

Running head: Global patterns in diet variation of a generalist predator.

Factors influencing diet variation in a generalist predator across its range distribution.

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1 **ABSTRACT:**

2 Factors linked with intraspecific variation in trophic diversity are still poorly understood in
3 generalist species like the Montagu's harrier (*Circus pygargus*). We described geographic
4 patterns of Montagu's harrier diet across Eurasia, gathering diet data from 30 studies in 41 areas
5 from 11 countries. We grouped prey as invertebrates, reptiles, small mammals, large mammals,
6 eggs, small birds and large birds, and calculated the contribution of each prey type to the diet (as
7 % biomass) and Shannon's Diversity Index for each study site. We analysed the diversity index
8 and qualitative estimates of prey abundance in relation to latitude and longitude, then diet
9 composition in relation to habitat of the study area and prey abundance estimates. Diet diversity
10 of Montagu's harriers increased from north to south, while abundance of all prey groups other
11 than small mammals showed the opposite trends. Agricultural areas in northern latitudes seemed
12 to hold high densities of small mammals, but low densities of alternative prey. Overall, birds
13 were the main prey in most of Montagu's harrier's distribution range, although the relative
14 importance of each prey type in the diet was significantly explained by its local abundance and
15 habitat, confirming the opportunistic foraging strategy of this raptor species. Consumption of
16 mammals was an exception to this trend, being negatively associated with the abundance of
17 alternative prey, suggesting that this prey is not preferred. Trophic diversity in this species could
18 be influenced by land-use changes through variations in the abundance and availability of prey,
19 which could impact its population dynamics. This may be particularly important for northern
20 populations of Montagu's harriers breeding in agricultural habitats, where trophic diversity is
21 already low.

22
23 Keywords: diet variation, generalist predator, biogeographical patterns, land-use changes,
24 conservation, *Circus pygargus*.

1 INTRODUCTION

2
3 An organism's diet is a fundamental aspect of its ecological niche. Knowledge of diet and
4 factors affecting its variation across individuals or populations therefore has important
5 implications for the understanding of population and community dynamics. Understanding how
6 diet change in response to variations in abundance, availability and the relative value of
7 different prey, remains a major issue in modern ecology.

8 Individuals are considered trophic specialists if they feed primarily on one food resource,
9 regardless of its abundance. On the other hand, generalists behave opportunistically, in such a
10 way that they may change their diet in response to changes in availability of different prey types
11 (Glasser, 1982). In practice, there is a continuum from specialization to generalization within
12 and between species (Bernays et al. 2004; Egan & Funk, 2006; Partridge & Green, 1985; Durell,
13 2000; Woo et al, 2008). The question of why and when individuals focus on certain prey types
14 is still not entirely understood. However, spatiotemporal adjustments in diet composition are
15 probably of great significance to the survival of individuals and their reproductive success (Roth
16 et al. 2007). Thus, behind the ecological questions of when, where and why species exploit
17 particular resources, there are practical implications for the conservation of animal populations.

18 Understanding of a species' trophic ecology can benefit from comparisons between
19 populations occupying different regions or habitats, which can lead to the assessment of factors
20 associated with changes in diet. The abundance of potential prey may explain local patterns of
21 diet diversity and composition in generalist predators (Elmhagen et al. 2000; Revilla &
22 Palomares, 2002; Moleón et al. 2009). At a geographical scale, abundance of different prey
23 types is likely to depend on climate, which in turn depends on latitude. A latitudinal gradient in
24 species abundance and diversity has been described in Eurasia (Pianka, 1966; Blondel &
25 Aronson, 1999), so more diverse diets are expected at lower latitudes (Rosenzweig, 1995).
26 Indeed, several studies have shown that trophic variation of medium-sized carnivores is linked
27 to latitude, with higher trophic diversity in Mediterranean climates (Clavero et al. 2003; Lozano
28 et al. 2006), or to climatic variables, like xericity (Virgós et al. 1999).

29 Furthermore, the composition of a predator's diet can be influenced by a variety of
30 factors including anti-predator behavior or vulnerability of prey. Prey behavior can indirectly
31 influence predator choice. Indeed, relative encounter rates with different prey may depend on
32 predator/prey habitat and microhabitat overlap, prey refuge within the habitat, and prey versus
33 predator activity, movement speed and reactive distances (Sih & Christensen, 2001). Habitat
34 structure can therefore influence the relative vulnerability of different prey groups to a particular
35 hunting strategy (Redpath et al. 2002).

36 Among raptors, several studies have found a relationship between latitude and diet
37 diversity (Herrera, 1974; Korpimäki & Marti, 1995; Watson, 1997). However, these studies did
38 not explicitly consider variables such as habitat or prey abundance, so it remains unclear
39 whether latitudinal variation in diet arises due to variation in prey abundance or availability, to
40 differences in preference of predator, or to a combination of both.

41 Montagu's harrier (*Circus pygargus*) is a medium-sized raptor species that breeds
42 throughout the Palearctic, from the Iberian Peninsula to central Asia (Cramp & Simmons
43 1980), thus occurring in different biogeographic areas in a wide variety of open and shrub-
44 dominated habitats. It takes many different types of prey, and is considered to be a generalist
45 species over the majority of its range (Cramp & Simmons 1980, Arroyo 1997). However, it
46 can behave locally as a specialist on a particular type of prey. Montagu's harrier populations
47 have been described as specialized on lagomorphs in central Spain (Arroyo & García, 2006)
48 and on insects in Portugal (Onofre, 1994), and have been shown to exhibit numerical
49 responses to vole abundance in western France (Salamolard et al. 2000). The diet of many
50 other populations is dominated by birds, particularly ground-nesting passerines (Underhill-

Day, 1993; Martínez et al. 1999). The spatial variation in diet diversity observed across the distribution range combined with different patterns of local specialization make the Montagu's harrier a good model species to study local variation in diet composition and specialization level of a generalist predator.

We compare the diet of this species across its breeding range. We first evaluate the geographical patterns in diet variation, assessing whether diet diversity varies according to longitude or latitude. We go on to test whether observed patterns relate to variations in prey abundance or with habitat. We hypothesize that, as a generalist species, Montagu's harriers prey more frequently on particular prey types when the conditions make them profitable (e.g. when its abundance increases or when it is more accessible, for example in certain habitats).

MATERIAL AND METHODS

Literature review and data standardization

We gathered data (from published papers or reports, Appendix 1) on diet of the Montagu's harrier from 30 studies in 41 areas from 11 countries (Table 1, Fig. 1). Several publications from different years referred to the same study area. Some multi-year studies did not differentiate data from each year separately, so we pooled together data from all the study years for each area. This method masks small inter-annual oscillations in diet, which is helpful when inferring geographical patterns at a continental scale (Donazar et al. 1989). The only exceptions were studies in two areas (Vendee and Flevoland) that were carried out 30 years apart. We considered those studies as separate, as habitat and/or prey availability had changed during the intervening period (Table 1).

