

## Influence of seasonality, temperature and rainfall on the winter diet of the long-eared owl, *Asio otus*

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**A b s t r a c t.** In this study we analysed whether the diet composition of a wintering population (40–70 individuals) of long-eared owls (*Asio otus*) in northern Italy showed within-season variation, and whether it was influenced by ambient temperature and rainfall. Diet composition was determined by pellet content, and over 5500 prey items were analysed; pellets were collected at 2-wk intervals over two consecutive winters (October to April), 1996–1998. Three out of five main prey categories showed a marked within-season variability in relative frequency in diet, both considering the number of prey items and prey biomass, whereas between-year variability was shown only by a single prey category (Savi's pine vole). Although rainfall had no influence on diet composition, temperature affected negatively the prevalence of harvest mouse, a relatively unimportant prey category. Thus, the considered weather variables seem to have little influence on the winter diet composition (at the level of individual prey categories) of these owls. However, diet breadth (estimated by the Levins' index of niche breadth) increased with increasing rainfall and decreasing temperature, when calculated on the proportion of prey items: hence it seems that the owls become more generalists under unfavourable weather conditions.

**Key words:** weather conditions, nocturnal raptors, small mammals, niche breadth, seasonal variation

### Introduction

Meteorological conditions can affect the diet and hunting success of raptors. For example, rain seems to have a negative impact on the hunting performance of some species, hampering flight or perceptive ability (Barbieri et al. 1975, Wijnandts 1984, Michelat & Giraudoux 1992, Olsen & Olsen 1992, Henrioux 1999). In the long-eared owl (*Asio otus* Linnaeus, 1758), a low ambient temperature and presence of rain seems to reduce flying activity, although the effect varied according to season (Henrioux 1999). Also, surface activity patterns of small mammals (the commonest prey of the long-eared owl; Marti 1976) are influenced by the weather to varying degrees (e.g. Sidorowicz 1960, Getz 1961, Maguire 1999). Further, diet composition may also depend on seasonal variation (hereafter defined as seasonality) in prey choice by the owls and/or prey activity, as shown by previous analyses of the owl's diet (Nilsson 1981, Pirovano et al. 2000a). The most comprehensive study so far is that of Nilsson (1981) in southern Sweden, which investigated changes in diet composition throughout several year cycles. However, the data were grouped by month, and were mostly discussed in terms of between-year and between-season variations in prey and habitat choice, whereas no effort has been devoted to the analysis of within-season variability patterns in diet composition.

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To our knowledge, few studies addressed whether there are relationships between weather conditions and diet composition in free-living raptors, while accounting for seasonal variation in diet (e.g. C a n o v a 1989). Here we analysed within-season variation in diet composition (determined by pellet content) in a population of long-eared owls studied over two consecutive winter seasons (October to April), 1996–1998. The diet and behaviour of this urban wintering population has been described elsewhere (P i r o v a n o et al. 2000a,b): the brown rat (*Rattus norvegicus*) was the most abundant prey in terms of biomass, and the monthly proportion of rats in the diet was inversely related to mean monthly rat weight (P i r o v a n o et al. 2000a), suggesting a selection on young rats (90–100 g). The aim of the present study was to assess the effect of seasonality on diet and the relationships between diet composition and meteorological variables (mean temperature and amount of rainfall preceding pellet collection) and determine which of these factors explained the largest variation in diet.

