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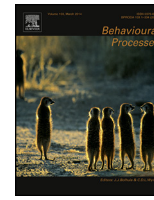

Saving the best for last: Differential usage of impaled prey by red-backed shrike (*Lanius collurio*) during the breeding season

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ABSTRACT

We compared the prey composition of the red-backed shrike's (*Lanius collurio*) larders in agricultural habitats in Italy, France and Poland. This species exhibits the behaviour of impaling prey in larders, a behaviour attributed not only to storing food, but also as a social indication for sexual selection and/or demarcation of territories.

A total of 426 impaled items were identified in 244 larders. Most common prey were identified for each country: Insecta (Hymenoptera) in Italy, Amphibia, Insecta (Diptera) and Clitellata in Poland, and Insecta (Orthoptera, Lepidoptera) in France. We found no relationship between type of prey impaled and height of impalement, however, we noted a negative relationship between the height of impalement and the distance to the nearest road. Furthermore, impaled toxic prey were found in all three countries, strengthening the possibility that prey are exposed to expedite the degradation of toxins or used as a social signal.

Our results showed that the average weight of impaled prey was greater during the last reproductive stage (hatching and feeding young), providing evidence of differential usage of impaled prey during the breeding season. We therefore hypothesize that larger animals provide more energy, then vertebrates are preferred to invertebrates, especially when parents are feeding their nestlings.

1. Introduction

Access to critical resources, especially food, is crucial for effective conservation of declining farmland species (O'Connor and Shrubb, 1990; Tryjanowski et al., 2011). A good example of an avian family whose distribution and population stability is strongly related to the availability of appropriate foods, are the True Shrikes Laniidae (Yosef, 1994). This family employs the unique behaviour of impaling prey and, like many other avian species, of creating larders (Tryjanowski et al., 2003b; Yosef and Pinshow, 2005). The Laniidae use a typical sit-and-wait strategy and their diet is predominantly composed of insects supplemented by vertebrates (Karlsson, 2004; Morelli et al., 2013; Tryjanowski et al., 2003a). Prey is captured from elevated observation posts or perches (Lefranc and Worfolk, 1997), and this capability is shown to affect the total territory defended by a pair (cf. Yosef and Grubb, 1992).

Short-term food storage is affiliated primarily with shrikes, birds of prey (Lefranc and Worfolk, 1997; Newton, 2010) and in some Cracticids, Parids and Corvids (Pizzey and Knight, 2012; Smith and Reichman, 1984; Vander Wall, 1990). However, the most conspicuous in this behaviour are the Laniidae (Antczak et al., 2005a; Nikolov et al., 2004), frequently resulting in the layman's animosity towards shrikes (e.g., Swanson, 1927). In Europe, the behavioural trait of impaling prey is restricted to the different shrike species (Yosef and Pinshow, 2005), and the behaviour of food storing amongst birds is assumed mainly for deposition of food items in a particu-

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lar location for subsequent consumption (Shettleworth et al., 1995). However, in shrikes the use of larders has been shown to have originated because of morphological limitations (Cade, 1995; Schon, 1994) and has evolved into a variety of different exaptations (cf. courtship, polygyny – Yosef and Pinshow 2005; extra-pair copulations – Tryjanowski and Hromada, 2005; overcome toxic prey – Yosef and Whitman, 1992; Fuisz and Yosef, 2001). Impaling appears to have evolved as a tool that facilitates dismemberment of prey, allows the Laniidae to broaden the prey spectrum that would otherwise not be included in their diet (Cade, 1995; Yosef and Pinshow, 2005), and develops in the days immediately after the young fledge the nest (Smith, 1973). In contrast to raptors, shrikes are Passerines that do not have talons or strong feet to manipulate the prey, but have a bill similar to the *Falco* spp. with a tomial tooth which enables them to dismember prey with minimal energetic investment and maximizes butchering capabilities (Cade, 1995; Hromada et al., 2008; Yosef and Pinshow, 2005).

Several studies have proposed that impaled prey also plays a social role, with sexual selection, signalling territory quality and the hunting prowess of the owner (Antczak et al., 2005b; Yosef and Pinshow, 1989). Sloane (1991) thought that impaled prey in exposed places might serve as landmarks for territory demarcation, in spite of kleptoparasitism by other avian species on a regular basis (Yosef and Pinshow, 2005). In many Laniidae species, males are the first to arrive at the breeding grounds, so the appropriate demarcation of the territory would increase the individual's chances of being chosen earlier in the season by the earliest arriving females. This advantage over their conspecifics results in better fitness levels (Antczak et al., 2009; Yosef and Pinshow, 2005), and in some species even leads to polygyny for males that have especially large larders (Yosef and Pinshow, 1988; Yosef, 1992; Yosef et al., 1991).

