Prey diversity is affected by climate and differs between age classes in the Red-backed Shrike (*Lanius collurio*)

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When breeding, food availability is essential for optimal reproductive output and is potentially one of the main factors limiting breeding success, especially in single brooded long-distance migratory birds. In this study, we examined the diet (as a measure of prey availability) of two Red-backed Shrike (*Lanius collurio*) populations in Denmark, based on more than 11,000 prey items covering seven years. We found a negative correlation between prey diversity and temperature, indicating that Red-backed Shrikes feed on preferred prey items in warmer summers (low diversity) while forced to feed on a larger variety of species in colder summers. Adults had a more diverse diet and generally fed on smaller prey items than did young birds. Thus, age- and environment-related differences must be taken into account when describing the diet of the Red-backed Shrike. Direct nest observations produced different results for diet composition than did nest and pellet samples, underlining the importance of using different methods in diet assessments. Detailed knowledge on limiting factors on the breeding grounds, such as food availability, is crucial for mitigating population declines of vulnerable species, such as the Red-backed Shrike.

1. Introduction

Migratory birds face many challenges at every stage in their life cycle (Newton 2008). Some of the most important challenges are deterioration of habitat on both wintering and breeding grounds, loss of staging areas, and climate changes. Furthermore, climate-induced phenological changes may cause increased competition and problems with optimizing arrival time and breeding in relation to peaks of food abundance (Both *et al.* 2006, Wilcove & Wikelski 2008). As a consequence, migratory birds – especially long-distance migrants – have suffered severe population declines during the past three decades (Sanderson *et al.* 2006, Heldbjerg & Fox 2008). In addition, long-distance migratory birds typically have fewer broods, smaller clutches and lower annual fecundity than short-distance migrants and resident species (Böhning-Gaese *et al.* 2000). They are, therefore,

particularly dependent on habitat quality in the breeding areas to sustain population size.

Food availability on breeding grounds is one of the main factors limiting breeding success in birds (Martin 1987, Granbom & Smith 2006). Knowledge on the diet of long-distance migratory birds is therefore important, as it can provide information about habitat quality that can be used to guide conservation efforts in breeding areas.

The Red-backed Shrike (*Lanius collurio*) is a long-distance migratory bird wintering in Southern Africa (Tøttrup *et al.* 2012). In the 20th century, the species went through a decline throughout its range, especially in northern and western Europe (Hagemeijer & Blair 1997, Lefranc & Worfolk 1997, Birdlife International 2004, Pasinelli *et al.* 2011). However, stable and even increasing populations still occur (Birdlife International 2004). In Denmark, the population seems to thrive in Jutland, but has declined in the eastern part of the country where only a few populations remain (Grell 1998). The Red-backed Shrike arrives to its North European breeding sites during May and June, and leaves again in August to September (Tøttrup *et al.* 2012). It inhabits open areas or forest clearings, with scattered bushes and low trees that are used as nest sites and perching posts for hunting. The species is insectivorous, although it also consumes small vertebrates such as mice, shrews and lizards. Like most other shrike species, it sometimes impales prey items on thorns, barbed wires or sharp branches for handling and storage or as part of its display behaviour.

The aims of the present paper are threefold, and concern the effects of (1) temperature and (2) age on, and (3) the consistency of different assessment methods of, bird diet. High summer temperatures are often associated with high insect abundance, and may therefore also affect the Red-backed Shrike through influencing the diversity of the species' diet. The diet diversity might also be potentially related with bird age, but thus far only a few studies have focused on this aspect (Hernandez 1993; Tryjanowski *et al.* 2003b). Many different methods have been used to describe the food choice and diet composition in the Red-backed Shrike (Tryjanowski *et al.* 2003b, Golawski 2006; for an earlier summary, see Cramp & Perrins 1993). Both invasive (e.g. analyses of stomach contents) and non-invasive methods (e.g., analy-

