The diet of insectivorous bird species differs when staging spring and autumn in the same habitat

KARSTEN LAURSEN

(Med et dansk resumé: Insektædende fuglearters fødevalg er forskellig under rast i samme habitat både forår og efterår)

Abstract Many insectivorous passerine bird species are morphologically almost similar and are mainly separated by different habitat types at their sympatric breeding areas. In this study, a natural experiment was used to examine how species segregated by habitat perform when occurring together in the same habitat. The study focused on diet and took place on the small island of Christiansø in the Baltic Sea used by large numbers of passerines for stopover during migration. The aim was to analyse the diet of insectivorous bird species with small morphological differences during conditions of an assumed high level of competition among the birds for food. Due to morphological differences between species such as body size, wing length and beak size, it was assumed that the diet differed between the species. Gizzard content was obtained by a non-destructive method from 13 passerine species totalling 1141 individuals. In total 25 056 food items were identified to 72 taxonomic and ecological groups. These groups were pooled into 12 groups of food items during statistical analyses. Ten of the 13 bird species were studied in both spring and autumn. The availability of food, mainly insects, was recorded on a daily basis using different sampling methods. The results showed that (1) for the 10 species there were significant interspecific differences in diet and in size of food items taken during spring and autumn, (2) for nine of the ten bird species examined during both seasons, significant differences were found in diet between the two seasons, (3) the diet reflected the daily amount of insects recorded, (4) the diet of the species differed according to where the birds were caught on the island, and (5) the body weight of the bird species increased in autumn during the day but no change in body weight was found in spring, indicating that Christiansø could be a sink during spring. These differences between the seasons were caused by a four to eight fold increase in insect abundance in autumn. In conclusion, insectivorous bird species demonstrated interspecific differences in their diet, probably due to minor morphological and behavioural differences between the species, and opportunism in food choice between spring and autumn.

Dansk Orn. Foren. Tidsskr. 116 (2022): 45-60.

Introduction

Several insectivorous passerine species in Europe are morphologically related, with only small differences (Glutz & Bauer 1991a, 1991b, 1993). Due to the evolutionary outcome of interspecific competition, these species segregate into different habitat types during the breeding season (Cody 1978, Rosamond *et al.* 2020). The aim of this study was to examine how these species perform when they share the same habitat type with limited space. A natural experiment was used to examine this question. During migration, a large number of passerine birds use the island of Christiansø as a stopover site during spring and autumn (Lausten & Lyngs 2004). During stopovers, the birds forage to replenish body reserves and subsequently continue the migration to reach their destination within a certain time frame (Alerstam 1990, Cohen *et al.* 2020). The conditions for the species on Christiansø suggest at least two possibilities in relation to their diets: either the species may take what they encounter, and their diets become similar, or they utilize their morphological and behavioural differences and diet may differ between species. Cody (1974), who stated that bird species generally are opportunistic feeders, supports the first option. Schoener (1965) and Hespenheide (1971) support the second. In this study, we test the hypothesis based on the second option that the diet of the species differs due to morphological and behavioural differences (Miles & Ricklefs 1984, Price 1991, Rabøl 1992).

In addition to the primary study of diet, more aspects were analysed: (A) how much food (mainly insects) was available in the two seasons, (B) the influence of weather conditions on the abundance of food, (C) did the diet reflect the site on the island where the birds were caught, and (D) did the birds increase in body weight during stopover on the island and for how long on average did they remain on the island in spring and autumn.

Darwin (1859) was among the first to describe how bird species have adapted to utilize different habitats and available food types through natural selection, by having different body sizes and forms of beaks. Later MacArthur (1958) demonstrated that passerine species that utilizing different parts and heights of tree canopies vary in foraging behaviour corresponding to differences in their diet. Haftorn (1956) and Alatalo *et al*. (1986) showed that tits utilized different parts of tree branches for feeding, and that the size of these parts changed depended on the amount of food present.

Morse (1971) described insectivory as an adaptive strategy to utilize the worldwide, enormous abundance of insects. About 60% of all bird species depend on insects and have developed beak, body and flying abilities to utilize this food resource (Morse 1971). The development of this strategy has taken place as an adaptation to utilize different and often special habitat types during breeding. During migration, birds utilize different habitat types compared to during the breeding season at stopover sites and wintering grounds (Alerstam 1990). The shifts between geographical regions cause physical, morphological and ecological challenges for migratory birds (Howlett *et al.* 2000, Thorup *et al.* 2017, Sjöberg *et al.* 2018). Most studies have focused on breeding conditions and a few on the ecological conditions at wintering grounds, for example in Africa (Alerstam 1990, Rabøl 1987, 1990, Thorup *et al*. 2017). However, less is known about the ecological conditions at stopover sites during migration (Rabøl 1988, Berthold 2001).

Before migration, bird species use different strategies to replenish body reserves before flying over long distances (Howlett *et al*. 2000, Cohen *et al.* 2020, Klinner *et al.* 2020). During spring, an estimated 138 million migratory birds pass over the Baltic Sea and Eastern Europe while 150 million birds do so in the other direction in autumn (Nussbaumer *et al*. 2021). Most of these birds take off in Southern and Central Europe and aim for breeding grounds in Scandinavia, Finland and Russia. However, some of these birds while crossing the Baltic Sea make a stopover at the small island of Christiansø to rest, refuel or for other reasons. Among the 13 species in the present study, nine were among the 16 most numerous migratory species in Europe (Hahn *et al*. 2009) so their behaviour may be indicative of some general ecological features of these species when resting at a stopover site during migration.

Study site

The study took place on Christiansø, the largest island in the archipelago of Ertholmene, which also includes the island Frederiksø and several smaller rocky islands and skerries. Ertholmene is situated in the Baltic Sea 18 km northeast of Bornholm (Fig. 1). Christansø is 22 ha in size, and about half of the island is a plateau 20 m above sea level covered by open vegetation and some bushes. Slopes make up the other half, covered by trees, bushes and gardens surrounded by stone fences. There are a few ponds that serve as water reservoirs. The island is inhabited and has a long tradition of bird studies. A field station has been running for several decades with the primary task of catching and ringing migratory birds (Christiansø 2021). The birds are caught in mist nets placed in or near taller vegetation (Fig. 1; Lausten & Lyngs 2004).

Methods

Diet samples

Diet samples were taken from 13 insectivorous passerines, with samples from 10 species taken in both spring and autumn. The 10 species were Wood Warbler *Rhadina sibilatrix*, Willow Warbler *Phylloscopus trochilus*, Common Chiffchaff *P. collybita* (Chiffchaff), Eurasian Blackcap *Sylvia atricapilla* (Blackcap), Garden Warbler *S. borin*, Lesser Whitethroat *Curruca curruca*, Common Whitethroat *C. communis* (Whitethroat), Spotted Flycatcher *Muscicapa striata*, European Pied Flycatcher *Ficedula hypoleuca* (Pied Flycatcher) and Common Redstart *Phoenicurus phoenicurus* (Redstart). In addition, samples of diet were collected from three other species, when time and possibilities allowed either during spring for Icterine Warbler *Hippolais icterina* and European Robin *Erithacus rubecula* (Robin) or during autumn for Goldcrest *Regulus regulus*.

Birds for the diet samples were caught in mist nets during the daily ringing routine in autumn 1977, spring and autumn 1978 and spring 1979 (Tab. 1). The ringers selected the birds for the diet study and, if possible, chose those individuals with the highest body weight. The birds were brought to the ringing station in a cloth bag with information of the specific net in which it was caught. At the station, wing length was measured with a linear (1 mm) and the height, width and length of the beak with callipers (0.1 mm). The body weight was measured by a Pesola spring balance (0.1 g). Next, the non-destructive method described by Moody (1970) was used to extract the contents of the digestive tract. Each bird was placed in a plastic bag with its head outside a hole. The beak was opened and a soft, plastic tube with a syringe at the end was carefully inserted through the oesophagus and into the gizzard. Lukewarm, isotonic water was slowly pressed through the tube, and shortly afterwards the contents of gizzard and intestine were expelled down in the plastic bag. Surplus water and remaining gizzard contents were subsequently drawn up by the syringe. The birds were placed in a closed bucket for 10-15 min. for observation, before they were released.

Identification of the diet composition

The gizzard contents were identified using a stereo microscope (× 20). The contents were very fragmented and remains from insects and other arthropods consisted of body parts, mandibles and fragments of wings and legs. Heads from beetles Coleoptera and wasps Hymenoptera were often intact. To support the identification a reference collection was made of identified insects that have been subsequently fragmented. The gizzard contents were quantified by counting the identified fragments as for example, number of heads from beetles and wasps, typical wing structures from bugs Psylloidea, aphids Aphididae and mosquitos Bibionidae and Chironomidae, sclerites from fungus gnats Mycetophilidae, mandibles from larvae of butterflies Lepidoptera and sawflies Thenthredinoidae, and chelicera from spiders Araneae (Laursen 1979).