Furthermore, larders can also provide benefits during inclement weather (Tryjanowski and Goławski, 2004) or when energetic requirements increase rapidly, for example during egg laying and the rapid growth of nestlings immediately after hatching (Carlson, 1985a; Degen et al., 1992). They seem to be a very important strategy, mainly for avian species living in agro ecosystems that may not always be compatible to their specific requirements. Agricultural landscapes are human-modified, artificial mosaics of different land uses and types, that represent one of the most common habitats for several avian guilds in Europe, and covers up to 60% of some countries (Donald et al., 2006). These landscapes constitute the breeding habitats of the red-backed shrike (*Lanius collurio*), a species that is widespread in areas where the traditional model of field division with perennial field margins is retained and edge-habitats are created, as in some regions of Poland and Central Italy (Morelli, 2013a; Wuczyński et al., 2011). That said however, it is important to note that farmland biodiversity is currently under threat across much of Europe (Tryjanowski et al., 2011). Despite the basic understanding that shrike's impale their prey in order to exploit a wider range of species, the relationship with habitat modifications remains obscure. In addition, the red-backed shrike is suffering from population declines across most of Europe, especially in the western countries (Yosef, 1994; Kristín et al., 2004).

Our aim was to compare the prey composition of the red-backed shrike's larders, in agro-ecosystems in Italy, France and Poland, in order to further our understanding of the reasons the red-backed shrike (being the most common of the Laniidae in Europe) have for impaling their prey. Additionally, by evaluating the larders in relation to a variety of environmental parameters, we wished to elucidate possible advantages conferred upon the red-backed shrike. We hypothesized that larders placed conspicuously may play a role in the form of some social function (sexual selection, territory demarcation, etc), while those hidden inside foliage would function as a larder per se i.e., for consumption at a time of greater need. We examined the changes in prey impaled during the different stages of the seasonal reproductive cycle, and also thought that the inclusion of inedible objects or toxic prey could be a manner in which males display their hunting prowess to the females. In addition, because shrikes are also known to scavenge, we assumed that the distance of the larder from the nearest road would be indicative of the proportion of energetic investment in accessing a food source or storing it. However, because roads are known to modify wildlife behavior (Shannon et al., 2014), it is of interest to see whether they also influence the prey dispersal and impaling behavior of the red-backed shrike. Finally, we tried to underline potential conservation applications of our findings.

2. Material and methods

2.1. Study area

Data were collected in three European countries: (a) extensive farmlands of central Italy, in the foothills of the Apennines, in the Northern Marche region (43.76°N 12.64°E); (b) extensive farmlands of Eastern Poland, near the Siedlce (52.14°N 21.93°E), (c) and extensive farmlands of Central France, in the Limousin's region (45.85°N 0.88°E). The three areas were selected because long term studies of red-backed shrikes have already been conducted in these regions (e.g. Bussière, 2014; Golawski and Golawska, 2013; Morelli, 2012; Tryjanowski and Goławski, 2004), and they are predominantly agro ecosystems. Dominant habitats in the study areas included pastures, meadows, cultivated and fallow fields, small forest patches, shrub lands and small urban areas.

2.2. Bird data collection and environmental variables

Breeding areas of red-backed shrike were visited from mid-May to late July of 2013, simultaneously in Italy, France and Poland. The surveys were performed by expert observers in each country. On arrival at the respective study areas, individual birds, breeding pairs and their relative behaviours — territory establishment, courtship, or nest-building were identified by direct observation. Every one of the territories was marked with the help of GPS readings. Subsequently, these areas, were visited again following a constant sampling effort procedure (days of search) in order to cover the entire area in as uniform a manner as possible. We defined a specific spot within the territory as the larder if the resident red-backed shrike impaled prey at the site either more than on one occasion, or two or more prey were clustered at the same site.

In order to locate and quantify all the prey contents of the larders we divided the reproductive stages of the red-backed shrike according to phenological stages: courtship and egg laying which occurs throughout the second half of May, hatching and first half of the nestling and brooding stage that takes place in the first half of June, the second phase of the nestlings in the nest when they are feathered during the second half of June, and the feeding of the fledglings when they leave the nest over the first and second half of July (Hernández, 1995). Previous studies indicate that mating and incubation are the periods most suitable to detect larders because they are displayed openly and there is a relatively low rate of food consumption (Antczak et al., 2005b; Yosef and Pinshow, 1989).