ses of pellets or impaled prey found at larders) have been applied for the Red-backed Shrike. It is an ideal species for diet studies as it regurgitates indigestible fragments of consumed prey items in small pellets (Cramp & Perrins 1993, Lefranc & Worfolk 1997). Direct nest observations are time consuming, and increased predation with prolonged disturbance by observers has been reported (Tryjanowski & Kuzniak 1998). Therefore, it is worth to examine if the collection of pellets during breeding season or collecting nests after fledging of the young will provide sufficient information about the diet of the Red-backed Shrike. These latter two methods are – in spite of the effort to identify prey fragments – less time consuming and will disturb the birds less. However, few attempts have been made to directly compare different approaches and validate their outputs (Tryjanowski *et al.* 2003b, Golawski 2006). Furthermore, no attempts have to our knowledge been made to use diversity estimators and indices to describe the diversity of the diet in Red-backed Shrikes.

The aim of the present study was to examine how the species diversity in diet is correlated with environmental factors, and if specific species can explain differences in the diversity of diet between years. Furthermore, we compared the diet of young and adults in terms of diet diversity and composition and prey size. Finally, by using available data we compared three diet-assessment methods: prey remains from nests, prey remains from pellets, and direct observations made at nests.

2. Material and methods

2.1. Study sites and field data collection

Two study sites were examined: Gribskov and Hulsig Hede. Gribskov (56°0' N, 12°20' E) is a forested area in northern Sealand, located in a moraine area. The many clearings are surrounded by bushes and trees such as beech and spruce, making it an ideal breeding site for the Red-backed shrike (Pedersen *et al.* 2011). Hulsig Hede (57°41' N, 10°28' E) is a dune-heath area south of Skagen in the northernmost part of Jutland. It is a complex landscape that provides a wide range of different habitat types, from drifting-sand dunes to wet bogs. The heath is partly bordered by coniferous

plantations (Beusink *et al.* 2003, Van Duinen *et al.* 2004). Both areas host valuable habitat types to a variety of species, and they are part of the NATURA 2000 network of the European Union.

A total of 24 nests were collected from Gribskov at the end of July 2008 (three nests), July and September 2009 (15 nests) and January 2010 (six nests). Because of remarkable variation in the amount of prey fragments in the nests, we collected data on nest site and height to test the influence of these factors on the amount of prey fragments in the nests. As expected, generally more prey items were identified from nests containing more fragments (analysis not shown). The number of prey items identified from each nest was therefore used as a measure of the amount of fragments left in the nest.

In Hulsig Hede, 318 pellets from nestlings and young fledglings (underneath nests), juveniles (from regular feeding locations near the nest) and adults (underneath perches) were collected in July 2001–2002, June and July 2004–2005 and in July–August 2007–2008 (28 different pairs). Four nests were collected in Hulsig Hede; three in 2007 and one in 2008. To determine nestling diet by direct nest observations, three nests were examined each year in Hulsig Hede during June–August 2002 and 2003. Nests were observed from 06:00 h to 09:00 h every second day, from shortly after hatching until fledging. All prey species were identified to the highest possible taxonomic level (for details, see Hornman *et al.* 1998).

Climate data were obtained from the Danish Meteorological Institute (DMI 2010) as mean values for the region of Northern Jutland and for the area of Copenhagen and Northern Sealand. We used the averaged mean temperature of two months (June–July), mean precipitation and number of days with precipitation.

2.2. Sorting and identification of pellet and nest samples

We identified prey remains in pellets and nests to the highest possible taxonomic level (Kuper *et al.* 2000). Nests were torn apart and pellets crumbled so that important fragments for identification and quantification could be collected. These fragments consisted mainly (depending on prey group) of

Table 1. Percentage of prey items identified to the highest possible taxonomic level, determined by three different methods (*N* = number of prey items).