## Material and Methods

The roost site, occupied by 40–70 owls during winter (October to April), was located in the southern tip of the city of Milan (northern Italy, 45°28'N – 9°12'E). Owls hunt in the suburbs and cultivated fields surrounding the city (P i r o v a n o et al. 1997, 2000a,b). The owls' likely hunting range consisted mainly of winter stubbles (cereal crops, colza), poplar plantations, meadows, together with patches of network habitats (copses, hedgerows along field margins), which are actively selected by owls whilst searching for prey in our study region (G a l e o t t i et al. 1997). Mean monthly rainfall in the study period was 80 mm per month (ranging from 150 mm in December to 6 mm in March), while mean monthly temperatures ranged from 14.6°C in October to 3.9°C in January. The study was carried out over two consecutive winters (November–April 1996–97 and October–April 1997–98). Pellets were collected at 2 wk-intervals each month (first collection: 15<sup>th</sup> of each month; second collection: 30<sup>th</sup>/31<sup>st</sup>) and analysed following standard techniques (Y a l d e n & N o r r i s 1990). Possible biases associated with pellet collection were minimised by collecting all the intact pellets at each visit, always along the same trail below the owls' perches. A preliminary cleaning-up of all pellet remains was undertaken 2 wk before the first collection for each of the two study years. As in other studies, mammals were determined to species level, and birds were considered as a single category (G a l e o t t i & C a n o v a 1994, P i r o v a n o et al. 2000a). Weather variables were recorded at Brera-Duomo Meteorological Observatory (3 km from the roost site) at hourly intervals. In the analyses, we concentrated only on main prey categories (those constituting at least 5% of prey items over the two years, following the definition given in P i r o v a n o et al. 2000a): they were wood mouse (*Apodemus sylvaticus*) (38.5 %), brown rat (21.7 %), Savi's pine vole (*Microtus savii*) (17.3 %), birds (9.6 %), harvest mouse (*Micromys minutus*) (5.5 %). Main prey categories made up 93 % of prey items over the two years. The complete dataset used in the analyses is reported in the Appendix.

## Statistical analyses

Using mean hourly temperature data, we calculated the daily mean temperatures for 2-week periods, and rainfall was measured as the amount of rain (in mm) recorded in the fortnight preceding pellet collection, i.e. the timeframe during which pellets were produced. We used

both proportion of prey items (%N), which represents hunting acts, and proportion of prey biomass (%B), representing an index of energy intake by the owls. This latter index may be relevant in an energetic context, especially during winter, an energetically stressful period for raptors (e.g. O v e r s k a u g et al. 1997, N e w t o n 1998). Estimates of prey biomasses were derived from the literature (D i P a l m a & M a s s a 1981, G a l e o t t i & C a n o v a 1994) and from specimens collected in the study area. Birds were assigned a mean mass of 20 g each (G a l e o t t i & C a n o v a 1994, P i r o v a n o et al. 2000a). The body mass of predated brown rats was estimated by measuring mandible length and using the regression equation given in D i P a l m a & M a s s a (1981). In biomass calculations, rats were thus assigned the mean monthly weight.

The proportions of prey categories (both as %N and %B) were calculated for each fortnight. The number of prey items for each fortnight varied between 29 and 580 (median = 198 prey items, see Appendix): overall, 25 fortnights were included in the analyses. All variables were normally distributed (Kolmogorov-Smirnov test,  $P > 0.18$ ), so that no data transformation was performed before variables being used in parametric statistical analyses. For each fortnight we calculated diet breadth using the L e v i n s ' (1968) index of niche breadth ( $NB = 1 / \sum p_i^2$ , where  $p_i$  is the proportion of the  $i^{\text{th}}$  prey category); compared to other diversity indices, this index gives more weight to dominant diet components (which can be hypothesized to have more biological relevance), and its value is less sensitive to stochastic variation in the occurrence of the least abundant prey categories. Diet breadth was calculated on all prey categories, including those not listed above.

In order to separate seasonal variation in diet composition from the effect of weather (temperature and rainfall), we first built maximal models in which diet parameters were expressed as a function of year of pellet collection and date of sampling. Given that a preliminary look at the variation of prey categories in relation to date of sampling revealed mostly non-linear patterns, we also included in the maximal models the quadratic term of date, together with all the year by date interactions. Models were built using Type I sum of squares (hierarchical sum of squares), in which each term is corrected only for those preceding it in the model definition (N o r u s i s 1988). Thus, the factor year was always entered first in the model, followed by date and its quadratic term, whereas interactions (year x date, year x date<sup>2</sup>) were entered after main effects. Before testing the additive effects of temperature and rainfall, non-significant higher order terms and interactions were dropped from the model, and the model was run again with significant terms included only (this is termed Step 1 hereafter). Note that if higher order terms were significant, then the corresponding lower order terms were also left in the model, even if they did not reach statistical significance. Then we tested for the effects of temperature and rainfall, which were entered separately in the models (Step 2a and Step 2b, respectively). If the initial model (before Step 1) was non significant, then the effects of weather variables on diet parameters were tested alone in an analysis of covariance (ANCOVA).