The location of the breeding pairs was carried out by direct observation during the red-backed shrike's arrival, courtship or nest-building activities, then, the occupied territories were surveyed. The territories occupied were determined following repeated and simultaneous observations of two or more individuals of the same sex. Because this species has a markedly territorial behaviour, such observation methods are suitable in defining an occupied territory (Karlsson, 2004; Tryjanowski and Goławski, 2004). When a territory was attributed to a breeding pair, it was

Table 1
Environmental variables collected in the field in Central Italy, Central France and Eastern Poland.

Parameter	Description
Geo-position	Latitude and longitude, expressed as decimal degrees
Surrounding land-use	Land-use typology: cultivated, uncultivated, badland, forest, grassland, hedgerows, isolated trees, shrubs, urban, road, river, expressed as % coverage in 100-m radius around the larder
Road distance	Distance to the nearest road, meters
Landscape to exposition	Main type of land-use in the direction opposite to the larder
Type of support of larder	Type of structural support used to build the larder (e.g. plant species, barbed wire, other)
Vegetal species and height	Plant species, height of the top of the vegetal species were larder is built, meters
Hidden	Level of concealment of the prey from a frontal view of the larder, using a ranking from 0 = totally visible, 1 = partially covered by some foliage, to 2 = almost completely covered by foliage
Stuck	Type of fixation of the prey (impaled or wedged)
Prey type	Classified as vertebrate or invertebrate
Prey species	Systematic determination of prey species impaled in the larder
Prey number	Total prey in the same larder
Prey height	Measured from the impaled prey to the ground, meters
Prey weight (average)	The average weight of the most frequent type of prey found in the larders was derived from bibliography

classified with a code (sampled site 1, sampled site 2, etc). The surveys were conducted on all viable shrubs characterized by activities of both males and females (prey transport and territorial behaviour) with the aim of identifying impaled prey. Each larder was considered a single unit of study and was attributed to a particular breeding pair in whose territory it was located (sampled site). In situ we noted the habitat composition in a 100-m radius around the larder in order to quantify the surrounding land-use, marginal vegetation typologies, and structural characteristics (Morelli, 2012; Table 1).

All prey found in the larders was photographed in order to subsequently determine the taxon of the species with the appropriate taxonomic guides and experts. The prey was initially classified into major taxonomic groupings: Invertebrates: Arachnida, Insecta, Vertebrates: Amphibia, Reptiles, Aves and Mammalia. Moreover, in France, we found four cases of impaling of inedible objects — two of egg-shells and two of fruits (cf. Yosef and Pinshow, 2005).

In order to estimate the average weight of prey recorded in the larders, we used the masses reported in the literature for each of the identified species. For insects, the mass ranged between 0.3–1.2 g (Holzer et al., 2003; Ryszkowski and Karg, 1977; Ulrich, 2006), for Amphibia (*Rana* sp.) average mass was estimated at 22 g (Tryjanowski and Hromada, 2005) and for Reptilia (Colubridae) *Hierophis viridiflavus* mass was ca. 30 g (Zuffi, 2011).

2.3. Statistical analysis

In order to study the prey characteristics of the red-backed shrikes' larders in each of the above mentioned countries, we used the indicator value method (IndVal analysis; De Cáceres et al., 2010; De Cáceres and Jansen, 2012). The IndVal analysis is based on specificity, which is the conditional probability of a positive predictive value of a given prey as an indicator of the target plot group, and sensitivity (or fidelity) which is the conditional probability that the given prey will be found in a newly surveyed plot belonging to the same plot group (Dufrene and Legendre, 1997), producing a percentage indicator value (IndVal) for each prey type. IndVal analysis needs two kinds of input that can be either occurrence or abundance values: plot-by-prey table containing the occurrence data of prey type at sampled sites (larders) and partition of the sampled sites into groups (countries). In order to be considered a characteristic of a certain country, a prey type has to be found reliably and almost exclusively within that country. Here, prey type that has an IndVal statistic value higher than 20% and $p < 0.05$ is considered an indicator prey type for each country that is statistically significant (Della Rocca et al., 2014).