Insects have a certain body size as adults, therefore the body length of the individual specimens can be esti-

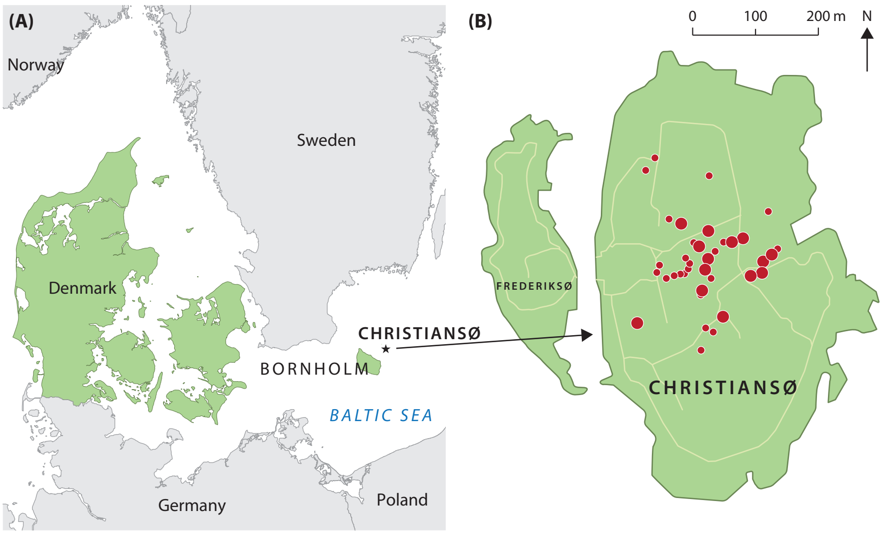


Fig. 1. Map showing Christiansø in the Baltic Sea and locations of the mist nets for bird ringing. Large circle = 12 m net; small circle = 6 m net (from Lausten & Lyngs 2004).
Kort over Christiansø og dens placering i Østersøen (A). På kortet over Christiansø (B) er vist placering af spejlnet til fuglefangst. Store cirkler viser 12 m net og små cirkler 6 m net.

Tab. 1. Number of food samples collected on Christiansø arranged by year and season for 13 passerine species.
Antal indsamlede fødeprøver fra 13 insektædende spurvefugle på Christiansø, fordelt på år og årstid.

Year, season *År, årstid*	Icterine Warbler *Gulbug*	Wood Warbler *Skovsanger*	Willow Warbler *Løvsanger*	Chiffchaff *Gransanger*	Blackcap *Munk*	Garden Warbler *Havesanger*	Lesser Whitethroat *Gærdesanger*
1977 autumn *1977 efterår*	0	4	101	6	20	46	30
1978 spring *1978 forår*	9	4	78	17	35	28	49
1978 autumn *1978 efterår*	0	0	74	15	50	59	54
1979 spring *1979 forår*	0	0	71	20	31	31	58
Sum *Sum*	9	8	324	58	136	164	191
	Whitethroat *Tornsanger*	Goldcrest *Fuglekonge*	Spotted Flycatcher *Grå Fluesnapper*	Robin *Rødhals*	Pied Flycatcher *Broget Fluesnapper*	Redstart *Rødstjert*	Sum *Sum*
1977 autumn *1977 efterår*	5	0	19	0	31	66	328
1978 spring *1978 forår*	38	0	5	6	15	16	300
1978 autumn *1978 efterår*	5	18	0	0	0	0	275
1979 spring *1979 forår*	27	0	0	0	0	0	238
Sum *Sum*	75	18	24	6	46	82	1141

mated (1.0 mm). However, the body length of larvae and adult spiders vary. Thus, to obtain estimates of the body length of these arthropods the length of mandibles and chelicera found in the diet samples were measured and compared to the relationships between lengths of mandible and chelicera and body length of intact larvae and spiders. These relationships were estimated as follows: from a selection of intact larvae the body lengths were measured (1.0 mm) and subsequently desiccated and the mandibles measured (0.1 mm); from these two measurements, relationships were estimated between body length and mandible lengths. The same procedure was used for adult spiders, using the length of the chelicera (0.1 mm). With these relationships it was possible to relate the fragments identified to number and size of food items (individuals) ingested by the birds. Berries were identified and quantified by the kernels in the pulp. Stamens from flowers were counted.

Snails in the diet were identified to phylum and arthropods such as spiders and harvestmen Opiliones to order. Arthropods such as insects were in few cases identified to species, but mostly they were identified to subfamilies, families or higher taxonomic units. The diet was separated into 72 systematic and ecological groups that were then merged into 12 food item groups for the statistical analyses (see Appendix 1). One of the 12 food item groups, the wingless arthropods, is based on these organisms way of moving around on the ground, in grass and on herbs. This group included snails (although not an arthropod), wood lice Oniscidea, centipedes Myriapoda, spiders and harvestmen (Appendix 1). A separate group included eggs and unidentified food items, although the eggs could derive from insects ingested. The 12 food item groups reduce the diversity in the diet, which means that the statistical tests may be considered as conservative.

Samples of arthropods

As a measure of food availability, arthropods, mainly insects, were sampled using three methods: by suction trap, by glue traps and by vegetation sampling. One suction trap was placed at a sheltered position and was active 24 hours on (almost) all days during the four periods. The trap had an opening of about 30 cm and caught insects that passed within a certain distance. The trap was emptied every day. Later, the caught insects were

Tab. 2. Weather conditions measured three hours after sunrise on Christiansø. Values for wind speed, cloud cover and temperature show means for the period (Danish Meteorological Institute).
Vejrforhold målt tre timer efter solopgang på Christiansø. Tal for vindstyrke, skydække og temperatur angiver gennemsnit for perioden (DMI).

Year, season *År, årstid*	Precipitation, number of days *Nedbør, antal dage*	Wind speed, m/s *Vindstyrke, m/s*	Cloud cover, x/8 *Skydække, x/8*	Temperature, °C *Temperatur, °C*
1977 autumn *1977 efterår*	5	4.0	4.4	13.8
1978 spring *1978 forår*	3 (1 day snow) *3 (1 med sne)*	3.4	2.4	7.0
1978 autumn *1978 efterår*	8	9.5	4.9	13.0
1979 spring *1979 forår*	9	13.4	3.6	7.9

identified, counted, dried and weighed (0.1 mg). The average dry weight of insects per day was estimated (total weight per day/total number per day). Glue traps were placed at 4-6 positions with two traps in each group. The insects were identified, counted and their body lengths measured every day, with some exceptions. After being recorded the insects were removed. The glue traps were applied in three seasons (spring and autumn 1978 and spring 1979). Neither the suction trap nor the glue traps caught insects during conditions of strong wind (gales).

Sampling of insects and arthropods on branches was done by putting a plastic bag around a branch, closing it and cutting off the branch. The contents were poisoned by chloroforming, and later the arthropods were identified, counted, dried and weighted (0.1 mg). The contents were related to the length (0.1 m) of the branch. Samples were taken from 5-7 of the dominant tree and bush species during spring (1978 and 1979) and from 4-6 species during autumn (1977 and 1978) with 5-10 samples taken from each tree or bush species. In late autumn 1977, samples (N = 20) were taken only from elm trees *Ulmus scabra*. In spring, sampling of branches took place in early, mid and late May and in autumn in late August and late September.

Weather conditions

Weather conditions were recorded daily at the official weather station on Christiansø (Danish Meteorological Institute) and included here are precipitation (mm), wind speed (m/sec), cloud cover (8/8) and air temperature (°C).

The weather in May 1978 was cold with snowfall and a mean temperature of 7.0 °C, whereas the weather in May 1979 was wet and windy with a mean temperature of 7.9 °C (Tab. 2). The temperature in both spring seasons increased from about 4 °C in the beginning of May to 13-15 °C by the end of the month (Fig. 2). Weather in the autumn seasons of 1977 and 1978 was mild with mean temperatures of 13.8 °C and 13.0 °C, respectively, and in both years there were 5-8 days precipitation (Tab. 2, Fig. 2). The average wind speed in autumn 1977 was 4.0 m/sec, but autumn 1978 was windy with a wind speed of 9.5 m/sec. The mean temperature in both autumn seasons declined from 15-19 °C in late August to about 11-14 °C in late September (Tab. 2).