Identification class	Pellets (*N* = 2,650)	Nests (*N* = 357)	Nest obs. (*N* = 7,319)
Unknown to class	0.5	0	26.7
Order	5.5	3.6	21.1
Family	16.6	9.0	6.8
Genus	35.2	43.1	7.8
Species	42.2	44.3	37.6

different parts of head and wing, and legs and mandibles. We counted fragments belonging to the same taxon and estimated the minimum number of individuals for each sample. Identification and estimation of lengths of different invertebrate items were based on a reference collection and identification literature (e.g., Chinery 1988, Harde & Severa 1989, Bellmann 1995), with additional help of databases of invertebrate images (e.g., http://www.koleopterologie.de). Nomenclature was based on the Dutch Species Catalogue (2010). We divided taxa into six body-length classes: 1–5, 6–10, 11–15, 16–20, 21–25 and >26 mm (modified from Kuper *et al.* 2000). If a taxon fell into more than one length class, the number of individuals counted for the taxon in the sample was divided equally among the different classes.

In Hulsig Hede, we identified 2,650 prey items in pellets and 357 in nests, and identified 7,319 prey items using direct nest observations. In the nests from Gribskov, we found 1,181 prey items. We identified a total of 293 different taxa, of which 176 from nest and pellet samples (for details on prey groups, see supplementary material at http://www.ornisfennica.org).

For all three methods, identification to species could be performed in about 40% of the cases. However, a relatively high amount of prey items could not be determined higher than class using the nest-observation method (Table 1). Over 90% of prey items belonging to the order Coleoptera (beetles) were identified to genus or even to species using all three methods. For the order Hymenoptera (bees, wasps and ants) the same was true, although for pellet remains only about 80% could be identified to at least the genus level. Eighty-five percent of the vertebrate prey items were identified

Table 2. Slope values, Spearman rank (*r*) values and probabilities (*p*) of Chao2, Jackknife1 and Bootstrap species estimators and Shannon-Wiener and Simpson's diversity indices, showing the correlation between mean temperature (June–July) and prey diversity (*N* = 6 years).

Estimator/Index	Slope	*r*	*p*
Chao2	–17.91	–0.65	0.081
Jackknife1	–8.02	–0.25	0.545
Bootstrap	–4.78	–0.12	0.776
Shannon-Wiener	–0.22	–0.62	0.098
Simpson	–2.77	–0.57	0.133

to at least family level. For nest observations, over 50% of the vertebrates could not be identified, because they were mostly brought to the nest in pieces.

2.3. Data analyses

We used EstimateS (Colwell 2009) to calculate species-diversity estimators and indices. To compare species richness, we used computed number of individuals instead of number of samples, as recommended by Colwell (2009). We used the diversity estimators Chao2, Jackknife 1 and Bootstrap (Chao 2005) and the Shannon-Wiener and Simpson's diversity indices (Magurran 2004) to describe the diversity of diet. The number of randomizations was set at 1,000 runs, and samples were randomized without replacement. For Chao2, we used the classic instead of the bias-corrected formula in cases where the incidence distribution was above 0.5, as recommended by Colwell (2009). However, for comparability reasons the classic formula was not used – albeit being recommended in three out of eight cases – in the comparison of diversity between years and climate data.

We used linear regression to determine correlations between environmental factors and the diversity of prey. Because abundant prey items may potentially drive the diversity calculations, we determined the correlation between diversity and the proportion of an abundant prey item in the diet, the scarabid beetle *Anomala dubia*. We used one-sample *t* test to evaluate the significance of the mean correlation between environmental factors and diversity.

We compared the three diet-assessment methods using *G* test. We tested the similarity in the number of prey items and taxa in nests from Gribskov and Hulsig Hede using Mann-Whitney *U* test, and one-way ANOVA, *t* test and linear regression to test the influence of nest site, date of nest collection and nest height on the amount of prey items in the nests. When performing multiple similar tests, we adjusted the significance level using the sequential Bonferroni probability adjustment (Rice 1989). All statistical tests were performed using SAS 9.1.

