Spatial structure in the diet of imperial eagles *Aquila heliaca* in Kazakhstan

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We evaluated the relationship between spatial variability in prey and food habits of eastern imperial eagles *Aquila heliaca* at a 90,000 ha national nature reserve in north-central Kazakhstan. Eagle diet varied greatly within the population and the spatial structure of eagle diet within the population varied according to the scale of measurement. Patterns in dietary response were inconsistent with expectations if either ontogenetic imprinting or competition determined diet choice, but they met expectations if functional response determined diet. Eagles nesting near a high-density prey resource used that resource almost exclusively. In contrast, in locations with no single high-density prey species, eagles' diet was more diverse. Our results demonstrate that spatial structuring of diet of vertebrate predators can provide important insight into the mechanisms that drive dietary decisions.

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Dietary decisions by individual top predators can have consequences that are expressed at the population and community level. Those dietary decisions are influenced by a variety of factors, including foraging strategies in response to prey distributions (Holling 1959, Korpimäki and Norrdahl 1991, Jaksic et al. 1992, Morgan et al. 1997, O'Donoghue et al. 1998a,b), inter-species interactions that limit resource access (Korpimäki 1987, Korpimäki et al. 1991), and learned behavioural preferences (Peacock and Jenkins 1988, Annett and Pierotti 1999). In a spatially heterogeneous environment, predators that otherwise behave similarly may use different subsets of the available habitat and, consequently, may show high within-population variability in diet that is linked to the spatial scale at which birds forage. In the case of wide-ranging birds of prey, individuals can forage at one of three spatial scales: across all breeding territories and all surrounding habitat (a landscape scale), across multiple neighbouring territories and the immediately adjacent areas (a regional scale), or exclusively within or around a single territory (a territory scale). Therefore, the scale at which a predator forages should be a function of the spatial distribution of prey and should underlie variability in dietary response (Fretz 2002).

We assessed the extent and structure of variability in diet within a population of eastern imperial eagles *Aquila heliaca* inhabiting a spatially variable prey environment at a protected nature reserve in north-central Kazakhstan. We addressed this question by evaluating variation in eagle diet in the context of multi-scale analysis of territory spacing and locations. The resulting correlative

patterns provide a framework by which we interpret the role of territory-, regional- and landscape-wide influences on eagle foraging.

Materials and methods

Study area

This research was conducted during summers 1998–2000 at the Naurzum *Zapovednik* (National Nature Reserve) in the Kostanay Oblast of north-central Kazakhstan (51°N, 64°E). The reserve is composed of three mixed-forest patches named Tersec, Sip-sin and Naurzum in a matrix of wetlands and shrub- and grassland-steppe. We evaluate data from north and south Naurzum separately because eagle ecology differs between these regions (Katzner et al. 2003). To avoid confusion, we distinguish between the name of the Zapovednik (the Naurzum Zapovednik) and the names of the two regions of that forest (north Naurzum and south Naurzum).

These diverse habitats support a remarkably diverse community of breeding raptors, including eastern imperial eagles, of which there are approximately 40 active territories (Bragin 2000), resulting in the highest known breeding density for this species. Eagles in this area have eaten more than 150 different prey species (Bragin and Katzner, personal observations); the most important of these are listed in Appendix I and in Katzner et al. (2005).

Further details on the reserve's location, climate, history and floral and faunal communities and on Imperial Eagle ecology are provided in Katzner et al. (2003, 2005).

Data collection

Annual surveys for eagle territories and monthly surveys for reproductive activity are described in detail in Katzner et al. (2003, 2005). Regurgitated pellet castings and prey remains were collected at nests and associated roosts on each visit to a nest (Katzner et al. 2005). Pellet contents and prey remains were identified to the lowest taxonomic level possible based on comparison with reference materials and the minimum number of individuals (MNI) in each pellet or prey remain was estimated from body parts and from quantities of fur or feathers, as is described in Katzner et al. (2005).