Variables selected

We grouped prey into the following main prey types: invertebrates (mostly orthopterans), reptiles (mainly lizards), small mammals (mainly voles), large mammals (mainly lagomorphs), eggs, small birds (mainly passerines) and large birds (mostly game birds or wader nestlings). All the studies included in this analysis gave information on the relative frequency of the different prey categories in relation to the total number of prey. However, data for six sites (three studies) did not separate large from small birds. In these cases, we assumed that the proportion of large birds was 11.4 % (mean % of large birds in the other 35 areas).

When evaluating diets formed by prey types of very different size, biomass estimates are the most useful data because they may be considered a direct measure of the energetic value of the different prey consumed (Reynolds & Aebisher, 1991). Thus, for each study area, we estimated the percentage of biomass supplied by each prey type. When transforming frequency data in biomass, we adopted the following mean weights for each prey category: 5 g for grasshoppers, 2 for crickets, 1 for other invertebrates, 20 for small mammals, 120 for large mammals, 30 for small birds, 100 for large birds, 15 for eggs, and 10 for reptiles. These figures were rounded up from the average weight of consumed species within each category for small mammals, small birds, insects, eggs and reptiles. In the case of large mammals and large birds, we used minimum values assuming that part of the animal is discarded or that only younger individuals are caught (Arroyo, 1997). For each study area, we also calculated the Diet Diversity Index (Shannon-Weaver).

We then noted the "type of sampling" carried out in each study, coded as "pellets" (if information came from pellets only), "mixed" (if it came from a combination of pellets and remains, or pellets and observations) and "observations" (when only observations were used). Additionally, we classed information for each study area in relation to the time of sampling, as "nestling" (information taken mainly in the nestling period) or "all" (data collected throughout the breeding season).

1 Descriptions of the habitat in each study area were obtained from the publications.
2 From those descriptions, habitat in each area was categorized as “scrub” (dominated by shrub
3 vegetation); “wetlands” (dominated by marshes, reeds, etc); “grasslands” (dominated by
4 herbaceous natural vegetation, including dry grasslands, steppe or dunes); or “agricultural”.
5 Within the latter, we differentiated three types according to vegetation cover: “cereal”
6 (agricultural areas dominated by cereal and other annual crops); “cereal-bareground”
7 (agricultural areas with cereal, and bareground habitats including ploughed fallow fields,
8 vineyards and olive groves); and “cereal-pastures” (agricultural areas with cereal and areas of
9 grazed land).

10 Latitude and longitude of each study site were obtained from the publications or through
11 Google earth (<http://earth.google.com>).

12 Quantitative data on prey abundances were not available for any of the study sites. In
13 order to include some qualitative information on prey abundance in the models, we categorized
14 prey abundance of each main prey in each study area as follows: absent or unimportant (1);
15 particularly abundant (3); and everything in-between the previous statements (2) (Table 2). This
16 categorization was based on the qualitative descriptions in some of the publications included in
17 this analysis ($n = 4$, including those published in the 1970’s), and also on published literature
18 giving information on distribution and abundance of birds, small mammals and lagomorphs
19 across Europe (Myllymäki, 1977; Hagemeyer & Blair, 1997; Villafuerte et al., 1998; Mitchell-
20 Jones et al., 1999; Virgós et al., 2007). More precisely, for lagomorphs and small mammals we
21 used published data on the distribution of the main Montagu’s harrier mammal prey species in
22 order to determinate their presence/absence in each study site included in the analysis (Mitchell-
23 Jones et al. 1999). If a species was present in a study area, we assessed whether its abundance
24 warranted a classification of 3 (particularly abundant) by referring to other literature sources,
25 such as maps, like maps of small rodent outbreaks (Spitz, 1977; Myllymäki, 1977, Delattre et al.
26 1992, Olea et al. 2009) and maps of lagomorph abundance (Villafuerte et al., 1998; Rogers et al.
27 1994). In the case of birds, we used the European atlas of breeding birds (Hagemeyer & Blair,
28 1997) to assess how many of the species known as regular prey of the Montagu’s harrier (larks,
29 pipits, wagtails, wader and galliform chicks) were present at each study site, and created an
30 index of abundance by adding the number of bird species present at each site. We categorized as
31 3 (particularly abundant) the sites that had more than 75% of the potential prey species present,
32 as 1 those that had less than 30%, and as 2 everything in between. In the case of birds, thus, we
33 made the assumption that higher species diversity is an indicator for higher overall abundance.
34 Indeed, this assumption of a relationship between species richness and abundance is
35 commonly explained by the ‘More Individuals Hypothesis’ (MIH) by Srivastava & Lawton
36 (1998), and assumes that (1) areas with greater food resources should support more
37 individuals, and (2) communities with more individuals are able to support more species
38 populations above some minimum viable size. The relationships between species richness and
39 abundance is further supported by an increasing number of studies conducted in numerous
40 taxa, (Poulin et al. 2003; Bock et al. 2007) and particularly in avian assemblages (Hurlbert,
41 2004; Pautasso & Gaston, 2005).

42 In the case of insects and reptiles, the information was qualified with expert opinion for these
43 two groups (Miguel Carretero and José Manuel Grosso, CIBIO, Porto, Portugal), having
44 extensive knowledge on the distribution and abundance patterns of these two groups across
45 Eurasia. Overall, the qualitative estimates on prey abundances used here are crude and are likely
46 to contain some errors, but we believe that the crudeness itself (the use of only three categories)
47 makes it relatively robust, and is likely to reflect the overall situation in each study site.

48 To test if the abundance of alternative prey influenced the percentage of biomass of each
49 prey group, we also calculated the “abundance of alternative prey” for each prey group as the
50 sum of abundance scores for all other prey groups.

Statistical analyses

Factors affecting spatial variations in diet diversity were tested using a General Linear Model (GLM), with a normal error distribution and an identity link function, using latitude and longitude as explanatory variables.

For analyses of the variation in prey abundance estimates in relation to latitude and longitude, an ordinal regression was carried out with prey abundance as a dependent variable, using SPSS 14.0 (SPSS Inc, 2005). The SPSS ordinal regression procedure or PLUM (Polytomous Universal Model) is an extension of the general linear model to ordinal categorical data. All other analyses were carried out with SAS v.9.1. (SAS Institute, 2003).

We simplified the variation in the prey group abundance data by carrying out a Principal Component Analysis (PCA), to understand the general factors affecting prey abundance variation as a whole. We analyzed the relationship between the axes of the PCA and other variables (latitude, habitat) using a GLM, with a normal error distribution and using an identity link function. For this analysis, we considered the main four habitat categories (bushes, grasslands, wetlands and agricultural).