3. Results

3.1. Diversity and environmental factors

We found negative relationships between mean temperature (June–July) and prey diversity, with the overall mean significantly different from 0 ($r = -0.45$, $t_4 = -3.89$, $p = 0.018$) (Table 2). Diversity correlated with mean precipitation and days of precipitation positively, albeit only marginally significantly ($r = 0.34$, $t_4 = 2.5$, $p = 0.067$ and $r = 0.28$, $t_4 = 2.25$, $p = 0.088$, respectively). Similarly, the diversity estimators and indices negatively and marginally significantly correlated with diet diversity and the proportion of *Anomala dubia* in the diet (mean $r = -0.28$, $t_4 = -2.66$, $p = 0.057$).

3.2. Adult and nestling diet

A comparison of the diet between young and adults indicated that the latter had a more diverse diet, which was confirmed by Chao2 and Jackknife1 estimators and Shannon-Wiener and Simpson's indices (Table 3). These indices all indicated a higher diversity of prey items in the diet of adults than in the diet of young. The result was also consistent when compared to the diet of nestlings in nest observations from Hulsig Hede. Only Jackknife1 was higher in nestlings than in adults based on nest observations (although the standard variations overlapped slightly). There was no distinct difference in the diversity of prey items found in the diet of nestlings in Gribskov and nestlings in Hulsig Hede (Table 3).

The proportions of orders in the diet of nest-

Table 3. Chao2 and Jackknife1 diversity estimators (mean ± SD) and Shannon-Wiener and Simpson's diversity indices, applied to the diet of the Red-backed Shrike for Hulsig Hede and Gribskov and for young and adults in Hulsig Hede only (*N* = number of nests and/or collections of pellets from the same nest).

Population	Method	Age	N	Individuals	Chao2	Jackknife1	Shannon-Wiener	Simpson's
Hulsig Hede	Pellets	Adults	16	1,398	215 ± 32	181 ± 21	3.5	13.49
Hulsig Hede	Nests and pellets	Nestlings and juveniles	18	1,433	200 ± 35	161 ± 14	3.15	9.61
Hulsig Hede	Nests and pellets	Nestlings	12	888	144 ± 27	119 ± 11	2.97	7.76
Hulsig Hede	Nest observations	Nestlings	6	7,319	203 ± 15	208 ± 10	3.15	10.14
Gribskov	Nests	Nestlings	23	1,181	136 ± 23	120 ± 6	2.92	7.63

lings, juveniles and adults in Hulsig Hede (pellet and nest-remains data) were significantly different ($G_{18} = 227$, $p < 0.01$). This was mainly due to the amount of Hemiptera (true bugs) in adult diet (14%, compared to 2% and 3% in the diets of nestlings and juveniles, respectively) and the amount of Dermaptera (earwigs) in the diet of juveniles (7%, compared to 0.4% in the diet of nestlings and adults) as well as the amount of Hymenoptera in the nestling diet (45%, compared to 35% and 36% in the diets of adults and juveniles, respectively). Among Coleoptera, Scarabaeidae (dung and ground beetles) dominated in the diets of nestlings, juveniles and adults, comprising 46%, 67% and 50% of the beetles, respectively. Within the Hymenoptera order, *Bombus* (bumblebees) constituted a higher proportion of the diet of nestlings, whereas a higher proportion of Formicidae (ants) was found in the diet of adults. Vespidae (wasps) were

mainly found in the diets of nestlings and adults (Fig. 1).