Owing to the strict non-linear covariation between temperature and date of sampling (temperature as a function of date:  $R^2 = 0.73$ , 2<sup>nd</sup> order polynomial function,  $P < 0.0001$ ), with temperature being lower in mid-winter months, effects of seasonality *per se* and temperature on diet could be difficult to disentangle. Hence, the same models as above (Step 2a) were also run entering temperature before the effects of date of sampling: to evaluate which model performed best, we compared the change in  $R^2$  ( $\Delta R^2$ ) between

model types (i.e. those with temperature entered after date vs. those with temperature entered before date) after entering the first term (note that seasonal terms, e.g. date and date<sup>2</sup>, are considered altogether in calculating the change in R<sup>2</sup>). Means are shown together with their standard deviations.

## Results

In total, 5509 prey items were examined over the two years (see Appendix). The 2-wk proportions of prey items and prey biomasses were strictly correlated (mean  $r_s = 0.93$ ; range 0.85–0.96;  $N = 5$  prey categories; all  $P < 0.0001$ ). Three out of five prey categories showed a clear seasonal variation in prevalence in the diet (Table 1, Fig. 1), both in terms of number and biomass (i.e. wood mouse, brown rat and harvest mouse). Birds showed a seasonal variation in prevalence only when considering %N, whereas no variables were significant in the initial model for %B (Table 1). Savi's pine vole was the only prey category showing a significant between-year variation in prevalence (Table 1). In both years, the dietary response over the winter season was non-linear, the prevalence of rats and birds decreasing around mid-winter being replaced by wood mice and birds. As mid-winter was the period with the lowest temperatures, the prevalence of rats, harvest mice and birds trend could also be modelled as a function of mean temperature (see significant effects at Step 2a in Table 1).

**Table 1.** Summary of ANCOVA models (type I sum of squares) describing the relationships between long-eared owl diet parameters (diet composition, expressed both as % number (%N) and % biomass (%B)), seasonal variation and weather variables during two consecutive study winters (October to April), 1996–1998. See Material and Methods for a detailed description of variables and model definition.

Diet parameters	Model steps						
	Step 1 <sup>§</sup> (year, season)		Step 2a <sup>^</sup> (temperature)			Step 2b <sup>^</sup> (rainfall)	
	Variables	R <sup>2</sup> (%)	P	ΔR <sup>2</sup> (%)		P	ΔR <sup>2</sup> (%)
<i>Apodemus sylvaticus</i>	%N	date, date <sup>2</sup>	70.7	0.25 - 0.14	-	0.68	-
	%B	date, date <sup>2</sup>	61.9	0.62 - 0.17	-	0.72	-
<i>Rattus norvegicus</i>	%N	date, date <sup>2</sup>	66.8	0.39 - 0.00*	66.8 - 14.5	0.10	-
	%B	date, date <sup>2</sup>	48.7	0.49 - 0.15	-	0.24	-
<i>Microtus savii</i>	%N	year	43.9	0.22 - 0.19	-	0.88	-
	%B	year, date	38.1	0.07 - 0.17	-	0.47	-
<i>Micromys minutus</i>	%N	date <sup>2</sup>	47.5	0.07 - 0.00*	47.5 - 51.3	0.39	-
	%B	date <sup>2</sup>	45.3	0.15 - 0.00*	45.3 - 41.8	0.32	-
Birds	%N	date, date <sup>2</sup>	59.6	0.29 - 0.02*	59.6 - 11.0	0.76	-
	%B	-	-	0.49	-	0.10	-

<sup>§</sup> Only significant terms are shown; associate model R<sup>2</sup> is shown when overall models significant at  $P < 0.05$ .

<sup>^</sup> P-values for additional effects of temperature and rainfall are shown; for temperature: left value: temperature entered after other variables (those selected with Step 1); right value: temperature entered before other variables. Significant P-values ( $P < 0.05$ ) are marked with an asterisk (\*). Corresponding changes in % R<sup>2</sup> (ΔR<sup>2</sup>) for the two model types (after entering the first term; seasonal terms are considered altogether in calculating the change in R<sup>2</sup>, see Materials and Methods for details) are also shown when P-values for temperature were significant at  $P < 0.05$ .