Territories were used as our sampling unit to avoid potential problems of psuedoreplication that occur when the number of pellets is used to assess raptor diet (Swanson et al. 1974, Hurlbert 1984). The accuracy of our identification of territories (Katzner et al. 2003) has recently been verified through use of genetic analyses (Rudnick et al. 2005). We assumed that the prey in

pellets and remains from each month represented unique observations of individuals that did not occur in pellets or prey remains from any other month. MNIs were summed separately by both territory and month and the monthly MNIs were added together to estimate MNI of each prey type over the whole field season (Katzner et al. 2005).

Data analysis

We conducted a series of statistical tests on these dietary data designed to (1) identify the presence and characteristics of regional and temporal differences in diet; and (2) evaluate the relationships between dietary overlap and geographic distances between territories. At our study site, the "landscape" included all breeding territories and all the surrounding habitat (the entirety of Fig. 1 in Katzner et al. 2005). "Regions" within the landscape were the four forested components of the Zapovednik (North Naurzum, Sip-sin, South Naurzum, and Tersec) and the immediately adjacent habitat. At the smallest scale, "territories" within regions were the defended areas around eagle nests.

To minimize the impact of unequal sampling at different territories, we analysed only data from those territories at which we collected >20 items (pellets or prey remains) in a breeding season. Most analyses were conducted on the 10 or the 25 most common prey types because these composed the majority of observations. Remaining prey types are often grouped together into a single "miscellaneous" or "other" category (Steenhof and Kochert 1985, Steenhof and Kochert 1988, Watson et al. 1992). Because the heaviest "other" items in this study, ∼5000 g geese and cranes, were 2,500 times heavier than the lightest, ∼2 g locusts, we did not group these disparate types together.

Proportional within-year dietary differences among regions were evaluated for the 10 most commonly used prey species with a chi-square analysis (Watson et al. 1992, Zar 1999). If the chi-square indicated a significant difference in diet among forest regions, 10 nonparametric Kruskal-Wallis tests were employed to compare use of the most commonly taken prey groups among those regions (Zar 1999). A sequential Bonferroni's technique was used to evaluate significance of these tests (Rice 1989, Fedriani and Kohn 2001), and when significant, this was followed by Dunn's multiple comparison to determine differences between regions (Zar 1999).

