COEXISTENCE IN A MULTISPECIES ASSEMBLAGE OF EAGLES IN CENTRAL ASIA

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Abstract. We evaluated factors that permit species coexistence in an exceptional assemblage of similar raptor species at the Naurzum Zapovednik (a national nature reserve) in north-central Kazakhstan. White-tailed Sea-Eagle (*Haliaeetus albicilla*), Imperial Eagle (*Aquila heliaca*), Golden Eagle (*A. chrysaetos*), and Steppe Eagle (*A. nipalensis*) all breed at the Zapovednik. Steppe Eagle use of nesting resources was distinct from that of tree-nesting species. We evaluated differences in nest tree and nest habitat characteristics, nest dimensions and positions, and nest spacing among the three forest-dwelling eagle species to distinguish between the effects of inter- and intraspecific resource limitations on species coexistence. Although the different species bred in similar habitat and sometimes reused other species' nests, the dimensions, positions and locations of their nests often differed. These differences did not appear to result from interspecific competition. Nest spacing trends were also species specific; Imperial Eagles generally nested farther from other eagle nests than did Golden Eagles and White-tailed Sea-Eagles. Intraspecific variation in habitat, physical characteristics, and spacing patterns of Imperial Eagle nests was extensive throughout the nature reserve. Although interspecific partitioning of nesting habitat may allow coexistence of ground-nesting Steppe Eagles, interspecific competition did not appear to be a primary determinant of the use of nest habitat, space, or nests by tree-nesting species. Rather, interspecific effects appeared secondary to intraspecific effects in determining coexistence of tree-nesting eagles at this site.

Key words: Aquila chrysaetos, Aquila heliaca, Aquila nipalensis, *habitat use,* Haliaeetus albicilla, *Kazakhstan, species coexistence.*

Coexistencia en una Asamblea Multiespecífica de Águilas en Asia Central

Resumen. Evaluamos los factores que permiten la coexistencia de varias especies de aves rapaces similares en Naurzum Zapovednik, una reserva natural nacional, en la región norcentral de Kazakhstan. Las águilas *Haliaeetus albicilla*, *Aquila heliaca*, *A. chrysaetos* y *A. nipalensis* se reproducen en Zapovednik. El uso de los recursos de nidificación por *A. nipalensis* fue diferente al de las otras especies, las cuales nidifican en árboles. Evaluamos las diferencias en los árboles y características de los hábitats de nidificación y las dimensiones, posición y distribución de los nidos entre las tres especies de águilas que habitan ambientes boscosos, para distinguir entre los efectos de limitación por recursos a nivel interespecífico e intraespecífico sobre la coexistencia de estas especies. A pesar de que las diferentes especies se reprodujeron en hábitats similares y a veces reutilizaron los nidos de otras especies, las dimensiones, posiciones y localizaciones de sus nidos difirieron a menudo. Estas diferencias no parecen ser un resultado de competencia interespecífica. Las tendencias de la distribución en el espacio de los nidos también fueron especie-específicas; Las águilas de la especie *A. heliaca* nidificaron generalmente más alejadas de nidos de las otras especies que las águilas *H. albicilla* y *A. chrysaetos*. La variación intraespecífica en el hábitat, características físicas y patrones de distribución de *A. heliaca* fue considerable a través de la reserva natural. A pesar de que la partición interespecífica del hábitat de nidificación podría permitir la coexistencia de la especie *A. nipalensis* (la cual nidifica sobre el suelo), la competencia interespecífica no pareció ser importante en determinar el uso del hábitat de nidificación, de los nidos o su distribución para las especies de águilas que nidifican en árboles. En cambio, los efectos interespecíficos parecieron ser secundarios con relación a los efectos intraespecífcos en determinar la coexistencia de las águilas que nidifican en árboles en este sitio.

INTRODUCTION

Interspecific partitioning of limited resources may permit species to coexist in complex assemblages (Cooper and Dobzhansky 1956, MacArthur 1958, Hutchinson 1959, Connell 1961). This theory of resource partitioning usually is based on interspecific relationships and the ability of a species to specialize along some critical resource dimension or environmental gradient to competitively exclude other species (MacArthur and Levins 1967). The mechanisms that permit generalist species to coexist on similar resources are less clear and may include interspecific differences in local reproductive output, survivorship, or response to stress and disturbance (Dudgeon et al. 1999, Beckerman 2000). Therefore, the structure of a community is a function of resource use and individual responses among and within species (Wiens 1977, Saetre et al. 1999).