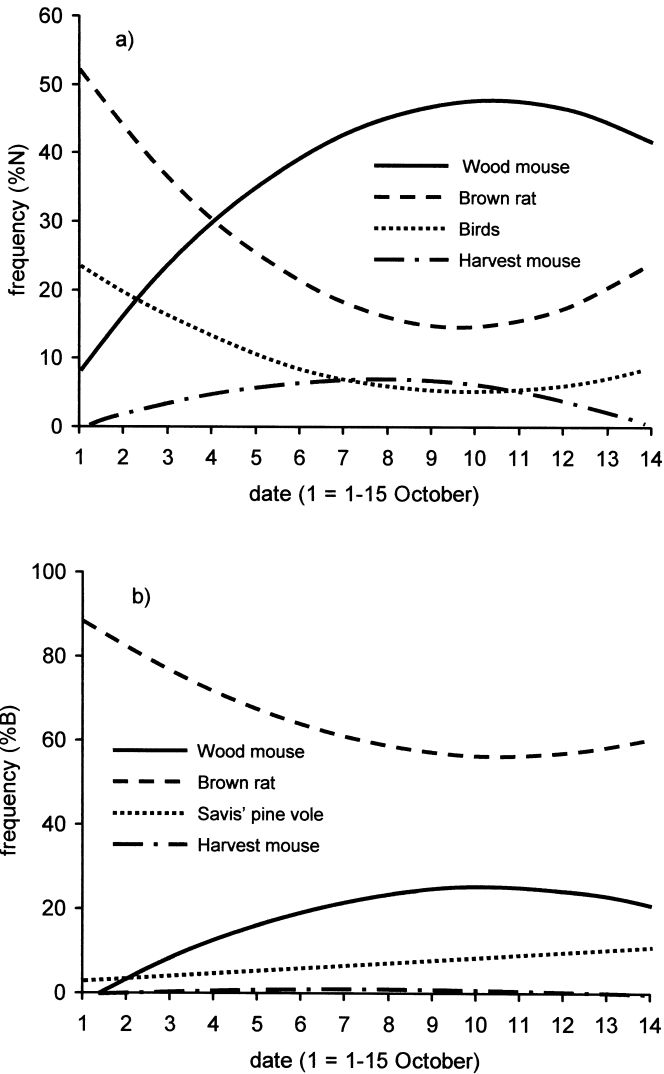
However, the only prey category that showed a consistent covariation in frequency with mean temperature upon the general effect of seasonality was the harvest mouse, which increased in proportion when temperature was lower, whereas seasonality seems to be far more important for other prey categories (Table 1). No correlation was found between the amount of rainfall and the percentages of any prey category (all  $P > 0.10$ , Table 1).

Diet breadth calculated on %N was not correlated with the same index calculated on %B ( $r_s = -0.11$ ;  $N = 25$ ;  $P = 0.59$ ), suggesting that different factors could be affecting this index at these two levels of analysis (%N or %B). The maximal model was non-significant for %N diet breadth ( $F_{5,19} = 2.16$ ,  $P = 0.10$ ), whereas date ( $P = 0.004$ ) and date<sup>2</sup> ( $P = 0.04$ ) were significant predictors of %B diet breadth after running Step 1, with breadth mostly increasing from winter to spring (model:  $F_{2,22} = 7.59$ ,  $P = 0.003$ ). %N diet breadth increased with decreasing temperature ( $F_{1,23} = 9.29$ ,  $P = 0.006$ ) (Fig. 2a) and with increasing rainfall ( $F_{1,23} = 5.62$ ,  $P = 0.026$ ) (Fig. 2b), but there were no correlations between weather variables and %B diet breadth (both entering weather variables after and before date terms, all  $P > 0.05$ ). The breadth indexes were not dependent on the total number of prey items included in each fortnight sample (%N:  $r_s = 0.30$ ;  $N = 25$ ;  $P = 0.14$ ; %B:  $r_s = 0.08$ ;  $N = 25$ ;  $P = 0.70$ ). Mean diet breadth calculated on %B was significantly lower than that calculated on %N ( $2.12 \pm 0.50$  vs.  $3.53 \pm 0.59$ , respectively; paired t-test:  $t_{24} = 8.57$ ,  $P < 0.0001$ ): this is because of the strong dominance of rats in biomass (mean fortnight proportion of rat biomass in diet is  $64.9 \pm 12.9\%$ , range 36.8–88.5%, see Fig. 2, Appendix). In fact, %B diet breadth was dependent on %B of rats in diet ( $r_s = -0.98$ ;  $N = 25$ ;  $P < 0.0001$ ), emphasizing that the brown rat is by far the most important prey and that the niche breadth in this apparently specialist predator is basically a function of the prevalence in the diet of the most important single prey type. However, in this particular situation, the Levins' index calculated on %B, being heavily influenced by dominant prey categories, may not be able to provide an adequate representation of the seasonal variations in diet breadth.