Concerning prey size (nest and pellet samples), most of the prey items fell into the length class 11–15 mm, regardless of the age of the Red-backed Shrike (45%, 51% and 39% for nestlings, juveniles and adults, respectively). However, the proportions of prey items in different size classes differed significantly among nestlings, juveniles and adults ($G_{10} = 87$, $p < 0.01$). For juveniles, we identified an equal amount of prey items above and below 11–15 mm. Nest and pellet samples contained a higher proportion of prey items below 11 mm for adults than for nestlings and juveniles, whereas the proportion of prey items above 15 mm was higher for nestlings. Prey items below 5 mm contributed 2% to the diet of nestlings. Comparing nestling diet from Gribskov and Hulsig Hede, the proportions of prey items in different size classes differed

Fig. 1. The proportion of different Hymenopteran taxa in the diet of nestlings, juveniles and adults of the Red-backed Shrike, based on pellet and nest samples from Hulsig Hede, corrected for prey size (*N* = number of prey items).
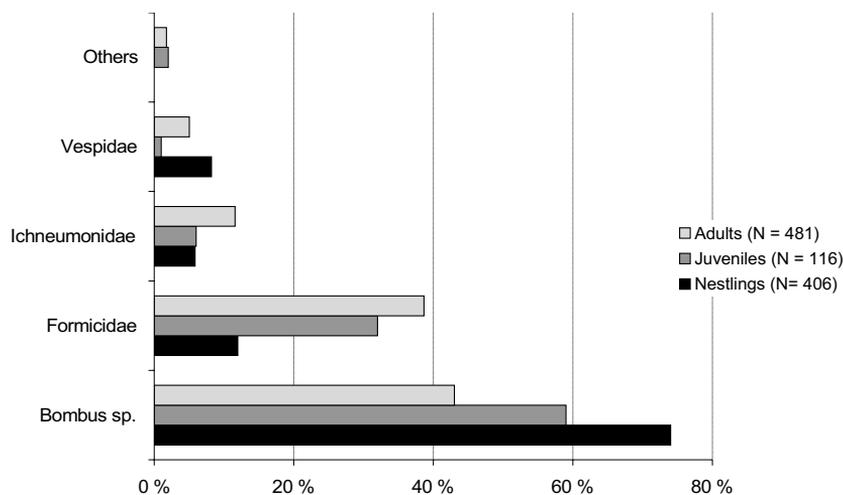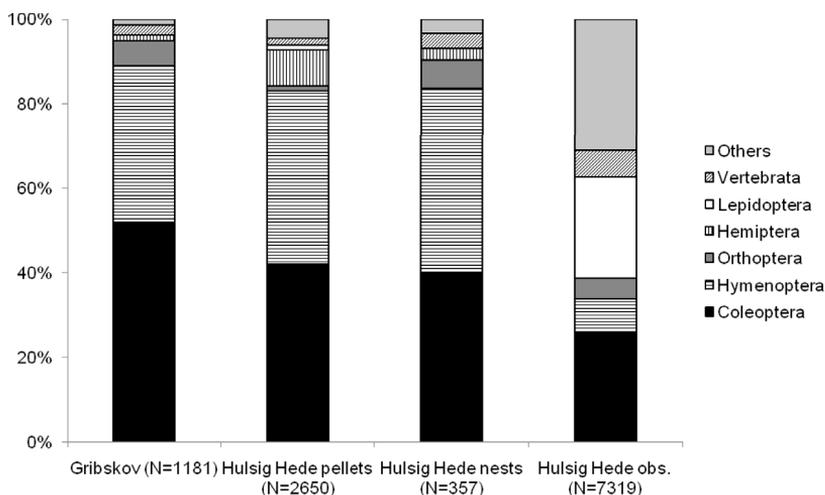
Fig. 2. Differences in the diet composition of nestlings of the Red-backed Shrike determined by three methods in Hulsig Hede and compared with nests from Gribskov (*N* = number of prey items). Results on pellets from Hulsig Hede show only the diet of nestlings for comparison.

significantly ($G_5 = 71.4$, *p* <0.01). Nest and pellet samples for nestlings contained more above-15-mm prey items in Gribskov than in Hulsig Hede.

3.3. Comparing methods

In pellets and nests from Hulsig Hede, 98.2% of the total prey number consisted of invertebrates and 1.8% of vertebrates. The visual nest observations based on number of prey deliveries resulted in 75.3% invertebrates, 5.8% vertebrates (including partial prey items) and 18.9% unknown taxa. In Gribskov, the nests contained 97.7% invertebrates and 2.3% vertebrates.

