24.00 (11.79)	38.25 (12.97)	46.40 (20.12)	2.091	0.210

**Figure 7** Box plot of the duration of the oviposition period in captivity for the five different moth groups according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").

6.2.2.2 Realised fecundity

Average realised fecundity varied between moth groups from 153 (*Allophyes*) to 757 (*Eupsilia* HF) eggs. Within the moth species, access to different food resources had no significant influence on the number of eggs laid per lifetime in captivity.

Table 17 Realised fecundity (per eggs) of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of one-way ANOVAs (with Welch correction)

Species	Banana	Vitamins	Sugar	F	p
<i>Allophyes oxyacanthae</i>	149.04 (91.30)	146.42 (93.12)	160.73 (71.74)	0.209	0.812
<i>Conistra vaccinii</i> HF	172.15 (102.06)	167.41 (123.36)	160.41 (162.13)	0.029	0.972
<i>Conistra vaccinii</i> HL	315.00 (119.01)	240.40 (145.55)	189.67 (160.24)	0.569	0.602
<i>Eupsilia transversa</i> HF	643.43 (374.33)	712.31 (230.48)	883.94 (299.19)	2.356	0.114
<i>Eupsilia transversa</i> HL	410.00 (203.93)	250.25 (162.43)	376.80 (80.10)	1.679	0.278

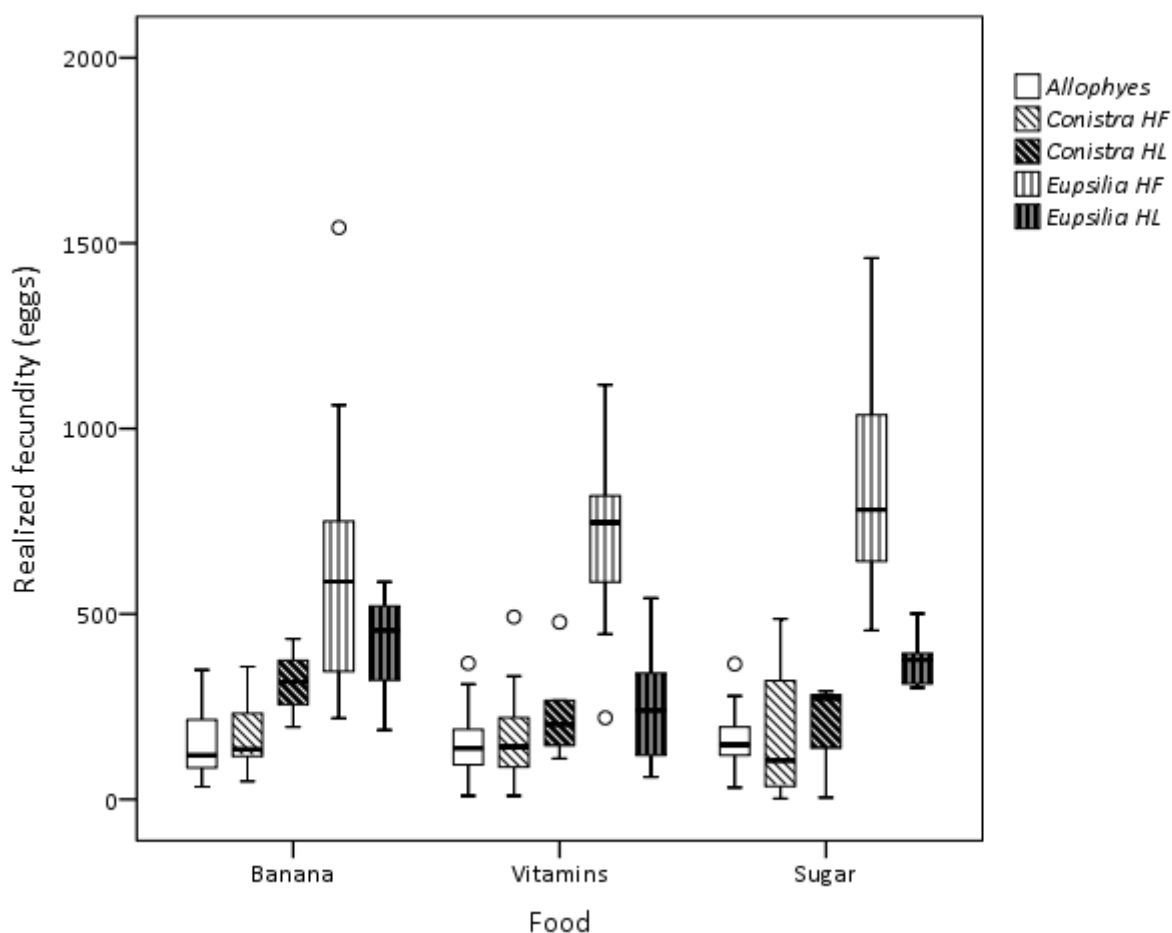


Figure 8 Box plot of realised fecundity in captivity for the different moth groups according to the three food treatments. Small circles represent outliers.

6.2.2.3 Mature oocytes remaining within the abdomen

Mean number of mature oocytes retained within the abdomen after the death of the females varied between moth groups from 31 (*Allophyes*) to 502 (*Conistra* HL) eggs. Access to different food resources had significant influence on the number of eggs remaining in the abdomen in the species *Allophyes* and *Eupsilia* when hibernating in the field. Females in both species groups feeding on banana had the most and those feeding on sugar the fewest eggs left in the abdomen.

Table 18 Eggs within the abdomen of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of one-way ANOVAs (with Welch correction)

Species	Banana	Vitamins	Sugar	F	p
<i>Allophyes oxyacanthae</i>	37.96 (37.26)	34.95 (28.27)	21.23 (15.16)	3.363	0.046
<i>Conistra vaccinii</i> HF	309.38 (171.75)	297.12 (133.31)	306.00 (146.90)	0.28	0.972
<i>Conistra vaccinii</i> HL	622.33 (156.72)	461.60 (281.38)	449.67 (57.40)	1.389	0.344
<i>Eupsilia transversa</i> HF	142.00 (104.52)	98.15 (103.08)	75.18 (72.19)	4.098	0.031
<i>Eupsilia transversa</i> HL	694.33 (240.20)	173.63 (139.58)	218.00 (229.48)	5.456	0.063

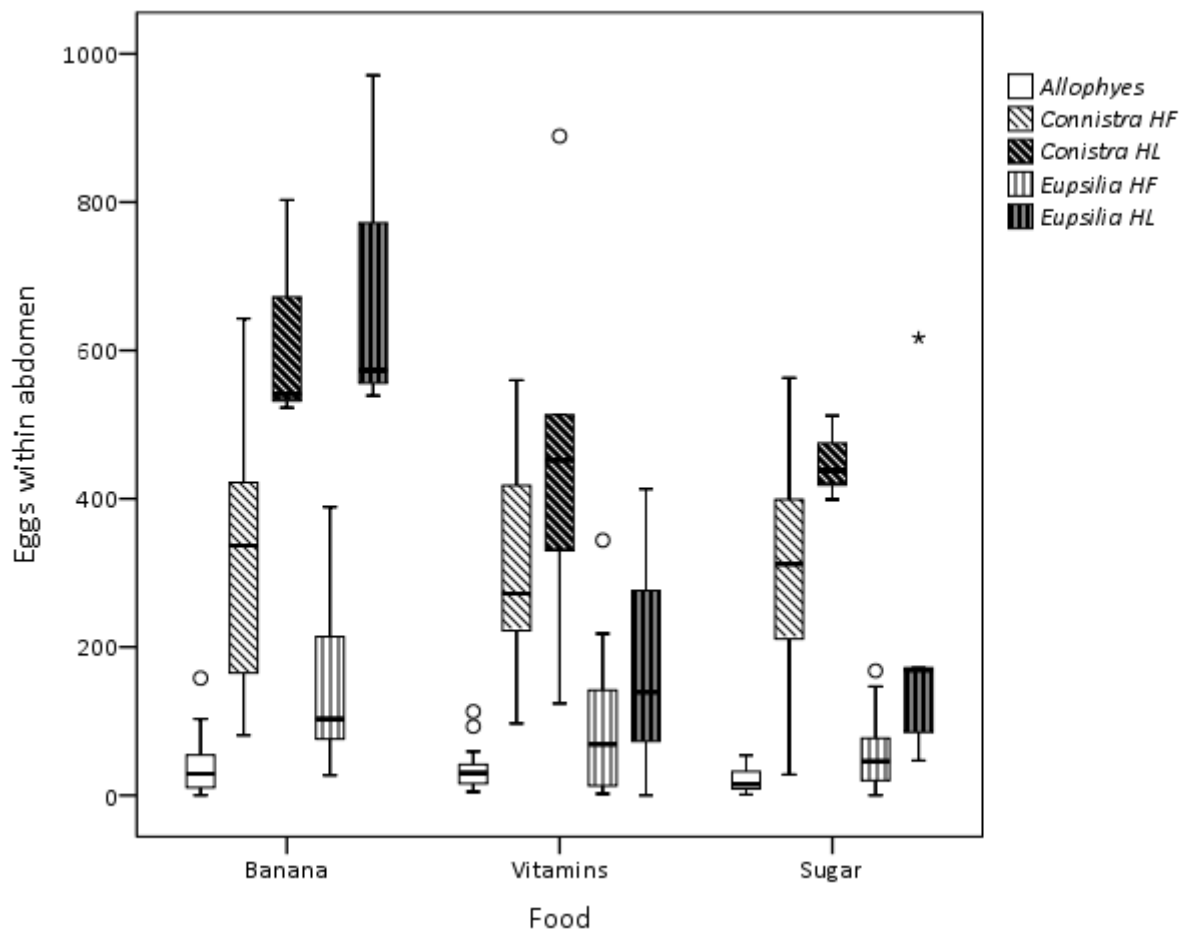


Figure 9 Box plot of the mature oocytes remaining within the abdomen after female's death in captivity for the different moth groups, according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").

6.2.2.4 Potential fecundity

Average potential fecundity in captivity varied between moth groups from 184 (*Allophytes*) to 853 (*Eupsilia* HF) eggs. Within most moth species, access to different food resources had no significant influence on the number of eggs. Only in individuals of *Conistra vaccinii* which hibernated in the laboratory a statistically significant difference was observed, with females feeding on banana having the most and those feeding on sugar the fewest eggs.