Statistical methods

For analysing data with several variables, a linear ANOVA-model with GLM procedure was used. This approach performs a least squares regression to describe statistical relationships between several predictors and a continuous response variable. The GLM procedure performs multiple comparisons between factor level means to find significant differences (SAS 2021). These analytical procedures are termed ANOVA-model for short. Some specific tests with ANOVA-models are: (1) analyses of the daily catch of insects in relation to weather conditions with insect abundance (log number of insects and log total daily weight of insects analysed separately) as dependent variable and weather conditions as explanatory variables, (2) differences between food items in spring and autumn analysed for 10 bird species with 12 groups of food items as dependent variables (each group of food item analysed separately) and year, season (spring, autumn) and 10 insectivorous bird species as explanatory variables, (3) increase in body weight during the day was analysed with standardized body weights (see below) as the dependent variable and species, hours after sunrise and the daily number of insects caught as ex-

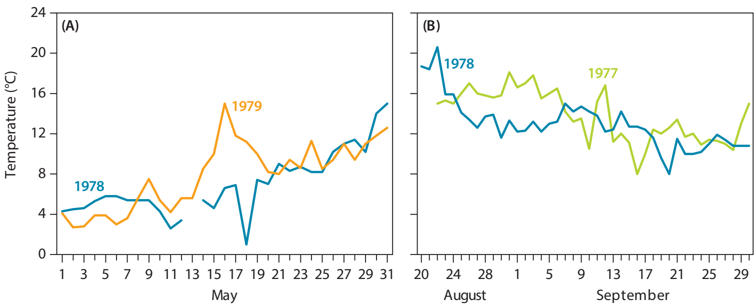


Fig. 2. Air temperature (°C) on Christiansø during spring (A) and autumn (B), 1977-1979.
Lufttemperatur (°C) på Christiansø forår (A) og efterår (B), 1977-79.

planatory variables, (4) differences in average number of arthropods in the gizzards between years and seasons were tested with log number of insects as the explanatory variable and species, year and hours after sunrise as dependent variables.

When analysing simple relationships, linear regression analysis was used. When analysing change in body weight during the day, values for body weight were standardized to account for differences in body weight between the species. The formula for the standardization was ($x_{standardize} = (x_{obs} - x_{mean})/x_{st.de}$) where x is body weight, x_{obs} is the observed body weight, x_{maen} is the mean body weight and $x_{st.de}$ is the standard deviation of body weight. By using this formula, the mean body weight of all species obtained the value =0 with variations that reflect heavy individuals (above the mean value) or light individuals (below the mean value; see Fig. 11) compared to mean body weight. For comparison of arthropod abundance between years a t-test was used. Log10 transformations were used to reduce variation. The statistical program SAS Enterprise Guide version 7.1 was used for the tests (SAS 2017). To facilitate reading, only a few test-values are given in the text. In several cases, only significant ($p < 0.05$) tests of correlation or differences between two datasets are indicated. For larger analyses, the test-results are given in tables.

Results

Abundance of insects and other arthropods

The suction trap caught mostly (>98%) flying insects. In the first half of May 1978 the catch of insects was 4.7 individuals per day, which subsequently increased to 98.0 per day in the second half of May. In 1979, the numbers of insects throughout May were more or less stable with an average number of 27.7 insects per day (Fig. 3). The mean weight per insect in 1978 was 0.16 mg per insect and 0.33 mg in 1979. However, there were no significant differences between the two years in the mean number of insects per day, but the mean weight per insect increased significantly from 1978 to 1979.

During the two autumn seasons, the daily catch of the suction trap was about 300-450 insects in late August, which declined to 100-200 insects by the end of September (Fig. 3). The decline was most pronounced in 1977. The average daily catch was 189.1 insects in 1977 and 240.1 in 1978, and these values were significantly different. The average weight per insects in the two autumn seasons was 0.35 mg and 0.48 mg, which was a statistically significant difference. The large variation in the average weight per insects was caused by a few, large insects, such as moths Lepidoptera, net-winged insects Neuroptera and large flies, large Muscidae.

The daily numbers of insects caught by the suction trap in spring were significantly correlated with the daily numbers of insects caught by the glue traps. However, there was no significant correlation during autumn.

There were significant positive relationships between temperature and the daily number of insects caught by the suction trap in spring and autumn (Fig. 4), whereas the relationship between temperature and the daily average weight per insect was significant during autumn but not in spring (Fig. 4).

In spring, the number and weight of arthropods per metre branch increased significantly from the beginning to the end of May. In autumn, the number of arthropods per metre branch increased significantly from end of August to end of September, whereas the weight of arthropods remained stable. There was no significant difference between years in the numbers of arthropods or the total weight of arthropods per metre branch in spring and in autumn. Between May and late August and September, the number of arthropods and the weight of arthropods per metre branch increased two fold for weight and eight fold for numbers (Fig. 5). However, from the end of May until late August and September only the number of arthropods per metre branch increased significantly, not the weight of arthropods per metre branch (Fig. 5).

Fig. 3. Numbers and weights (mg) of insects caught by suction trap during spring 1978 (A), spring 1979 (B), autumn 1977 (C) and autumn 1978 (D) on Christiansø. Absence of bar represents days with no information. *Fangst af insekter med sugefælde og den gennemsnitlige vægt pr. insekt (mg) i foråret 1978 (A), foråret 1979 (B), efteråret 1977 (C) og efteråret 1978 (D) på Christiansø. På dage uden søjle eller kurveforløb er der ikke foretaget fangst.*

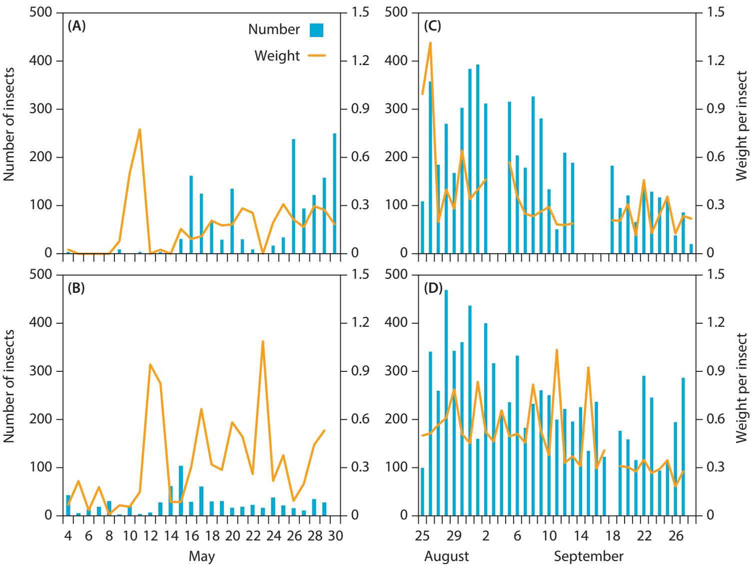


Fig. 4. Relationships between air temperature (°C) and (A) number of insects and (B) mean weight per insect caught by suction trap during spring and autumn on Christiansø. Data are log-transformed. *Sammenhæng mellem temperatur (°C) og (A) antallet af insekter og (B) den gennemsnitlige vægt pr. insekt fanget pr. dag i sugefælde, for- og efterår på Christiansø. Antal og vægt er log-transformeret.*

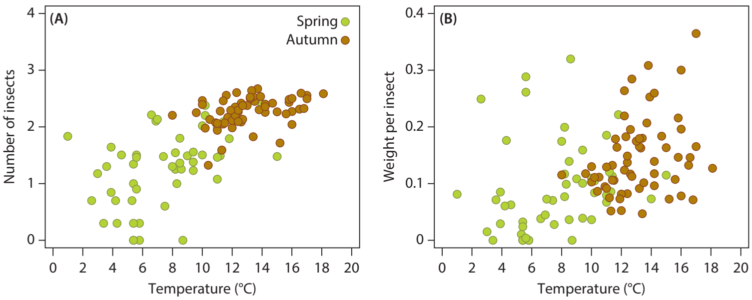
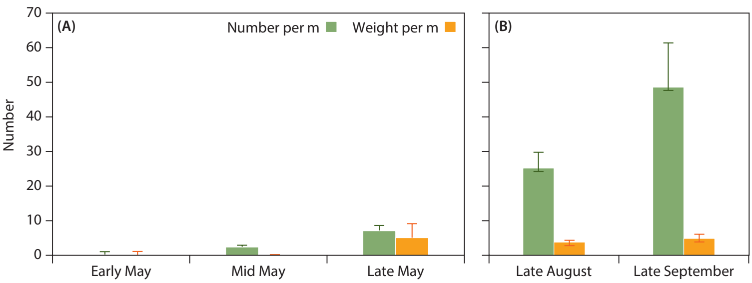


Fig. 5. Number and weight (mg) of arthropods per metre branch in spring (A) and autumn (B) on Christiansø. Numbers were estimated as the mean and standard error (+se) of all arthropods from the dominant trees and bushes during spring (1978-1979) and autumn (1977-1978). *Antal og vægt (mg) af leddyr pr. meter gren forår (A) og efterår (B) på Christiansø. Antallet er beregnet som gennemsnittet af leddyr på de dominerende træ- og buskarter, forår (1978-79) og efterår (1977-78). Grøn viser antal og orange vægten af leddyr pr. m gren. Standardfejlen (+se) er vist.*



Diet of bird species

The most abundant food items for all 13 bird species during the four seasons were Chironomidae 26.2%, followed by Hemiptera 13.9%, Hymenoptera 12.2%, Mycetophilidae 9.6% and anthers together with petals from flowers 7.8% (Fig. 6). The size of the smallest food item was 0.5 mm, the mean size of all food items was 3.3 mm, the mean of the largest food item in each gizzard was