In nests and pellets from Gribskov and Hulsig Hede, Coleoptera and Hymenoptera constituted 80–90% of identified prey items. The remaining prey items were mainly insects of Orthoptera (grasshoppers) and Hemiptera (Fig. 2). Only a small proportion of invertebrates from other orders were found in pellets and nest remains; these were Araneae (spiders), Odonata (dragonflies), Dermaptera, Diptera (flies) and Lepidoptera (butterflies). However, according to the nest observations some of these orders appeared rather common, especially Lepidoptera which comprised about 21% of the identified prey items consumed by nestlings. Hymenoptera, on the other hand, constituted only 7% of the prey items identified in nest observations.

Both pellet and nest samples from Hulsig Hede differed significantly from nest observations in terms of the proportions of prey orders (G_{14} = 2,121, *p* <0.01, $\alpha_{bonferroni}$ = 0.0125). A comparison between nest and pellet samples from Hulsig Hede suggested no significant differences between the two methods ($G_7 = 11$, *p* >0.05, $\alpha_{bonferroni}$ = 0.025). However, in terms of proportions of orders, the nests of Gribskov differed significantly from both pellets and nests of Hulsig Hede ($G_7 = 45$, *p* <0.01, $\alpha_{bonferroni}$ = 0.0167 and $G_7 = 22$, *p* <0.01, $\alpha_{bonferroni}$ = 0.0167, respectively).

Scarabaeidae constituted the majority of beetle items in Hulsig Hede, mainly due to *Anomala dubia* which was found in almost every pellet and nest sample there, and comprising 21% of the diet. Similarly, based on the nest observations during 2002–2003, *Anomala dubia* accounted for >75% of beetles in the diet. In Gribskov, the longhorn beetle *Corymbia rubra* (Cerambycidae) dominated, constituting 22% of the diet. Different species of ground beetles (Carabidae, mainly *Pterostichus niger*) were common in both Gribskov and Hulsig Hede, although they only comprised a small part of the diet in nest observations (potentially not recognized as carabids). The dominating Hymenopteran taxon in Gribskov and in the pellet and nest samples from Hulsig Hede was the genus *Bombus*, comprising 27% and 36% of the diet, respectively. Among vertebrates, the most common items in all three methods were lizards (*Lacerta agilis* and *Zootoca vivipara*), while shrews (*Sorex* sp.) and mice (Muridae) constituted a smaller part of the diet. In Gribskov the proportions of different vertebrate items were roughly equal.

No significant difference in the number of items found in nests occurred between Gribskov and Hulsig Hede (median values 53.0 and 67.5, respectively; $U = -221.5$, $p > 0.05$). The numbers of taxa found in nests were also relatively similar between Gribskov and Hulsig Hede (16.0 and 17.5, respectively; $U = -233.5$, $p > 0.05$). The number of prey items found in nests in Gribskov was not significantly associated with the nesting-tree species (ANOVA; $p = 0.868$), the time of the year in which nests were collected ($t_{22} = 2.29$, $p = 0.487$) or the height of the nest (slope $= -0.15$, $r = -0.32$, $p = 0.131$).

4. Discussion

4.1. Diet is related to summer temperature

Breeding success in the Red-backed Shrike is higher during warm and dry summers (Hušek & Adamík 2008, Hušek *et al.* 2009; but see Passinelli *et al.* 2011). We found that temperature negatively affects prey diversity, resulting in a more diverse diet during cold summers. In addition, there was a tendency that precipitation positively affects prey diversity, suggesting that Red-backed Shrikes feed on a wider variety of prey items during wet summers. Our findings also suggest that Red-backed Shrikes will switch to preferred food items when conditions are good but under less favourable conditions a broader spectrum of food items is utilized. This pattern was confirmed by investigating whether the species *Anomala dubia*, found in nearly all samples from Hulsig Hede, could explain the low diversity in the diet in warm summers.