We modelled the contribution of each prey type to the diet in terms of biomass using GLMMs (General Linear Mixed Model) with a binomial error distribution (the response variable was expressed as a proportion of the total diet) and a logit link function. We used a binomial error distribution in this analysis because the response variable was equivalent to a proportion. Because the distribution of studies was not homogeneous in space, and to avoid potential problems associated to pseudo-replication, we included factors in these models, specified as random effects, that grouped studies carried in close geographical proximity to one another (Fig. 1). Two different grouping variables were used: in one, studies that were closer than 200 km were grouped. In the other, we grouped studies according to general regions (Iberian Peninsula, central France, northern Europe, central Europe, Far East). Results were similar whether using one or the other random variable, so we present only the results from the models with groups specified according to region. In the initial models, we included the following explanatory variables: habitat (with six categories), abundance of the prey type being modelled, abundance of alternative prey groups (as the sum of scores of all other prey types) and the interactions between habitat and prey abundance. Because diet estimates can vary between different studies according to the technique by which it is determined (Arroyo, 1997; Sanchez-Zapata & Calvo, 1998), "type of sampling" was also included as a factor in the models. Diet may also vary according to the breeding season (Arroyo, 1997), so time of sampling may also affect the results and was thus initially included in the models. In all models, we also included the log of the number of years when diet had been studied in each given area, times the total number of prey items on which the diet was estimated, as a weight in the models (with the statement WEIGHT in SAS), to give relatively less influence to short-term studies or based on small number of prey. Differences among categories within class variables were tested two by two using the LSmeans statement implemented within SAS. Backward selection was finally used to determine the most parsimonious model.

RESULTS

General diet composition and spatial variations in diet diversity

From all identified prey (Of ca. 40000 identified prey items, Table 2), more than half (53.1%) were invertebrates, 22.8% were small mammals, 17.7% were small birds, 4.8% were reptiles, 2.6% were big mammals, 2.1% were large birds and 1.8% were eggs.

There were large variations in diet composition among studies. In terms of biomass, small birds (Passeriformes) appeared to be the most dominant prey type, constituting at least a

third of the diet biomass in 24 out of 41 areas, and at least half in seven (Table 2). The next most important prey were small mammals, comprising at least a third of the biomass in 12 out of 41 areas, and at least half in seven (Table 2). Next in importance were large birds, lagomorphs and invertebrates, although they accounted for half of the biomass in only one study each (Table 2). The proportion of reptiles in the diet was typically negligible, but in a few cases constituted more than 25% (Table 2), while eggs were the least important group, never accounting for more than 8% of diet biomass (Table 2).

Overall, birds (whether large or small) were the most commonly consumed prey, representing at least half of the biomass in 22 of the 41 areas, and more than a third in 33 (Table 2).

Diet diversity ranged from 0.20 to 0.60 (Table 2). Diet diversity across Montagu's harrier' distribution range decreased with latitude and increased almost significantly with longitude, once controlling for latitude ($\chi^2_1 = 7.37$, $P = 0.007$; $\chi^2_1 = 3.61$, $P = 0.06$ respectively). The relationship with longitude was strongly influenced by the two easternmost sites, as it disappeared when excluding them from the analyses ($\chi^2_1 = 4.54$, $P = 0.03$ for latitude; $\chi^2_1 = 0.26$, $P = 0.60$ for longitude).

Prey abundance variations in relation to latitude and habitat

Ordinal regression analyses showed that invertebrate, reptile, small bird and lagomorph abundance decreased with latitude, whereas small mammal abundance increased with latitude (Table 3). Additionally, invertebrate and reptile abundance increased with longitude (and this relationship was still significant at the 0.05 level when excluding data from Russia and Kazakhstan), but the abundance of no other prey group varied longitudinally (Table 3). Large bird abundance did not vary with either latitude or longitude (Table 3).

The PCA with prey abundances produced two orthogonal axes with eigenvalues higher than 1 (which together explained more than 75% of the variance, Table 4). The first axis can be interpreted as a gradient from sites with high to low small mammal abundance and low abundance of all other prey to sites with low abundance of small mammal abundance and low to high abundance of other prey types (Table 4). This axis was (unsurprisingly given the results above) significantly and negatively related to latitude, but there was much higher variability in northern sites than in southern sites (Fig. 2). The variability arose because of a significant interaction between habitat and latitude ($\chi^2_1 = 25.23$, $P = 0.0001$ for latitude; $\chi^2_3 = 7.90$, $P = 0.049$ for habitat; $\chi^2_3 = 11.34$, $P = 0.01$ for the interaction), the decline of PC1 with latitude being particularly marked for agricultural habitats (Fig. 2).

Factors explaining variations in the contribution of each prey type to the diet

Type of sampling had a significant effect on the identified proportion of biomass of all prey types except big birds (Table 5). In particular, there were significant differences between "combined" and "pellets" for all prey types (LSMeans diff, $\chi^2_1 = 8.76$, $P = 0.003$; $\chi^2_1 = 18.80$, $P = 0.0001$; $\chi^2_1 = 25.8$, $P = 0.0001$; $\chi^2_1 = 8.29$, $P = 0.004$; $\chi^2_1 = 11.72$, $P = 0.0006$ for small mammals, big mammals, insects, reptiles and small birds respectively; all other two-way comparisons non-significant). Lagomorphs and small birds were under-represented in pellet-only studies (or over-represented in studies including remains), whereas pellet-only studies over-represented small mammals, reptiles and insects (or they were under-represented in studies including remains).

Controlling for type of sampling, the biomass contributions of all prey types was positively related to their abundance (Fig. 3). The dietary contributions of lagomorphs and small mammals were also related (negatively) to the abundance of alternative prey, indicating that consumption

of these two groups increased when availability of alternative prey was low. The biomass of all prey types apart from mammals were also related to habitat. The relative importance of invertebrate prey was higher in cereal-pasture farmland than in other habitats (Fig. 4), while that of large birds was highest in bushes and that of small birds in grassland (Fig. 4). The reptile component of the diet was smallest in cereal farmland and greatest in cereal-bareground (Fig. 4). The interaction between habitat and abundance was not retained in any of the models.

DISCUSSION

We found that birds are the preferred prey group of this raptor species across its range distribution, although Montagu's harriers seem to take prey opportunistically, according to its availability, depending on local abundance and type of habitat. As a result, diet diversity varied geographically, being higher in southern populations, associated to an overall higher abundance of different prey groups in those areas. The only exception seemed to be mammals, which were consumed more frequently when alternative prey was lacking, which suggests that they are suboptimal prey. We subsequently discuss these results.

Diet diversity

Diet of Montagu's harrier was generally diverse, but trophic diversity varied widely among areas. The studies we reviewed cover the majority of this species' geographic range, which is sufficiently large to encompass marked local and regional variations in the diversity of prey types and the abundances of particular prey. In general, predator diets are expected to be more diverse at lower latitudes (Rosenzweig, 1995) due to the diversity and abundance of prey types such as lizards and insects (Blondel & Aronson, 1999) and terrestrial birds (Hawkins et al. 2003). Our results support this prediction: Montagu's harrier diet diversity was higher at lower latitudes, and this was related to patterns in prey abundance variations, as our qualitative estimators of abundance of all prey groups except large birds and small mammals decreased with latitude.