Although intraspecific effects may explain patterns in communities composed of divergent species, they are invoked less frequently to explain coexistence among similar species (Poole and Bromley 1988). We evaluated potential mechanisms permitting coexistence of four similar species of eagles breeding in the Narzum Zapovednik (a national nature reserve) in north-central Kazakhstan. We focused on nesting ecology as a manifestation of behaviors that reflect composition and persistence in many avian communities (Schmutz et al. 1980, Hayward and Garton 1988, Restani 1991, Selas 1997, Bakaloudis et al. 2001).

We examined intra- and interspecific patterns of eagle nest tree and nest habitat characteristics, nest dimensions and positions, and nest spacing, to evaluate two possible models of species coexistence. The first model, based on niche theory and interspecific effects, is often considered the primary mechanism structuring communities (Hairston et al. 1960, Schoener 1982, Kelt et al. 1995, Bardsley and Beebee 1998, Beckerman 2000). If interspecific interactions determine the composition of the eagle community in Kazakhstan, habitat use should be limited by interspecific competition. Under such conditions, we expected that nests and nest habitat would differ among species and that mated pairs would defend their territories against eagles of other species as well as against conspecifics (Cheylan 1973, Schmutz et al. 1980, Rothfels and Lein 1983, Hayward and Garton 1988, Restani 1991).

Alternatively, intraspecific processes may explain species coexistence (Wiens 1977, Connell 1983, Jaksic and Braker 1983, Saetre et al. 1999). In this scenario, habitat use by eagles should be limited by interactions with conspecifics, and we expected that habitat and characteristics of eagle nests would be similar among species but vary within species. Under an intraspecific model, we also expected that breeding pairs should be intraspecifically territorial, but not interspecifically territorial.

METHODS

SPECIES AND STUDY AREA

This research was conducted during April–August 1997–2000 at the Naurzum Zapovednik in the Kostanay Oblast of north-central Kazakhstan (51°N, 64°E). This region of northern Kazakhstan supports about 25 species of breeding raptors, including four similarly sized eagle species: Imperial Eagles (*Aquila heliaca*), about 40 active territories within the Zapovednik; White-tailed Sea-Eagles (*Haliaeetus albicilla*), about 20 active territories; Steppe Eagles (*A. nipalensis*), about 13 active territories; and Golden Eagles (*A. chrysaetos*), about 4 active territories (Bragin and Katzner, unpubl. data). Each of these species is internationally or locally recognized as threatened (Kovshar 1993, Hilton-Taylor 2000). Although these species have wide geographic ranges, they apparently nest together only in this area. Where they occur independently, these birds are generalists whose behavior and diet are often so similar that they are thought to replace each other in their respective habitats and geographic ranges (Grossman and Hamlet 1964, LeFranc and Clark 1983, Watson 1997).

Earlier studies indicate that these species share many resources, and that while the number of territories of each species in the reserve has fluctuated, the species assemblage has remained constant (Bragin 1989). All four species breed at the same time and their diets overlap extensively (Katzner 2002). Primary prey in the region are steppe marmots (*Marmota bobac*), ground squirrels (*Spermophilus* spp.), and several species of waterfowl, corvids, raptors, game birds, and small mammals.