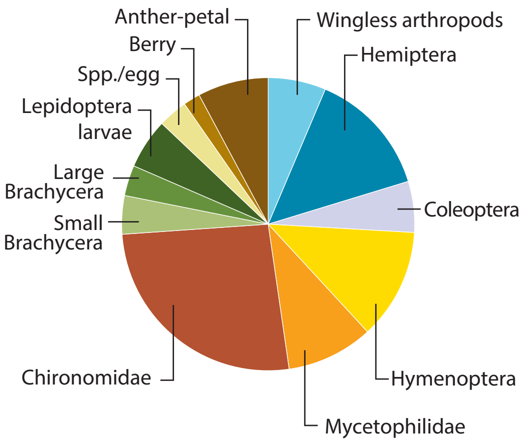


Fig. 6. Diet of 13 insectivorous bird species on Christiansø, spring and autumn 1977-1979 based on 25 056 food items. The diet was organised in 12 groups of food items. For the food item groups, see Appendix 1.
Den samlede føde for 13 insektædende fuglearter på Christiansø, forår og efterår, 1977-79 baseret på 25 056 fødeemner. Føden er samlet i 12 grupper af fødeemner. Se Appendiks 1 for alle fødeemner. Danske navne på fødegrupperne er vist i Tab. 3.

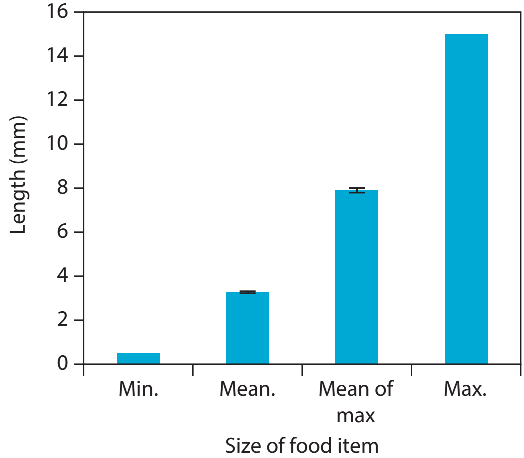


Fig. 7. Size of diet items shown as minimum, mean and standard error (se), mean and standard error of maximum (se) and absolute maximum size (mm) of all food items in 13 insectivorous bird species on Christiansø.
Den minimale, gennemsnitlige og maksimale størrelsen af alle fødeemner taget af 13 insektædende fuglearter angivet som det mindste fødeemne (Min.), den gennemsnitlige størrelse af fødeemner (Mean), gennemsnittet af det største fødeemne for hvert individ (Mean of max), og det største fødeemne blandt alle individer (Max.). For den gennemsnitlige størrelse og for gennemsnittet af de maksimale størrelser er standardfejlen (± se) vist.

7.9 mm, and the overall largest food item was 15.0 mm (Fig. 7). An overview of the diet of all species is shown in Appendix 1.

An overall analysis of food items taken by the 10 bird species caught in both seasons showed significant differences between the bird species for eleven food items and significant differences between spring and autumn for 10 food items (Tab. 3). No significant differences were found for the group of non-identified food items including eggs. Moreover, the size of food items showed significant differences between the bird species for mean and the maximum size of food items (Tab. 3).

Comparison of diet in spring and autumn

More detailed analyses of food items between spring and autumn were made for the 10 passerine species sampled in both seasons. The proportions of the five most common food items taken in the two seasons for the species were for Chironomidae (spring: 13.0%, autumn: 28.3%), Hemiptera (spring: 13.1, autumn: 14.1%), Hymenoptera (spring: 7.5%, autumn: 15.3%), Mycetophilidae (spring: 18.5%, autumn: 3.4%) and anthers from flowers (spring: 6.6%, autumn: 9.1%). Among these food items, the largest differences between spring and autumn were found for Chironomidae, Hymenoptera and Mycetophilidae.

Comparisons of the diet of the 10 species in spring and autumn showed significant differences between the two seasons for nine species (Fig. 8). Only Wood Warbler did not show any significant differences, probably due to small sample size (Tab. 1). For the other species, there were significant differences in the diet between spring and autumn in one food item for Chiffchaff, three food items for Whitethroat and Spotted Flycatcher, four food items for Pied Flycatcher, five food items for Redstart, six food items for Blackcap, seven food items for Lesser Whitethroat and eight food items for Willow Warbler and Garden Warbler (Fig. 8).

Comparing the food items taken in spring and autumn, seven bird species showed significant differences in the amounts of Mycetophilidae (include also Bibionidae, Cecidomyiidae, Tipulidae) and small sized Brachycera (Syrphidae, Chloropidae, Agromyzidae), four bird species showed differences in the amounts of wingless arthropods, Hemiptera, Hymenoptera and berries, three bird species showed differences in Coleoptera, Chironomidae and big sized Brachycera (Tachinidae, Muscidae, Calliphoridae), and two bird species showed differences in Lepidoptera larvae, non-specified food items (including eggs) and anthers from flowers (Fig. 8). In short, during spring the bird species took mainly Mycetophilidae

Tab. 3. Results of linear ANOVA models with GLM procedure analysing relationships between 12 food item groups (dependent variable) and year, season (spring, autumn) and 10 insectivorous passerine species as explanatory variables. Each food item group was analysed separately. Statistically significant values are shown in bold. The food item groups given are a mixture of ecological and systematic groups; see Appendix 1.
Resultaterne af lineære ANOVA-modeller med GLM-procedure til analyse af relationerne mellem 12 grupper af fødeemner (afhængig variabel) og år, årstid (forår og efterår) og 10 insektædende fuglearter som forklarende variable. Hvert fødeemne er analyseret separat. Statistisk signifikante værdier er angivet med fed skrift. Fødeemnerne er opdelt i en blanding af systematiske og økologiske grupper; se Appendiks 1.

		Year *År*		Season *Årstid*		Bird species *Fuglearter*	
Food item groups *Fødeemne grupper*	*df*	*F*	*p*	*F*	*p*	*F*	*p*
Wingless arthropods *Vingeløse leddyr*	1,1104	30.76	**0.0001**	15.71	**<0.0001**	37.35	**<0.0001**
Hemiptera *Næbmunde*	1,1104	29.52	**<0.0001**	3.13	0.0771	176.42	**<0.0001**
Coleoptera *Biller*	1,1104	1.64	0.2008	6.00	**0.0145**	5.60	**0.0181**
Hymenoptera *Årevinger*	1,1104	3.22	0.0728	93.31	**<0.0001**	12.89	**0.0003**
Mycetohpilidae *Svampemyg*	1,1104	68.67	**<0.0001**	265.12	**<0.0001**	44.10	**<0.0001**
Chironomidae *Dansemyg*	1,1104	3.17	0.0753	29.04	**<0.0001**	283.01	**<0.0001**
Small Brachycera *Små fluer*	1,1104	52.29	**<0.0001**	198.04	**<0.0001**	39.31	**<0.0001**
Large Brachycera *Store fluer*	1,1104	9.96	**0.0016**	227	0.1321	16.80	**<0.0001**
Lepidoptera larvae *Sommerfugle larver*	1,1104	4.69	**0.0306**	12.17	**0.0005**	5.62	**0.0179**
Spp. and eggs *Spp. og æg*	1,1104	0.55	0.4567	6.890	**0.0008**	0.30	0.5844
Berries *Bær*	1,1104	39.29	**<0.0001**	177.19	**<0.0001**	110.37	**<0.0001**
Anthers and petals *Støvblade og kronblade*	1,1104	9.70	**0.0019**	24.27	**<0.0001**	126.32	**<0.0001**
Diet size *Fødeemne, størrelse*							
Mean *Gennemsnit*	1,1093	6.34	**0.0119**	5.20	**0.0228**	179.70	**<0.0001**
Maximum *Maksimum*	1,1093	1.44	0.2303	20.73	**<0.0001**	12.04	**0.0005**

and Lepidoptera larvae and in autumn mostly Hymenoptera, Chironomidae and anthers.

The average number of insects in the gizzard of the 10 passerine species was significantly higher in spring 1978 than in spring 1979 (mean (se) 20.8 (1.4) vs. 14.4 (1.2)), whereas no differences were found between the average number of insects in gizzards in autumn 1977 and 1978.

Diet during spring

In spring, significant differences between the diet of the bird species were found for the numbers of wingless arthropods, Coleoptera, Hymenoptera, Chironomidae, small sized Brachycera, large sized Brachycera, berries and anthers. In addition, the mean size and the maximum size of the food items were significantly different between the bird species. Of more specific food items, ladybirds Coccinellidae and ants Formicidae were especially taken in spring.

