Relationship between demographics and diet specificity of Imperial Eagles *Aquila heliaca* in Kazakhstan

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The demographic consequences of within-population variability in predator foraging are not well understood. We assessed the relationship between the degree of diet specialization and two demographic parameters, population density and reproductive output, within a single population of Imperial Eagles *Aquila heliaca* at a nature reserve in north-central Kazakhstan. Nearest-neighbour distances between eagle nests throughout the reserve, and thus population density, were correlated with the degree to which diets were specialized. Diet diversity showed an extensive regional variability that was linked to prey distributions, but within-year analyses of reproductive output did not show similar linkages. However, multi-year analyses of breeding performance showed inter-regional differences in nesting success that were paralleled, and probably driven by, similar trends in diet diversity. In contrast, brood size at fledging was not linked to diet diversity and was more probably driven by reserve-wide influences such as weather. Finally, the decision to initiate breeding was associated neither with diet diversity nor with environmental variability. Our results indicate that the degree of dietary specialization is linked to the demographics of Imperial Eagle populations. For these and other raptor populations, it is possible that management could be used separately to increase or decrease nesting success, brood size at fledging, and the likelihood that a pair will initiate breeding.

Predator foraging response has well defined demographic consequences for avian populations (Steenhof & Kochert 1988, Korpimäki & Hakkarainen 1991, Jaksic *et al*. 1992, Silva *et al*. 1995, Rohner & Krebs 1998). However, while the existence of individual variation in foraging is well documented, the demographic effects of within-population variability in predator behavioural strategies are less well understood (reviewed in Durell 2000; Bolnick *et al*. 2003). The few studies of avian systems that have investigated this question have shown important links between fecundity and foraging behaviour (Annett & Pierotti 1999, Golet *et al*. 2000, Marshall *et al*. 2002).

Because the composition of predator diet is determined by foraging behaviour, when foraging behaviour influences demographics, variability in diet should also be related to variability in many fundamental population parameters. The mechanism thought to underpin this relationship is that individuals specializing on one prey type will be more efficient than generalist foragers (MacArthur & Pianka 1966). Watson (1997) therefore predicted that the degree of dietary specialization by Golden Eagles *Aquila chrysaetos* should correlate with the number of fledglings they produce (their reproductive output). Using results from several published studies, he regressed diet breadth against reproductive output and showed that this was in fact the case. However, his macroecological analysis (Brown 1995) evaluated country-wide and global trends, but did not address whether these same patterns occurred on a smaller, regional scale.

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Theory also predicts that areas of 'good' habitat should support higher densities of predators than areas of 'bad' or marginal habitat (Fretwell & Lucas 1969, Schoener 1971). For raptors, habitat quality and population density are often determined by the distribution and availability of prey (Dunk & Cooper 1994, Newton 1998, Wiklund 2001). Therefore, because foraging should be more efficient in better quality habitat, raptor population density should correlate with the degree of dietary specialization. Under these conditions, such patterns should be apparent between geographically distinct populations and also within single populations distributed across a heterogeneous environment.

We assessed the demographic impacts of dietary response within a single population of predators that rely on a spatially variable prey base in north-central Kazakhstan. The area of the Naurzum *Zapovednik* (the Naurzum National Nature Reserve), supports large numbers of Imperial Eagles *Aquila heliaca*, and is surrounded by a habitat matrix with abundant, diverse, and patchily distributed prey. Earlier studies have demonstrated that the foraging response of these eagles is affected by prey distribution and density (Katzner 2003). The goal of this study was to assess the demographic correlates of their foraging response and to evaluate possible mechanisms for these relationships. Specifically, we asked: (a) whether predator breeding density was correlated with the degree of dietary specialization, (b) whether reproductive output by predators was related to their degree of dietary specialization, and (c) given these relationships and the spatial and temporal environmental variability that also influence populations, what is the extent of, and what are possible mechanisms for, the link between the degree of dietary specialization and demographics of the *Zapovednik*'s Imperial Eagles.

MATERIALS AND METHODS

Study area

This research was conducted during the summers of 1998 to 2000 at the Naurzum *Zapovednik* in the Kostanay Oblast of north-central Kazakhstan (51°N, 64°E). Most of the reserve is located in the Torgay Hollow, an historic wetland draining south toward the Aral Sea. The regional climate is continental, dry, and windy, with temperatures as low as −45 °C during winter and as high as 41 °C in summer. Average annual temperature is 2.4 °C, and average annual precipitation is 233 mm (T. Bragina pers. comm.).