The Zapovednik, established in 1931, encompasses an area of 87 700 ha (Fig. 1). About one-third of the reserve and much of the interstitial
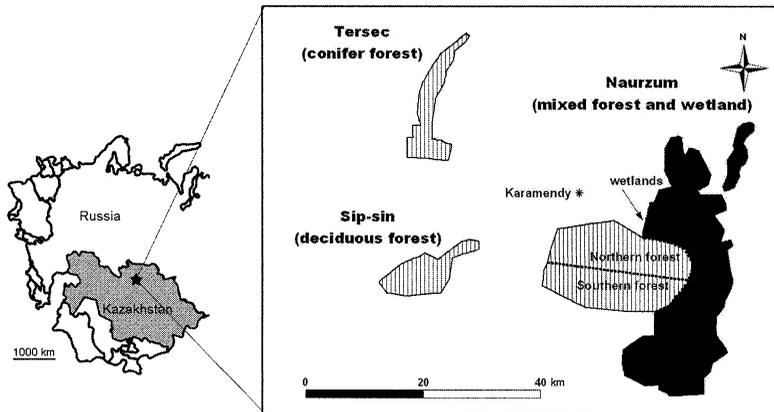
FIGURE 1.   The Naurzum Zapovednik, Kazakhstan, and its location (indicated by the shaded star) in the former Soviet Union. Boundaries of the three protected regions of the reserve (Naurzum, Sip-sin, and Tersec) and the village of Karamendy are shown. For analysis of Imperial Eagle nest dispersion, we divided Naurzum forest into northern and southern components on the basis of ecological differences between the two. Hatched gray areas are forested, solid black areas are wetland; the vast majority of surrounding unprotected land (white) is steppe or converted steppe (agriculture).

surrounding area is treeless, dominated by feather grass (*Stipa* spp.) and many types of bunchgrasses, or low sagebrush (*Artemisia* spp.) and other shrubs and grasses. More than 50% of this steppe was plowed during the virgin lands program initiated by Khrushchev in the 1950s. Interspersed within the steppe matrix are three woodland patches named Tersec, Sip-sin, and Naurzum that make up much of the protected reserve land (Fig. 1). To avoid confusion, we refer to the reserve as a whole (the Naurzum Zapovednik) as the Zapovednik; we use ''Naurzum'' to refer to the largest forested region. Forests are dominated almost exclusively by 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. The remaining protected area includes dry steppe and permanent and ephemeral wetlands with saline or fresh water. 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. M. Bragina, pers. comm.).

DATA COLLECTION

We measured habitat, nest, and location variables that are known parameters of niche separation in other settings, and that were logistically feasible to collect and pertinent to evaluating our predictions. Measurements were taken once at each nest, regardless of how many years the site was used for breeding.

Field surveys. Each spring, we surveyed established eagle territories and new sites throughout the region for signs of breeding activity. Surveys were conducted on foot, by car, or from a motorcycle as early as weather permitted, usually by the end of April or the start of May. Because this is during the vulnerable egg-laying and incubation phases, we never stayed at a nest longer than 5 min on the first visit (Fyfe and Olendorff 1976, Grier and Fyfe 1987). Nests were revisited monthly for the remainder of the summer (June, July, and August) to check activity and to collect regurgitated pellets as part of an associated project investigating eagle diet and productivity. To monitor reproductive success we climbed to each nest near the end of the breeding cycle; we confirmed these data at subsequent visits whenever possible (Steenhof and Kochert 1982, Steenhof 1987). The location of each nest was recorded with a Garmin GPS 12 or 12XL receiver (Garmin International, Olathe, KS). Because most of these locations were recorded prior to May 2000 when selective availability was removed, we averaged readings over 2–3 min to improve their accuracy. We estimate the resulting location error to be less than 50 m.

We located and monitored all Steppe Eagle nests we found in and around the Zapovednik and we discuss their habitat use in the context of coexistence with other eagle species. How-

ever, we did not include this species in statistical analyses for two reasons. First, while other species are tree-nesters, Steppe Eagles usually nest on the ground. Their nests are so different from nests of other species that statistical comparison is unnecessary. Second, whereas our survey of tree-nesting species was close to a complete population count, we cannot make the same claim for Steppe Eagle nests, which were more difficult to find. It is therefore inappropriate to compare nest spacing among these species.

Nest tree and nest habitat characteristics. At each nest we recorded the species of the nest tree, its height, diameter at breast height (dbh), the proportion of the tree composed of living branches, and the percent canopy cover it provided (Mosher et al. 1987, Katzner and Parker 1997). For the eight trees closest to each nest tree and >12.5 cm dbh, we recorded the species, dbh, and distance to the nest tree. In addition, we estimated the proportion of bare ground, shrubs, and forbs and grasses in a 10-m circle centered at the nest tree. Finally, we estimated the proportion of pine, aspen, and birch trees in the forest patch where the nest tree was located. The largest forest patches used by eagles were 400 m in diameter, the smallest were composed of a single tree.