All of the preceding tests were repeated on proportional data adjusted for our best estimate of the weights of the prey and of prey-specific wastage factors calculated for golden eagles (Appendix 1; Brown and Watson 1964, Steenhof and Kochert 1985, Silva et al. 1995, Watson 1997, Redpath et al. 2001). Mass-adjusted
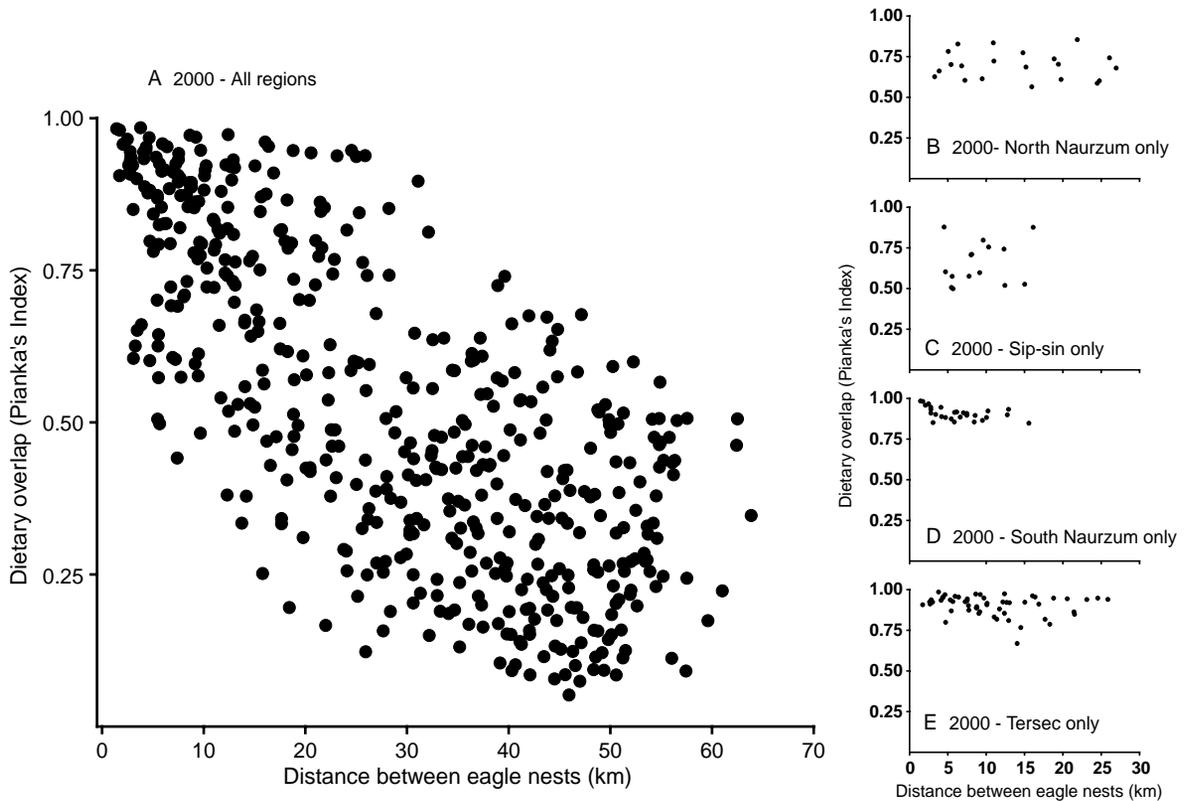
Fig. 1. Relationships at two different spatial scales between dietary overlap and geographic distance between nests for imperial eagles at the Naurzum Zapovednik, Kazakhstan in 2000. At the landscape scale (A) dietary overlap and distance between nests are highly spatially autocorrelated. At the regional scale (B,C,D,E) dietary overlap and distance between nests are not spatially autocorrelated. Data from other years are similar (see Table 1 for details and significance tests).

analyses were not extended beyond this point because interpretation of mass-adjusted dietary information has at least two critical limitations. First, eagles eat large prey and digest bone effectively, making it difficult to identify the number, age, sex or mass of prey in pellets (Duke et al. 1975), particularly for those species whose body size varies greatly over the course of their lifetimes. To illustrate this point, it is useful to consider that although a juvenile bobak marmot *Marmota bobac* can weigh 225 g, 1/25th as much as a 5.7 kg adult (Shubin et al. 1978), eagle pellets rarely contain information useful for aging this species. Second, even after adjusting for wastage, many prey are larger than the largest meal an eagle can consume. For example, adult bald eagles *Haliaeetus leucocephalus* rarely eat more than 200 g/day (Duke et al. 1975, Duke et al. 1976), and even the fastest growing golden eagle chicks do not eat more than 700 g/d (Collopy 1986). Nevertheless, eastern imperial eagles regularly feed on marmots, sheep and other prey weighing many kilograms. Our data did not allow us to determine effectively the mass of eagle prey, nor to interpret the functional difference to an eagle between a 2 kg marmot and a 5 kg goose, and to assume otherwise would be misleading.

Pianka's index was used to estimate dietary overlap among all possible combinations of eagle territories (Pianka 1973, Krebs 1989). Because infrequently used prey are important to dietary overlap measures, this statistic was calculated with the 53 diet classes that could be identified accurately in pellets and prey remains.