As shown here, *Anomala dubia* constituted a high proportion of the diet in years with low diet diversity, indicating that a single prey species is preferred when available. However, the occurrence of this beetle shows only one strong peak during the season and is also influenced by preceding temperatures (authors' own observations, Bargerveen Foundation). As the collection of pellets and nests were not equally spread out over June–July each year, however, some bias may have existed. In addition, Van Duinen *et al.* (2004) found that the abundance of *Anomala dubia* in Hulsig Hede is indirectly influenced by sand

spray; the strong dependence of its larvae on vital roots of the marram grass *Ammophila arenaria* makes this beetle much more abundant in dynamic than in more stable areas. This shows that food availability may vary within a given area, and therefore differences in diet within the population should be taken into account when analysing diet.

4.2. The diet differs between adults and young

The present study revealed a difference in both prey composition and prey size of nestlings, juveniles and adults. Coleopterans and Hymenopterans were the most common orders in the diet of both young and adults. However, unlike other groups the proportional distribution of different Hymenopteran taxa varied among nestlings, juveniles and adults; nestlings ate a larger amount of bumblebees and adults consumed a larger amount of ants, supporting Nikolov (2002), and juveniles fell between these two age groups. Prey sizes reflected this difference, adults generally eating smaller prey items than did nestlings. However, Hernandez (1993) found that nestlings were fed with prey items <10 mm whereas adults preferred larger prey. Prey length as an estimate of size appears problematic because insects have greatly varying body proportions, and longer insects tend to be narrower (Schoener 1980); it is therefore recommendable to use biomass estimates. However, in the present study this potential bias probably did not affect the results, as ants (relatively small) and bumblebees (relatively large) accounted for most of the variation in prey size.

4.3. Variation in diet between habitat types

Diet diversity of nestlings in Gribskov and Hulsig Hede was remarkably similar. In Gribskov, however, nestlings were fed larger prey than nestlings in Hulsig Hede. This was mainly due to the predominating species *Corymbia rubra* in Gribskov which fell into the size classes 11–15 and 16–20 mm. In comparison, the species *Anomala dubia*, which dominated the diet of nestlings in Hulsig Hede, consistently fell into the size class 11–15 mm. These two species are good examples of variation in overall prey shape, *Corymbia rubra* being

narrow and flat while *Anomala dubia* is almost spherical in shape.

However, longer insects are not necessarily heavier. Differences between a forest and a heath could potentially lead to differences in the insects inhabiting these areas (Golawski & Golawska 2008). Furthermore, visibility and availability of prey items is likely to differ between habitat types and can thereby cause differences in diet composition. Bumblebees did, however, constitute a major part of the diet of nestlings in both habitat types.

4.4. The choice of method affects the results of diet analysis

Our results support previous studies on diet composition of the Red-backed Shrike in that insects dominated over vertebrates (Tryjanowski *et al.* 2003a, Tryjanowski *et al.* 2003b, Golawski 2006). Beetles and hymenopterans (especially bumblebees) were the most important prey groups in both study populations. Although the proportions varied among sites, the dominance of these orders has also been documented in other studies using pellets to describe the diet (Olsson 1995, Arcas 1998, Tryjanowski *et al.* 2003a). Diet composition is influenced by many external factors, such as the quality of habitat, geographical location, weather conditions, time of day, and season (Cramp & Perrins 1993, Esselink *et al.* 1995, Hornman *et al.* 1998). All these factors need to be accounted for when performing diet analyses. However, the method on which the diet analysis relies might also affect the result (Tryjanowski *et al.* 2003b).