Nest dimensions and position in tree. We measured the greatest and shortest diameters of each nest, the height of the nest (on the outside, from the lowest point to the highest point), the distance to the ground from the top of the nest, the distance to the top of the tree from the top of the nest, the number of branches supporting the nest, and we estimated the percent canopy cover at the nest (Mosher et al. 1987). We calculated the relative position of the nest in the tree by dividing the distance to the ground by total tree height.

Nest location. In the Naurzum region, the only area with a clearly defined interior and edge, we measured the distance from nests to the edge of the forest. We used a GIS to overlay a plot of active eagle nests onto a digitized habitat map originally created on paper by reserve cartographers (ArcView 3.2, ESRI, Inc. 1999). We delineated forests from this generalized habitat map, buffered the forest boundary by 150 m to include the forest-steppe transition zone, which was not well represented in the original map, and measured the shortest distance from each nest to the buffered forest edge.

Territoriality. We evaluated both interspecific and intraspecific territoriality in the three tree-nesting eagle species. In each year of the study, we calculated the distance (in meters) between each nest and the nearest neighbor of the same species, the nearest neighbor of another species, and the nearest neighbor of any species. We calculated internest distances (a) for all occupied territories (for occupied territories in which birds did not breed or build a new nest, we measured from the nest that was occupied the previous year); (b) for all territories where breeding occurred; and (c) for all territories where successful breeding occurred. Since decisions about nest placement occur early in the breeding season when nonbreeding territories may be defended (Steenhof 1987, Watson 1997), and because nest spacing patterns were the same for occupied, breeding, and successful territories, we limit our discussion here to characteristics of occupied eagle territories. Two eagle nests were excluded from this analysis because they were located in small, isolated patches of trees >3 km from any other suitable nesting habitat.

STATISTICAL ANALYSES

Statistical analysis of our data presented special problems because of their discontinuous multi-year character. For example, a repeated-measures approach was precluded because most eagle territories had active nests in only one or two of the three years of the study. Furthermore, some pairs bred several times in one nest, but others used different nest sites in each year. As a consequence, application of general linear models that included a year effect would have been inappropriate (Hurlbert 1984). We therefore performed separate statistical analyses for each year of the study.

We used a series of discriminant function analyses (DFA) to test (a) if nest tree and nest habitat characteristics were different for each species of eagle; and, (b) if these characteristics were different for Imperial Eagles (the most numerous species) in the three regions of the Zapovednik. Because Imperial Eagles are the only species that regularly nests in birches and aspens as well as in conifers, we used another DFA on eagle nests in conifer trees to evaluate among-species differences in that subset of the nest sites. All habitat characteristics from active nests (those where eggs were laid) were included in these analyses. We did not consider unused nests

because of the possibility that their habitat or structural characteristics made them unsuitable for breeding. Proportional data were arcsine transformed and we averaged two variables (size of and distance to the eight nearest neighbor trees) before analysis. We evaluated these nest tree and nest habitat variables with a principal components analysis to graphically show underlying multivariate patterns in our data.

We used a series of DFAs to test (a) whether nest dimensions and position were different among eagle species; and (b) whether dimensions and position of nests were different among Imperial Eagles in the three regions of the Zapovednik. As above, only active nests were considered, proportional data were arcsine transformed, and Golden Eagles were only included in 2000. We used a Mann-Whitney U-test to evaluate differences in the average distance from occupied eagle nests to the forest edge. Golden Eagle nest location data ($n \leq 2$) are reported but not statistically analyzed.