Table 19 Potential fecundity of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of one-way ANOVAs (with Welch correction)

Species	Banana	Vitamins	Sugar	F	p
<i>Allophyes oxyacanthae</i>	187.00 (103.94)	181.37 (88.98)	181.96 (67.57)	0.024	0.977
<i>Conistra vaccinii</i> HF	481.54 (115.09)	464.53 (108.19)	466.41 (116.23)	0.093	0.912
<i>Conistra vaccinii</i> HL	937.33 (71.84)	702.00 (193.78)	639.33 (106.37)	8.154	0.027
<i>Eupsilia transversa</i> HF	785.43 (319.47)	810.46 (180.73)	905.83 (320.86)	1.392	0.266
<i>Eupsilia transversa</i> HL	1104.33 (353.80)	423.88 (129.17)	594.80 (185.96)	5.503	0.066

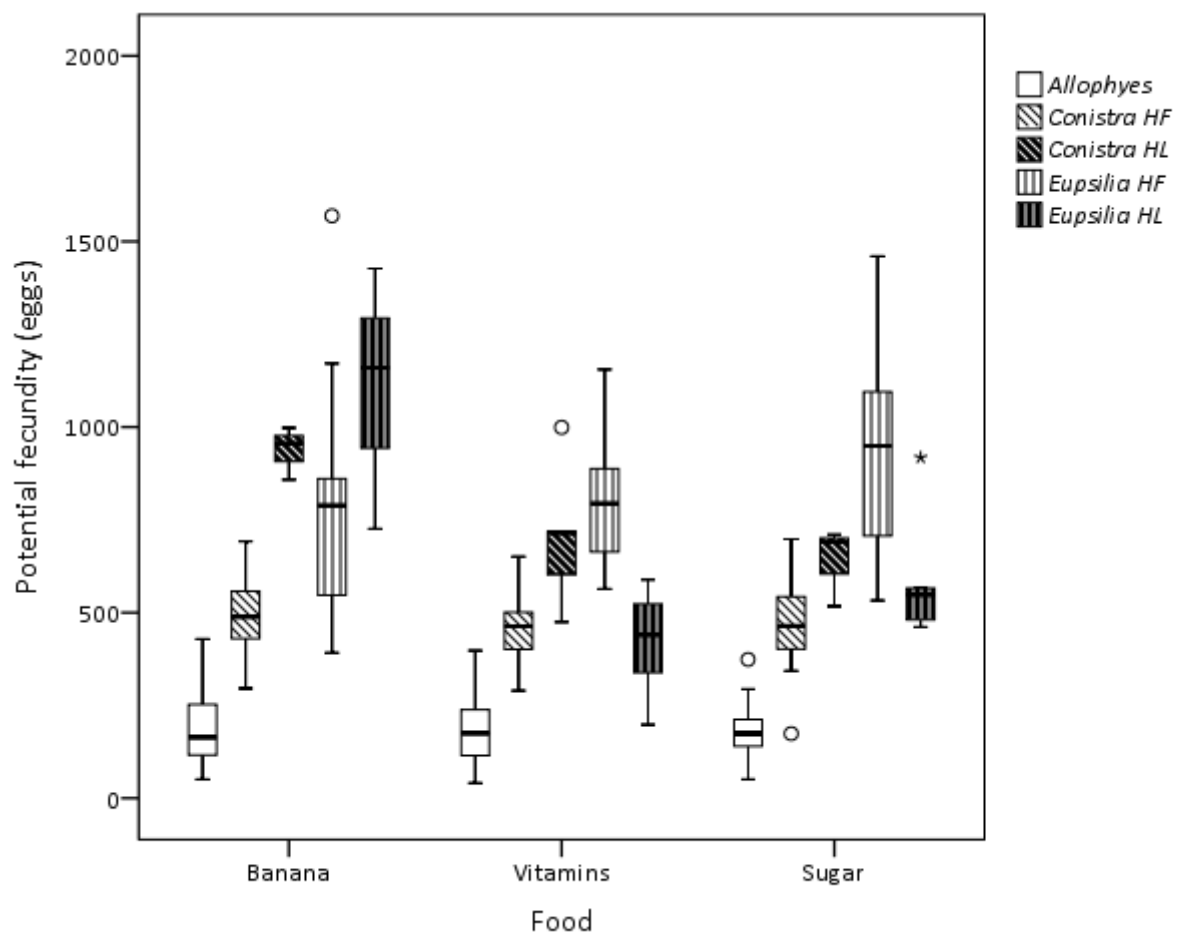


Figure 10 Box plot of potential fecundity in captivity for the different moth groups, according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").

6.2.2.5 Egg size

To determine the impact of food on the egg size, the egg size of each individual was analysed. Mean egg size per individual show significant results only in the species *Eupsilia transversa* when moths hibernated in the laboratory.

A comparison across the species (*Allophytes*, *Eupsilia* and *Conistra* from which enough data could be sampled for data analysis) revealed that *Allophytes oxyacanthae* laid by far the largest eggs and *Eupsilia transversa* the smallest (Figure 11). *Conistra vaccinii* moths which had hibernated in the field laid distinctly larger eggs than those individuals that hibernated in the laboratory, whereas no such difference was obvious in the other adult hibernator, *Eupsilia transversa*. Within each species or hibernation type, no significant effect of adult resource access on mean egg size produced per female was apparent.

Table 20 ANOVA on mean egg size of *Allophytes*, *Conistra* and *Eupsilia*

Species	Banana	Vitamins	Sugar	F	p
<i>Allophytes oxyacanthae</i> A	0.686 (0.049)	0.707 (0.050)	0.698 (0.053)	0.995	0.378
<i>Conistra vaccinii</i> HF	0.514 (0.017)	0.514 (0.025)	0.516 (0.022)	0.047	0.954
<i>Conistra vaccinii</i> HL	0.453 (0.003)	0.405 (0.051)	0.426 (0.025)	0.047	0.266
<i>Eupsilia transversa</i> HF	0.441 (0.029)	0.439 (0.027)	0.442 (0.032)	2.587	0.954
<i>Eupsilia transversa</i> HL	0.432 (0.028)	0.403 (0.026)	0.442 (0.011)	6.462	0.042

A Games-Howell post hoc Test shows significant differences among sugar and vitamins at *Eupsilia transversa* HL.

Table 21 Games-Howell post hoc Test on mean egg size of *Eupsilia transversa* hibernating in the laboratory

Species	Life cycle	Food_min	Food_min	p
<i>Eupsilia transversa</i>	HL	Banana	Sugar	0.838
			Vitamins	0.359
		Sugar	Banana	0.838
			Vitamins	0.008
		Vitamins	Banana	0.359
			Sugar	0.008

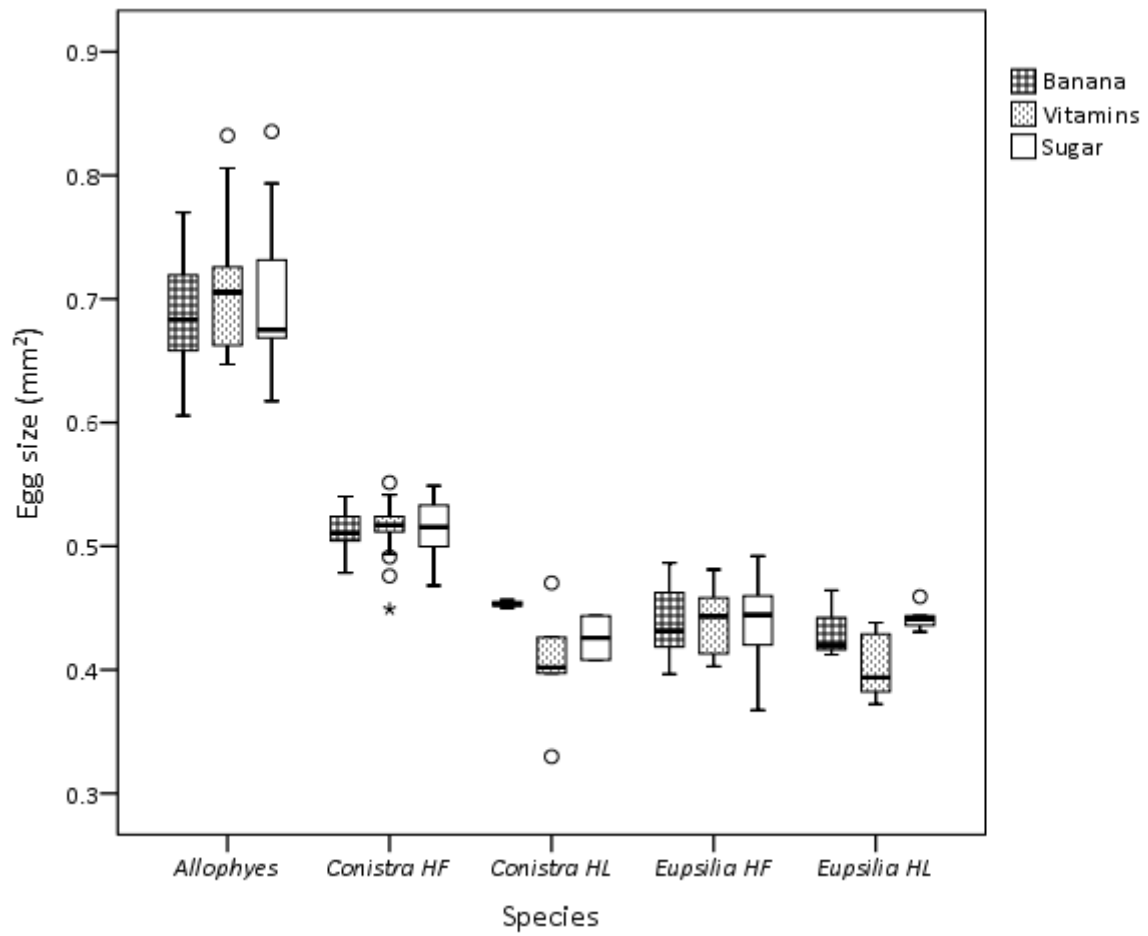


Figure 11 Box plot of the mean egg size of eggs laid by females of frugivore noctuid species in captivity, in relation to the food resources offered. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").

6.2.3 3-way mixed model ANOVA to show influences of predictors

Finally, to more rigorously assess possible effects of different predictors on different target variables related to reproductive success, a 3-way mixed model ANOVA was performed on the two species, overwintering as adults, namely *Eupsilia transversa* and *Conistra vaccinii*. Here species identity was modelled as a random factor and food and mode of hibernation (in the lab or in the field) were modelled as fixed factors.