Diet during autumn

The diet in autumn showed significant differences between the bird species in the number of wingless arthropods, Hemiptera, Hymenoptera, Chironomidae, Mycetophilidae, small sized Brachycera, large sized Brachycera, berries and anthers from flowers. In addition, there were significant differences between the mean size of the food items taken by the bird species, but not for the maximum food size taken.

Diet of three bird species in either spring or autumn

The three species studied only in one season are interesting because they are different from the 10 species already presented. Goldcrest has the smallest body size, Robin takes food items at or near the ground, and Icterine Warbler forages in the canopies (Glutz & Bauer 1988, 1991a). The diets of Icterine Warbler and Robin, both sampled in spring, were significantly different. The Robin took mainly Hemiptera, Coleoptera and Hymenoptera (mostly ants, Formicidae), whereas the Icterine Warbler mainly took Chironomidae, Mycetophilidae and large sized Brachycera (Fig. 9). The diet of the two species confirms that they forage at different heights of the vegetation. There was no difference between the sizes of the prey taken by the two species.

Goldcrest and Chiffchaff were the morphologically most similar species among the warblers in autumn 1978, when both were sampled. Nevertheless, there were significant differences between their diet. Gold-

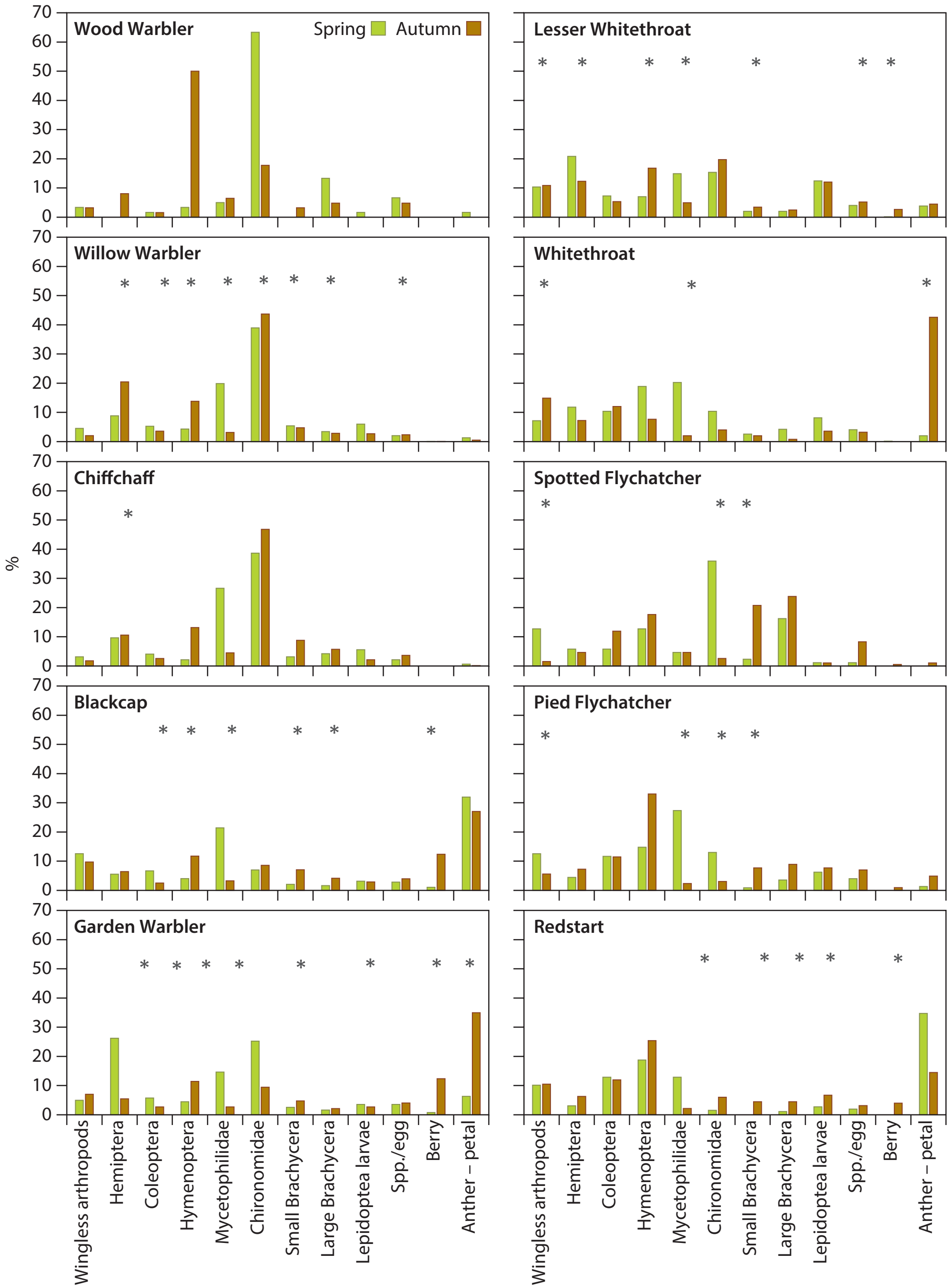


Fig. 8. Diet organised in 12 groups of food items of 10 insectivorous bird species on Christiansø during spring and autumn. An asterisk indicates statistically significant differences between spring and autumn ($p < 0.05$).
Ti insektædende fuglearters føde på Christiansø for- og efterår fordelt på 12 grupper af fødeemner. En stjerne angiver at der er signifikant (p < 0,05) forskel på fødeemnet forår (grøn) og efterår (brun). Arterne er fra venstre øverst og nedefter: Skovsanger, Løvsanger, Gransanger, Munk, Havesanger, Gærdesanger, Tornsanger, Broget Fluesnapper, Grå Fluesnapper og Rødstjert. Danske navne på fødeemnerne er vist i Tab. 3.

crest mostly took Hemiptera and Lepidoptera larvae, whereas Chiffchaff took small and large sized Brachycera. It was moreover remarkable that the Goldcrest, the species with the smallest body size, took significantly larger food items than Chiffchaff.

Diet in relation to catch site

The analyses showed that the amounts of wingless arthropods, large sized Brachycera and Lepidoptera larvae in the diet were significantly different between the catch sites in spring. During autumn, there were significant differences in the amounts of wingless arthropods and Chironomidae between the catch sites. These results indicate that diet reflects the habitat adjacent to the catch sites.

Availability of insects and diet

To compare the diet of the bird species with the daily number of insects caught by the suction trap, the food items of the birds were pooled into two groups: non-flying and flying food items. The non-flying food items were primarily arthropods that move around in and on the vegetation and seldom fly or are incapable of flying (wingless arthropods, Coleoptera and Lepidoptera larvae). The flying food items were Hemiptera, Chironomidae, Mycetophilidae, Hymenoptera, and small and large sized Brachycera. Both in spring and autumn, significant and positive relationships were found between the numbers of flying food items in the diet and the daily number of insects caught. However, a significant correlation was also found between the number of non-flying food items in the diet and the daily catch of insects (Fig. 10, Tab. 4). Using the daily total weight of insects caught, instead of the number of insects, the significant level of the test increased for both spring and autumn (Tab. 4).

Increase in body weight during the day

Increase in body weight indicates whether during stopover the birds replenish their body reserves to continue migration. Thus, whether body weight increased in spring and autumn while staying on the island was analysed for the six *Phylloscopus* and *Sylvia/Curruca* species. In spring, the results showed no significant relationships between body weight and hours after sunrise. However, there were significant differences between the two spring seasons in that body weight decreased more in 1979 than in 1978.

In autumn, body weight increased with numbers of hours after sunrise (Tab. 5, Fig. 11). The trend line in Fig. 11 is described by the equation: $y = 0.0294x - 0.0119$, where y is body weight and x is number of hours after sunrise, which shows that body weight in autumn increased by 0.24 g after eight hours. From Fig. 11 it appears that the number of birds caught in the mist nets decreased after about 4 hours, i.e. the overall mean catch time in hours after sunrise on the island was significantly shorter during spring compared to autumn (3.76 hours vs. 4.19 hours; see discussion).