We used Mantel tests (Mantel, 1967) to test for spatial autocorrelation. The Mantel statistic (r_M) is a measure of the correlation between the two matrices and results from the cross-product of the matrix elements after standardization. This test evaluates the similarity between two matrices: one measuring ecological distance (prey height in the larder in this case) (Legendre and Legendre, 2012) and the other geographical distance (among sampled sites). If a spatial autocorrelation exists, and the plots are closer in geometric space, the more similar the pattern of values between the matrices will be. Thus, the Mantel test measures the correlation between the Euclidean plot-to-plot dissimilarity matrices for testing for plot-level associations. We used Monte Carlo permutations with 999 randomizations to test for significance (Oksanen, 2014). We did not find spatial autocorrelation in the dataset ($r_M = 0.08$, $P = 0.15$, 999 randomizations), hence models were performed without including latitude and longitude as (spatially structured) random effect into the model specification.

Mixed effects models refer to a variety of models which have both fixed and random effects as a key feature. In this work, Generalized Linear Mixed Models (GLMMs) were used to study the patterns of average prey weight found in larders in relation to the reproductive stage, whilst taking the level of concealment of the prey in the larder into consideration as well. Sampled site and country were included as random effects in the models. Other GLMM models were performed using the prey height in the larder as a response variable, and the other environmental variables as predictors, sampled site and country were also included as random effects in these models. Models were fitted with REML *t*-tests using Satterthwaite approximations for degrees of freedom, and the package 'lme4' (Bates et al., 2014) in R. The minimal models were chosen using only those terms retained, showing a significant effect on the predictors values at a >5% rejection probability.

All tests were performed with R (R Core Team, 2014) (Fig. 1).

3. Results

A total of 426 impaled items of prey were identified in 244 larders of red-backed shrike in all three countries — 63 prey in 36 larders in Italy, 140 prey in 66 larders in Poland, and 223 prey in 142 larders in France. Larders that were exhibited openly were in cultivated and grassland habitats, and were found at a range of 0.3–350 m from the nearest road.

Prey was impaled mostly on plants and barbed wire (ratio 62:38 %). The plant species most used were: *Prunus spinosa, Rubus* sp., *Crataegus* sp. and *Rosa canina* (>95% of total). The average plant height used as a larder was similar among the three countries (total mean = 2.5, SD = 1.2, $n = 263$, $F_{2,259} = 0.77$, $P = 0.46$). Most prey in the larders was impaled ($n = 418$; 98%) and only a few were wedged ($n = 8$; 2%).

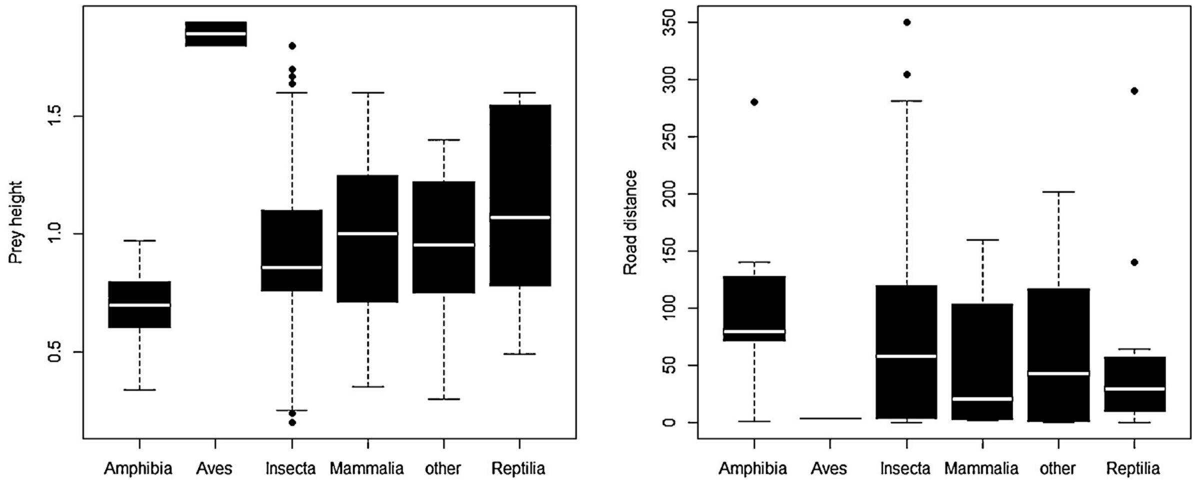

Fig. 1. The relationship between type of prey impaled in the larder of red-backed shrike (*Lanius collurio*) with the height of impaling above-ground and distance to the nearest road. The *y*-axis represents the prey height and road distance in meters. The boxplots show the median (white bar in the middle of black rectangles), upper and lower quartiles and extreme values.

Table 2
Number of impaled prey of each category, per country, and percentage of total found in the larders of red-backed shrike (*Lanius collurio*).