Established in 1931, the *Zapovednik* encompasses an area of 87 700 ha (Fig. 1) at the juncture of the northern Siberian forest and the southern Eurasian steppe. About one-third of the reserve and much of the surrounding interstitial area is comprised of sandy and mixed soils with feather *Stipa* spp. and bunch grasses, or denser clay soils with low sagebrush *Artemisia* spp. and other nutrient-rich shrubs and grasses (Formozov 1966). More than 50% of this steppe was ploughed during the failed 'virgin lands' programme initiated in the 1950s. Although many of these fields are now fallow, their outlines are still visible in satellite images, even while they are being recolonized by their original floral and faunal communities (Katzner & Knick pers. obs.). Interspersed within the steppe matrix are three distinct woodland patches – named Tersec, Sip-sin, and Naurzum – that comprise much of the protected reserve land (Fig. 1). To avoid confusion, we distinguish between the name of the *Zapovednik* (the Naurzum *Zapovednik*), the name of the largest forest (the Naurzum forest), and the names of the two regions of that forest (North Naurzum and South Naurzum). All three forests are dominated almost exclusively by Scots Pine *Pinus sylvestris*, birch *Betula* spp. and aspen *Populus* spp., in single-species (Tersec and Sip-Sin) and mixed-species stands (Naurzum) of various sizes (Fig. 1). The remaining protected area includes dry steppe and numerous permanent and ephemeral lakes holding saline or fresh water. These wetlands provide important breeding habitat for a wide variety of passerines and waterbirds, and the permanent ponds serve as critical stopover, moulting, and staging areas for many thousands of waterfowl. In this paper we evaluate data from the four different regions of the *Zapovednik*, North Naurzum, Sip-sin, South Naurzum and Tersec (Fig. 1), because eagle ecology differs between these regions (Katzner *et al.* 2003).

The Naurzum *Zapovednik* supports nearly 25 species of breeding raptors, including Imperial Eagles, of which there are approximately 40 active territories (Bragin 2000). There are also breeding territories of White-tailed Sea Eagles *Haliaeetus albicilla*, Steppe Eagles *A. nipalensis*, and Golden Eagles. Each of these species is internationally or locally recognized as threatened or endangered (Kovshar 1996, Hilton-Taylor 2000). Imperial Eagles forage throughout the *Zapovednik* but appear to focus their effort in the vast steppe surrounding the forest zones. We have
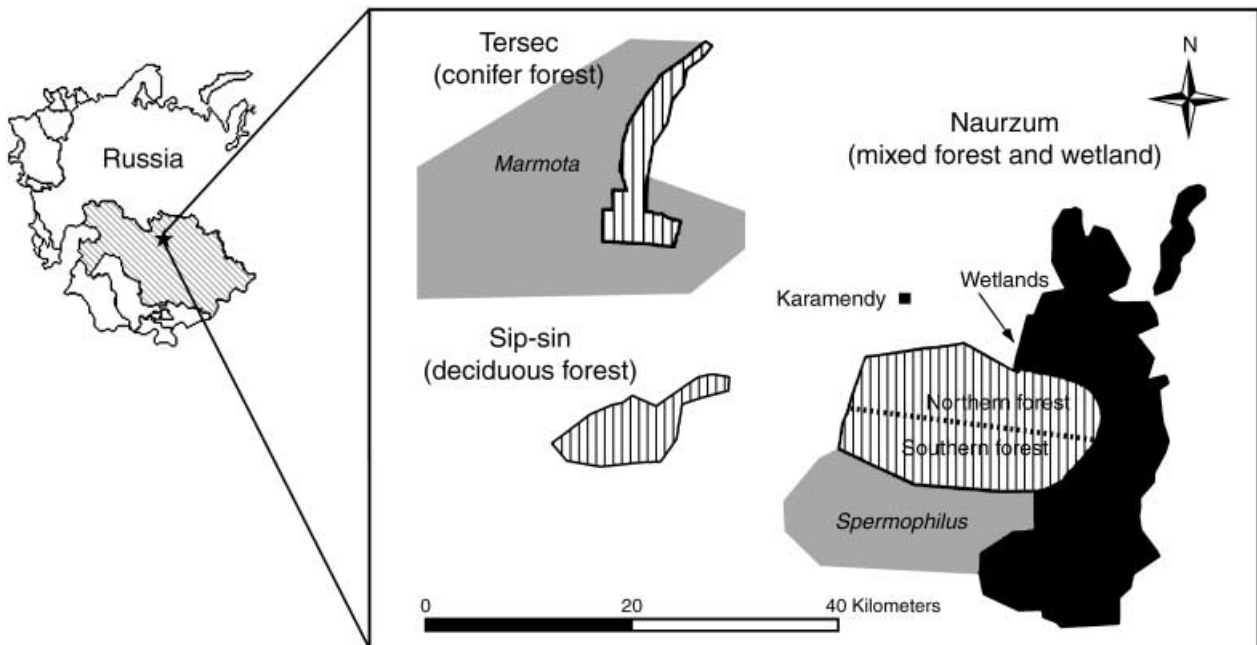
Figure 1. Map of the Naurzum *Zapovednik*, Kazakhstan, showing its location in the former Soviet Union, the three administrative and four biotic forest regions of the reserve, and the approximate locations of marmot and ground squirrel colonies.