6.2.3.1 Duration of oviposition period

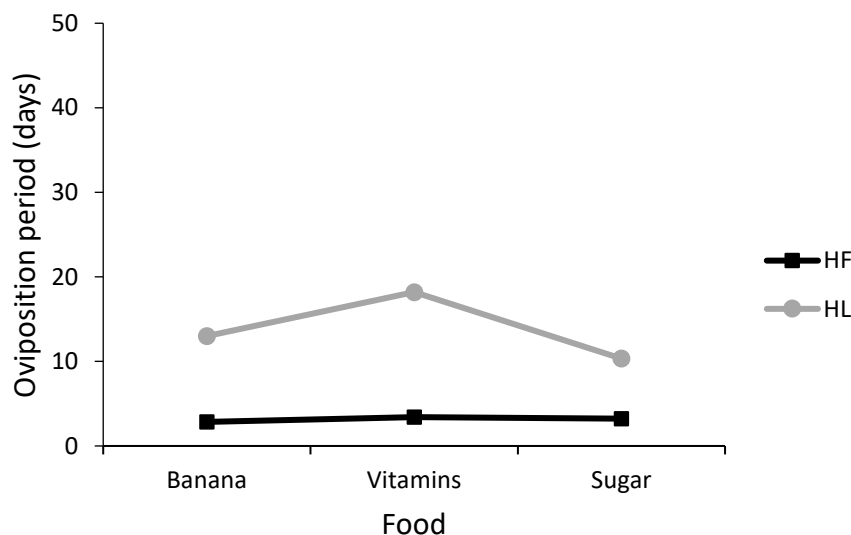
The length of the oviposition period was strongly influenced by all investigated factors and their interactions (Table 22, Table 23). In both species, females that maintained in the laboratory laid eggs over a substantially larger period than those hibernating in the field over winter, because while hibernating in the field data could not be documented. Generally, the oviposition period lasted longer in *Eupsilia transversa* (HL: grand mean $38.13 \pm \text{SD } 16.36$; HF: grand mean $\pm \text{SD}$: 12.84 ± 5.52) than in *Conistra vaccinii* (HL: grand mean $14.64 \pm \text{SD } 8.44$; HF: grand mean $\pm \text{SD}$: 3.19 ± 2.72). Effects of food treatment (or interactions between food treatment and other factors) were rather weak, as indicated by the higher p- and lower F-values. In both species, banana-fed females tended to have shorter egg-laying periods than females in the other two food treatments (Figure 12 and Figure 13). Multiple significant interactions further show that factors that regulate oviposition period are contingent on species identity, food and the dormancy history of the individuals in question.

Table 22 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on the duration of the oviposition period. Significant results marked in bold face.

Source	Df1	Df2	F	p
Species	1	107	98.16	<0.0001
Hibernation	1	107	110.90	<0.0001
Food	2	107	5.14	0.007
Species × Hibernation	1	107	15.42	<0.0001
Species × Food	2	107	5.31	0.006
Hibernation × Food	2	107	2.37	0.098
Species × Hibernation × Food	2	107	4.23	0.017

Table 23 Duration of the oviposition period (days) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.

Species	Banana	Vitamins	Sugar
<i>Conistra vaccinii</i> HF	2.85 \pm 5.31	3.41 \pm 5.23	3.24 \pm 5.23
<i>Conistra vaccinii</i> HL	13.00 \pm 6.39	18.20 \pm 5.85	10.33 \pm 6.39
<i>Eupsilia transversa</i> HF	10.71 \pm 5.29	14.46 \pm 5.31	13.33 \pm 5.22
<i>Eupsilia transversa</i> HL	24.00 \pm 6.39	38.25 \pm 5.53	46.40 \pm 5.85

**Figure 12** Estimated marginal means of the egg laying duration of *Conistra vaccinii* in the three food treatments and different hibernation

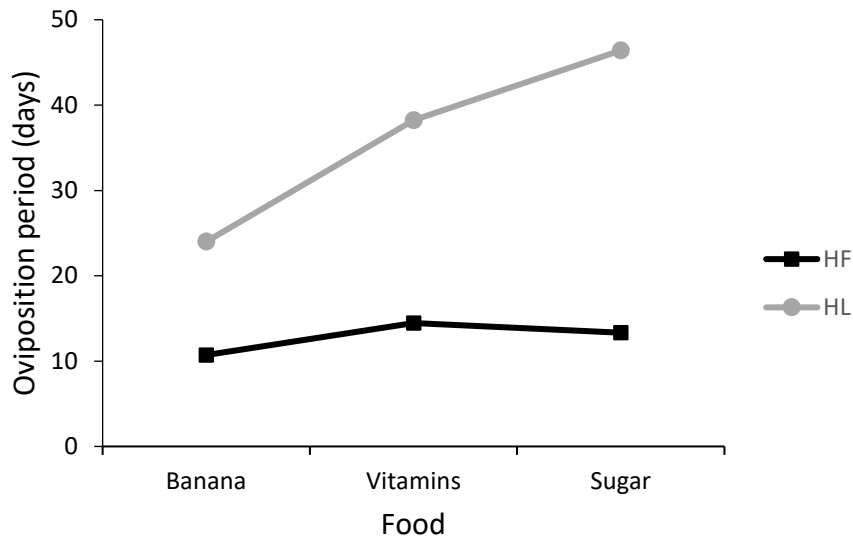


Figure 13 Estimated marginal means of egg laying duration of *Eupsilia transversa* in the three food treatments and different hibernation

6.2.3.2 Realised fecundity

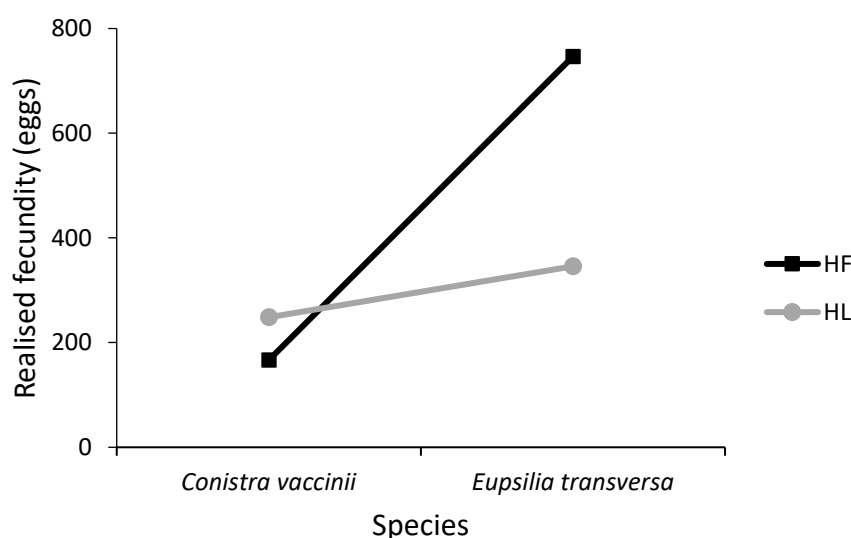
Overall, *Eupsilia transversa* females laid distinctly more eggs (HL: grand mean \pm SD: 319.75 ± 157.66 ; HF: grand mean \pm SD: 739.89 ± 334.79) than those of *Conistra vaccinii* (HL: grand mean \pm SD: 246.91 ± 137.25 ; HF: grand mean \pm SD: 166.19 ± 131.06) (Table 25, Figure 14). This difference was particularly strong in females that had hibernated in the wild. Apart from species identity and hibernation history, none of the investigated factors affected realised fecundity (Table 24). In particular, food treatment did not play any role.

Table 24 Statistical test results (*F*- and *p*-values) from a 3-way mixed model ANOVA on realised fecundity. Significant results marked in bold face.

Source	Df1	Df2	F	p
Species	1	106	44.20	<0.0001
Hibernation	1	106	9.82	0.002
Food	2	106	0.58	0.560
Species × Hibernation	1	106	22.44	<0.0001
Species × Food	2	106	1.35	0.263
Hibernation × Food	2	106	1.14	0.323
Species × Hibernation × Food	2	106	0.24	0.786

Table 25 Realised fecundity (number of laid eggs) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.

Species	Banana	Vitamins	Sugar
<i>Conistra vaccinii</i> HF	172.15 \pm 61.06	167.41 \pm 53.40	160.41 \pm 53.40
<i>Conistra vaccinii</i> HL	315.00 \pm 127.11	240.40 \pm 98.46	189.67 \pm 127.11
<i>Eupsilia transversa</i> HF	643.43 \pm 58.84	712.31 \pm 61.06	883.94 \pm 53.40
<i>Eupsilia transversa</i> HL	410.00 \pm 127.11	250.25 \pm 77.84	376.80 \pm 98.46

**Figure 14** Estimated marginal means of laid eggs per species and hibernation

6.2.3.3 Oviposition rate

The number of laid eggs per oviposition period was only influenced by the different dormancy histories of the moths, other investigated factors had no effect (Table 27). Hibernators in the field laid more eggs per period (*Eupsilia*: grand mean \pm SD: 66.62 ± 45.54 ; *Conistra*: grand mean \pm SD: 64.18 ± 57.29) than hibernators in the laboratory (*Eupsilia*: grand mean \pm SD: 9.77 ± 6.24 ; *Conistra*: grand mean \pm SD: 18.29 ± 9.69) (Table 26, Figure 15, Figure 16).

Table 26 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on oviposition rate. Significant results marked in bold face.

Source	Df1	Df2	F	p
Species	1	106	0.10	0.751
Hibernation	1	106	24.11	<0.0001
Food	2	106	1.16	0.317
Species \times Hibernation	1	106	0.17	0.680
Species \times Food	2	106	0.26	0.776
Hibernation \times Food	2	106	0.30	0.740
Species \times Hibernation \times Food	2	106	0.23	0.792

Table 27 Oviposition rate (eggs per oviposition period) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.