As expected based on the fact that nests remains are in fact crumbled pellets, our study revealed no significant difference in nestling diet between pellet and nest samples, supporting Golawski (2006). Diet composition described by pellet and nest remains as compared with direct nest observations differed remarkably. This difference is mainly due to differential digestion of prey items from specific taxonomical groups, especially nonsclerotized invertebrates, such as Araneae, larvae of different orders (e.g., caterpillars) and adult Lepidoptera and Diptera. These taxa are poorly preserved in pellets, and even if some parts are preserved they might be overlooked because of difficulties in identifying them (Nikolov 2002, Tryjanowski *et al.* 2003b).

As there are advantages and drawbacks with all diet-analysis techniques, more than one method should be applied to complement each other (Rosenberg & Cooper 1990, this study). As for analysis of both pellet and nest remains, the major advantages are the precision in identification of prey items without having to disturb the bird. In addition, the researcher is independent on the season to identify prey items. These methods can provide good qualitative insights to the presence or absence of different families, genera or in many cases even species. Furthermore, pellets can be collected from both young and adults, thereby providing information regarding variation in diet composition between age classes. Differences in the digestibility of prey items (Nikolov 2002, Tryjanowski *et al.* 2003b) and in the handling of prey before eating (Tryjanowski *et al.* 2003b) are, on the contrary, drawbacks that will certainly lead to underestimations of prey items. For nests, another drawback is that the amount of identifiable prey fragments might be reduced because of environmental factors such as wind and rain or parasites decaying the fragments. However, we found no significant differences between nests in the amount of identified prey items.

In terms of absolute prey numbers, direct nest observations provide the best quantitative measure of prey items fed to nestlings. The use of nest observations is the only way of gaining knowledge on prey items not preserved in pellets. Another major advantage is the amount of additional information that can be gathered from such studies, mainly feeding rates, parental behaviour, and diurnal and age-related variation in diet. Our observational study showed a relatively high amount of prey items that were not even identified to order (16–32% per nest), underlining the importance of using complementary methods.

Our study supports three general conclusions regarding diet studies in shrikes. Firstly, we recommend using direct observations in diet studies whenever time and funding can support the respective costs. These observations should be supplemented by studies of either nest or pellet remains. Secondly, when focusing on the diet of nestlings, collection of nests at the end of the season will be sufficient. Thirdly, to obtain data on adult diet, collection of pellets underneath perches during the season will be necessary.

Pikkulepinkäisen saaliskirjoon vaikuttavat ilmasto ja ikäluokka

Pesimäkautena ravinnon saatavuus on tärkeää optimaaliselle jälkeläistuotolle ja potentiaalisesti yksi pesimämenestystä määrittävistä päätekijöistä eritoten yksipesyeisillä muuttolinnuilla. Selvitimme pikkulepinkäisen (*Lanius collurio*) ravintoa (saaliin saatavuuden mittari) kahdessa tanskalaisessa populaatiossa perustuen yli 11 000 saaliseläimeen seitsemän vuoden ajalta. Saaliin diversiteetti ja lämpötila korreloivat keskenään negatiivisesti, mikä viittaa siihen, että pikkulepinkäiset käyttävät pääravintokohdettaan lämpimämpinä kesinä (jolloin saalisdiversiteetti on alhaisempi) ja ovat pakotettuja laajentamaan ravintokohdevalikoimaansa kylmempinä kesinä. Nuorten ja vanhojen yksilöiden saaliin koostumus oli erilainen: vanhojen ravinto oli monipuolisempaa ja koostui pienemmistä saaliseläimistä. Siten ikä- ja ympäristöerot tulisi huomioida pikkulepinkäisen ravintoa tutkittaessa. Suorat havainnot pesiltä tuottivat erilaisen kuvan ravintokirjosta kuin oksennuspalloja pesäpohja-aineistot; siten ravintotutkimuksissa olisi suotavaa käyttää useampia menetelmiä. Yksityiskohtainen tieto pesimäseuduilla rajoittavista tekijöistä, kuten ravinnon saatavuudesta, on tärkeää vähenevien ja uhanalaisten lajien, kuten pikkulepinkäisen, suojelussa.

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