recorded more than 150 prey species taken by eagles in this area. Among the most important of these are mammals, primarily Bobak (Steppe) Marmots *Marmota bobac*, susliks (ground squirrels) *Spermophilus fulvus*, *S. major*, *S. pygmeus*, hares *Lepus* spp., and small mammals (Muridae), and birds including corvids *Corvus corone*, *C. frugilegus*, *Pica pica*, Little Bustard *Tetrax tetrax*, and several species of waterfowl and raptors. There is a large suslik colony (> 15 km wide; primarily *S. fulvus*) just to the south of Naurzum forest and there is a large marmot colony (> 20 km wide) to the west and south of Tersec (Fig. 1).

Data collection

Field data collection
In spring 1998–2000 we surveyed established eagle territories and new sites for signs of breeding activity. Once located, we revisited active nests monthly for the remainder of the summer (June, July and August). The location of each nest was recorded with a Garmin GPS receiver (Model 12XL or 12; Garmin International, Olathe, KS); locations were not corrected. We climbed to each nest near the end of the breeding cycle to monitor reproductive successes, and we confirmed these data at subsequent

visits whenever possible (Steenhof & Kochert 1982).

We collected regurgitated pellet castings and prey remains at nests and associated roosts on each visit to a nest. Pellets and remains from roost sites were gathered only from roosts within ~200 m of the nest, within sight of the nest, or at a nearby nest-site previously used by the same pair of eagles.

Description of pellet contents and prey remains
We used the territory as our sampling unit to avoid pseudoreplication that occurs when the number of pellets is used to assess raptor diet (Swanson *et al.* 1974, Hurlbert 1984). 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. All pellet contents and prey remains (fur, feathers, bone, claws, bills, etc.) were identified by comparison with reference materials. We were generally able to identify prey in pellets and remains to the species level. However, for those groups for which this was not possible we characterized the samples at the lowest identifiable taxonomic level.

Whenever possible, the minimum number of individuals (MNI) in each pellet or prey remain was

estimated from the number of skeletal or keratinized body parts present (Marti 1987). However, eagles often eat large prey whose bones do not appear in pellets, making it difficult to count individuals (Collopy 1983, Watson *et al*. 1992, 1993, Bochenski *et al*. 1997). When body parts were not useful in determining the number of individuals present, the MNI was estimated as follows. First, the quantity of fur, feathers and bone of each species in the pellet was evaluated relative to that observed in pellets where body parts could be counted. This quantity was then scored using a scale of relative 'intensity' of occurrence from 0 to 2. If a prey species was represented by only a very few feathers, hairs or body parts, it was scored as zero. Occurrences with '0' intensity scores were also assigned a MNI of '0', unless that was the only time in the collection period that the species occurred in pellets or remains from that territory. In such cases they were assigned an MNI of '1'. This interpretation was justified because the components of a previous meal (e.g. small feathers, bones and bits of fur) may remain in the crop after a pellet is regurgitated and often turn up in subsequent pellets (Mersmann *et al*. 1992). If significant quantities of fur, feathers or body parts from a single species were present in a pellet, that occurrence of the species was scored with an intensity of '1' and assigned an MNI of '1' (Watson *et al*. 1992, Ramakrishnan *et al*. 1999). This interpretation was justified because studies of captive and wild raptors suggest that the contents of most pellets represent food eaten during a discrete period of time (usually a day), and only rarely do large quantities of fur or feathers from a single meal appear in several pellets (Duke *et al*. 1976, Mersmann *et al*. 1992, Watson *et al*. 1992). Finally, if body parts clearly underestimated the number of individuals present, we assigned an intensity of '2' and added '1' to the MNI estimate. Justification for this adjustment can best be explained with the following example. Consider a large eagle pellet composed entirely of small mammal (Muridae) fur and a single vole skull. Skeletal evidence alone would suggest an MNI of '1', but this pellet clearly contains more fur than can be found on the body of a single vole. Because this situation was relatively common, there was a real need to reflect this by adjusting the MNI.

This scoring technique is a conservative modification of that proposed for mammals (Kelley & Garton 1997). In that study, MNI estimates were more accurate when based on the quantity of fur present than when based on counting bones. Such an approach is especially relevant because there is extensive evidence that diurnal raptors digest bone more effectively than hair (Duke *et al*. 1975, Mersmann *et al*. 1992, Houston & Copsey 1994, Bochenski *et al*. 1997).

We summed MNI estimates from pellets and from prey remains separately by both territory and month. We used only the higher MNI estimate (from pellets or from prey remains) for each prey species or group, and added monthly MNIs together to estimate the MNI of each prey type over the whole field season. As pellets and prey remains may provide different perspectives on diet, combining data from both should provide a more accurate picture of eagle diet than would data from either alone (Collopy 1983, Redpath *et al*. 2001).