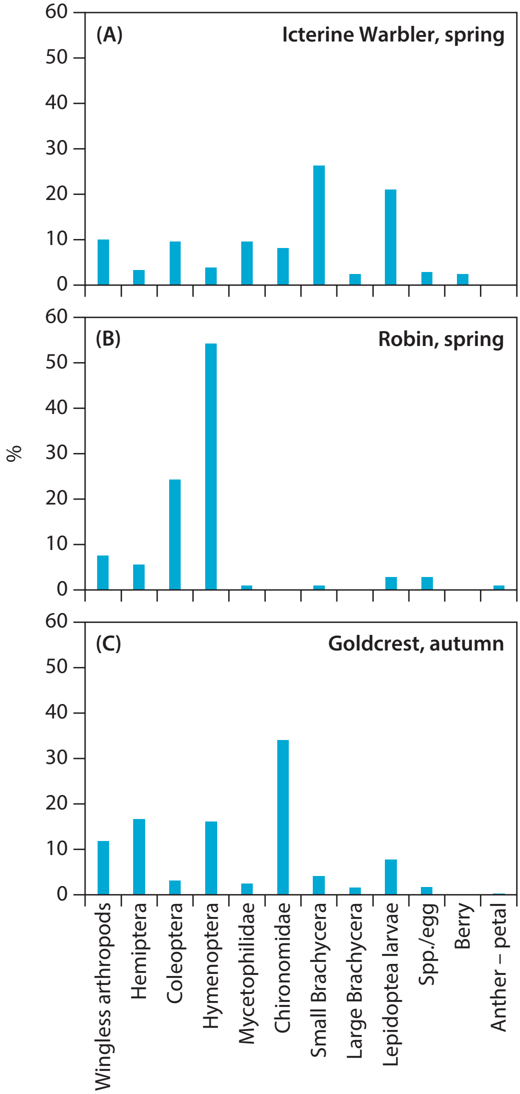


Fig. 9. Diet of three bird species on Christiansø: (A) Icterine Warbler, spring; (B) Robin, spring; (C) Goldcrest, autumn.
Fødeemner for tre fuglearter på Christiansø: (A) Gulbug, forår; (B) Rødhals, forår; (C) Fuglekonge, efterår. Danske navne på fødeemnerne er vist i Tab. 3.

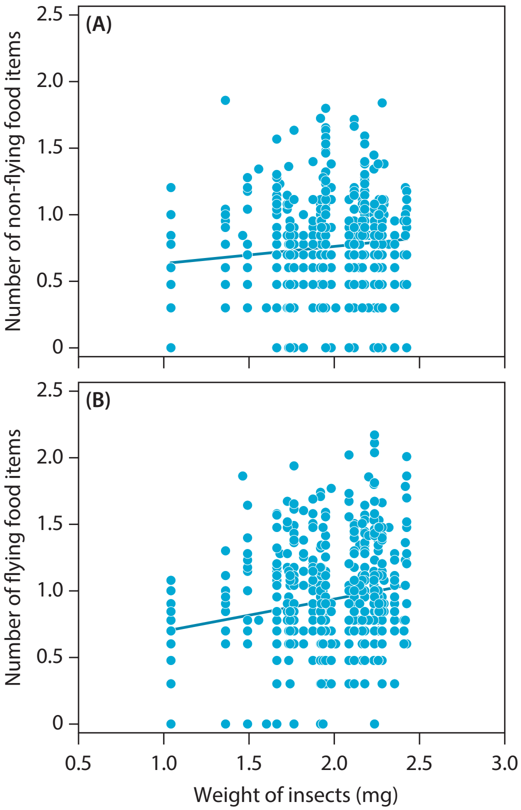


Fig. 10. Relationship between number of non-flying food items (A) and flying food items (B) taken by 10 insectivorous bird species during autumn on Christiansø in relation to the total, daily weight of flying insects caught by suction trap on the day the bird was caught and the diet analysed. Data are log-transformed. For definition of non-flying food items and flying food items, see Tab. 4.
Antal fødeemner af ikke flyvende byttedyr (A) og fødeemner fra flyvende byttedyr (B) taget af 10 insektædende fuglearter i relation til den daglige vægt af insekter fanget med sugefælde om efteråret på Christiansø på den dag, fuglene blev fanget og deres føde analyseret. Data er log-transformeret. For gruppering af ikke flyvende og flyvende insekter, se Tab. 4.

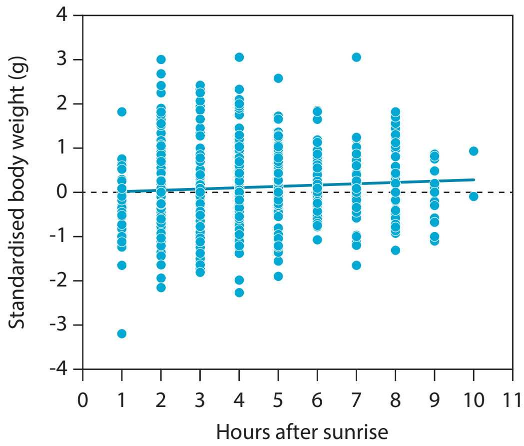


Fig. 11. Standardised body weight (g) of six insectivorous bird species during autumn in relation to number of hours after sunrise on Christiansø. The trend line is shown (y = 0.0294x – 0.0119). Based on 453 birds.
Standardiseret kropsvægt (g) hos seks insektædende fuglearter i relation til antal timer efter solopgang om efteråret på Christiansø. Tendenslinjen er vist (y = 0,0294x – 0.0119). Baseret på 453 fugle.

Discussion

Diet of bird species

The results from Christiansø show that the species demonstrated differences in diet within seasons, confirming the main hypothesis. In addition, the species also demonstrated opportunistic food choice by taking different food items in spring and autumn while still demonstrating differences in diet between the species. The differences in diet may be caused by morphological and behavioural differences. The bird species move through the vegetation in different ways and at different speeds (Rabøl 1992), taking the food items they encounter and are able to catch and hold. Most species are primarily gleaners like Willow Warbler, Chiffchaff, Lesser Whitethroat, Whitethroat, Blackcap and Garden Warblers that take insects from leaves or twigs, some are able to hover like Chiffchaff and Willow Warbler and take insects from the vegetation when flying, and some are perching species that spot prey from the distance and take it on the ground such as Redstart, or in the air such as Pied and Spotted Flycatchers (Miles & Ricklefs 1984, Rabøl 1992). However, it is not only feeding behaviour that may influence the diet, and species body size and wing and beak morphology may also be involved. On Christiansø more than half of the food items are small flying insects such as mosquitos, flies and wasps, which may be easier to catch for bird species with a small body size and for species with long wings. These morphological aspects in relation to prey species will be treated later (Laursen submitted).

Compared to breeding season, diet studies of migrating passerines are few and generally show that the diet is more opportunistic than during the breeding season; for example Lesser Whitethroats in Israel took 138 different food items, compared to 58 during the breeding season (Boren & Safriel 1974). Insects such as ants and aphids that occur in large numbers in southern Europe

Tab. 4. Results of linear regression analyses of numbers of non-flying and flying food item groups taken by 10 insectivorous passerine species (dependent variables) in relation to daily catch of insects (number), weight of insects caught (mg) and mean weight per insect caught (mg) as explanatory variables in spring (upper panel) and autumn (lower panel). Non-flying food items: Wingless arthropods, Coleoptera and Lepidoptera larvae. Flying food items: Hemiptera, Chironomidae, Mycetophilidae, Hymenoptera, small and large Brachycera. Statistically significant results are given by bold.
Lineære regressions analyser af antallet af ikke flyvende og flyvende fødeemner taget af 10 insektædende fuglearter (afhængig variabel) i relation til den daglige fangst med sugefælde af antal insekter, vægten af insekterne (mg) og den gennemsnitlige vægt (mg) pr. insekt (forklarende variable) henholdsvis forår (øverst) og efterår (nederst). Ikke flyvende fødeemner: Vingeløse leddyr, biller og sommerfuglelarver. Flyvende fødeemner: Næbmunde, dansemyg, svampemyg, årevinger, små og store fluer. Statistisk signifikante sammenhænge er markeret med fed skrift.

Food item groups *Fødeemner*	Number, insects caught *Antal fangede insekter*		Weight, insects caught *Vægten af fangede insekter*		Weight per insect caught *Vægt pr. fanget insekt*	
	T	*p*	*T*	*p*	*T*	*p*
Spring, n = 511 *Forår, n = 511*						
Non-flying food items *Ikke flyvende fødeemner*	0.728	0.4348	3.17	**0.0016**	4.41	**<0.0001**
Flying food items *Flyvende fødeemner*	2.67	**0.0078**	3.90	**0.0001**	0.94	0.3484
Autumn, n = 523 *Efterår, n = 523*						
Non-flying food items *Ikke flyvende fødeemner*	2.06	**0.0402**	2.73	**0.0065**	2.77	**0.0058**
Flying food items *Flyvende fødeemner*	2.67	**0.0078**	3.90	**0.0001**	0.94	0.3484

were taken by Robin and Pied Flycatcher, together with grasshoppers, woodlice and earth worms (Glutz & Bauer 1988). Goldcrests in spring in Denmark took springtails (Collembola), spiders, and plant lice (Psylloidea) (Laursen 1976). The diet of *Sylvia/Curruca* warblers during autumn in Germany and Spain was made up of plant materials that could made up to 90% of the diet (Krool 1972, Glutz & Bauer 1991b). Other plant based items such as anthers and nectar were taken during spring in Denmark (Laursen 1979).