Species	Banana	Vitamins	Sugar
<i>Conistra vaccinii</i> HF	92.93 \pm 12.66	51.24 \pm 11.07	55.13 \pm 11.07
<i>Conistra vaccinii</i> HL	25.10 \pm 26.36	15.35 \pm 20.42	16.37 \pm 26.36
<i>Eupsilia transversa</i> HF	73.02 \pm 12.20	55.64 \pm 12.66	73.67 \pm 11.07
<i>Eupsilia transversa</i> HL	17.05 \pm 26.36	7.40 \pm 16.14	9.19 \pm 20.42

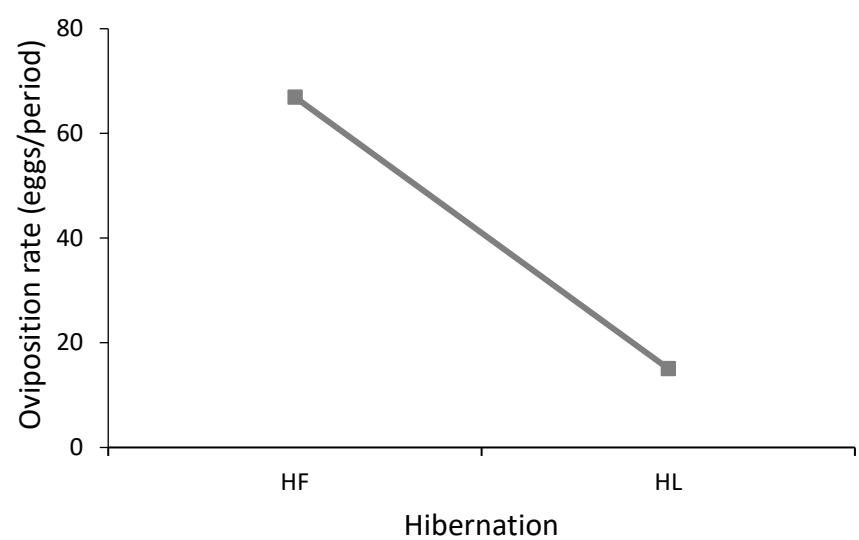


Figure 15 Estimated marginal means of laid eggs per oviposition period of the moths with different dormancy history

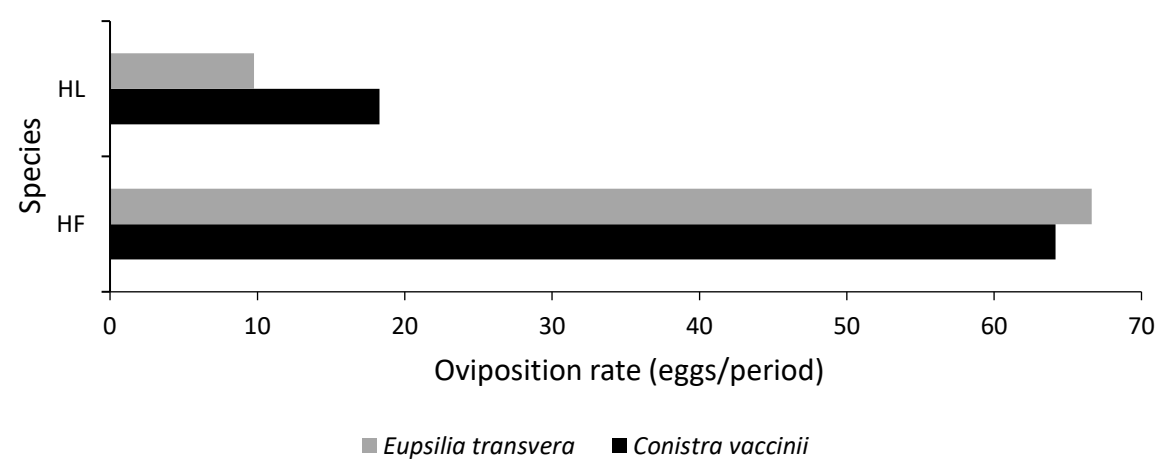


Figure 16 Means of the oviposition rate of two different species hibernated in the laboratory and in the field

6.2.3.4 Mature oocytes remaining within the abdomen

Species identity, hibernation history and food treatment influenced the number of mature oocytes remaining within the abdomen (Table 28). Individuals that had access to banana had more eggs left within the abdomen (Table 29). Whereas hibernators in the laboratory had more eggs remaining in the abdomen and were greatly affected by food treatment individuals that hibernated in the field had fewer eggs remaining in the abdomen and were less affected by food treatment (Figure 17). Individuals of *Conistra vaccinii* (HL: grand mean \pm SD: 502.18 \pm 207.90; HF: grand mean \pm SD: 303.72 \pm 146.32) had more mature oocytes left within the abdomen than individuals of *Eupsilia transversa* (HL: grand mean \pm SD: 285.13 \pm 269.17; HF: grand mean \pm SD: 100.93 \pm 95.10).

Table 28 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on the mature oocytes remaining within the abdomen. Significant results marked in bold face.

Source	Df1	Df2	F	p
Species	1	105	26.29	<0.0001
Hibernation	1	105	50.71	<0.0001
Food	2	105	11.53	<0.0001
Species \times Hibernation	1	105	0.77	0.383
Species \times Food	2	105	3.03	0.052
Hibernation \times Food	2	105	7.89	0.001
Species \times Hibernation \times Food	2	105	1.81	0.168

Table 29 Mature oocytes remaining within the abdomen of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.

Species	Banana	Vitamins	Sugar
<i>Conistra vaccinii</i> HF	309.39 \pm 39.56	297.12 \pm 34.60	306.00 \pm 34.60
<i>Conistra vaccinii</i> HL	622.33 \pm 82.36	461.60 \pm 63.80	449.67 \pm 82.36
<i>Eupsilia transversa</i> HF	142.00 \pm 38.13	98.15 \pm 39.57	75.18 \pm 34.60
<i>Eupsilia transversa</i> HL	694.33 \pm 82.36	173.63 \pm 61.39	218.00 \pm 63.80

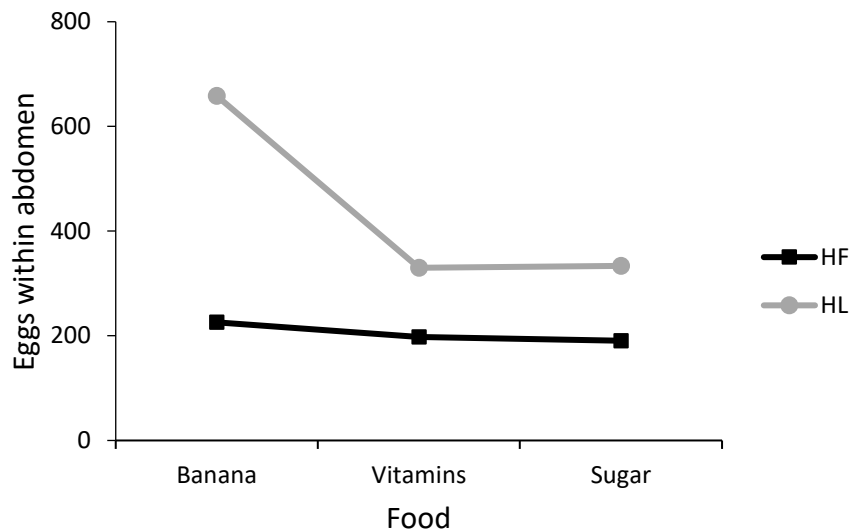


Figure 17 Estimated marginal means of eggs left within the abdomen of hibernators in the field and hibernators in the laboratory with different food treatments

6.2.3.5 Potential fecundity

Species identity and food treatment had significant influence on potential fecundity (Table 30, Table 31). Hibernators in the laboratory laid most eggs when fed with banana (Figure 18).

Females of *Conistra vaccinii* had more eggs when hibernating in the laboratory (grand mean \pm SD: 749.09 ± 183.49) than when hibernating in the field (grand mean \pm SD: 469.91 ± 110.81), whereas females of *Eupsilia transversa* had more eggs when hibernating in the field (grand mean \pm SD: 840.82 ± 286.04) than hibernating in the laboratory (grand mean \pm SD: 604.88 ± 317.96) (Figure 19).

Table 30 Statistical test results (*F*- and *p*-values) from a 3-way mixed model ANOVA on potential fecundity. Significant results marked in bold face.

Source	Df1	Df2	F	p
Species	1	107	10.27	0.002
Hibernation	1	107	2.80	0.097
Food	2	107	7.50	0.001
Species × Hibernation	1	107	18.27	<0.0001
Species × Food	2	107	1.84	0.164
Hibernation × Food	2	107	8.84	<0.0001
Species × Hibernation × Food	2	107	2.12	0.125

Table 31 Potential fecundity (total number of eggs) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.

Species	Banana	Vitamins	Sugar
<i>Conistra vaccinii</i> HF	481.54 \pm 58.25	464.53 \pm 50.94	466.41 \pm 50.94
<i>Conistra vaccinii</i> HL	937.33 \pm 121.26	702.00 \pm 93.93	639.33 \pm 121.26
<i>Eupsilia transversa</i> HF	785.43 \pm 56.13	810.46 \pm 58.25	905.83 \pm 49.50
<i>Eupsilia transversa</i> HL	1104.33 \pm 121.26	423.88 \pm 74.26	594.80 \pm 93.93

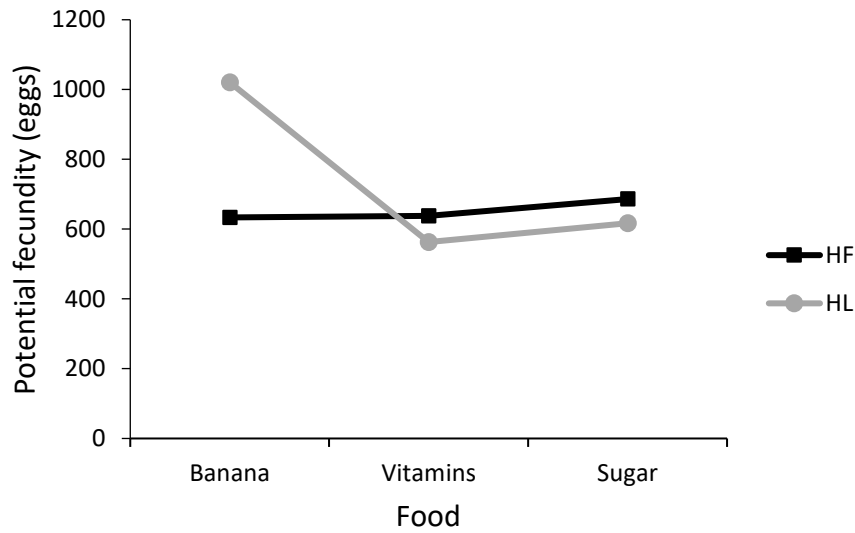


Figure 18 Estimated marginal means of the total number of eggs within the different food treatments and hibernation

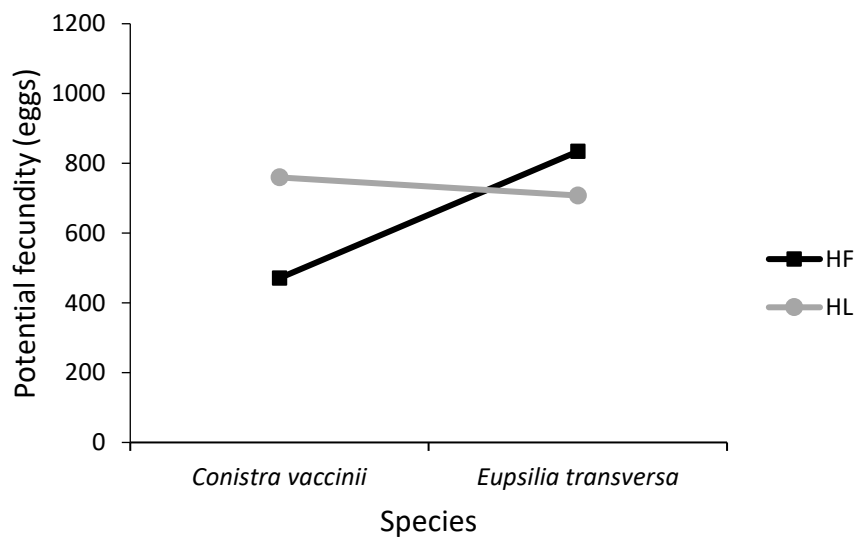


Figure 19 Estimated marginal means of the total number of eggs of the different species and hibernation

6.2.3.6 Egg size

Egg size was strongly influenced by all investigated factors and their interactions (Table 32, Table 33). Hibernators in the field showed no food differences, whereas hibernators in the laboratory of the species *Conistra* had smallest eggs when fed with sugar and largest when fed with banana (Figure 20, Figure 21). Eggs of females that had hibernated in the field (*Eupsilia*: grand mean \pm SD: 0.44 ± 0.03 ; *Conistra*: grand mean \pm SD: 0.51 ± 0.02) were larger than eggs of females that had hibernated in the laboratory (*Eupsilia*: grand mean \pm SD: 0.41 ± 0.03 ; *Conistra*: grand mean \pm SD: 0.41 ± 0.07).