We used a series of ANOVAs and Bonferroni-adjusted t-tests to evaluate (a) whether nearest-neighbor distances were different among tree-nesting eagle species; and (b) whether nearest-neighbor distances of Imperial Eagle nests were different in four forested subregions of the Zapovednik. For the former analysis, the number of Golden Eagles in the reserve was so low that we were able to statistically compare only nearest-neighbor distances of Imperial Eagle and White-tailed Sea-Eagle nests. We used pooled t-tests when variances were equal and Satterthwaite tests when variances were not equal (SAS Institute 1999). For the latter analysis, we assigned nests in the largest of the three forests (Naurzum) into northern and southern sections based on field observations of ecological differences in habitat and prey distributions between these two regions (Fig. 1; EAB and TEK, pers. obs.). We then tested the significance of differences in Imperial Eagle nest spacing among the four resulting subregions of the Zapovednik (Tersec, Sip-sin, north Naurzum, and south Naurzum). Finally, we used a corrected nearest-neighbor analysis to evaluate whether nests in the entire Naurzum region were randomly distributed or evenly spaced (Krebs 1989). In cases where two nests were closer to each other than to all other nests, we only counted that nearest-neighbor distance once for the ANOVAs and t-tests. This limited our sample size, but elimi-

nated nonindependence among measurements. All analyses were performed with SAS software (SAS Institute 1999). Unless otherwise noted, statistical significance was evaluated at $P < 0.05$ and values reported are means $\pm$ SD.

RESULTS

In each year we observed signs of occupancy at 32–35 Imperial Eagle territories, 11–16 White-tailed Sea-Eagle territories, 7–9 Steppe Eagle territories and 4–5 Golden Eagle territories. We noted breeding attempts at the majority of these: 25–34 Imperial Eagle nests, 8–13 White-tailed Sea-Eagle nests, 2–5 Steppe Eagle nests, and 1–3 Golden Eagle nests. We measured nest and nest habitat variables at most of these nests (Table 1).

Our data should be evaluated in the context of two important trends that we observed. First, in each year of this study, there were previously occupied eagle territories that were no longer used by any species. These included up to 14 Imperial Eagle, 7 White-tailed Sea-Eagle, 9 Steppe Eagle, and 2 Golden Eagle territories. Second, eagles of one species often bred in nests previously built or occupied by eagles of another species with no apparent reproductive costs. This trend has been well documented over the past 20 years at the Naurzum Zapovednik (EAB, unpubl. data). Two Golden Eagle nests were at sites originally used by Imperial Eagles (one of those sites has also been used by sea-eagles). Another historically occupied Golden Eagle nest site was originally occupied by sea-eagles. Likewise, several current sea-eagle territories included nests built by Imperial or Golden Eagles, and in 2000 there were two instances where sea-eagles established new territories and successfully bred in nests originally built by Imperial Eagles. In both of these cases the pair of Imperial Eagles that built the nest maintained occupancy of their territory and successfully bred in another nearby nest 370–600 m from the sea-eagles.

NEST TREES AND NEST HABITAT CHARACTERISTICS

All tree-nesting eagles nested in similar habitats throughout the Zapovednik in 1998, 1999, and 2000 (1998: Wilk's lambda = 0.47, $F_{11,16}$ = 1.7, P = 0.17; 1999: Wilk's lambda = 0.18, $F_{11,8}$ = 3.3, P = 0.05; 2000: Wilk's lambda = 0.47, $F_{22,54}$ = 1.1, P = 0.35). Because only one Golden Eagle nest was active in 1998 and 1999, data

TABLE 1. Measurements (means ± SD) of nest habitat and nests of tree-nesting eagles at the Naurzum Zapovednik, Kazakhstan, in 2000. Data from other years are similar. Imperial Eagle nests were analyzed separately for the three regions of the Zapovednik (Naurzum, Sip-sin, and Tersec). Number of nests is in parentheses; not all measurements were taken at all nests. Dbh = diameter at breast height.