When information obtained from studies of migration at other localities is compared with the diets described here for Christiansø, the species take mainly the same food items, although there are some differences. The passerines studied on Christiansø took a great number of Chironomidae, Mycetophilidae and stamens from flowers together with food items that normally are avoided due to bad taste, such as ladybirds and ants (both especially in spring), or items of low energetic value such as ticks, springtails and small butterflies Psychididae. These food items support the interpretation that the diet on Christiansø was opportunistic, but may also indicate that the amount of available food was low. The food amount was especially low in spring 1979 after cold weather in March and April (Lindhardt & Rosenørn 2007), which was reflected in lower numbers of food items in the gizzards compared to spring 1978. The scarcity of food during spring was underlined by observations on Christiansø when Chiffchaffs and Willow Warblers were perched around small ponds wait-

Tab. 5. Results of linear ANOVA analyses with GLM procedure of standardized body weight (g) of six insectivorous passerine species in autumn (dependent variable) on Christiansø in relation to bird species, number of hours after sunrise and daily number of flying insects caught (explanatory variables). Statistically significant results are given in bold.
Resultatet af en lineær ANOVA-analyse med GLM-procedure mellem kropsvægten (g) for seks insektædende fuglearter (afhængig variabel) på Christiansø i relation til årstid (for- og efterår), fugleart, antal timer efter solopgang og det daglige antal fangne insekter (forklarende variable). Statistisk signifikante forskelle er vist med fed skrift.

Variables *Variabler*	*df*	*F*	*p*	Estimat (se)
Bird species *Fuglearter*	1,513	0.42	0.5193	0.0087 (0.0135)
Hours after sunrise *Antal timer efter solopgang*	1,513	5.54	**0.0190**	0.0480 (0.0204)
Number of flying insects *Antal flyvende insekter*	1,513	9.28	**0.0024**	0.6500 (0.1330)

ing for Chironomidae to emerge from their pupae. The Chironomidae were taken either from the water surface or during a short flight. Similar behaviour was for Willow Warblers in Norway when food was scarce (Glutz & Bauer 1991b).

Diet and weather conditions

The positive relationship between the daily numbers of insects caught in the suction trap and the numbers of flying and non-flying items in the diet indicate that it is the same climatic factors that stimulate the activity of both flying and non-flying arthropods and expose them to birds (see also Lewis & Taylor 1964, Bale *et al.* 2002). The results show that temperature is the main factor for arthropod activity. However, as insects could not be collected during strong winds, the analysis of this relationship may be biased. An important factor, not included in this study, is the timing of leaf bloom in spring. This is related to the ambient temperature (Slagsvold 1976) and in other studies has been shown to govern insect appearance and abundance in the diet of insectivorous birds (Varley *et al.* 1973, Crawley & Akhteruzzaman 1988). In a larger perspective, the relationship between temperature and occurrence of insects has changed the phenology of bird migration recorded on Christiansø due to earlier increase in spring temperature in recent years (Tøttrup *et al*. 2006).

Diet in relation to catch site

The diet reflected the catch site of the birds on the island. This was an unexpected result due to the small size and rather uniform vegetation of the island. The result may indicate at least three issues. First, that diet studies may be an effective method when microhabitats of ecologically related species are studied, since small differences can be detected. Second, that the arthropod fauna was different in different parts of the island. Third, that the birds only move over short distances or that they stay in the same microhabitat (e.g. open vs. dense vegetation). However, the general impression of the activity of the birds on the island does not support the notion that the birds move over short distances. However, some species e.g. Pied Flycatcher and Lesser Whitethroat may defend small territories, a behaviour that has also been described for other species at stopover sites (Bibby & Green 1980, Carpenter *et al*. 1993).

Food and body weight

Competition for food and derived impact on weight gain among staging migrant passerines have been demonstrated both by observations and experiments (Moore & Yong 1991, Fransson 1998, Studds *et al.* 2005). At geographically extensive stopover sites, studies indicate that there is plenty of food available for staging birds (Buler *et al.* 2007, Carlie *et al.* 2012, Telleria *et al.* 2013, Cohen et al. 2020). However, at sites of limited size such as small islands, food is scarce, staging birds may consume a considerable proportion of the available insects (Moore & Yong 1991) and competition for food may exist between species (Laursen 1979).

On Christiansø, the weight of six insectivorous passerines increased during autumn, indicating that sufficient food was available during autumn. The increase found was of the same magnitude as found for a passerine species in Portugal in autumn (Bibby & Green 1980). However, this was not the case in spring when no change in weight on Christiansø could be detected. Another result that may indicate lack of food in spring is that the overall mean time taken to catch birds for ringing decreased; this observation may indicate that the birds decrease their activity earlier in spring than in autumn, i.e. that they stopped moving around on the island. Another explanation could be that birds leave the island earlier during spring, and during the daytime, than during autumn. Moreover, food conditions may vary during spring as found for 1979, where body weight was lower, compared to 1978. Taken together these results indicate strong competition for food in spring. In contrast to Christiansø, which appears to be less suited as a staging area for insectivorous migrants in spring, a study in spring on another small Danish island showed that Robins increased their weight by 2 g during the day (Petersen 1972), indicating that local conditions, diet food items taken and probably also temporal variation may play a role in food availability for the migrant birds.

In this diet study, the ringers chose the individuals with the highest body weight if possible. This choice may imply that the estimations of body weight presented here could be biased if the ringers selected relatively more birds with low body weight during the first hours after sunrise as well as relatively more birds with high body weight later during the day. However, it is assumed that the selection of birds was constant during the day, and if so, selection would probably not have had any effect on the result. However, more birds were weighed during the ringing activity than those included in this study. Analysing this large data set could provide more information than presented here about weight changes of birds staging at Christiansø.

Is Christiansø actually an ecological trap for less fit migrants in spring? This could be supported by several

passerine skeletons and corpses located in sheltered sites on the island in some springs (D. Boertmann *pers. com.*). However, the fraction of recaptured ringed passerines is almost the same for birds ringed in autumn and in spring, which suggests the same possibility of survival and recapture (Lausten & Lyngs 2004), which is an issue for further study.

Acknowledgements

The studies on Christiansø could not have been done without great help by the island's bird ringers. Special thanks go to Stefan Pihl and three now deceased ornithologists: Flemming Christensen, Peter Lyngs and Finn Dalberg Petersen. In addition, many thanks go to Jørgen Rabøl for several inspiring discussions and support, to Eigil Holm for at fruitful cooperation, and to David Boertmann for useful comments and suggestions. Nick Quist Nathaniels kindly corrected my English.

Ethical statement

The non-destructive methods used in this study to take diet samples from birds was described by Moody (1970), and the method has been used in several studies in a number of countries. An application for approval of the method to be used in Denmark was sent to the Danish Veterinary and Food Administration but approval was not granted. However, this response was received until most of the samples had already been taken. It was therefore decided to publish the results as they contain important information about the ecology of migratory birds in general and for one of the most studied island sites for staging passerines in particular.

Resumé

Insektædende fuglearters fødevalg er forskellig under rast i samme habitat både forår og efterår

I yngletiden forekommer insektædende fuglearter ofte i forskellige habitattyper, fordi de dermed reducerer deres indbyrdes konkurrence. Men hvordan reagerer arterne, når de af naturlige årsager er tvunget til at være i samme habitat og på en begrænset plads. Det er undersøgt ved et naturligt eksperiment, hvor deres indbyrdes relationer er belyst under forhold, hvor arterne forekommer sammen i stort antal i samme habitattype. Med fokus på arternes føde blev undersøgelsen udført på Christiansø gennem to forår og to efterår. Da Christiansø har en beskeden størrelse (22 ha) og ofte har et stort antal rastende småfugle, antages det at konkurrencen blandt de rastende fugle er stor. Som et resultat af arternes selektion og tilpasning forventes det, at de udnytter deres morfologiske forskelligheder som kropstørrelse, vingelængde og næb til at tage en føde, der er forskellig fra andre arters.

Føden blev undersøgt ved hjælp af en ikke destruktiv metode for 13 insektædende fuglearter, omfattende 1141 individer med bestemmelse af 25 056 fødeemner fra 72 taksonomiske og økologiske grupper. Under bearbejdningen blev disse samlet i 12 grupper af fødeemner. Ti af de 13 fuglearter blev undersøgt både forår og efterår. Insektmængden på øen blev registreret (næsten) dagligt.

Resultaterne viste, at 1) for de 10 arter, som forekom både for- og efterår, var der signifikante forskelle på fødeemnerne mellem arterne og på størrelsen af føden; 2) for ni ud af de 10 arter var der signifikante forskelle på fødeemnerne mellem de to årstider; 3) fuglearternes fødevalg afspejlede den daglige insektmængde; 4) arternes føde var forskellig alt efter, hvor på øen de blev fanget; 5) arterne forøgede deres kropsvægt om efteråret med gennemsnitlig 0,24 g fra solopgang og otte timer frem, hvorimod der ikke var signifikante ændringer af kropsvægten om foråret. Det er en forskel, som afspejler, at der var 4-8 gange så mange insekter på Christiansø om efteråret som om foråret.