Table 32 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on egg size. Significant results marked in bold face.

Source	Df1	Df2	F	p
Species	1	106	21.19	<0.0001
Hibernation	1	106	73.23	<0.0001
Food	2	106	3.84	0.024
Species \times Hibernation	1	106	40.42	<0.0001
Species \times Food	2	106	4.22	0.017
Hibernation \times Food	2	106	3.49	0.034
Species \times Hibernation \times Food	2	106	4.39	0.015

Table 33 Egg size (mm²) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.

Species	Banana	Vitamins	Sugar
<i>Conistra vaccinii</i> HF	0.51 ± 0.02	0.51 ± 0.02	0.52 ± 0.02
<i>Conistra vaccinii</i> HL	0.45 ± 0.03	0.40 ± 0.02	0.37 ± 0.03
<i>Eupsilia transversa</i> HF	0.44 ± 0.02	0.43 ± 0.02	0.44 ± 0.02
<i>Eupsilia transversa</i> HL	0.43 ± 0.03	0.39 ± 0.02	0.44 ± 0.02

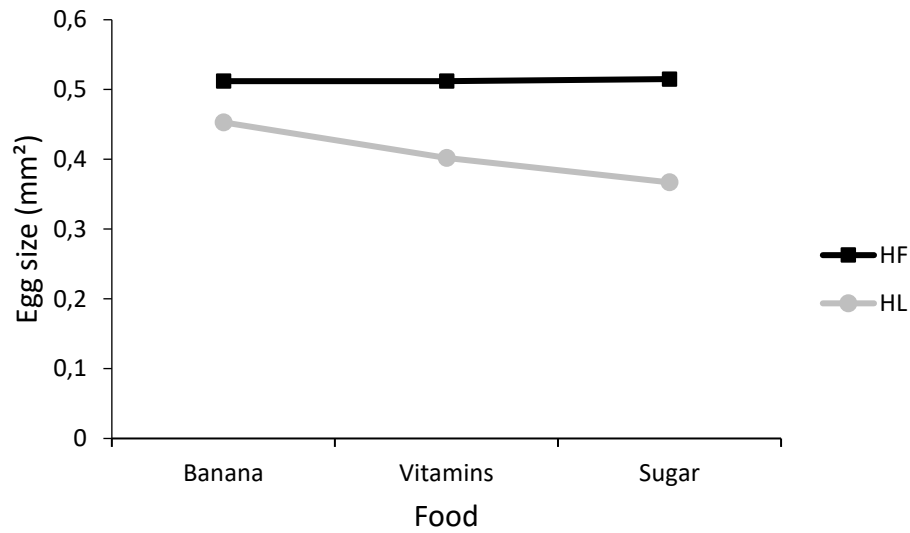


Figure 20 Estimated marginal means of egg size within different food treatments of *Conistra vaccinii*

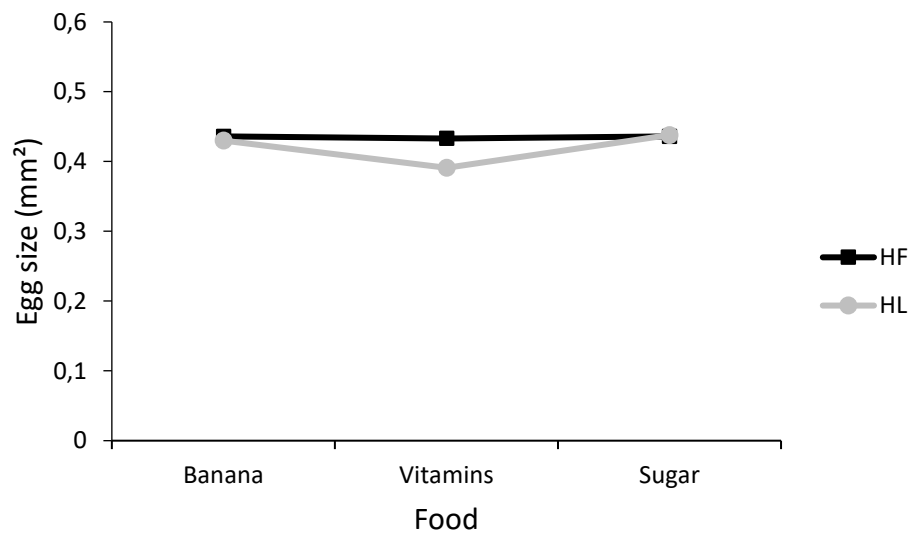


Figure 21 Estimated marginal means of egg size within different food treatments of *Eupsilia transversa*

7 Discussion

7.1 Biodiversity

Because of different vegetation and disturbance regimes of flooded and non-flooded areas differences in species richness, diversity and composition of moths visiting fruit baits were expected. In flooded regions lower numbers of the investigated factors were awaited, because flooding is a great mortality factor for the preimaginal stages of Lepidoptera (Konvicka, Nedved and Fric, 2002; Nicholls and Pullin, 2003). Other differences were anticipated due to habitat differences in flooded and non-flooded areas. Flooded habitats are dominated by poplars, willows and grey alder, non-flooded by oak, ash, hornbeam, maple, linden and elm trees (Willner and Grabherr, 2007).

Species richness

In non-flooded areas 256 individuals representing 29 species and in flooded areas only 188 individuals in 22 species were identified. No significant differences could be found in species richness. As shown in Beck and Schwanghart (2010) and Fiedler and Truxa (2012), diversity measures like Fisher's alpha and Shannon's exponential index stabilized faster with increasing sample size than mere species richness.

Truxa and Fiedler (2012a) found 251 individuals representing 51 species of the Noctuoidea superfamily, whereas only 34 species belonged to the family of Noctuidae. This study also identified altogether 34 species in the two different habitats. Although the same number of species was found, only 4 species (*Abrostola triplasia*, *Lacanobia oleracea*, *Scoliopteryx libatrix* and *Xestia c-nigrum*) were found in both studies in the same area under investigation (Donau-Auen Nationalpark near Orth/Donau). *Lacanobia oleracea* and *Xestia c-nigrum* were only found in non-flooded areas and also in Truxa and Fiedler (2012b) they were more abundant in non-flooded areas. The reason for the small overlap of the species seems to be that Truxa (2012) had only samling nights in June and so caught noctuids flying in summer and in this study sampling started in mid-September, covering mostly autumn species and species that hibernate in their imaginal state. Another reason for the small overlap of species could be due to the different catching method with baits.

Of all the 34 species, 17 could be found in both habitats among them hibernating species like *Conistra* and *Eupsilia* which beside feeding on nectar also have been found feeding on fruit and *Autographa gamma*, who is a typical migratory species feeding on nectar.

The following caught moth were on the red list of endangered species Austria (Rote Liste gefährdeter Tiere Österreichs): *Meganephria bimaculosa* (endangered), *Xylota* (*Xylota*) *exsoleta* (endangered), *Amphipyra* (*Amphipyra*) *livida* (vulnerable) and *Xestia* (*Xestia*) *castanea* (near threatened). (Huemer, 2007)

Species diversity

Species diversity showed differences with regard to both, Fisher's alpha and Shannon exponential mean. As expected in the non-flooded fraction of the forest moth diversity was higher than in the flooded part. In flooded areas, moth diversity may be lower, because many moth species spend at least part of their preimaginal stages on or near the ground and therefore could be severely influenced when flooding occurs during these preimaginal stages. At the Donau-Auen the typical flooding period is in summer where lots of the found moth have their more immobile development stages.

Truxa and Fiedler (2012b) found no clear pattern in abundance profiles between ground-layer and arboreal moths. Their study showed that most of the common wetland moth species were more abundant in flooded habitats. In contrast, this study found 5 species that only appeared in the flooded area with only one species that prefers wetlands *Agrochola* (*Anchoscelis*) *helvola*. There were no species that were more abundant in the flooded area. 12 species appeared only in the non-flooded area. As before, *Lacanobia oleracea* and *Xestia c-nigrum* were only found in non-flooded areas and also in Truxa and Fiedler (2012b) they were more abundant in non-flooded areas.

Truxa and Fiedler (2012b) showed no reduction on overall 'macro-moth' diversity in flooded habitats relative to non-flooded habitats. Looking at moths in the Danube floodplains which had their larval stages near the ground in contrary to all surveyed moth in general, moth diversity was lower in flooded regions than in non-flooded regions which conforms to the results in this study.

Species composition

In contrast to the hypothesis, species composition only differed with regard to phenology, viz. in early autumn other species could be found than in late autumn. With regard to the two habitat types, no significant differences in species composition could be found. Truxa (2012) shows very clear differences in species composition between forest parcels north and south the Hubertusdamm. This study could not proof the results from Truxa (2012), perhaps due to small sample size. Another possible reason could be the way of living of these frugivorous moths in the cold season, where they must travel long distances to find food resources at all. Differences in the season types are also explained by Summerville and Crist (2005), showing that sampling in temperate-zone ecosystems should be spread throughout the year because of the distinct phenological species turnover.

Agrochola circellaris, *Allophyes oxyacanthae*, *Autographa gamma*, *Eupsilia transversa*, *Conistra vaccinii* and *Conistra rubiginosa* are most responsible for seasonal differences. *Agrochola circellaris*, *Allophyes oxyacanthae*, *Eupsilia transversa* and *Conistra rubiginosa* were more common in late autumn samples, whereas *Autographa gamma* and *Conistra vaccinii* were more frequent in early autumn samples.