Our results also suggest a longitudinal gradient of diet diversity for this species across Eurasia. This was largely a reflection of the higher diversity found in the two easternmost sites, as the significance of the relationship disappeared when excluding these two sites. However, it could be also partly related to the west-east gradient of agriculture intensification (Thomas et al., 2008). Indeed, earlier agricultural intensification in western European countries (particularly those in higher latitudes) has had a long term impact on prey communities. The higher invertebrate and reptile abundance found in eastern areas supports this hypothesis.

Importance of birds

Notwithstanding, the large variability in diet composition among studies, birds were the most important prey, contributing to a greater proportion of diet biomass (36%) across all studies than any other prey type. Most birds consumed were passerines, but Montagu's harriers also included larger birds in their diet (which were occasionally dominant).

Prey that are easier to capture have higher prey value (higher expected net energy intake/handling time). Adult birds are clearly highly mobile prey and have high escape success so they should be low prey value. However, the bird species primarily consumed by Montagu's harriers (pipits, larks and bunting species, Arroyo et al., 2004) are medium-size and essentially terrestrial species, so relatively easy to locate and capture (particularly during the breeding season) by foraging harriers. Passerine birds also have the same daily activity rhythms as foraging harriers, increasing their probability of encounter with a Montagu's harrier during a foraging trip, in contrast to other prey types, like small mammals, whose crepuscular and nocturnal behavior is, at least in part, due to avoidance of predators (Eccard et al., 2008).

Furthermore, young passerines are typically more vulnerable to predation than adults, and become available to foraging harriers during the time that they are feeding nestlings and recently fledged young. These different reasons combined with the fact that the above-mentioned groups of passerines are present throughout Montagu's harrier's distribution range in the majority of habitats it breeds in (Table 2), could explain that birds were such an important element of the diet during the breeding period.

Alternative prey

Other than birds, Montagu's harriers consumed a variety of alternative prey, sometimes in important proportions. Overall, those prey were taken opportunistically, with their contribution to the diet depending on its local abundance.

Insects (the least energetically profitable prey) were consumed in most sites but appeared as dominant in the diet only in one locality in Portugal (Table 2). Similarly, reptiles were taken frequently where they were more abundant, but were rarely dominant. The marginal contribution of these prey groups to diet in most of the sites could be related to the trade-off between their low-medium net energy intake and relatively high handling time, indicating that these prey are only profitable when their abundance is extremely high.

Lagomorphs were taken as prey in many areas, and their contribution to the diet increased with their abundance, but lagomorphs featured most prominently in studies conducted within the range of the Iberian hare (*Lepus granatensis*) (Table 2), (Arroyo & García, 2006). In the rest of the Montagu's harrier distribution range, the European hare (*Lepus europaeus*) is present, but never constitute a significant part of its diet. This could be linked to the smaller size of Iberian hare (mean weight of 605 individuals in Spain: 2225 g; Farfan et al., 1999) in comparison with the other species (mean weight of 64 individuals in Poland: 4130g; Myslek et al., 2004). The small body size of Montagu's harrier is a constraint to the capture of large prey like hares, so it could be that only the smaller Iberian hare is a profitable prey for Montagu's harrier at the vulnerable leveret stage. Overall, this prey group was captured more frequently when alternative prey was not abundant, which suggests that this prey is counter-selected, probably because of the low capture success, high handling time and risk of injury resulting from the large size and high body weight of this prey group. Interestingly, the smaller wild rabbit (*Oryctolagus cuniculus*) is present through a large part of Montagu's harrier distribution range in Spain and Europe and reach locally high densities, but is much less prevalent in Montagu's harrier diet. This might be linked to differences in anti-predatory behavior between hares and rabbits (more particularly to the higher accessibility of leverets as living exclusively above ground).

The most important prey type after small birds was small mammals. Indeed, rodents constituted more than a third of the biomass in 12 areas of the 41 included in this study, and some of these populations also showed numerical responses (in either density or breeding parameters) to variations in vole abundance. Montagu's harriers breeding in Western France, are vole specialists and apparently the only ones across the species distribution range to behave as true specialists in a demographic point of view (Salamolard et al., 2000; Millon & Bretagnolle, 2008). Dutch, eastern France and German populations also show important variations in their breeding parameters in relation with vole abundance, although less marked (or non-existent) density numerical responses than in western France (Millon et al., 2002; Holker & Wagner, 2005; Koks et al., 2007). This could suggest that this species is a facultative specialist of this prey group. However, the negative relationship that we found between small mammal contribution to the diet and alternative prey abundance suggests that, as for lagomorphs, this prey group is counter-selected. Indeed, small mammal abundance, in general, was negatively related to the abundance of other prey, but the negative relationship between abundance of alternative prey and proportion of small mammals in the diet was independent of this fact. Thus,

even in areas where small mammals are relatively abundant, Montagu's harriers prefer to take other prey types when they are available. Consequently, these results suggest that the specialist strategy of Montagu's harriers to vole populations, mainly observed in agricultural areas at northern latitudes, may be a by-product of there being high abundance of voles in those habitats, and relatively few alternative prey (Fig. 2).

Habitat

After taking into account for variation in prey abundance, the importance of each prey type (except mammals) in the diet was significantly affected by habitat in the area.

For example, reptiles were least common in cereal-dominated agricultural areas and most common in agricultural areas with bareground, probably related to variations in accessibility. More particularly, vegetal cover could influence detection and capture of small and elusive prey, like lizards.

The importance of birds in the diet was particularly high in natural vegetation areas (grasslands and shrub), but small birds were also relatively important in cereal-dominated agricultural areas. In contrast, they were less present in the diet in agricultural areas with pasture or bareground, or in wetlands. These differences may be explained by variations in birds abundance and availability between the different habitats classes included in this study. Birds might be more abundant in natural habitats and because they are preferred, they should be prevalent in Montagu's harrier diet in those habitats, ahead of other prey types, even if those ones are also abundant. Furthermore, vegetation height and micro-scale habitat heterogeneity could influence prey escape possibilities and harrier capture success (as suggested by Madders, 2000, harriers may be more successful on natural habitats, as the common harrier hunting strategy of capture by ambush is better suited to patches of scrub and other tall vegetation).

Finally, insects were more important in areas dominated by cereal-pasture habitats, which may also reflect variations in abundance and accessibility: large orthopterans (the most commonly captured insects) reach higher densities in grassland patches within an agricultural matrix (Rodriguez & Bustamante, 2008), and might be easier to catch in ecotones.

Overall, results indicate that both abundance and accessibility to prey probably have additive importance in explaining diet variations.