Resultaterne viser, at Christiansø om foråret ikke bidrager til at forøge de insektædende fuglenes kondition, og at den kan fungere som en økologisk fælde i visse forår. For føden konkluderes det, at der var indbyrdes forskelle i arternes fødevalg både forår og efterår. Desuden demonstrerede arterne opportunisme i deres fødevalg ved bl.a. at have forskellig fødesammensætning i de to årstider.

References

Alatalo, R.V., L. Gustafsson & A. Lundberg 1986: Interspecific competition and niche shifts in tits Parus: evolution of non-experimental data. – Am. Nat. 127: 819-834.

Alerstam, T. 1990: Bird Migration. – Cambridge University Press.

Bale, J.S., G.J. Masters, I.D. Hodkinson, G.C. Awmack … & J.B. Whittaker 2002: Herbivory in global climate changes research: direct effects of rising temperature on insect herbivores. – Global Change Biol. 8: 1-16.

Berthold, P. 2001: Bird Migration: A General Survey. – Oxford University Press.

Bibby, C.J. & R.E. Green 1980: Foraging behavior of migrant Pied Flycatchers, *Ficedula hypoleuca*, on temporary territories. – J. Anim. Ecol. 49: 507-521.

Boren, N. & U. Safriel 1974: Food overlap and competition in temporally coexisting Sylviid species. – Israel J. Zool. 23: 219-220.

Buler, J.J., F.J. Moore & S. Woltmann 2007: A multi-scale examination of stop over habitats use by birds. – Ecology 88: 1789-1802.
Carlie, J.D., K.L. Olmstead & C.H. Richart 2012: Food availability, foraging behavior and diet of autumn migrant landbirds in the Boise foothills of Southwestern Idaho. – Condor 114: 449-461.
Carpenter, F.L., M.A. Hixon & E.J. Temeles 1993: Interference asymmetries among age-sex classes or Rufous Hummingbirds during migratory stopovers. – Behav. Ecol. Sociobiol. 33: 297-304.
Christiansø 2021: Christiansø field station. https://chroe.dk/
Cody, M.L. 1974: Competition and structure of bird communities. – Princeton University press.
Cody, M.L. 1978: Habitat selection and interspecific territoriality among Sylviid warblers of England and Sweden. – Ecol. Monog. 48: 351-396.
Cohen, E.B., K.G. Horton, P.P. Marra, H.L. Clipp … & J.J. Buler 2020: A place to land: spatiotemporal drivers of stopover habitat use by migratory birds. – Ecol. Lett. Doi. 10.1111/ele. 13618
Crawley, M. & M. Akhteruzzaman 1988: Individual variation in the phenology of oak trees and its consequences for herbivorous insects. – Funct. Ecol. 2: 409-415.
Darwin, C. 1859: On the Origin of Species. – Broadview Texts.
Fransson, T. 1998: A feeding experiment on migratory fueling in whitethroats, *Sylvia communis*. – Anim. Behav. 55: 153-162.
Glutz, U.N. & K.M. Bauer 1988, 1991a, 1991b, 1993: Handbuch der Vögel Mitteleuropas. – AULA-Verlag GmbH, Wiesbaden.
Haftorn, S. 1956: A comparative analysis of *Parus atricapillus* L., *P. cristatus* L. and *P. ater* L. – Kgl. Norsk. Vid. Selsk. Skr. 2: 1-54.
Hespenheide, H.A. 1971: Food preference and the extent of overlap in some insectivorous birds, with special reference to the Tyrannidae. – Ibis 113: 59-71.
Hahn, S., S. Bauer & F. Liechti 2009: The natural link between Europe and Africa – 2.1 billion birds migration. – Oikos 118: 624-626.
Thorup. K., A.P. Tøttrup, M. Willmoes, R.H.G., Klassen… & C. Rahbek 2017: Resource tracking within and across continents in long-distance bird migrants. – Sci. Adv. 3:e1601360
Howlet, P., I. Jüttner & S.J. Ormerod 2000: Migration strategies of Sylviid warblers: change patterns or community dynamics. – J. Avian Biol. 31: 20-30.
Klinner, T., J. Buddemeier, F. Barlain & H. Schmaljohann 2020: Decission-making in migatory birds at stopover. – Behav. Ecol. and Sociobiol. 74: 10. https://link.springer.com/article/10.1007/s00265-019-2784-7
Kroll, H. 1972: Nahrungsökologie der Gartengrasmücke beim Herbstzug 1969 auf Helgoland. – Voglwarte 26: 280-285.
Laursen, K. 1976: Feeding ecology of the Goldcrest during spring migration in Denmark. – Vogelwarte 28: 180-190.
Laursen, K. 1979: Interspecific relationships between some insectivorous passerine species illustrated by their diet during spring migration. – Ornis Scand. 9: 178-192.
Laursen, K. submitted: Prey size reflects morphology of insectivorous bird species when staging spring and autumn in the same habitat.
Lausten, M. & P. Lyngs 2004: Trækfugle på Christiansø 1976-2001. – Christiansø Naturvidenskabelige Feltstation.
Lewis, T. & L.R. Taylor 1964: Diurnal periodicity of flight by insects. – Trans. R. Ent. Sci. Lond. 116: 393-476.
Lindhardt, K. & S. Rosenørn 2007: Dansk vejr i 100 år. – Aschehoug Dansk Forlag A/S.
MacArthur, R.H. 1958: Population ecology of some warblers of northeastern coniferous forest. – Ecology 39: 599-619.
Miles, D.B. & R.E. Ricklefs 1984: The correlation between ecology and morphology in deciduous forest passerine birds. – Ecology 65: 1629-1640.
Moody, D.T. 1970: A method for obtaining food samples from insectivorous birds. – Auk 87: 579.
Moore, F.R. & W. Yong 1991: Evidence of food-based competition among passerine migrants during stopover. – Behav. Sociobiol. 28: 85-90.
Morse, D.H. 1971: The insectivorous bird as an adaptive strategy. – Ann. Rev. Ecol. Syst. 2: 177-200.
Nussbaumer, R., S. Bauer, L. Benoit, G. Mariethoz … & B. Schmid 2021: Modelling the flow of nocturnal bird migration with year-round European weather radar network. – BioRxiv. Doi: org/10.1101/2020.10.13.321844
Petersen, F.D. 1972: Weight-changes at Hesselø in night migrating passerine due to time of day, season and environmental factors. – Dansk Orn. Foren. Tidsskr. 66: 97-107.
Price, T. 1991: Morphology and ecology of breeding warblers along an altitudinal gradient in Kasmir. India. – J. Anim. Ecol. 60: 643-664.
Rabøl, J. 1987: Coexistence and competition between overwintering Willow warblers *Phylloscopus trochilus* and local warblers at lake Naivasha, Kenya. – Ornis Scand. 18: 101-121.
Rabøl, J. 1988: Fuglenes træk og orientering. – Bogans Forlag.
Rabøl, J. 1990: Competition between over-wintering Willow Warblers *Phylloscopus trochilus* and local warblers in the acacia-savanna in Kenya. – Proc. Seventh Nordic Congr. Ornithol.: 76-96.
Rabøl, J. 1992: Foraging behavior and habitat distribution of migrant passerines on Christiansø. – Unpublished report from Institute of population Biology, University of Copenhagen.
Rosamond, K.M., C.M. Kent, S.C. Hunter & T.W. Sherry 2020: Morphological traits influence prey selection by coexisting species of New World warblers (Parulidae). – J. Field Ornithol. 91: 393-408.
SAS 2017: Enterprise Guide 7.1. – SAS Institute.
SAS 2021: SAS user's guide 13.1. https://support.sas.com/documentation/onlinedoc/stat/131/glm.pdf
Schoener, T.W. 1965: The evolution of bill size differences among sympatric congeneric species of birds. – Evolution 19: 189-213.
Sjöberg, S., L. Pedersen, G. Malmiga, T. Alerstam … & J. Backman 2018: Barometer logging reveals new dimensions of individual songbird migration. – J. Avian Biol. 49: e01821. Doi: 10.1111/jav.01821
Slagsvold, T. 1976: Annual and geographical variation in time of breeding of Great tit *Parus major* and Pied flycatcher *Ficedula hypoleuca* in relation to environmental phenology and spring temperature. – Ornis Scand. 7: 127-145.
Studds, C.E. & P.P. Morra 2005: Nonbreeding habitat occupancy population processes: An upgrade experiment with migratory birds. – Ecology 86: 2380-2385.
Telleria, L.J., M. Blazquez & I. De La Hera 2013: Migratory and resident Blackcaps *Sylvia atricapilla* wintering in southern Spain show resource portioning. – Ibis 155: 750-761.
Tøttrup, A.P., K. Thorup & C. Rahbek 2006: Long-term phenological changes in spring migration through Northern Europe: a comparative approach. – J. Ornithol. 147: 51-52
Varley, G.C., G.R. Gradwell & M.P. Hassel 1973: Insect population ecology. – Blackwell. Oxford.

Appendix 1: https://pub.dof.dk/link/2022/2a.appendiks1

Author address:
Stavlundvej 11, DK-7540 Haderup, Denmark