Prey type	Central Italy	Eastern Poland	Central France	% of the total
Insecta	51	104	212	86.2
Amphibia	0	31	0	7.3
Reptilia	6	2	3	2.6
Aves	2	0	0	0.5
Mammalia	3	1	3	1.6
Other	1	2	5	1.9
Total	63	140	223	

Of the 426 prey found in larders, all were classified at the level of their Order or species (Table A1, Annex 1). The most common prey in all countries was insects (>86%, Table 2). Prey composition in the larders was country specific and the results of IndVal analyses showed the prey type described as being representative of the different countries and their combinations. The prey item specificity (degree to which a prey item is found only in a given group of sites, component “A”) and fidelity (degree to which a prey item is present at all sites of a group, component “B”; Table 3) was represented for each country or combination.

In all countries, a small number of potentially toxic species were found impaled in the larders of red-backed shrike ($n = 27$, 6.3%; prey type = 15, Table A1, Annex 1). In all cases the potential toxic prey was found mainly during the brooding phase of the breeding cycle (>80 % cases).

On the first level, the “multipatt” function produced the species that represent each of the countries, or their combinations. Of those, Insecta (Hymenoptera) was significantly characteristic of larders in Central Italy, Amphibia, Insecta (Diptera) and Clitellata were typical of larders in Eastern Poland, and other four prey types were significantly characteristic in combinations between the countries studied (Table 3).

The results of GLMM procedures showed that the average weight of prey items did not correlate with the distance from the

Table 3
Results of IndVal analysis of prey item composition of red-backed shrike (*Lanius collurio*) larders from Central Italy, Eastern Poland and Central France. Component A refers to the specificity, while component B refers to the fidelity of the prey type in each group. Only prey types with stat values higher than 0.20 at 0.05 *p*-level are statistically significant, and denoted by asterisks.

	Group Central Italy, number of prey type = 5				
Species	A	B	Stat	*p*-value	
Insecta (Hymenoptera)	0.92838	0.30556	0.533	0.0010	****
Aves	1.00000	0.02778	0.167	0.340	
Insecta (Mantodea)	1.00000	0.02778	0.167	0.365	
Reptilia (Colubridae)	1.00000	0.02778	0.167	0.350	
Insecta (Larvae)	1.00000	0.02778	0.167	0.333	
	Group Eastern Poland, number of prey type = 4				
Species	A	B	Stat	*p*-value	
Amphibia	1.00000	0.39394	0.628	0.001	****
Insecta (Diptera)	0.99041	0.24242	0.490	0.001	****
Clitellata	0.89590	0.06061	0.233	0.061	.
Arachnida	0.89590	0.03030	0.165	0.261	
	Group Central France/Eastern Poland, number of prey type = 2				
Species	A	B	Stat	*p*-value	
Insecta (Orthoptera)	0.95056	0.61143	0.762	0.001	***
Insecta (Odonata)	1.00000	0.02857	0.169	0.668	
	Group Central Italy/Eastern Poland, number of prey type = 4				
Species	A	B	Stat	*p*-Value	
Insecta (Lepidoptera)	0.95296	0.13043	0.353	0.007	**
Reptilia (Lacertidae)	0.90424	0.07246	0.256	0.091	.
Insecta (Heteroptera)	1.00000	0.05797	0.241	0.031	*
Mammalia	0.84323	0.04348	0.191	0.434	

Table 4
Fixed-effect parameters in the GLMM, accounting for variation in weight of prey items impaled in larders in relation to the reproductive stage of red-backed shrike (*Lanius collurio*). The full model is based on 426 observations and is the result of an automated model selection procedure including possible interactions between covariates (sampled sites and country). Sampled site (groups = 244), country (groups = 3) and interactions between them were added as the random factor in the model. Significant variables selected in the best model are in bold.

Fixed effects	Estimate	SE	df	*t* value	*P*
(Intercept)	2.798	2.090	3.250	1.339	0.266
Reproductive stage — nestling (first half)	0.488	1.240	223.89	0.394	0.694
Reproductive stage — nestling (second half)	−0.036	2.110	228.71	−0.017	0.986
Reproductive stage — hatching, feeding chicks	4.950	1.322	205.87	3.744	**0.000*******