Data analysis

To minimize the impact of unequal sampling in different territories, we only analysed data from territories in which we collected more than 20 items (pellets or prey remains) in a breeding season. We estimated dietary specialization in each eagle territory with Levins' index of diet breadth, using the 53 prey groups that we could identify accurately in pellets and prey remains (Levins 1968, Krebs 1989). Further details on these preliminary analyses are described in greater detail elsewhere (Katzner 2003).

Our statistical tests on these data were designed to identify spatial patterns in, and to clarify the interaction between, diet diversity and eagle demographics. We first evaluated patterns in the data from a territory, rather than from a regional perspective. To understand the within-year relationships between the degree of dietary diversity and the breeding density of Imperial Eagles we regressed nearest-neighbour distance against diet diversity. We used analyses of variance (ANOVAS) to look for within-year differences in diet diversity among occupied territories where zero, one, two or three chicks were produced (an occupied territory is one in which two adults were regularly observed; such a territory may or may not have active nests). We also used a regression to evaluate the relationship between the average diet diversity at each occupied territory and the average number of chicks they fledged. This last analysis was limited to the subset of 27 nests for which suitable dietary information was available in at least two of the three years of the study.

Because of the many factors that can affect reproductive output, relationships between reproductive

output and diet diversity were often more apparent at a regional scale than at the scale of individual territories. We compared the average number of chicks fledged among the regions of the *Zapovednik* with a Kruskal–Wallis test for each year of the study (Zar 1999). We used an ANOVA to test for within-year differences in average degree of dietary specialization among the four regions of the *Zapovednik*, and a Scheffe's multiple comparison to identify differences between regions (Zar 1999). For the subset of 21 territories for which suitable dietary information was available in all years of the study, we compared diet breadth within regions and across years with a multivariate repeated measures ANOVA.

If the mean reproductive output of eagles differs among regions, it is still possible that the reproductive response to inter-annual environmental differences can be similar (Watson *et al.* 2003). However, when reproductive response varies across regions, understanding the way that this variability is manifested can provide an important mechanistic insight into the relationships between dietary, environmental and reproductive parameters. We investigated possible mechanisms for reproductive response by evaluating the following average annual reproductive parameters: (1) the proportion of occupied territories in which breeding was attempted ('active' territories), (2) the proportion of active territories in which breeding was successful ('successful' territories), and (3) the number of chicks fledged in (3) active and (4) successful territories. We used a repeated measures ANOVA to evaluate year-to-year differences in these parameters and a Friedman's test (test statistic *W*) to evaluate regional differences (Daniel 1990, Zar 1999). For both analyses our sampling unit was the region rather than the territory. For the Friedman's test we used average annual regional productivity as our treatment effect and year as our blocking variable. Finally, we used the same tests to evaluate year-to-year and regional differences in average annual dietary diversity. We performed these analyses to facilitate the comparison between regional-based dietary and reproductive data, in spite of the fact that their outcomes were expected to be nearly identical to those from the territory-based ANOVAs on diet diversity that were mentioned earlier.

All analyses were performed with either SAS software (SAS version 8.01, SAS Inc., Cary, NC) or within a spreadsheet (Excel 2000, Microsoft, Redmond, WA). Inter-nest distances were calculated in a GIS (ArcView 3.2, ESRI Inc., Redlands, CA).

RESULTS

Dietary diversity and inter-nest spacing were positively correlated in each year of the study (Fig. 2). The exclusion of one outlier in both 1998 and 2000 further improved the significance of our correlations. Shorter nearest-neighbour distances were common in the South Naurzum and Tersec regions; longer nearest-neighbour distances were usually found in North Naurzum and Sip-sin (Katzner 2003, Katzner *et al.* 2003). Most territories contained one or more unused eagle nests, suggesting that the nest spacing was not driven by the availability of nest-sites.