Spatial autocorrelation and the scale of eagle dietary choices were evaluated with Mantel tests on a matrix of dietary overlap between all nests and a second matrix of geographic distance between all nests (Mantel 1967, Fortin and Gurevitch 2001). The Mantel nonparametric test calculator (Liedloff 1999) was employed to calculate matrix correlation coefficients and to simulate a probability distribution for the comparison based on 5000 iterations for each pair of matrices (Sokal and Rohlf 1995). To better understand the relationships between inter-nest distances and dietary similarity, this analysis was conducted at both the regional and landscape scales.

Multivariate repeated measures ANOVA were used to evaluate Zapovednik-wide, year-to-year differences in use of the 25 prey species most commonly encountered in diet at the 21 nests where > 20 pellets were collected in each of the three years of the study (Zar 1999). Univariate repeated measures ANOVAs were also used

to evaluate year-to-year differences in use of the 10 most commonly taken prey and 4 other prey whose numbers were observed to fluctuate – foxes (*Vulpes vulpes* and *V. corsac*), harriers (*Circus* spp.), owls (*Asio flammeus* and *A. otus*) and steppe pika (*Ochotona pusilla*).

Unless otherwise noted all analyses were performed with either SAS software (SAS, Cary, NC, version 8.01, 1999), or within a spreadsheet (Excel 2000, MicroSoft, Redmond WA, 1999). Distances between eagle nests were calculated in a GIS (ArcView 3.2, ESRI, Inc. Redlands, CA, 1999).

Results

Foraging response-regional patterns

We identified 11 079 prey items in 5 759 eastern imperial eagle pellets collected from 1998 to 2000. The 10 most commonly used prey classes were rooks, ducks of several species, kestrels, hares, bobak marmots, mice and voles, magpies, russet susliks, yellow susliks, and little bustard (scientific names are given in Appendix 1). Overall use of prey by eagles was different among regions in each year of the study (1998: $\chi^2_{27} = 149.1$, P <0.001; 1999: $\chi^2_{27} = 240.8$, P <0.001; 2000: $\chi^2_{27} = 298.0$, P <0.001). When prey were adjusted for mass, use patterns did not change but χ^2 values were more highly significant.

Because overall use of all prey by eagles was consistently different among regions, regional differences were evaluated for each of the 10 most commonly taken prey in each year of the study. Use of yellow susliks, bobak marmots and russet susliks was regionally different in each year of the study and use of Murids was different in 1998 and 2000. In general, yellow susliks were most frequently taken by eagles inhabiting south Naurzum and least frequently taken by those in Tersec. Bobak marmots and Murid rodents showed the opposite trend, and russet susliks were taken in all regions except Tersec.

Similar trends were apparent when pellet contents were adjusted for prey mass and wastage. Three species (marmots, yellow and russet susliks) were used differently among regions in each year of the study, but Murid rodents were only taken in different amounts in 2000. Use patterns were the same as those associated with unweighted proportions. However, in 2000, rook, magpie and bustard were all used more heavily in north Naurzum and Sip-sin than in other regions.

Foraging response-spatial scale

Mean dietary overlap among eastern imperial eagles was generally similar in each year of the study, averaging about 0.5, or 50% overlap (1998: mean =0.54, range = 0.17–0.98; 1999: mean =0.41, range =0.01–0.98; 2000: mean =0.52, range =0.05–0.98). Mean dietary overlap

within regions averaged 0.68 in north Naurzum, 0.64 in Sip-sin, 0.84 in south Naurzum and 0.85 in Tersec. Nearest neighbour distances between eagle nests were generally 2–4 km (Katzner et al. 2003), and mean inter-nest distance (the average distance between all nests in the population) at the landscape scale was about 29 km in each year of the study (1998: mean =29.34 km, range = 1.68–63.79 km; 1999: mean =28.38 km, range = 1.68–56.09 km; 2000: mean =28.85 km, range =1.44–63.86 km).