| | | Imperial Eagle | | | White-tailed |
	Golden Eagle (3)	Naurzum (14–16)	Sip-sin (6)	Tersec (8–11)	Sea-Eagle (8–12)
Nest tree and nest habitat					
Nest tree height (m)	17.7 ± 4.5	15.5 ± 2.8	10.6 ± 0.8	11.5 ± 2.9	16.5 ± 2.9
Nest tree dbh (cm)	174.0 ± 26.9	176.8 ± 38.9	95.7 ± 28.1	144.7 ± 54.6	181.5 ± 50.2
Nest tree dead (%)	25 ± 13	34 ± 16	56 ± 40	34 ± 29	33 ± 28
Nest tree canopy cover (%)	73 ± 12	71 ± 13	48 ± 35	67 ± 15	70 ± 15
Bare ground at nest tree (%)	67 ± 28	57 ± 15	8 ± 10	27 ± 19	64 ± 18
Grass and forb cover (%)	17 ± 4	33 ± 17	59 ± 30	52 ± 20	32 ± 18
Shrub cover (%)	19 ± 27	10 ± 14	22 ± 29	18 ± 19	2 ± 3
Dbh of 8 neighbors (cm)[a]	55.9 ± 27.8	58.9 ± 38.3	54.9 ± 14.3	36.7 ± 21.5	36.1 ± 18.3
Distance to 8 neighbors (m)[a]	6.3 ± 3.2	27.1 ± 39.6	20.7 ± 9.5	6.3 ± 7.2	7.5 ± 8.1
Pine in patch (%)	68 ± 47	59 ± 45	0	67 ± 42	72 ± 33
Aspen in patch (%)	2 ± 3	3 ± 10	17 ± 41	24 ± 43	0
Nest dimensions and position					
Greatest diameter (cm)	148.3 ± 30.1	127.9 ± 23.9	112.5 ± 19.9	111.3 ± 23.5	148.3 ± 24.6
Shortest diameter (cm)	115.7 ± 5.1	84.4 ± 20.0	91.3 ± 11.8	76.2 ± 13.5	106.9 ± 19.0
Base to lip (cm)	48.0 ± 10.6	51.2 ± 17.4	58.3 ± 8.8	41.8 ± 16.8	75.0 ± 29.2
Height above ground (m)	13.5 ± 5.0	14.5 ± 2.7	7.7 ± 1.1	10.2 ± 2.8	13.2 ± 3.4
Distance to top of tree (m)	4.2 ± 1.6	1.0 ± 0.5	3.3 ± 1.1	0.8 ± 0.3	3.3 ± 2.0
Supporting branches (n)	6.3 ± 3.1	5.0 ± 1.1	5.3 ± 1.6	5.7 ± 1.6	8.9 ± 5.0
Cover at nest (%)	61 ± 37	19 ± 14	35 ± 20	16 ± 14	45 ± 29

[a] Mean measurement of the eight trees >12.5 cm dbh nearest the nest tree.

TABLE 2. Variables with factor loadings above 0.5 or below –0.5 from nine discriminant function analyses (DFA) used to evaluate within-year differences in eagle nest characteristics in the Naurzum Zapovednik, Kazakhstan, 1998–2000. The analyses addressed nest tree and habitat characteristics of Imperial Eagle nests in the three forested regions of the Zapovednik; dimensions and position of Imperial Eagle nests in the same three regions; and dimensions and position of Imperial, Golden, and White-tailed Sea-Eagles in the entire Zapovednik. All first axes and one second axis (in the analysis of nest variables for Imperial Eagles in 2000) were significant.

| Comparison | Loadings | | |
Variable	1998	1999	2000
Nest-habitat variables, Imperial Eagle nests (n)[a]	(11, 2, 7)	(8, 4, 3)	(15, 6, 8)
% Bare ground within 10 m of nest tree	0.59	0.61	0.86
% Grass and forb cover within 10 m	−0.56		−0.54
Dbh of nest tree	0.57	0.71	0.72
Nest tree height		0.63	0.70
% Pine composition of nest patch			0.54
Mean distance to nearby trees[b]	−0.58		
Nest variables, Imperial Eagle nests (n)[a]	(11, 4, 7)	(10, 4, 6)	(14, 6, 10)
Distance from nest lip to top of tree	0.94	0.91	−0.93
Height of nest (base to lip)	0.53		
% Canopy cover at nest		0.82	
Position of nest in tree[c]	−0.61	−0.97	0.99
Height of nest above ground		0.69	0.68
			0.52[d]
Longest diameter of nest			0.50[d]
Nest variables, all eagle species (n)[e]	(22, 7, 0)	(20, 5, 0)	(30, 7, 3)
Longest diameter of nest	0.73	0.72	0.53
Shortest diameter of nest	0.71	0.74	0.70
Height of nest (base to lip)	0.68		
% Canopy cover at nest	0.58		0.79
Distance from nest lip to top of tree		0.81	0.81
No. of branches supporting nest		0.71	0.51
Position of nest in tree[c]		−0.53	−0.61