In each year of the study, dietary diversity was similar in nests fledging different numbers of chicks (1998: $F_{2,24} = 0.75$, $P = 0.4818$; 1999: $F_{3,19} = 2.49$, $P = 0.0911$; 2000: $F_{3,28} = 0.07$, $P = 0.9742$). The
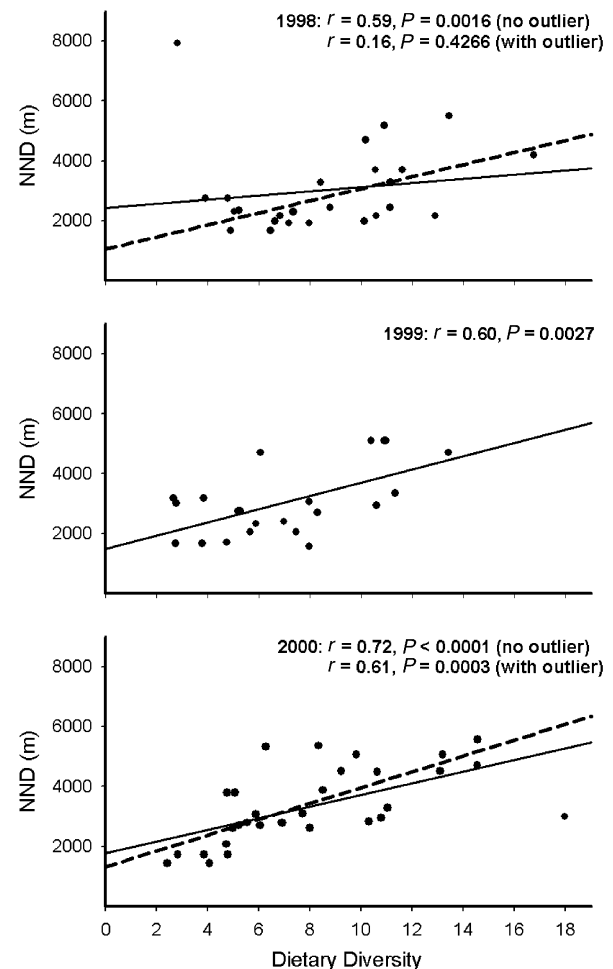
Figure 2. Correlation between dietary diversity (Levins' index) and nearest-neighbour distance (NND) for Imperial Eagles at the Naurzum *Zapovednik*, Kazakhstan, 1998–2000.
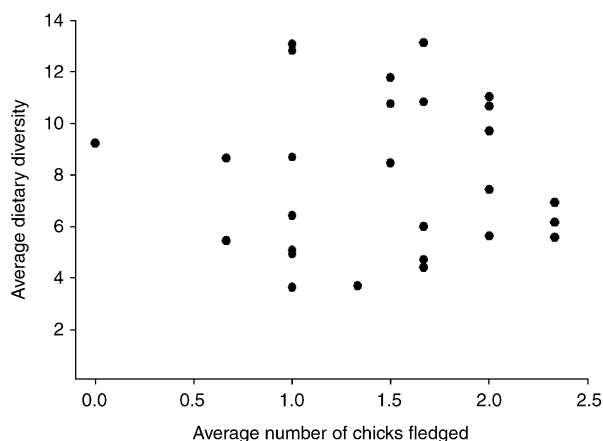
Figure 3. Average number of chicks fledged vs. degree of dietary diversity (Levins' index) at Imperial Eagle territories at the Naurzum *Zapovednik*, Kazakhstan, 1998–2000. Data from nests where < 2 years of dietary data were collected are not shown.

Table 1. Average dietary diversity (Levins' index) at occupied Imperial Eagle territories in the four regions of the Naurzum *Zapovednik*, Kazakhstan. Letters indicate similarity of groups as determined by a multiple comparison (Scheffe's test); sample sizes for each year (1998, 1999, 2000) are given below the names of each region.

Year	Sip-sin (5, 3, 6)	North Naurzum (5, 4, 7)	Tersec (9, 8, 11)	South Naurzum (8, 8, 8)	*P*-value
1998	12.50[a]	10.90[a,b]	5.96[c]	7.92[b,c]	< 0.0001
1999	9.14[a,b]	10.71[a]	6.22[a,b]	4.99[b]	0.004
2000	12.95[a]	10.23[a]	5.79[b]	4.91[b]	< 0.0001

average number of chicks fledged from Imperial Eagle territories was also independent of the average dietary diversity in those territories ($r^2 < 0.01$, $n = 27$; Fig. 3). In the few nests where productivity was highest ($\bar{x} > 2$), the eagles always had specialized diets; in nests where fewer chicks were produced, eagles had either specialized or generalized diets.

Within each year the number of chicks fledged in occupied territories was similar in all regions of the *Zapovednik* (1998: $\chi^2 = 0.2394$; 1999: $\chi^2 = 0.1074$; 2000: $\chi^2 = 0.2613$). However, the degree of dietary specialization in occupied territories, which averaged between 7 and 9 (1998: $\bar{x} = 8.60$, $n = 29$, range = 2.81–16.75; 1999: $\bar{x} = 7.11$, $n = 28$, range = 2.65–13.41; 2000: $\bar{x} = 7.81$, $n = 33$, range = 2.41–17.97), did vary among regions (Table 1). Eagle diet in South Naurzum and Tersec was more specialized than that of eagles in Sip-sin and North Naurzum. Repeated

measures analysis showed similar regional effects and neither a significant year effect (Wilk's $\lambda = 0.802974$, $F_{2,16} = 1.96$, $P = 0.1728$) nor a significant year–region interaction effect (Wilk's $\lambda = 0.512127$, $F_{6,32} = 2.12$, $P = 0.0783$).