## Discussion

Owing to the proportional nature of dietary data, with one prey type increasing in prevalence as others decrease, it may be difficult to identify the reasons behind changes in diet composition (statistically as well as biologically). Indeed, from our investigations, it is clear that the brown rat is the primary prey type in this wintering owl population, in which birds behave as rat specialists (see also P i r o v a n o et al. 2000a). The prevalence of rats reaches up to 80% of prey biomass and is around 20% in number of prey items. As a consequence, the prevalence of other numerically important mammalian prey types (wood mouse and Savi's pine vole) were negatively correlated to the percentage of brown rat and were thus seemingly alternative prey to the brown rat, given the dominance of rats by biomass (P i r o v a n o et al. 2000a).

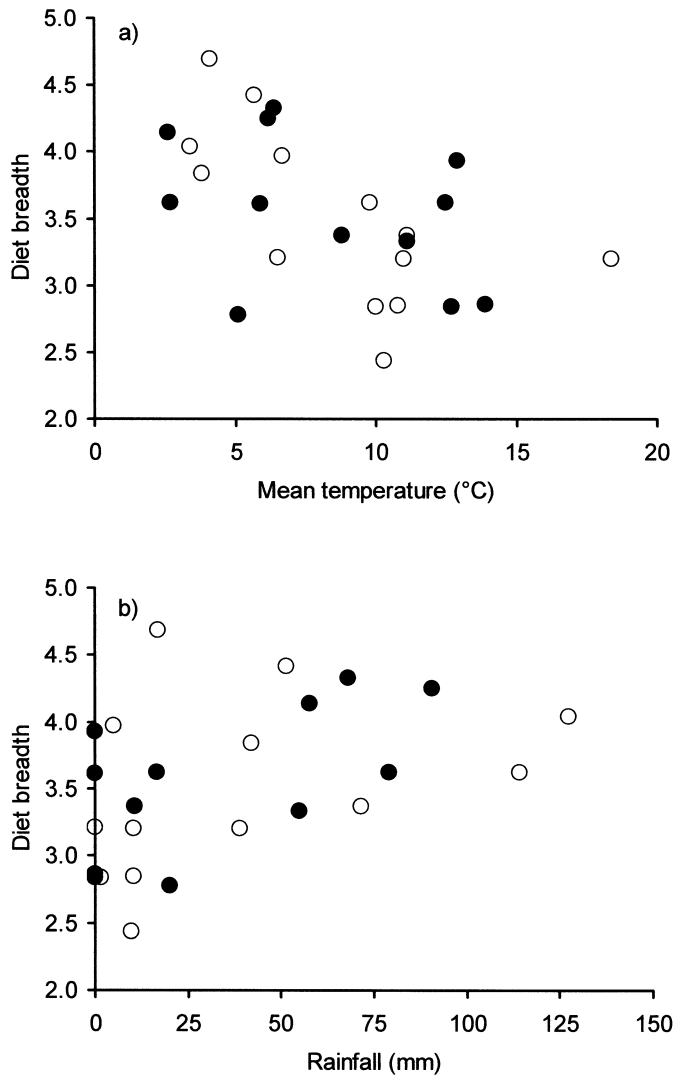
Overall, the most important prey categories showed clear within-season variations in prevalence throughout the winter. Weather variables had no or limited effects on the variation of individual prey categories: the only prey whose prevalence in diet was consistently affected by temperature was the harvest mouse, which, owing to its small size, makes a low contribution to the overall diet, and can thus be considered to have a low biological relevance (see Appendix). The increased prevalence of harvest mice with cold



**Fig. 1.** Seasonal variation in diet composition of long-eared owls, measured at 2-wk intervals. For clarity of presentation, only fitted lines for prey categories that showed significant seasonal variation in frequency are shown, according to patterns detected in Table 1; a) frequency of prey items (%N); b) frequency of prey biomass (%B).

weather may reflect a higher availability of this prey with lower temperatures, when a fraction of the population may be forced to leave cultivated fields by habitat deterioration, thus showing a more predictable occurrence in network habitats largely preferred by owls for hunting (Galeotti et al. 1997).