Conclusions

The Montagu's harrier core breeding range in western Europe, is centered on central-southern France and Spain (Clarke, 1996). So, the species could have evolved adaptations to Mediterranean and dry climates where abundance and diversity of potential prey are high but may show important inter and intra-annual variations. For example, in the Madrid region, leverets were selected in the pre-breeding and laying periods, young birds become regular prey during the nestling phase before the net dominance of insects in the diet in response to increased availability during the summer and the postfledgling phase (Arroyo, 1997; García & Arroyo, 2005). Our results indicate that birds are the staple prey group across its distribution range, particularly in natural habitats similar to original habitats of this raptor species (grasslands and bushy areas). Nevertheless, Montagu's harrier has been able to adapt to anthropised agricultural habitats, where passerines are usually abundant and accessible, switching when it is profitable from a bird-based diet to alternative prey in relation to their relative abundance, energy intake and vulnerability. This species can be thus qualified as an opportunistic generalist, able to exploit the most profitable prey according to their spatiotemporal variations in abundance. In addition, the species appears to be able to specialize locally in small mammals, particularly in agricultural areas of western and central Europe, where voles occur in high numbers, and where alternative prey is less abundant. Our analyses, however, suggest that this strategy is not necessarily optimal, as diet diversity in most areas increases when alternative prey is abundant.

1 Furthermore, we only consider, on this study, direct effects of prey abundance and diversity on
2 Montagu's harrier, but it is likely that indirect effects are also important. Insect abundance and
3 diversity could impact indirectly on Montagu's harrier diet by helping to sustain the populations
4 of some of its vertebrate types (lizards and passerine birds). Similarly, the effects of prey type
5 availability on Montagu's harrier diet composition could also be modified by intra- and inter-
6 specific competition, as it has been demonstrated in other predator species (Kortello et al. 2007;
7 Sidorovich et al. 2010).

8 Finally, our results have important conservation implications as trophic diversity could
9 be influenced by land use changes as has been shown in other raptor studies (Pedrini & Sergio,
10 2002). As stated above, diet of Montagu's harrier is dominated by birds, particularly in natural
11 or semi-natural habitats, where small passerines probably reach higher densities than in
12 agricultural habitats. Historically, Montagu's harriers shifted from natural vegetation areas to
13 agricultural areas during the 20th century (Arroyo et al., 2003), maybe also helped by the
14 abundance and accessibility of passerines, their preferred prey, in extensive agricultural habitats.
15 Intensification of agriculture (which has occurred earlier and more strongly in northern Europe)
16 has led to a decrease in insect and bird abundance in those areas (Donald et al., 2001; Brotons et
17 al., 2005), probably producing a shift in Montagu's harrier's diet from a bird dominated diet to a
18 more mixed diet or even dominated by small rodents. Consequences of this shift in terms of
19 harrier demography are unknown, but from the latitudinal gradient in trophic diversity, northern
20 Montagu's harrier populations seem to be dependent on fewer prey groups, being eventually
21 more food restricted (or at least more vulnerable to prey abundance changes) than southernmost
22 populations. Furthermore, recent land use changes and further agriculture intensification have
23 been shown to induce strong declines in small mammal populations in last decades (Jacob,
24 2003). Changes in fluctuations patterns of vole populations are linked to alterations in the
25 landscape, in particular to the relative area occupied by permanent grasslands and the extension
26 of ploughed lands has probably reduced the amplitude of density fluctuations. For example, the
27 threshold value of 100 voles per hectare for optimal productivity of Montagu's harriers is now
28 rarely reached in western France (Butet & Leroux, 2001). Thus, on intensified agrosystems at
29 the northern limits of their range, populations of Montagu's harriers could be threatened by
30 further decline of their main prey (vole) populations and unable to shift to alternative prey,
31 which would lead to a contraction of the species distribution range to the south. However, raptor
32 species breeding at their distribution range limits are strongly affected by climatic conditions
33 (García & Arroyo, 2001; Ontiveros & Pleguezuelos, 2003). Predictions of the impact of climate
34 change on Montagu's harrier distribution are for a decrease in the favorability of the most
35 southern areas (Estrada et al., in press), so distribution range may contract in both limits of the
36 range through different processes, leading overall to lower resilience of the species to global
37 changes. Conservation actions aimed to maintain biodiversity in agricultural areas, through
38 implementation of agri-environment schemes (increasing set-aside habitats and natural
39 vegetation on field edges) would be highly beneficial to Montagu's harriers (Koks et al. 2007).
40 Two recent examples, in central France and Netherlands, showed that Montagu's harrier's local
41 populations breeding in intensive farmland habitats, exhibited a shift from a diet mainly
42 dominated by small mammals to a progressive higher inclusion of passerine birds (Bretagnolle,
43 pers comm.; Koks, pers comm.). This shift was mainly the consequence of the positive impact,
44 agri-environment schemes had on passerine bird's local abundance (mainly by expanding the
45 proportion of extensive grasslands and manipulating mowing regime), and confirm the
46 importance of birds as a preferred food source for this raptor species.

47 Further research is clearly needed to evaluate the implications of differential prey
48 preferences or availability across the distribution range of the Montagu's harrier in terms of
49 breeding success and survival, which is essential to understand the dynamics of the European
50 metapopulation.

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SUPPORTING INFORMATION

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Table 1. Studies used in this review with an indication of study location, the length of the study (number of years), type and time of sampling, habitat, and abundance (1 = unimportant; 2 = regular; 3 = particularly abundant) of each prey group (I: insects, SM: small mammals, R: reptiles, L: lagomorphs, SB: small birds, terrestrial passerines, BB: big birds, game birds or waders) for each study location.

Site	References	Region	Country	Study length	Type of sampling	Time of sampling	Habitat	I	SM	R	L	SB	BB
1	Malvoisin, 1999	Vendée	France	3	pellets	all	pasture	2	3	1	1	2	2
2	Millon et al., 2002	Barrois	France	5	combined	nestling	cereal	1	2	1	1	1	1
3	Schipper, 1977	Crau	France	1	combined	nestling	grasslands	3	1	3	3	3	3
4	Millon et al., 2002	Crayeuse	France	5	combined	nestling	cereal	1	2	1	1	1	1
5	Malvoisin, 1999	Deux Sevres	France	3	pellets	all	cereal	1	3	1	1	1	1
6	Salamolard et al., 2000	Rochefort	France	11	pellets	all	pasture	2	3	1	1	2	2
7	Thiollay, 1968	Vendée	France	1	pellets	nestling	pasture	2	3	1	1	3	3
8	Holker & Wagner, 2006	Westfalia	Germany	10	combined	all	cereal	1	3	1	1	2	2
9	Miklós, 1934	Lebeny	Hungary	1	combined	nestling	wetlands	3	2	2	2	3	3
10	Giacchini & Pandolfi, 1994	Pesaro-Urbino1	Italy	4	combined	all	cereal	3	1	2	3	2	2
11	Giacchini & Pandolfi, 1994	Pesaro-Urbino2	Italy	4	combined	all	bushes	2	1	3	2	2	2
12	Giacchini & Pandolfi, 1994	Pesaro-Urbino3	Italy	4	combined	all	grasslands	3	1	3	2	2	2
13	Faralli, 1994	Sub-Apenine	Italy	1	obs	nestling	bushes	3	1	3	2	2	2
14	Terraube et al., in press	Naurzum	Kazakhstan	1	combined	nestling	grasslands	3	3	3	1	3	3
15	Schipper, 1977	Ameland	Netherlands	3	obs	nestling	grasslands	2	1	1	1	3	3
16	Koks, 1993; Koks & Visser, 1997, 2000a, 2000b; Koks et al., 1994, 2002	East Groningen	Netherlands	7	combined	nestling	cereal	1	2	1	1	1	2
17	Koks & Visser, 1997, 2000b; Koks et al., 2002	Flevoland	Netherlands	4	combined	nestling	cereal	1	2	1	1	1	1
18	Schipper, 1977	Flevoland	Netherlands	1	combined	nestling	pasture	2	3	1	2	3	3
19	Schipper, 1977	Groote Peel	Netherlands	1	combined	nestling	bushes	1	1	1	1	2	2
20	Koks & Visser, 1997; Koks et al., 2002	Lauwersmeer	Netherlands	2	combined	nestling	wetlands	2	2	1	1	2	3
21	Schipper, 1977	Terschelling	Netherlands	4	obs	nestling	grasslands	2	1	1	1	3	3
22	Leroux & Krogulec, 1992	Chelm marshes	Poland	4	combined	all	wetlands	2	3	1	2	3	2
23	Reiss et al., 2001; Franco et al., 1998; Onofre, 2001	Castro verde	Portugal	3	pellets	nestling	pasture	3	1	3	3	3	2
24	Silva et al., 1995	Serra da Malcata	Portugal	1	pellets	all	bushes	3	1	3	2	3	2
25	Davygora, 1995	Urals	Russia	6	obs	nestling	grasslands	3	3	3	1	3	3