Some average regional measures of reproductive output varied between the years. The number of chicks produced at active ($F_{2,6} = 14.32$) and at successful ($F_{2,6} = 10.03$) Imperial Eagle nests was highest in 2000 and lowest in 1998 ($\alpha_{0.01,2,6} = 13.3$, $\alpha_{0.5,2,6} = 8.43$). However, the two other measures we considered – the proportion of occupied territories where breeding was attempted ($F_{2,6} = 1.10$) and the proportion of active territories where breeding was successful ($F_{2,6} = 1.66$) – were similar in each year of the study ($\alpha_{0.5,2,6} = 8.43$).

In the analysis of regional dietary diversity, the proportion of occupied territories where breeding was attempted ($W_{3,4} = 0.20$) and the number of chicks produced at successful breeding territories ($W_{3,4} = 0.5889$) were similar across regions ($\alpha_{0.05,3,4} > 0.778$; Fig. 4). However, the proportion of active territories in which breeding was successful ($W_{3,4} = 0.911$), and the number of chicks fledged from active territories ($W_{3,4} = 0.911$) were greater in Tersec and South Naurzum than in Sip-sin and North Naurzum ($p_{0.911,3,4} = 0.017$).

Finally, as expected, the average regional measures of dietary diversity (Fig. 4) showed the same general trends as had been identified by the ANOVAs (Table 1) for which territories were the sampling unit. In this analysis, dietary diversity within regions was similar across the 3 years of the study, regardless of whether we considered all occupied territories ($F_{2,6} = 1.45$) or only active ($F_{2,6} = 1.30$) or successful ($F_{2,6} = 1.47$) ones ($\alpha_{0.5,2,6} = 8.43$). However, dietary diversity within years always differed between the four regions of the *Zapovednik*, regardless of whether we considered all occupied territories ($W_{3,4} = 0.822$), or only active ($W_{3,4} = 0.822$), or only successful ($W_{3,4} = 0.822$) territories ($p_{0.822,3,4} = 0.026$).

DISCUSSION

Nesting density was correlated with the diet diversity of Imperial Eagles at the Naurzum *Zapovednik*, Kazakhstan. Eagles that had a relatively specialized diet usually nested close to their neighbours. Shorter nearest-neighbour distances and high diet specificity were more common in South Naurzum and Tersec, both of which are situated near high-density colonial prey resources (Katzner 2003, Katzner *et al*.
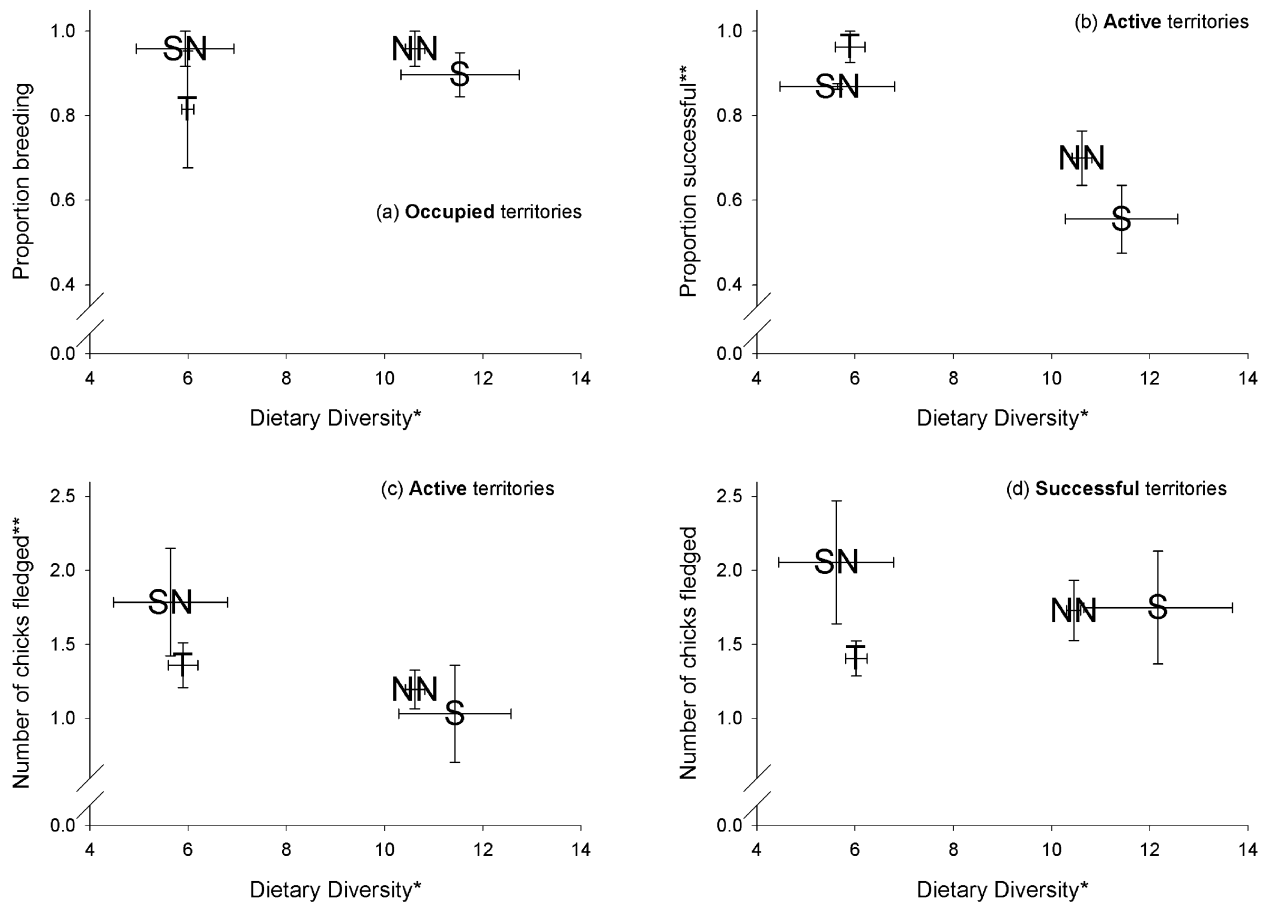
Figure 4. Bi-directional error plots of regional 3-year average degree of dietary diversity (Levins' index; ± se) vs. (a) the proportion of occupied territories where breeding was attempted; (b) the proportion of active territories where breeding was successful; (c) the mean number of chicks fledged at active territories; and (d) the mean number of chicks fledged at successful territories. Regions are north Naurzum (NN), Sip-sin (S), south Naurzum (SN) and Tersec (T; see Figure 1 for details). Significant differences among regions are indicated by an *(P = 0.026) or **(P = 0.017) by the label of the axis along which differences existed (see text for details).