Foraging response was different when we considered different scales of measurement. At the landscape scale, geographic distance and dietary overlap between nests were strongly negatively spatially autocorrelated (Table 1, Fig. 1A), indicating that diet was more similar at nests that were closer together and less so at nests further apart. However, at the regional scale, geographic distance between nests was neither positively nor negatively spatially autocorrelated with dietary overlap (Table 1, Fig. 1B,C,D,E). Mean inter-nest distances within regions in the three years of the study averaged 15.3 km in north Naurzum, 8.7 km in Sip-sin, 6.4 km in south Naurzum and 9.4 km in Tersec.

Foraging response-temporal patterns

Overall diet of eastern imperial eagles did not change from year to year (Wilks' Lambda: $F_{2,499} = 0.49$, P = 0.611). However, the significant interaction between year and prey species used (Wilks' Lambda: $F_{48,998} = 4.42$, P <0.001) indicated temporally variable use of some prey groups. Significant among-year differences were found in use of six types of prey: harriers ($F_{2,19} = 4.92$, P =0.019), mice and voles ($F_{2,19} = 19.1$, P <0.001), owls ($F_{2,19} = 7.99$, P =0.003), magpie ($F_{2,19} = 4.67$, P = 0.022), yellow suslik ($F_{2,19} = 3.92$, P =0.038), and foxes ($F_{2,19} = 6.65$, P =0.006). The remaining nine species we evaluated were used similarly across the three years of the study ($F_{2,19} < 3.52$, P >0.05).

Discussion

If competitive interactions determine dietary response in a spatially heterogeneous prey environment, nests close together should have less dietary overlap than those farther apart. However, our analyses were not consistent with this interpretation. First, we observed negative spatial autocorrelation in dietary overlap at the landscape scale, indicating that nests farther apart had less dietary overlap than those closer together. Second, we observed no autocorrelation at the regional scale, indicating no within-region relationship between dietary overlap and the distance between nests. If behavioural preferences determine eagle dietary response, there

Table 1. Mantel tests for correlations between matrices of distance between nests and of dietary overlap between nests at the Naurzum Zapovednik, Kazakhstan. Probability values are derived from 5000 simulations; in cases where a range of P-values was generated the lowest are reported. Within each year $\alpha = 0.05/4 = 0.0125$.

Year	Region	N	Z	r	g	P
1998	All regions	27	4940043	−0.56	−10.03	0
	North Naurzum	5	84162	−0.54	−1.38	0.0882
	Sip-sin	5	42007	0.04	0.11	0.4412
	South Naruzum	8	144294	0.16	0.68	0.2894
	Tersec	9	284543	−0.44	−2.37	0.023
1999	All regions	23	1990867	−0.75	−12	0
	North Naurzum	4	72494	−0.15	−0.86	0.203
	Sip-sin[†]	3	20789	0.02	–	–
	South Naruzum	8	138982	−0.44	−1.56	0.1066
	Tersec	8	170992	0.06	0.27	0.4084
2000	All regions	32	5928578	−0.73	−15.84	0
	North Naurzum	7	205367	−0.09	−0.49	0.3162
	Sip-sin	6	89952	0.2	0.76	0.2758
	South Naruzum	8	157211	−0.5	−2.14	0.0168
	Tersec	11	530628	−0.18	−1.05	0.146

[†] Probability values could not be determined because of the small sample size.

should be continuity in eagle diets that was decoupled from temporal variability in prey availability. Our data are not conclusive in this regard. Use by eagles of six types of secondary prey fluctuated annually and apparently in relation to annual variation in numbers of some of those prey. Such a finding, if also linked to fluctuations in primary prey, is not consistent with that expected for predators that specialize on certain prey. Although competition or behavioural preferences may influence eastern imperial eagle diet at the Zapovednik, our results suggest that these were likely not the primary forces structuring diet.

If a functional response determines diet, a foraging predator should always take the most abundant prey, regardless of prey densities at other times or in other places. In our analyses, spatial variation in eagle diet was extensive at the regional scale and autocorrelated at the landscape scale. Differential occurrence in diet of the most heavily used prey correlated well with distribution of those prey in the environment. Specifically, marmot distributions and the use of marmots by eagles were both almost exclusively limited to the Tersec area. Yellow suslik density and use of yellow susliks by eagles were highest near south Naurzum, and use and density of russet suslik and bustard were highest in and around Sip-sin.