In general, the relationships between diet composition and weather conditions may have different origins: either (1) predation by the owls is influenced by weather conditions, given a uniform availability of prey species, or (2) activity/availability of prey



**Fig. 2.** Correlation between an index of long-eared owl diet breadth (Levins' index), calculated for each fortnight on %N, and: a) 2-wk mean ambient temperature; b) total amount of fortnight rainfall (in mm); filled circles = winter 1996-97; open circles = winter 1997-98.

species depends on weather variations and the owls eat what is available. Of course, these possible processes are not mutually exclusive, and what is actually found in the owls' diet may derive from their combination: a thorough investigation of the factors influencing diet should link dietary data to small mammal and owl's activity pattern and habitat use. Future efforts should thus include the quantification of the above-mentioned variables, and perhaps simultaneous trapping of small mammals in different habitats and quantification of owls habitat use (by e.g. radio-tracking), while taking into account weather conditions, may provide adequate answers.

With regards to our results, possible reasons for the observed generalized lack of effect of weather variables on individual prey frequencies may include the relatively mild winter climate and the interval at which pellets were collected, that may have been too long and may have obscured the effect of weather on diet. Previous studies of resident raptors wintering at high latitudes have shown food availability, related to climatic factors, to be of major importance in determining the survival probability throughout winter (Newton 1998, Sundé 2002), but weather conditions are likely to have a limited importance in our study area on both owl activity and food abundance: hence, it would be interesting to investigate longer time series including harsh winter seasons, which may exacerbate the effect of weather on diet composition.

Diet breadth (calculated on %N) was positively related to rainfall and negatively to temperature. This may simply reflect a decrease in diet breadth when many young rats are available, i.e. when temperatures are high (Perry 1946, Pirovano et al. 2000a): however, this would imply a negative correlation between %N diet diversity and abundance of rats (both %N and %B), but this is not the case (Spearman Rank:  $P = 0.60$  and  $P = 0.30$ , respectively). Hence, either overall average prey activity may be higher at lower temperatures and elevated soil moisture (Maguire 1999), or owls may become more euryphagous under inclement weather conditions, which seems a likely explanation (Cánova 1989). In fact, lower prey selectivity under relatively unfavourable weather conditions, which may negatively affect the energy budget of the owls or the abundance of food resources, is to be a generally expected ecological response to climatic variability (e.g. MacArthur & Pianka 1966). When analysing diet diversity from an energetical point of view (%B diet breadth), given that rats dominate the diet, diversity increased when the prevalence of rats decreased during mid-winter months (probably in response to a lower availability of young rats), with owls shifting to other prey types (wood mouse, Savi's pine vole). Thus, diet diversity seems to be influenced both by climatic factors and by the abundance of the preferred prey, depending on the measure used (%N or %B).

To conclude, the diet composition of the long-eared owl in our study area appeared to be independent of rainfall and slightly influenced by temperature, while a measure of diet variability increased with decreasing temperature and with an increasing amount of rainfall. Taken together, these results suggest that further studies investigating the diet of owls should consider seasonal variation and weather conditions as potentially influential variables, and emphasize that the winter diet composition of the long-eared owl in Southern Europe show marked within-season fluctuations.

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**Appendix.** Diet parameters (for both N and B) of long-eared owls in the suburbs of Milan, northern Italy, from October to April, according to year (Y) (1 = winter 1996/97; 2 = winter 1997/98) and date (D) of collection (1 = 1-15 October; 14 = 16-30 April). Diet breadth, number of prey items considered (N items) and weather variables (Temp = temperature; rain = rainfall) are also shown (see Material and Methods for details).