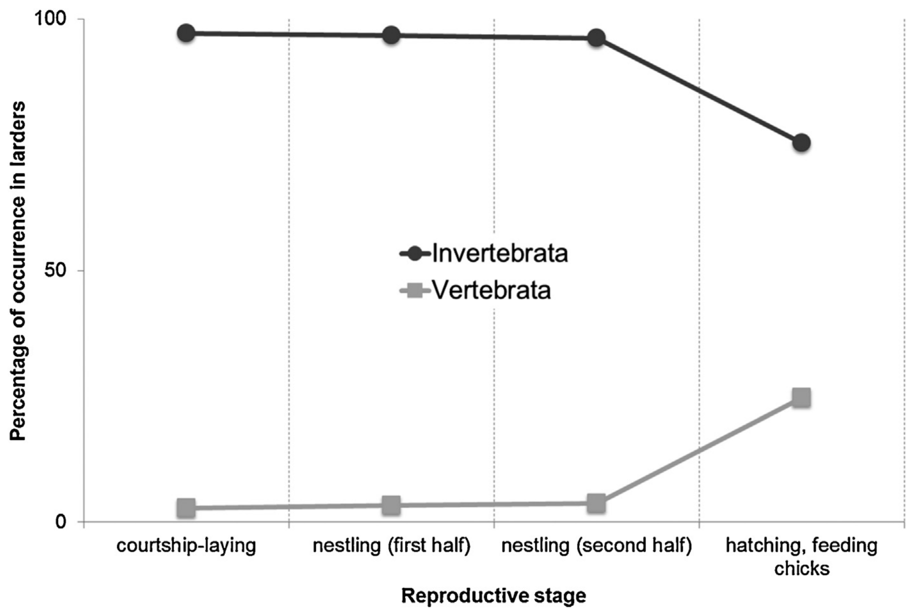

Fig. 2. Change in composition of impaled prey in larders of red-backed shrike (*Lanius collurio*), during the different reproductive stages.

road or other environmental variables as, for instance, the surrounding land-use composition, but was greater during the last reproductive stage (hatching and feeding young) when compared to all the earlier reproductive stages (Table 4, Fig. 2). In contrast, the GLMM model of prey height in the larder was influenced by the coverage of uncultivated, fallow lands which resulted in a small increase in the height of impaled prey in the larders. Similarly, a small increase in the height of the impaled prey was found during the second half of the nestling stage. Furthermore, height of impaled prey above the ground was negatively correlated with the distance to the nearest road (Table 5). Level of concealment of the prey items in the larder was not selected as a predictor in the best models.

4. Discussion

Specific prey was found as typical of the larders for each of the study countries. We used the IndVal analysis, a procedure normally used to study the species indicators of communities, to determine the prey items characteristic for each country. The indicator species are often determined using an analysis of the relationship between the species occurrence or abundance values from a set of sampled sites and the classification of the same sites into site groups, which may represent habitat types (De Cáceres et al., 2012). In this study, we applied the analysis to the composition of prey items in the larders. The comparison was useful to highlight the congruence

Table 5
Fixed-effect parameters in the GLMM, accounting for variation in height of prey in the larders in relation to environmental parameters and reproductive stage of red-backed shrike (*Lanius collurio*). The full model is based on 426 observations and is the result of an automated model selection procedure including possible interactions between covariates (sampled sites and country). Sampled site (groups = 244), country (groups = 3) and interactions between them were added as the random factor on the model. Significant variables selected in the best model are in bold.

Fixed effects	Estimate	SE	df	*t* value	*P*
(Intercept)	0.996	0.211	0.181	4.726	**0.000*******
Road distance	−0.150	2.1e-4	0.041	−1.048	**0.029***
Surrounding land-use					
– Cultivated	−2.3e-4	2.2e-3	3.7e2	−0.102	0.918
– Uncultivated	4.1e-3	2.4e-3	3.7e2	1.679	0.094.
– Forest	3.3e-3	2.8e-2	3.9e2	1.178	0.239
– Grassland	−1.7e-3	2.8e-3	3.0e2	−0.845	0.398
Reproductive stage — hatching, nidicolous young	5.9e-2	4.2e-2	4.1e-2	1.411	0.159
Reproductive stage — nestling (first half)	−4.2e-3	4.2e-2	4.1e-2	−0.098	0.922
Reproductive stage — nestling (second half)	0.161	5.3e-2	4.1e-2	3.023	**0.002****

and divergences on most typical prey items related to the three countries and combinations.