26	Sanchez & Calvo, 1998	Ajauque, Murcia	Spain	1	combined	all	wetlands	2	1	3	2	2	2
27	Hiraldo et al., 1975	Campiña de Gerena	Spain	1	pellets	all	bareground	3	1	3	3	3	2
28	Arroyo et al., 2008	Campiña,Extremadura	Spain	2	pellets	all	cereal	2	1	2	3	3	2
29	Limñana et al., 2008	Castellón	Spain	6	pellets	nestling	bushes	3	1	3	2	3	2
30	Guixé, 2003	Lleida	Spain	4	combined	nestling	cereal	2	2	2	2	2	2
31	Castaño, 1995	Ciudad Real	Spain	2	combined	nestling	bareground	2	1	2	3	2	2
32	Corbacho et al., 2005	Cornalvo,Extremadura	Spain	2	combined	all	bareground	2	1	2	3	3	2
33	Hiraldo et al., 1975	Isla cristina, Huelva	Spain	1	pellets	nestling	wetlands	3	1	3	2	3	3
34	Martinez et al., 1999	La Mata, Murcia	Spain	1	combined	all	grasslands	2	1	3	2	2	2
35	Arroyo et al., 2008; Corbacho et al., 2005	La Serena,	Spain	4	combined	all	pasture	3	1	3	2	3	2
36	Corbacho et al., 2005	Llanos de Badajoz	Spain	2	combined	all	bareground	2	1	2	3	3	2
37	Arroyo, 1997	Madrid	Spain	4	combined	all	bareground	2	1	2	3	2	2
38	Corbacho et al., 2005	Orellana, Extremadura	Spain	2	combined	all	cereal	2	1	2	3	3	2
39	Hiraldo et al., 1975	Sierra pelada, Huelva	Spain	1	pellets	all	bushes	3	1	3	2	3	2
40	Arroyo et al., 2008	Tierra de Barros	Spain	2	pellets	All	bareground	2	1	2	3	3	2
41	Underhill-Day, 1993	East Anglia	UK	2	combined	Nestling	cereal	1	1	1	2	1	2

Table 2. Sample size (N, number of identified prey), diet composition (percentage of the biomass provided by each prey type) and diet diversity (H) in each study location.

Site	Region	N	Invert.	Reptiles	Small mammals	Lagomorphs	Small birds	Big birds	Eggs	Total bird	H
1	Baie de l'Aiguillon	760	17.7	0.1	69.4	0.0	12.1	0.0	0.7	12.8	0.36
2	Barrois	2477	3.5	0.0	50.0	15.1	30.2	1.2	0.0	31.5	0.48
3	Crau	140	15.2	1.9	2.3	0.0	61.3	19.3	0.0	80.5	0.27
4	Crayeuse	1995	0.6	0.0	42.1	3.8	48.2	5.3	0.0	53.5	0.37
5	Deux Sevres	822	10.4	0.0	80.9	0.0	8.4	0.0	0.3	8.7	0.27
6	Rochefort	8797	42.6	0.5	49.9	0.0	7.0	0.0	0.0	7.0	0.40
7	Vendee	1663	16.4	0.1	70.4	0.5	10.6	0.0	2.0	12.6	0.36
8	Westfalia	1525	2.3	0.0	50.5	7.7	33.0	6.0	0.5	39.5	0.43
9	Lebeny	146	0.5	3.0	10.6	18.1	31.3	36.3	0.2	67.7	0.41
10	Pesaro-Urbino1	44	6.9	0.0	16.6	11.1	47.0	18.4	0.0	65.4	0.44
11	Pesaro-Urbino2	60	7.7	11.0	18.1	15.5	34.8	12.9	0.0	47.7	0.60
12	Pesaro-Urbino3	298	7.5	4.3	15.3	9.7	44.4	18.8	0.0	63.2	0.49
13	Sub-Apenine	39	4.0	4.4	26.7	0.0	29.3	35.6	0.0	64.9	0.39
14	Naurzum	246	4.9	38.9	24.6	0.0	30.9	0.0	0.8	31.7	0.53
15	Ameland	255	0.0	0.0	13.7	10.1	36.8	39.4	0.0	76.2	0.31
16	East Groningen	2880	0.9	0.0	37.0	13.2	28.1	18.2	2.6	48.9	0.45
17	Flevoland	387	0.4	0.1	47.7	6.9	27.2	16.2	1.4	44.9	0.40
18	Flevoland	162	0.0	0.0	6.5	24.8	48.8	19.2	0.7	68.7	0.34
19	Groote Peel	88	0.0	0.0	16.1	4.6	70.0	7.6	1.7	79.3	0.27
20	Lauwersmeer	164	1.7	0.9	32.2	7.9	32.5	19.9	5.0	57.3	0.43
21	Terschelling	307	0.0	23.1	4.9	0.9	61.7	9.4	0.0	71.1	0.34
22	Chelm marshes	386	5.4	0.4	44.2	0.0	34.6	15.5	0.0	50.1	0.38
23	Castro verde	4006	68.8	1.8	2.2	11.7	12.9	0.7	1.8	15.5	0.41
24	Serra da Malcata	135	26.8	18.9	10.5	0.0	33.2	10.5	0.0	43.7	0.55
25	Urals	141	0.8	29.5	16.4	0.0	53.3	0.0	0.0	53.3	0.45
26	Ajauque, Murcia Campiña de	100	9.1	5.0	0.9	5.5	79.5	0.0	0.0	79.5	0.33
27	Gerena	828	13.1	16.7	2.9	7.8	46.3	13.1	0.0	59.3	0.51
28	Extremadura	814	12.9	0.6	13.3	19.2	34.9	14.8	4.3	54.0	0.53
29	Castellón	623	19.6	7.4	11.8	0.0	60.9	0.0	0.3	61.3	0.46
30	Lleida	393	5.2	0.7	52.8	0.0	38.6	0.0	2.8	41.3	0.39