According to Ebert (1997) *Agrochola circellaris* is more common later in the year. *Allophyes oxyacanthae* is most common in October and there are no big differences in season types. *Eupsilia transversa* is more common late in the year, and these moths may fly very late in the year when night temperature is mild. *Autographa gamma* is a migratory moth and gets less common later in the year, when they either die or migrate back into the Mediterranean area Ebert (1997). *Conistra vaccinii* is most common in September and October then they have dormancy, whereas *Conistra rubiginosa* is common later in the year and is more active in winter than *Conistra vaccinii*. (Ebert, 1997)

7.2 Fitness

Butterflies in temperate zones mostly feed on nectar, whereas for most species other food sources are negligible (Karsholt *et al.*, 2015). In contrast, many noctuid species in central Europe also feed on rotting fruits, at least opportunistically (Ebert, 1997). In tropical zones fruits play a valuable role as food and energy resource, where they may be available the whole year and fruit feeding butterflies live longer than nectarivorous ones (Molleman *et al.*, 2007).

However, the role fruit feeding may play in temperate-zone moth communities has attracted far less attention, apart from the use of fruit baits for faunistic studies (Süssenbach and Fiedler, 1999).

Data on life expectancies and fecundity in my study are underestimates of true potentials, since moths from natural populations were sampled. Hence, their age and individual history at the onset of the experiment was unknown. However, this was true for all moths tested from all species and life cycle types in the same manner. Moths had been randomly assigned to food treatments, so that differences in pre-experimental age should be levelled out. Also, for statistical evaluations all those individuals were excluded which had died very early during the experiments, since these individuals were suspected to be 'over-aged' already when captured or they might have suffered from some damage during capture and transfer.

Fruit-feeding among adult Lepidoptera is generally associated with high life expectancy, fecundity and viability of eggs (Bauerfeind and Fischer, 2005; Mevi-Schütz and Erhardt, 2005; Bauerfeind *et al.*, 2007; Dierks and Fischer, 2008). This relationship holds true for specialist fruit-feeders and remains robust in large-scale multi-species comparisons across many butterfly taxa and biogeographical regions (Beck and Fiedler, 2008). Therefore, we also expected enhanced lifespan and fecundity when moth had access to banana. My data indicates that noctuids in temperate zones show significant differences in some fitness factors when confronted with different food treatments. Contrary to expectation, however, Central European cold season noctuid moths did not derive benefits from feeding on fruits, relative to mere nectar-feeding, regarding their longevity.

Longevity

Where subtle food effects could be determined at all, they were in opposite direction: fruit-feeders tended to live shorter than nectar-feeders in the laboratory. Further enrichment of the nectar mimic with a vitamin mixture appeared to be positive for the lifespan. Also in Molleman *et al.* (2008) *Charaxes fulvescens* females fed banana lived shorter than those feeding on a sugar solution. In comparison in Lepidoptera (*Papilionidea* and *Hesperioidea*) adult feeding shows a strong influence on lifespan. Fruit feeders exceed nectar feeders and pollen feeders exceed fruit feeders in longevity (Beck and Fiedler, 2008).

My results show significance only in two species (viz. *Agrochola*, *Eupsilia* hibernating in field), where females lived longer than males. For adult hibernators, high life-expectancy pays off especially for females because they mate very soon after hibernation. Hence, egg-laying can be extended over a period of months, starting in February or March and lasting until May. Longer adult life can have fitness pay-offs for the females because so they have more time to lay their eggs, whereas for the males the chance of finding an unmated female will become smaller in time.

Adult hibernators in the laboratory lived longer than hibernators in the field as was expected, because hibernators in the field had a longer lifetime before they were captured after winter and so their lifetime could only be measured after hibernation.

Conistra lived longer than *Eupsilia*. Referring to Ebert (1997) both species show similar imaginal life expectancies. Ebert (1997) notes, that the latest appearance of *Conistra* (21.05) is six days later than of *Eupsilia* (16.05), which could explain differences in lifespan.

Overall, longevity under laboratory conditions well matched the expectations, with *Allophyes* adults typically surviving for 2 weeks (maximum: 22 d), *Agrochola* for about 3 weeks (maximum: 69 d), *Conistra* (mean 111.3 d, maximum 198 d), *Eupsilia* (mean 124.5, maximum 159 d), and the early spring species *Anorthoa* about 2 weeks (maximum: 21 d). These high life expectancies reached in captivity indicate that conditions were suitable for the moth species concerned. The outstanding lifespan of 198 days results in a lifetime as imago for more than half a year. This long lifespan is only possible because they hibernate as imagos. Another reason for these long lifespans could be, because hibernators in the lab were not mated, and virgin life longer than mated females. According to Wang, Fang and Zhang (2005) longevity of females and males is affected significantly by their mating history. Virgin females or virgin males showed the longest lifespan, the lifespan of both sexes decreased with increased male mating times. Virgin females had the longest life which was significantly longer than once-and twice-mated females.

My results are somehow surprising at a first glance, since in other studies on butterflies feeding extensively on rotting fruits emerged as being associated with unusually long adult lifespans (Molleman *et al.*, 2007; Beck, 2008). However, in contrast to these studies that focused on specialist fruit-feeders, which rarely if ever visit flowers (mostly butterflies in the

family Nymphalidae from tropical realms), the European cold season moths in the experiment are all opportunistic feeders. They drink flower nectar whenever available (e.g. willow and willow flowers in early spring; see also (Ebert, 1997) for records of flower visits in SW Germany). Apparently, concentrated sucrose solution enriched with vitamins provides such moths with all nutrients relevant to attain high longevity. When banana slices were offered in addition to the nectar mimic, moths in my experiments seemed to experience a slightly elevated risk of premature mortality. Regarding longevity, the habit of avidly feeding on rotting fruits as seen in these cold-season moths does not offer them an advantage over nectar feeding. Rather, our results suggest that this peculiar habit just helps cold-season moths to survive periods of very restricted food availability, when they do not have access to floral nectar. They only use rotting fruits to supplement their diet when needed, this behaviour does not necessarily yield longevity benefits. Rather, the opposite came true in the extremely long-lived noctuid genus *Conistra*. This failure of fruit availability to enhance longevity might indicate some constraints in the digestive physiology of these essentially nectarivorous moths. Sucking at the banana slices will evidently yield dissolved mono- and disaccharides. Other nutrients that may also be contained in the fluid that a moth takes up with its proboscis when licking at a fruit, can apparently not be used to such a degree that longevity benefits might accrue, as seen at other fruit feeding specialists. (Dierks and Fischer, 2008; Molleman *et al.*, 2008) At the same time, fruit slices showed quick microbial decay during my experiments, and even though frequently replaced this decay may have been the reason for premature death in some individuals.

Oviposition period

Different food had significant effects on the duration of the oviposition period. As with longevity, banana seemed to be the least conducive nutrition and sucrose solution enriched with vitamins the most conducive one. Adult hibernators in the laboratory had a longer oviposition period than hibernators collected in spring in the field. This was expected since hibernators in the laboratory stayed in the experimental treatment for a much longer time, whereas hibernators in the field had a longer undefined lifetime and oviposition period before they were caught. *Eupsilia* showed a longer oviposition period than *Conistra*, although their total lifespan was shorter. A possible reason to extend oviposition over a longer period is that

Eupsilia laid 3.5 times more eggs than *Conistra* and therefore needed more time to mature the oocytes.

Realised fecundity

Concerning realised fecundity, *Conistra vaccinii* HF and HL and *Eupsilia transversa* HL laid most eggs when fed with banana whereas *Eupsilia transversa* HF and *Allophytes oxyacanthae* laid most eggs when fed with sugar, although there was no significant difference in different food treatment. *Eupsilia* laid more eggs ($629.69 \pm \text{SD}:350.90$) than *Conistra* ($181.50 \pm \text{SD}:134.85$). The strong differences among egg production seems to be the main reason for the longer oviposition period of *Eupsilia*. In contrary to *Conistra*, where total differences were only marginal (HF: $166.19 \pm \text{SD}: 131.06$, HL: $246.91 \pm \text{SD}: 137.25$) *Eupsilia* laid significantly more eggs when hibernating in the field than when hibernating in the laboratory (HF: $739.89 \pm \text{SD}: 334.79$, HL: $319.75 \pm \text{SD}: 157.66$). Apparently *Eupsilia* hibernating in the laboratory holds back their eggs, because they were not mated yet. They may need a spermatophore as nuptial gift for higher egg production. In other studies fecundity increased in mated, and also in multiply mated females (Boggs and Gilbert, 1979; Boggs, 1990; Hou and Sheng, 1999; Wang, Fang and Zhang, 2005). Wang, Fang and Zhang (2005) show, that virgin females lay less eggs than mated females and that their eggs were infertile. This would explain the different numbers in realised fecundity in *Eupsilia* hibernating in the field and hibernating in the laboratory.

Oviposition rate

Hibernators in the field had a higher oviposition rate than hibernators in the laboratory, presumably caused again by the fact that hibernators in the field had all been mated, whereas lab-hibernated females were not. Moths tended to lay more eggs per day when fed with banana.

Looking at the number of eggs laid over time, for individuals that were fed for only a short period of time, the number of eggs flattens out rather fast, viz. they lay less and less eggs. Hibernators with longer feeding time lay lot of eggs in the beginning, but also show some peaks in egg production later during their adult life time. The hibernators in the laboratory with a longer oviposition period seemed to profit from their food source, by laying more eggs later. In general, long-lived lepidopteran species appear to be more dependent on their adult diet (Bauerfeind and Fischer, 2005).

Eggs left within the abdomen

Hibernators in the laboratory ($373.56 \pm \text{SD}:265.02$) had more eggs left in the abdomen than hibernators in the field ($204.53 \pm \text{SD}:159.95$). When fed with banana ($301.82 \pm \text{SD}:236.46$) moths significantly had more eggs left in the abdomen than with sugar ($207.42 \pm \text{SD}:177.81$) or vitamins ($233.12 \pm \text{SD}:186.49$). Banana seems to boost egg production in general. Hibernators in the laboratory profit significantly more from banana ingredients than hibernators in the field (HL: $658.33 \pm \text{SD}:185.63$, HF: $222.59 \pm \text{SD}:162.30$).

Allophytes oxyacanthae had also more eggs left within the abdomen when fed with banana. This could be because oocytes gradually develop, but unless mating occurs, a large proportion of the oocytes never mature. For female multiple mating increases their average egg and offspring production and fertility. Most virgin females began to lay eggs later than mated females, indicating that mating stimulated female oviposition. (Wang, Fang and Zhang, 2005)

Potential fecundity

Potential fecundity differed significantly (HL: B: $1020.83 \pm \text{SD}:245.97$, V: $530.85 \pm \text{SD}:205.14$, S: $611.50 \pm \text{SD}:153.38$) between feeding treatments among hibernators in lab, but almost no difference was seen among individuals that had hibernated in the field. As before regarding the eggs remaining in the abdomen after death, hibernators in the lab overall produced most eggs when fed with banana.

Banana shows clear advantages in hibernators in the lab in all terms regarding fecundity: realised fecundity and eggs laid per day and its total potential fecundity (including eggs within the abdomen).