Similar to previous studies, beetles and hymenopterans dominated the prey species of the red-backed shrike (Goławski, 2006; Karlsson, 2004; Tryjanowski et al., 2003b). Besides these two orders, among the dominant taxa there were Heteropterans (Hernández, 1995; Tryjanowski et al., 2003b), Orthopterans (Hernández, 1995; Karlsson, 2004), and Dermapterans (Olsson, 1995). The percentage (both by number and biomass) of hymenoptera in the diet of red-backed shrike was high. This is surprising because if one considers that capture of bees and wasps requires an aerial chase that is energetically costly, we would expect these groups to be less energetically important for shrikes (Tryjanowski et al., 2003b), and yet they continue to comprise the most common prey in Central Italy, and in other European countries (Mielewczyk, 1967; Randik, 1970). These data are also similar for loggerhead shrikes (*Lanius ludovicianus*) in North America (cf. Yosef and Grubb, 1993)

The occurrence of some toxic species, impaled conspicuously in the larders of red-backed shrike in all countries (6.3% of total cases) but not subsequently consumed, confirms the possible use of prey also as a social signal or for territorial demarcation (Antczak et al., 2005b; Sloane, 1991). Nonetheless it is also possible that toxic prey is placed in open areas exposed to the sun in order to expedite the degradation of the toxins (Yosef and Whitman, 1992; Antczak et al., 2005a).

It is well known that vertebrates supplement the diet of the red-backed shrike (Lefranc and Worfolk, 1997) and are represented by a wide range of taxa such as small passerines, small mammals, lizards, frogs and even fish (Hernández, 1995; Morelli et al., 2012). However, the results of our study show a significant increase in the number of vertebrate prey in the larders during the last stages of the breeding period. Almost 88% of vertebrate prey was found during the last two reproduction stages in all three countries: the second phase of the nestlings (second half of June) and the feeding of fledglings (first and second half of July). Larger animals provide more energy for the birds, so vertebrates are preferred compared to the smaller invertebrates. A lot of food is required especially when the parents are feeding their nestlings. During this period, the prey in the larders of red-backed shrike increased not only numerically (Carlson, 1985a), but in body size as well. This result could also be related to the large number of amphibians found in eastern Poland during the later part of the breeding season, when the young frogs leave the ponds and are easy prey for shrikes. The study area in Poland is situated in wet meadows with small reservoirs in which there are many breeding amphibians.

We did not find a relationship between the type of prey impaled by red-backed shrikes and the height of placement in the larder.

Several studies have underlined a positive relationship between the distribution of Laniidae and linear habitats such as roads or the roadside hedgerows and fence-lines (Ceresa et al., 2012; Morelli, 2013b; Yosef and Grubb, 1993). Luukonen (1987) found that shrikes nested closer to roads than was expected. Howbeit, we found a significant and negative relationship between the height of impaled prey in the larder, placed in vegetation, and the distance between the larder and the nearest road. We hypothesized that this relationship could be explained by the structural differences between shrubs and their distance to the roads. Many roadside shrubs are subject to public works maintenance, especially cutting of lower branches in order to keep the roads clear of obstacles. This could lead to a situation where the only branches most suitable for larders are the remaining highest ones. Furthermore, shrikes are known to frequent roads in order to scavenge on fresh road-kills, which can be an important food resource for shrikes (Morelli et al., 2014).

An additional explanation for the increase in height of prey in larders, when in close proximity to roads, could be in order to avoid excessive exposure of impaled prey to potential kleptoparasites (cf. Yosef and Pinshow, 2005), like corvids, that are also very common scavengers and patrol the roads foraging for food (Dean and Milton, 2003; Mason and Macdonald, 1995). Moreover, the small mammals and reptiles that frequent roads in order to scavenge roadkill can also avail of the impaled prey. Similarly, we found that the average weight of prey items was positively correlated with the distance to the road. We rationalize this finding by the cost: the benefit ratio of the energetic investment in carrying a heavy prey decreases with distance (Carlson, 1985a,b). Also, shrikes are limited in the manner in which they can carry their prey, making the distance to the larder and important factor(cf. Yosef, 1993).

This study underlined the importance of studying the complete food spectrum of the red-backed shrike, as well as the temporal variation of these resources, especially in relation to the breeding season. We recommend that future conservation strategies, based on the species ecology, focus not only on the easily accessible food but also on availability and temporal changes. This is important because, as demonstrated in our study, there are differing energetic demands in the various breeding stages, requiring the breeding pair to maximize energetic gain for themselves and their progeny. Likewise, differences in prey weight in relation to land-use were not found in this study, even though all studied populations of red-backed shrike bred in extensive farmland areas. Therefore, comparisons between breeding populations in different kinds of habitats (farmland, grassland, mixed environment) could reveal new interesting insights. Besides, local differences can be tested in an experimental way.

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Annex 1.