2003). In contrast, eagles whose diet was more diverse usually had greater average inter-nest distances. Greater nearest-neighbour distances and lower diet specificity were common in North Naurzum and in Sip-sin, regions farther from high-density colonial prey. These data are consistent with the hypothesis that more efficient foraging, measured indirectly by dietary specialization, leads to a higher raptor nesting density. This greater foraging efficiency could be achieved by inherent individual variation, by a learning process that improved foraging, by increased encounter rates when foraging in areas with high density prey, or by a combination of these processes (MacArthur & Pianka 1966, Morgan *et al.* 1997, Bolnick *et al.* 2003). Regardless of which of these explanations applies in this situation, eagles at Naurzum with more specialized diets should require

less space for foraging and should defend smaller territories than their less specialized brethren. Defence of smaller territories is therefore an indirect effect resulting from an increased dietary specialization that subsequently allows breeding at higher population densities.

Thus, the degree of dietary specialization was a good correlate of breeding density and apparently of regional habitat quality for Imperial Eagles at the Naurzum *Zapovednik* (van Horne 1983). Throughout much of their range, the nesting density of Imperial Eagles is less than 0.2 pairs per 1000 km^2 (Bragin 2000). In good habitat, densities may reach 1.1 pairs per 1000 km^2, although densities higher than this have been reported (Davygora 1999, Bragin 2000). However, the breeding density of Imperial Eagles at this *Zapovednik* is considerably higher than in any

other known region (the exact difference depends on how the density is calculated). It is likely that the combination of abundant nesting sites and the possibility for efficient foraging allows this exceptionally high density of eagles at the Naurzum *Zapovednik*.

The degree of dietary diversity in eagles showed extensive variation among the different regions of the *Zapovednik*. Although access to habitat that allows dietary specialization should also have reproductive consequences, within-year patterns in reproductive output at the regional and *Zapovednik* scales provided little evidence of such consequences. However, because reproductive output may change significantly in response to annually variable environmental factors, we also considered differences in the multi-year average reproductive output, not just in individual observations within a single year. When we evaluated multi-year patterns, we found that: (a) although birds with a low productivity can have either specialized or generalized diets, the few birds with the highest productivity consistently showed high dietary specialization (Fig. 3); and (b) eagles breeding in regions where diets were more specialized usually had a greater reproductive output than those breeding in regions where the diets were less specialized (Fig. 4). In this analysis, some reproductive parameters were generally similar across regions and years, but others varied spatially and temporally in parallel with the degree of dietary specialization. As a consequence, evaluating this variability can provide some mechanistic insight into the possible relationships between reproductive output, diet and the environment.