Egg size

Eggs of *Conistra* were 26% larger when laid by females hibernating in the field than hibernating in the laboratory and eggs of *Eupsilia* were 6% larger (*Conistra* HF: $0.51 \pm \text{SD}:0.02$, HL: $0.41 \pm \text{SD}:0.07$, *Eupsilia* HF: $0.44 \pm \text{SD}:0.03$, HL: $0.41 \pm \text{SD}:0.03$). Hibernators in the field showed no food treatment differences, whereas among hibernators in the lab *Conistra* moths laid the biggest eggs when fed with banana (B: $0.45 \pm \text{SD}:0.00$, V: $0.40 \pm \text{SD}:0.05$, S: $0.36 \pm \text{SD}:0.10$). According to Fischer, Brakefield and Zwaan (2003) egg size correlates with egg viability, so

larger eggs increase the probability of reaching maturity, and so eggs of *Conistra* hibernating in the laboratory had the highest fecundity when fed with banana.

Conclusions

Conistra hibernating in the field showed no effect in realised fecundity, potential fecundity and egg size when fed with different resources. For *Conistra* hibernating in the laboratory banana was the most effective food and pure sugar the least effective one. Looking at *Eupsilia* hibernating in the laboratory, realised and potential fecundity were highest when moths were fed with banana.

Eupsilia showed 30% higher fecundity (total number of eggs multiplied by egg size) than *Conistra*, this may be due to larger body size of *Eupsilia*, since fecundity is known to correlate with body size (Tammaru and Haukioja, 1996; Garcia-Barros, 2000; Arendt, 2011).

Hence, fruit feeding seemed to have a positive effect on fecundity in particularly long-lived Central European cold season noctuid moths when fed with fruits over a long-time period, whereas no such effects were observed in more short-lived species that do not hibernate as adults. Fruit-feeding also did not shape longevity in the direction as had been expected, although a larger egg size enhances life expectancy of the next generation of moths (Fischer, Brakefield and Zwaan, 2003).

However, the data pool was small and differences between food treatments were minor. Further research on these moths is needed to confirm whether a positive effect of fruit-feeding on fecundity does exist, as seen in tropical butterflies (Bauerfeind *et al.*, 2007; Geister *et al.*, 2008; Molleman *et al.*, 2008, 2009).

To conclude, species richness and composition showed no differences between flooded and non-flooded areas in the Donau-Auen National Park, but species diversity was higher in the non-flooded parts.

Feeding experiments in the laboratory revealed that over a range of cold season moths, including some species with unusually long adult life, as they hibernate as adults, there was no indication that fruit-feeding would enhance longevity. However, fruit-feeding appeared to have minor, but significant positive effects on fecundity.

8 Summary

This thesis investigated two major hypotheses:

- Differences in species richness, diversity and composition between flooded and non-flooded areas of a riparian forest area in Eastern Austria.
- Possible fitness benefits that might accrue to these moths from feeding on rotting fruits.

First fruit-feeding noctuid moths were caught using sugar baits in flooded and non-flooded areas of the National Park Donau-Auen. Altogether, 695 moth-individuals belonging to the superfamily Noctuoidea were sampled, representing 53 species in 33 genera.

Second, for longevity a sample of 450 individuals representing 7 species and for fecundity a sample of 187 female individuals representing three life cycle types (autumn species, adult hibernators, and early spring species) were fed sucrose solution, sucrose solution enriched with vitamins, or banana slices plus sucrose solution, respectively, under identical greenhouse conditions.

Biodiversity results showed no significant differences between flooded and non-flooded areas regarding species richness. Species composition showed significant phenological differences, but not between areas. Species diversity (measured as Shannon's exponential index) was higher in non-flooded habitats than in areas prone to annual inundation (Shannon's Exponential Diversity non-flooded: $10.53 \pm \text{SD}:1.29$, flooded: $7.46 \pm \text{SD}:1.07$).

Fitness results showed positive effects on realised fecundity (i.e. number of laid eggs, HL: $B:1020.83 \pm \text{SD}:245.97$, $V:530.85 \pm \text{SD}:205.14$, $S:611.50 \pm \text{SD}:153.38$), potential fecundity (i.e. total number of eggs) (*Conistra vaccinii* HL: $B:937.33 \pm \text{SD}:71.84$, $V:702.00 \pm \text{SD}:193.78$, $S:639.33 \pm \text{SD}:106.37$) and the size of the eggs (HF: $0.48 \pm \text{SD}:0.05$, HL: $0.41 \pm \text{SD}:0.05$) for species with a particularly long lifespan as they overwinter as imago, when fed with banana.

In conclusion, species richness and composition showed no differences between flooded and non-flooded areas in the Donau-Auen National Park, but species diversity was higher in the non-flooded parts. Feeding experiments in the laboratory revealed that there was no indication that fruit-feeding would enhance longevity. However, fruit-feeding appeared to have minor, but significant positive effects on fecundity.

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10 List of tables

Table 1 Sample sizes for longevity experiment. A – autumn species; HF – hibernated in field; HL – hibernated in laboratory; S – spring species.....	11
Table 2 Sample sizes for fecundity assessment. A – autumn species; HF – hibernated in field; HL – hibernated in laboratory; S – spring species.....	12
Table 3 Sample sizes for egg size assessment – <i>Conistra vaccinii</i> HL.....	12
Table 4 Sample sizes for the 3-way mixed model ANOVA comparison in two noctuid species that hibernate as adults.	13
Table 5 Factors and their interactions included in ANOVA model with species as random factor and food and life cycle as fixed factors.....	14
Table 6 Noctuid and erebid moths captured in autumn 2005 near Orth/Donau according to time and location of capture.	15
Table 7 Estimates of total species richness of fruit-feeding noctuid and erebid moths in autumn 2005, according to the two flood regimes at sampling sites, in the National Park Donau-Auen. ACE – Abundance-based coverage estimator; Jack2 – second-order Jackknife estimator. 'Completeness' indicates the ratio of observed to expected species richness.	17
Table 8 Species diversity measures (\pm 95% confidence intervals) for fruit-feeding noctuid and erebid moths, segregated for sample sites in the two flood regimes.....	17
Table 9 Results of a two-way ANOSIM on moth species composition (expressed as Bray-Curtis similarities; 999 permutations). Significant results printed in bold.	19
Table 10 Results of a SIMPER analysis: Contribution of the 9 most diagnostic noctuid and erebid species to phenological dissimilarity of fruit-feeding moth species assemblages. Reported are mean numbers per nightly samples, mean and standard deviation of contribution to dissimilarity between groups; and individual as well as cumulative contribution of the 9 species. SD – standard deviation; EA – early autumn samples; LA – late autumn samples.....	21

Table 11 Outcome of t-tests with Welsh correction for sex differences in longevity of captive moths.	22
Table 12 Longevity (in days) of moths in the feeding experiment. Given are means and standard deviations (SD). Cases with significant sex difference are printed in bold. .	23
Table 13 t-test on different food treatment on male and female individuals of species with significant sex differences on longevity with Welch correction.	23
Table 14 Descriptive figures on different food treatment on male and female individuals of species with significant sex differences on longevity with Welch correction.	24
Table 15 Welch corrected ANOVA on longevity with different food treatment per species. .	24
Table 16 Oviposition period (in days) of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of ANOVAs (with Welsh correction).	27
Table 17 Realised fecundity (per eggs) of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of one-way ANOVAs (with Welsh correction).....	28
Table 18 Eggs within the abdomen of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of one-way ANOVAs (with Welsh correction).....	29
Table 19 Potential fecundity of female moths in captivity, in relation to the three food treatments. Given are means (SD in parentheses), as well as F and p values of one-way ANOVAs (with Welsh correction).....	31
Table 20 ANOVA on mean egg size of <i>Allophyes</i> , <i>Conistra</i> and <i>Eupsilia</i>	32
Table 21 Games-Howell post hoc Test on mean egg size of <i>Eupsilia transversa</i> hibernating in the laboratory	32
Table 22 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on the duration of the oviposition period. Significant results marked in bold face.	35

Table 23 Duration of the oviposition period (days) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.	35
Table 24 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on realised fecundity. Significant results marked in bold face.	37
Table 25 Realised fecundity (number of laid eggs) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.	37
Table 26 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on oviposition rate. Significant results marked in bold face.	38
Table 27 Oviposition rate (eggs per oviposition period) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.	38
Table 28 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on the mature oocytes remaining within the abdomen. Significant results marked in bold face.	40
Table 29 Mature oocytes remaining within the abdomen of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.	40
Table 30 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on potential fecundity. Significant results marked in bold face.	42
Table 31 Potential fecundity (total number of eggs) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA.	42
Table 32 Statistical test results (F- and p-values) from a 3-way mixed model ANOVA on egg size. Significant results marked in bold face.	44
Table 33 Egg size (mm ²) of the two adult hibernating moth species in the three food treatments (estimated marginal means \pm SE) from a 3-way mixed model ANOVA. ...	44

Table 34 Number of moths catching sites in different seasons, types, habitats. 67

Table 35 Superfamily tree of all caught (with fruit baits and light traps) individuals..... 67

11 List of figures

Figure 1 Randomized sample-based species accumulation curves (with 95% confidence intervals) for noctuid and erebid moths attracted to fruit baits in the two areas in the National Park Donau-Auen.	16
Figure 2 Species diversity of fruit-feeding moths, expressed as cumulative values of Fisher's alpha, as a function of the number of nightly samples.	18
Figure 3 Species diversity of fruit-feeding moths, expressed as cumulative values of Shannon's exponential index, as a function of the number of nightly samples.	19
Figure 4 Non-metric multidimensional scaling (NMDS) plot of samples of fruit-feeding noctuid and erebid moth species in autumn 2005 in the National Park Donau-Auen. Filled symbols – early autumn; empty symbols – late autumn. Circles – flood-prone sites; triangles – non-flooded sites. Early samples (to the left) are segregated from late ones (to the right).	20
Figure 5 Box plot of moth longevity in captivity for the seven different moth groups, according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").	25
Figure 6 Average longevity with different food treatment of all species, split in females and males.	26
Figure 7 Box plot of the duration of the oviposition period in captivity for the five different moth groups according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").	27
Figure 8 Box plot of realised fecundity in captivity for the different moth groups according to the three food treatments. Small circles represent outliers.	28
Figure 9 Box plot of the mature oocytes remaining within the abdomen after female's death in captivity for the different moth groups, according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").	30