31	Ciudad Real	68	1.7	0.2	0.4	57.5	6.3	33.3	0.6	40.2	0.34
32	Cornalvo,										
	Extremadura	275	36.5	1.0	1.3	0.0	20.5	32.5	8.3	61.2	0.33
	Isla cristina,										
33	Huelva	350	32.3	6.8	3.2	16.4	26.0	11.4	3.8	41.2	0.57
34	La mata, Murcia	297	0.5	0.7	13.7	0.0	85.0	0.0	0.0	85.0	0.21
35	La Serena	2096	16.1	4.0	3.8	26.3	42.7	0.0	7.0	49.8	0.54
36	Llanos de Badajoz	302	39.6	0.0	4.6	7.8	36.2	6.5	5.4	48.0	0.46
37	Madrid	3010	5.9	0.7	5.6	56.2	14.0	15.9	1.8	31.6	0.46
	Orellana,										
38	Extremadura	300	46.9	1.1	5.8	13.1	18.6	7.3	7.1	33.0	0.52
	Sierra pelada,										
39	Huelva	1630	12.4	6.4	2.5	7.0	40.8	30.9	0.0	71.7	0.41
40	Tierra de Barros	742	11.2	2.9	12.3	37.8	24.0	10.1	1.7	35.8	0.58
41	East Anglia	187	0.0	0.0	4.5	15.3	22.9	57.2	0.1	80.2	0.26
Total		39938	12 ± 16	5 ± 9	22 ± 22	11 ± 14	36 ± 19	13 ± 14	2 ± 2	51 ± 21	0.41 ± 0.09

Table 3. Type III results of the ordinal regression analyses explaining variation of abundance of each prey type with latitude and longitude.

Prey group	Latitude				Longitude			
	W	df	P	Parameter estimate	W	df	P	Parameter estimate
Invertebrates	14.75	1	0.0001	-0.47 ±0.12	8.03	1	0.005	0.18 ±0.06
Reptiles	16.61	1	0.0001	-0.63 ±0.15	10.51	1	0.001	0.19 ±0.06
Small mammals	11.97	1	0.001	0.30 ±0.09	0.680	1	0.41	0.03 ±0.03
Lagomorphs	8.75	1	0.003	-0.22 ±0.08	0.398	1	0.528	-0.02 ±0.03
Small birds	7.69	1	0.006	-0.19 ±0.07	2.21	1	0.14	0.05 ±0.03
Big birds	0.39	1	0.52	0.04 ±0.07	1.82	1	0.17	0.04 ±0.03

Table 4. Results of the Principal Component Analysis of abundance of each prey group.

Variable	PC1	PC2
Small mammal abundance	-0.32	0.594
Lagomorph ab.	0.387	-0.313
Reptile ab.	0.487	-0.109
Insect ab.	0.481	0.109
Small birds ab.	0.463	0.338
Large birds ab.	0.246	0.639
Eigenvalue	2.95	1.55
% Variance explained	49%	25%

Table 5. Results of the GLMM models explaining variations in the percentage of biomass provided by each prey type in each study site (cluster included as a random variable). Parameter estimates are presented for continuous variables.

	df	χ^2	P	Parameter estimate
<hr/> Small mammals <hr/>				
Type of sampling	2,15	3.45	0.059	
Abundance	1,15	12.84	0.003	0.65 ± 0.18
Abundance alternative prey	1,15	33.28	0.0001	-0.27 ± 0.04
<hr/> Lagomorphs <hr/>				
Type of sampling	2,15	6.22	0.011	
Abundance	1,15	25.46	0.0001	1.09 ± 0.22
Abundance alternative prey	1,15	5.26	0.037	-0.18 ± 0.08
<hr/> Invertebrates <hr/>				
Type of sampling	2,11	6.48	0.014	
Abundance	1,11	4.01	0.070	0.80 ± 0.39
Habitat	5,11	3.45	0.040	
<hr/> Reptiles <hr/>				
Type of sampling	2,11	8.29	0.006	
Abundance	1,11	65.49	0.0001	2.13 ± 0.26
Habitat	5,11	15.61	0.0001	
<hr/> Small birds <hr/>				
Type of sampling	2,11	4.41	0.039	
Abundance	1,11	6.31	0.028	0.626 ± 0.24
Habitat	5,11	3.16	0.051	
<hr/> Big birds <hr/>				
Type of sampling	2,11	1.30	0.31	
Abundance	1,11	7.08	0.02	1.29 ± 0.48
Habitat	5,11	6.61	0.004	

Figure 1. Location of the study sites and the two cluster variables used in the GLMM analyses.

Figure 2. Relationship between the first axis of the PCA of prey abundances (representing a gradient from sites with low abundance of small mammals and high abundance of other prey, to sites of high abundance of small mammal but low of other prey) and latitude and habitat.

Figure 3. Average (\pm SD) diet composition (% of the biomass provided by each prey type) of Montagu's harrier in relation to the abundance of each prey type.

Figure 4. Diet composition of Montagu's harrier in relation to habitat (Least Square Means from the GLMM model).

Fig 1:

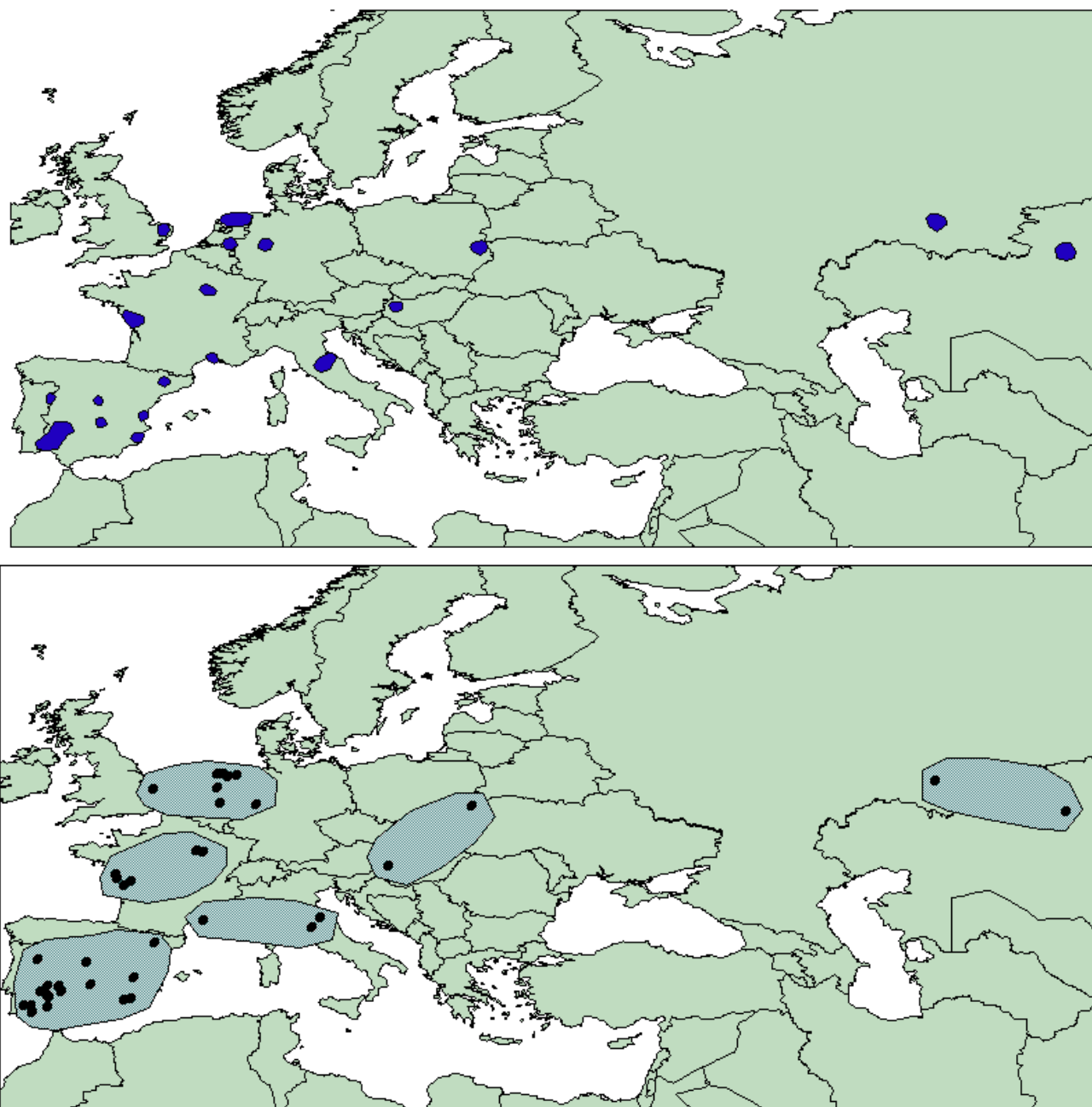


Fig. 2

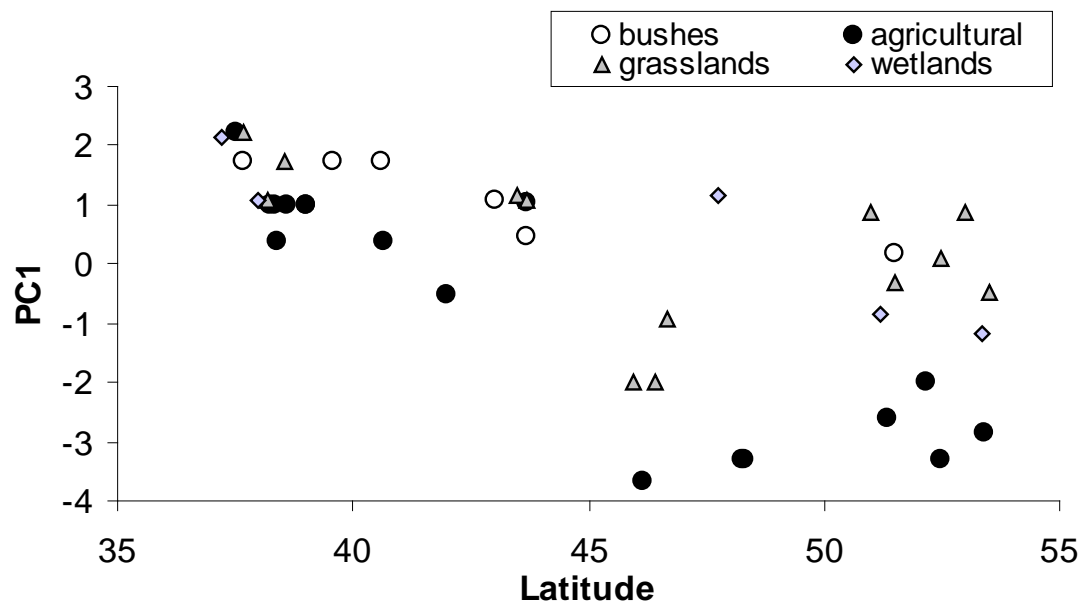


Fig. 3.

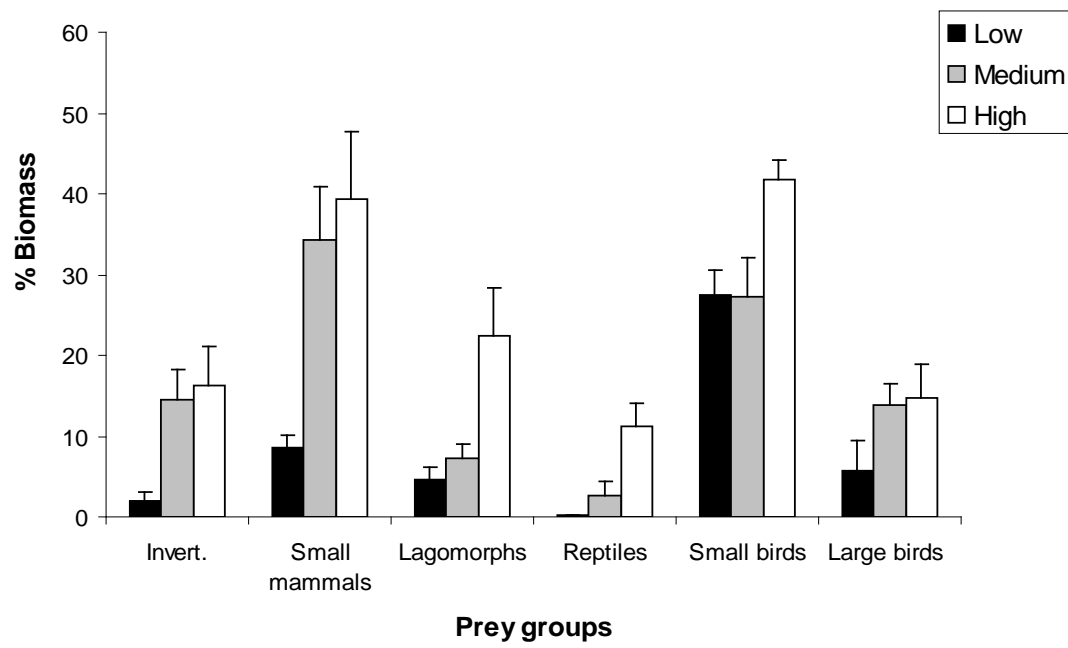


Fig 4.