Neither the proportion of active eagle territories at which breeding was attempted nor the average number of chicks fledged on successful territories differed between regions. Thus, the processes that controlled these parameters – the regulation of brood size at fledging and the annual decisions that determine whether or not to initiate breeding – appeared to be independent of the eagles' response among region spatial heterogeneity in the environment. In contrast, both the proportion of active territories in which breeding was successful and the number of chicks produced on active territories differed among regions. Therefore, the nest failure rate (the factor that determines both the difference between active and successful nests in the average number of chicks fledged, and the breeding success rate of active territories) was probably affected by spatial heterogeneity in the environment. Taken together, these results suggest that for Imperial

Eagles at the Naurzum *Zapovednik*: (1) the factors that control brood size at fledging and the decision to initiate breeding can vary independently of the factors that control nest failure rates; and (2) the mechanism producing regional variability in reproductive output probably acts by affecting nest failure rates and not brood size at fledging or the decision to initiate breeding.

Although there was an annual variation in the reproductive output of Imperial Eagles, neither the proportion of active territories in which breeding was successful, nor the proportion of occupied territories in which breeding was attempted, varied among years. These findings suggest that the processes controlling these parameters – nest failure rate and those that determine whether or not to initiate breeding – were similar in each year of the study and independent of temporal heterogeneity in the environment. However, year-to-year differences in the number of chicks produced in both successful and active nests indicate that the control of brood size at fledging is affected by temporal heterogeneity in the environment. Together, these results suggest that for Imperial Eagles at the Naurzum *Zapovednik*: (1) the factors that control nest failure rate and the decision to initiate breeding can vary independently of the factors that control brood size; and (2) the mechanism producing the annual variability in reproductive output acts by affecting brood size at fledging and not nest failure rates or the decision to initiate breeding.

These analyses point us towards several preliminary conclusions about the impact of eagle dietary decisions on demography. First, the factors that control nesting success, brood size at fledging, and the decision to initiate breeding were independent of each other in this system. Secondly, the factor that affects nesting success was related to regional differences within the *Zapovednik*. Possible candidates for this factor include either regional differences in nesting substrate (Katzner *et al*. 2003) or in prey availability and diet (Katzner 2003). However, differences in nesting substrate do not correlate well with differences in nesting success (nesting substrate in North Naurzum, a low-success area, is similar to that in South Naurzum, a high-success area), suggesting that increases in nesting success may be an important consequence of greater dietary specialization by these eagles. One reasonable hypothesis to explain this finding is that adult birds with more specialized diets may provide a more consistent food supply to their nests. Put in the context of the theory outlined earlier, the broods of more efficient foragers

are, on average, less likely to starve in bad years than the broods of less efficient foragers.

The factor that affects brood size at fledging was apparently controlled by a *Zapovednik*-wide, rather than regional, factor that varied annually. One of the best candidates for this mechanism may be the weather (Steenhof *et al*. 1997). If this theory is correct, it is unlikely that variability in the number of chicks fledged is tightly linked to variability in the degree of dietary specialization by Imperial Eagles. The number of chicks fledged therefore probably depends to some degree on the eagle's assessment of early spring environmental conditions and the decision of how many eggs to produce (Watson 1997). Finally, the decision whether or not to initiate breeding was independent of temporal or regional variations in this system. Other factors, such as the body condition of birds upon their return from spring migration, may have a greater impact on this decision.

Our results support earlier theories proposed to explain the effects of habitat heterogeneity on avian demography (Dhondt *et al*. 1992, Ferrer & Donazar 1996, Rodenhouse *et al*. 1997, Kruger & Lindstrom 2001). In this scenario, when avian reproductive output is limited by habitat quality, birds in a high quality habitat will produce more progeny than those in a marginal habitat. Some authors have proposed that the mechanism for this variability will function only if the habitat is heterogeneous at or near the scale of the individual territory (Dhondt *et al*. 1992, Ferrer & Donazar 1996). However, the scale of defended territories at Naurzum was considerably less than the scale of heterogeneity in prey distributions (for details see Katzner 2003 and Katzner *et al*. 2003), yet the results of our study show that reproductive output was still limited by habitat heterogeneity. Our data suggest that the scale of heterogeneity that influences reproductive output needs only be similar to the scale at which birds forage, not the scale of defended territories. Distinguishing between the space used for foraging and the space defended for territories is relevant, because while the two are often the same (e.g. Dhondt *et al*. 1992, Ferrer & Donazar 1996, Kruger & Lindstrom 2001), Naurzum's eagles apparently do not defend the area in which they forage (Katzner 2003).

The mechanistic explanations we propose to explain the links between dietary specialization and demography have conservation implications. They suggest that specific management approaches could be used separately to increase or decrease demographic characteristics such as nesting success, brood size at fledging, and the decision to initiate breeding. However, it is important to note that applying our analyses to management depends on our 3-year sample of eagle demography being an accurate window of the longer-term processes which determine population trajectories. Continued monitoring of these populations is therefore required to tune our conclusions more finely.

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