Correspondence between spatial variability in diet and in distributions of primary prey was consistent with that expected for predators whose diet was determined primarily by a functional response. An eagle whose diet is determined by a functional response should vary the spatial scale at which it forages in response to prey distributions. In this population, we observed negative spatial autocorrelation in the landscape scale analysis and no autocorrelation within regions, suggesting different population foraging responses at different spatial scales. Thus eagle foraging was a response to environ-mental gradients at a scale among, not within, the different regions of the Zapovednik. Furthermore, without directly monitoring individuals or prey distributions we were able to gain insight into the spatial scale of eagle foraging and derive considerable understanding of the determinants of that foraging behaviour. It is therefore likely that the among-region dietary variability and foraging response may also explain the patterns of nest spacing among the different regions of the Zapovednik (Katzner et al. 2003, Katzner et al. 2005).

The foraging ecology of eastern imperial eagles at the Naurzum Zapovednik is, from several perspectives, exceptional (Watson et al. 1993, Meyburg and Chancellor 1996, Watson 1997, Belik 1999, Riabtsev 2000, Ferrer 2001). First, although diets vary among different populations of eastern imperial eagles, the highly diverse diets and foraging modes within the single population of the Naurzum Zapovednik are unique (but see Solomatin (1970), who also worked at the Naurzum Zapovednik). Second, we did not observe a relationship between dietary overlap and nest distribution at the regional scale. However, dietary differentiation was greater among Spanish imperial eagles (*Aquila adalberti*) nesting close together than those nesting farther apart at Doñana National Park in Spain, suggesting that competitive exclusion determined eagle dietary response (Ferrer 2001). The difference between our results and theirs may be due to the relatively lower prey densities at Doñana, which causes Spanish imperial eagles sometimes to be food limited (Ferrer and Donazar 1996, Ferrer 2001).

The unusual foraging ecology of Naurzum's eagles has important implications for eastern imperial eagles and their conservation. The ability of this species to respond adaptively to prey distributions is likely a key factor that enables them to exist at viable population sizes across heterogeneous habitats in a manner impossible for

dietary specialists. Because of this behavioural plasticity, human-altered habitat mosaics encompassing sufficient prey populations may be suitable to sustain viable populations of imperial eagles.

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Appendix 1. Estimated weight and proportional wastage factor for the ten prey most frequently observed in diet of eagles at the Naurzum Zapovednik. Wastage was estimated from Brown and Watson (1964) and Watson (1997). When a range of adult weights was provided or when a species had a long juvenile growth period, weight was estimated from the lower end of the range to account for the many juveniles taken by eagles.

Prey species	Common name	Estimated weight (g)	Wastage	Sources
Corvus frugilegus	Rook	310	0.2	Snow and Perrins 1998
Anatidae	Duck	800	0.2	Snow and Perrins 1998
Falco tinnunculus, F. naumanni	Kestrel	200	0.2	Snow and Perrins 1998
Lepus spp.	Hare	1500	0.3	Sludskii et al. 1969a, MacDonald and Barrett 1993
Marmota bobac	Bobak marmot	1400	0.3	Sludskii et al. 1969a, Shubin et al. 1978
Murid	Mice, voles	30	0.1	Parker 1990, MacDonald and Barrett 1993
Pica pica	Magpie	200	0.2	MacDonald and Barrett 1993, Snow and Perrins 1998
Spermophilus fulvus	Yellow suslik	600	0.2	Sludskii et al. 1969b
Spermophilus major	Russet suslik	550	0.2	Sludskii et al. 1969b
Tetrax tetrax	Little bustard	600	0.2	Gavrin et al. 1962, Bogdanov 1992, Snow and Perrins 1998