Figure 10 Box plot of potential fecundity in captivity for the different moth groups, according to the three food treatments. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").	31
Figure 11 Box plot of the mean egg size of eggs laid by females of frugivore noctuid species in captivity, in relation to the food resources offered. Small circles and stars represent outliers, whereas circles mark "out" values and stars mark "far out" values (by SPSS referred as "Extreme values").	33
Figure 12 Estimated marginal means of the egg laying duration of <i>Conistra vaccinii</i> in the three food treatments and different hibernation	35
Figure 13 Estimated marginal means of egg laying duration of <i>Eupsilia transversa</i> in the three food treatments and different hibernation	36
Figure 14 Estimated marginal means of laid eggs per species and hibernation	37
Figure 15 Estimated marginal means of laid eggs per oviposition period of the moths with different dormancy history	39
Figure 16 Means of the oviposition rate of two different species hibernated in the laboratory and in the field	39
Figure 17 Estimated marginal means of eggs left within the abdomen of hibernators in the field and hibernators in the laboratory with different food treatments	41
Figure 18 Estimated marginal means of the total number of eggs within the different food treatments and hibernation	43
Figure 19 Estimated marginal means of the total number of eggs of the different species and hibernation	43
Figure 20 Estimated marginal means of egg size within different food treatments of <i>Conistra vaccinii</i>	45
Figure 21 Estimated marginal means of egg size within different food treatments of <i>Eupsilia transversa</i>	45

12 Appendix

Table 34 Number of moths catching sites in different seasons, types, habitats.

non-flooded		flooded	
early autumn	late autumn	early autumn	late autumn
10 sites	8 sites	4 sites	8 sites
site numbers		site numbers	
1, 7, 9, 11, 13, 17, 18, 20, 21, 24	29,36, 37, 40, 41, 44, 50, 51	12, 14, 16, 23	30, 31, 34, 38, 42, 43, 46, 47

Table 35 Superfamily tree of all caught (with fruit baits and light traps) individuals

Superfamily Noctuoidea				2005		2006
Family (3)	Subfamily (8)	Genus (33)	Species (53)	nf	f	nf
Erebidae	Erebinae	<i>Catocala</i>	<i>Catocala nupta</i>	2	1	
	Hypeninae	<i>Hypena</i>	<i>Hypena rostralis</i>		1	1
	Scoliopteryginae	<i>Scoliopteryx</i>	<i>Scoliopteryx libatrix</i>	6	13	18
Noctuidae	Amphipyridae	<i>Allophyes</i>	<i>Allophyes oxyacanthae</i>	64	59	
		<i>Amphipyra</i>	<i>Amphipyra (Amphipyra) berbera</i>	1		
			<i>Amphipyra (Amphipyra) livida</i>	1	1	
			<i>Amphipyra (Amphipyra) pyramidea</i>		1	
			<i>Amphipyra (Amphipyra) tragopoginis</i>	1	2	
		<i>Asteroscopus</i>	<i>Asteroscopus sphinx</i>		2	
		<i>Brachionycha</i>	<i>Brachionycha nubeculosa</i>			4
		<i>Meganephria</i>	<i>Meganephria bimaculosa</i>	1		
	Dilobinae	<i>Diloba</i>	<i>Diloba caeruleocephala</i>	1	5	
	Noctuinae	<i>Agrochola</i>	<i>Agrochola (Anchoscelis) helvola</i>		2	
			<i>Agrochola (Anchoscelis) humilis</i>	1		
			<i>Agrochola (Anchoscelis) litura</i>		1	
			<i>Agrochola (Anchoscelis) nitida</i>	1	1	
			<i>Agrochola (Leptologia) lota</i>	2		
			<i>Agrochola (Leptologia) macilenta</i>	13	1	
			<i>Agrochola (Sunira) circellaris</i>	65	59	
		<i>Agrotis</i>	<i>Agrotis ipsilon</i>	6	2	1
		<i>Ammoconia</i>	<i>Ammoconia caecimacula</i>	8		
		<i>Atethmia</i>	<i>Atethmia centrargo</i>	1		
		<i>Mniotype</i>	<i>Mniotype satura</i>	1		
		<i>Cerastis</i>	<i>Cerastis rubricosa</i>			2
		<i>Conistra</i>	<i>Conistra (Conistra) rubiginosa</i>	13	6	2
			<i>Conistra (Conistra) vaccinii</i>	19	6	85
			<i>Conistra (Dasycampa) erythrocephala</i>	1	1	2

			<i>Conistra (Dasycampa) rubiginea</i>			1
		<i>Episema</i>	<i>Episema glaucina</i>		1	
		<i>Eugnorisma</i>	<i>Eugnorisma (Metagnorisma) depuncta</i>	1		
		<i>Eupsilia</i>	<i>Eupsilia transversa</i>	18	12	66
		<i>Lacanobia</i>	<i>Lacanobia (Diataraxia) oleracea</i>	2		
		<i>Lithophane</i>	<i>Lithophane (Lithophane) ornitopus</i>	1	1	
		<i>Mythimna</i>	<i>Mythimna (Mythimna) conigera</i>	1		
			<i>Mythimna (Mythimna) vitellina</i>	2	1	
		<i>Noctua</i>	<i>Noctua pronuba</i>		1	
		<i>Orthosia</i>	<i>Orthosia (Cororthosia) gracilis</i>			1
			<i>Orthosia (Monima) cerasi</i>			4
			<i>Orthosia (Monima) cruda</i>			7
			<i>Orthosia (Monima) populeti</i>			3
			<i>Orthosia (Orthosia) incerta</i>			1
			<i>Orthosia (Semiophora) gothica</i>			2
		<i>Anorthoa</i>	<i>Anorthoa munda</i>			20
		<i>Phlogophora</i>	<i>Phlogophora meticulosa</i>	1	1	
		<i>Rhizedra</i>	<i>Rhizedra lutosa</i>	1	1	
		<i>Tiliacea</i>	<i>Tiliacea aurago</i>	1		
			<i>Tiliacea citrargo</i>	1		
		<i>Xestia</i>	<i>Xestia (Megasema) c-nigrum</i>	1		
			<i>Xestia (Xestia) castanea</i>	1		
		<i>Xylena</i>	<i>Xylena (Xylena) exsoleta</i>	4	3	1
	Plusiinae	<i>Abrostola</i>	<i>Abrostola triplasia</i>	2	2	
		<i>Autographa</i>	<i>Autographa gamma</i>	24	17	
Nolidae	Chloephorinae	<i>Nycteola</i>	<i>Nycteola asiatica</i>		1	
				269	205	221
			total			695

Abstract

The aim of this thesis was to investigate local biodiversity and reproductive biology of fruit feeding central European noctuid moths: firstly, if there are differences in species richness, diversity and composition between flooded and non-flooded areas of a riparian forest area in Eastern Austria, and secondly to determine possible fitness benefits that might accrue to these moths from feeding on rotting fruits. For tropical butterflies, it has been shown that feeding on rotting fruits, rather than nectar, is important to achieve high adult life expectancy and may have large positive effects on their reproductive output. Many European cold season noctuid moths also avidly feed on such resources.

Between September 2005 and November 2005, fruit-feeding noctuid moths were caught using sugar baits in flooded and non-flooded areas of the National Park Donau-Auen. This yielded a sample of 444 individuals from 34 species in 22 genera. Species richness showed no significant differences between flooded and non-flooded areas. Species composition showed significant phenological differences, but not between areas. Species diversity (measured as Shannon's exponential index) was higher in non-flooded habitats than in areas prone to annual inundation.

Field-caught individuals of 5 species were fed sucrose solution, sucrose solution enriched with vitamins, or banana slices plus sucrose solution, respectively, under identical greenhouse conditions. These moths represented three life cycle types (autumn species, adult hibernators, and early spring species). Benefits were expected to be especially pronounced in moths which overwinter as adults, in relation to their unusually long and thus nutrient-demanding imaginal lifespan (6–9 months). Indeed, adult food type significantly affected length of the oviposition period, mature oocytes remaining within the abdomen, potential fecundity and egg size. Some of these effects were contingent on species identity or life cycle type.

Keywords: *Noctuoidea, adult nutrition, longevity, nectar, fruit feeding, species composition, flooded area, fecundity, feeding experiments*

Abstract

Ziel dieser Arbeit war es, die lokale Biodiversität und Reproduktionsbiologie von fruchtsaugenden mitteleuropäischen Noctuoidea zu untersuchen: erstens, ob es Unterschiede in Artenreichtum, Vielfalt und Zusammensetzung zwischen überschwemmten und nicht überschwemmten Gebieten eines Auwaldes in Ostösterreich gibt, und zweitens, um mögliche Fitnessvorteile aus der Fütterung mit verrottenden Früchten zu ermitteln. Bei tropischen Schmetterlingen hat sich gezeigt, dass erwachsenen Falter die im Gegensatz zu Nektar mit verrottenden Früchten ernährt wurden eine hohe Lebenserwartung erreichen konnten, und dass Fruchtfütterung positive Auswirkungen auf die Fortpflanzungsleistung haben kann. Viele europäische Eulenfalter ernähren sich in der kalten Jahreszeit von solchen Ressourcen.

Zwischen September 2005 und November 2005 wurden in überschwemmten und nicht überschwemmten Gebieten des Nationalparks Donau-Auen mit Zuckerködern fruchtsaugende Noctuoidea gefangen. Daraus ergab sich eine Stichprobe von 444 Individuen aus 34 Arten in 22 Gattungen. Der Artenreichtum zeigte keine signifikanten Unterschiede zwischen überfluteten und nicht überfluteten Gebieten. Die Zusammensetzung der Arten zeigte signifikante phänologische Unterschiede, allerdings nicht zwischen den Gebieten. Die Artenvielfalt (gemessen als Shannon's Exponentialindex) war in nicht überschwemmten Lebensräumen höher als in Gebieten, die zur jährlichen Überschwemmung neigen.

Im Labor wurden 5 Arten mit Saccharose Lösung, mit Vitaminen angereicherte Saccharose Lösung bzw. mit Bananenscheiben und Saccharose Lösung gefüttert und unter identischen Gewächshausbedingungen gehalten. Diese verschiedenen Falterarten kamen aus drei Lebenszyklen (Herbstarten, erwachsene Überwinterer und frühe Frühlingsarten). Besonders ausgeprägt war der Nutzen für Arten, die als Erwachsene überwintern, da diese ungewöhnlich lange, und damit nährstoffintensive imaginäre Lebensdauern von 6-9 Monaten erreichen. Tatsächlich konnte man signifikante Unterschiede durch Fütterung mit unterschiedlicher Nahrung in die Eilegedauer, der Anzahl der reifen Eizellen die im Bauchraum verbleiben, der potentielle Fruchtbarkeit und der Eigröße feststellen. Einige dieser Effekte waren abhängig von der Art oder dem Lebenszyklustyp.

Stichworte: *Noctuoidea, Ernährung, Langlebigkeit, Nektar, Fruchtsauger, Artenzusammensetzung, Überschwemmungsgebiet, Fruchtbarkeit, Futterexperimente*