*Table A1. List of impaled prey recorded in the larders of red-backed shrike (*Lanius collurio*) in Central Italy, Central France and Eastern Poland. Toxic prey are denoted by a black dot, and is based on literature.*

	Prey type	Species (or Order)	Toxicity
Invertebrata	Clitellata	*Lumbricus terrestris*	
	Arachnida	*Steatoda paykulliana*	●
	Arachnida	*Araneus* sp.	●
	Insecta (Coleoptera)	*Melolontha melolontha*	
	Insecta (Coleoptera)	*Onthophagus* sp.	
	Insecta (Coleoptera)	*Palomena prasina*	●
	Insecta (Coleoptera)	*Rhizotrogini* sp.	
	Insecta (Coleoptera)	*Amphimallon solstitialis*	
	Insecta (Coleoptera)	*Emus hirtus*	
	Insecta (Coleoptera)	*Nicrophorus* sp.	
	Insecta (Coleoptera)	*Geotrupes* sp.	
	Insecta (Coleoptera)	*Meloe violaceus*	●
	Insecta (Coleoptera)	*Philonthus* sp.	●
	Insecta (Coleoptera)	*Feronia nigrita*	
	Insecta (Coleoptera)	*Capnodis tenebrionis*	●
	Insecta (Coleoptera)	*Geotrupes vernalis*	
	Insecta (Coleoptera)	*Geotrupes stercorarius*	
	Insecta (Coleoptera)	*Coleoptera sp.*	
	Insecta (Coleoptera)	*Meligethes aeneus*	
	Insecta (Coleoptera)	*Phyllopertha horticola*	
	Insecta (Coleoptera)	*Necrophorus investigator*	●
	Insecta (Coleoptera)	*Necrophorus vespilloides*	●
	Insecta (Coleoptera)	*Silpha carinata*	●
	Insecta (Diptera)	*Eristallis* sp.	
	Insecta (Diptera)	*Tabanus bovinus*	
	Insecta (Heteroptera)	*Lygaeus saxatilis*	●

	Prey type	Species (or Order)	Toxicity
	Insecta (Heteroptera)	*Coreus marginatus*	●
	Insecta (Heteroptera)	*Heteroptera* sp.	●
	Insecta (Hymenoptera)	*Bombus pascuorum*	
	Insecta (Hymenoptera)	*Andrena cineraria*	
	Insecta (Hymenoptera)	*Bombus* sp.	
	Insecta (Lepidoptera)	*Noctua pronuba*	
	Insecta (Lepidoptera)	*Aglais urticae*	
	Insecta (Lepidoptera)	*Zygaena filipendulae*	●
	Insecta (Lepidoptera)	*Vanessa cardui*	
	Insecta (Lepidoptera)	*Saturnia pyri*	●
	Insecta (Lepidoptera)	*Noctuidae* sp.	
	Insecta (Lepidoptera)	*Macrothylacia rubi*	
	Insecta (Lepidoptera)	*Eruca* sp.	
	Insecta (Mantodea)	*Mantis religiosa*	
	Insecta (Odonata)	*Cordulegaster boltonii*	
	Insecta (Odonata)	*Anax imperator*	
	Insecta (Odonata)	*Libellula depressa*	
	Insecta (Odonata)	*Odonata* sp.	
	Insecta (Orthoptera)	*Tettigonia viridissima*	
	Insecta (Orthoptera)	*Metrioptera roeselii*	
	Insecta (Orthoptera)	*Gryllus campestris*	
	Insecta (Orthoptera)	*Gryllotalpa gryllotalpa*	
	Insecta (Orthoptera)	*Chorthippus* sp.	
	Insecta (Orthoptera)	*Pholidoptera griseoaptera*	
	Insecta (Orthoptera)	*Oedipoda caerulescens*	
	Insecta (Orthoptera)	*Anomala dubia*	
	Insecta (Orthoptera)	*Orthoptera* sp.	
Vertebrata	Amphibia	*Triturus vulgaris*	
	Amphibia	*Rana* sp.	
	Reptilia (Colubridae)	*Hierophis viridiflavus*	
	Reptilia (Lacertidae)	*Podarcis muralis*	
	Reptilia (Lacertidae)	*Lacerta viridis*	
	Reptilia (Lacertidae)	*Zootoca vivipara*	
	Aves	*Serinus serinus*	
	Aves	*Passer domesticus italiae*	
	Mammalia	*Muridae* sp.	
	Mammalia	*Sorex araneus*	●
	Mammalia	*Apodemus sylvaticus*	
	Mammalia	*Microtus arvalis*	

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