Y	D	<i>Apodemus sylvaticus</i>		<i>Rattus norvegicus</i>		<i>Microtus savii</i>		<i>Micromys minutus</i>		Birds		Diet breadth <sup>§</sup>		N items	Temp (°C)	Rain (mm)
		%N	%B	%N	%B	%N	%B	%N	%B	%N	%B	N	B			
1	3	29.41	9.46	42.53	81.74	10.41	3.04	3.17	0.26	9.50	2.89	3.33	1.46	221	11.10	55.0
1	4	22.22	11.20	18.18	58.24	33.33	15.24	0.00	0.00	19.19	9.14	4.25	2.57	99	6.21	90.6
1	5	21.89	9.66	22.26	68.00	33.21	13.30	0.60	0.30	13.58	5.66	4.33	2.02	265	6.38	68.0
1	6	34.48	12.68	31.03	78.98	10.34	3.45	6.90	0.65	6.90	2.40	4.14	1.56	29	2.59	57.8
1	7	44.22	24.27	13.27	58.07	21.09	10.50	11.22	1.57	6.12	3.17	3.62	2.43	294	2.69	79.2
1	8	53.85	33.51	9.89	47.44	22.53	12.71	5.49	0.87	2.75	1.61	2.78	2.74	182	5.12	20.2
1	9	43.28	23.30	13.79	59.13	23.45	11.45	8.28	1.14	4.48	2.28	3.61	2.33	580	5.91	0.0
1	10	43.17	20.24	21.03	66.03	23.25	9.89	3.32	0.40	4.43	1.96	3.37	2.01	271	8.81	10.8
1	11	52.71	28.09	17.44	58.11	18.22	8.81	3.10	0.42	3.49	1.76	2.84	2.29	258	12.67	0.0
1	12	34.43	13.95	28.96	73.57	19.13	7.03	2.73	0.28	12.02	4.60	3.93	1.76	183	12.87	0.0
1	13	50.88	25.24	21.05	62.42	17.54	7.89	1.75	0.22	6.14	2.88	2.86	2.11	114	13.94	0.0
1	14	27.91	15.97	16.28	55.69	37.21	19.31	0.00	0.00	6.98	3.77	3.62	2.44	43	12.54	16.6
2	1	9.38	3.12	42.19	82.04	1.56	0.47	0.00	0.00	34.38	10.82	3.20	1.45	64	18.41	10.2
2	2	15.24	4.21	55.49	88.50	6.71	1.68	2.44	0.17	10.98	2.86	2.85	1.27	164	10.75	10.4
2	3	31.31	11.22	38.89	80.39	3.54	1.15	3.03	0.28	15.15	5.13	3.62	1.52	198	9.81	114.2
2	4	25.82	8.34	39.56	83.16	10.44	3.06	3.85	0.32	11.54	3.52	3.97	1.43	182	6.69	5.0
2	5	35.20	13.96	26.20	75.10	10.80	3.88	9.60	0.97	9.20	3.44	4.42	1.70	500	5.74	51.4
2	6	43.23	27.62	10.42	51.16	14.84	8.60	9.11	1.48	12.24	7.38	4.04	2.85	384	3.36	127.4
2	7	44.31	24.21	16.08	58.76	14.90	7.38	5.49	0.76	7.84	4.05	3.84	2.42	255	3.82	42.2
2	8	35.40	17.69	17.31	64.79	18.60	8.43	8.53	1.09	10.34	4.88	4.69	2.17	387	4.10	16.8
2	9	48.73	29.38	12.39	51.42	21.97	12.01	4.79	0.74	9.01	5.13	3.21	2.72	355	6.47	0.0
2	10	49.38	22.67	20.33	66.85	14.11	5.87	3.32	0.39	5.81	2.52	3.20	1.99	241	10.98	39.0
2	11	54.55	41.10	6.82	36.79	19.32	13.20	6.82	1.31	7.95	5.66	2.84	3.07	88	9.96	1.6
2	12	58.41	28.35	22.12	64.01	13.27	5.84	3.54	0.44	1.77	0.81	2.44	2.03	113	10.34	9.6
2	13	48.72	26.92	17.95	53.48	12.82	6.42	5.13	0.72	7.69	4.01	3.37	2.72	39	11.12	71.4

<sup>§</sup> According to the Levins' index of niche breadth (NB =  $1 / \sum p_i^2$ ) on all prey categories determined to species level (including birds, that were considered as a single category).

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