[a] Sample sizes are the number of Imperial Eagle nests in Naurzum, Sip-sin, and Tersec forests, respectively.
[b] The mean distance from the nest tree to the nearest 8 trees >12.5 cm dbh.
[c] Nest height above ground divided by total tree height.
[d] Factor loading on second significant axis.
[e] Sample sizes are the number of Imperial Eagle, White-tailed Sea-Eagle, and Golden Eagle nests, respectively.

from this species were included only in the 2000 analysis. A separate DFA on data from only Imperial and White-tailed Sea-Eagle nests in 2000 confirmed that the inclusion of Golden Eagle nests in that year did not hide new differences between those two species (Wilk's lambda = 0.57, $F_{11,25}$ = 1.7, P = 0.13).

Imperial Eagles nested in *Pinus*, *Betula* and *Populus* trees, whereas Golden and White-tailed Sea-Eagles nested only in *Pinus*. We therefore repeated our statistical analyses (DFAs) exclusively for eagle nests in *Pinus* to evaluate differences among species in the subset of nests in a similar substrate. There was no significant difference in habitat use among pine-nesting eagles in any year of the study, whether or not Golden Eagles were included (1998: Wilk's lambda = 0.42, $F_{10,14}$ = 1.9, P = 0.13; 1999: Wilk's lambda = 0.16, $F_{10,4}$ = 2.2, P = 0.24; 2000 [without Golden Eagle]: Wilk's lambda = 0.57, $F_{11,17}$ = 1.2, P = 0.38; 2000 [with Golden Eagle]: Wilk's lambda = 0.44, $F_{22,38}$ = 0.9, P = 0.61).

Habitat at Imperial Eagle nests differed among the three regions of the Zapovednik (1998: Wilk's lambda = 0.02, $F_{22,14}$ = 3.8, P < 0.01; 1999: Wilk's lambda < 0.001, $F_{22,4}$ = 14.5, P < 0.01; 2000: Wilk's lambda = 0.09, $F_{22,32}$ = 3.4, P < 0.001; Table 2). There were pairwise differences in habitat at Imperial Eagle nests between Sip-sin and Naurzum and between Sip-sin and Tersec in each year of the study, and also between Tersec and Naurzum in 2000. Of the variables analyzed, two (bare ground at the nest tree, and dbh of the nest tree) were consistently useful in discriminating between nest trees and nest habitat in the different forests.
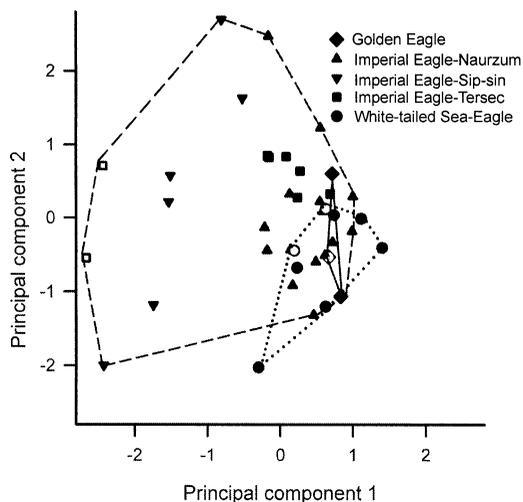
FIGURE 2. Factor plot of a principal components analysis of nest-tree and nest-habitat variables for three species of eagles nesting in the Naurzum Zapovednik, Kazakhstan, in 2000. This plot demonstrates interspecific similarity of nest habitat characteristics among Golden Eagles, Imperial Eagles, and White-tailed Sea-Eagles, as well as intraspecific differences among Imperial Eagle nests in three regions of the Zapovednik. Downward triangles (Imperial Eagle nests in Sip-sin) and the two unfilled squares on the left side of the figure were nests in deciduous trees, all other nests were in conifers. The three other unfilled symbols (2 White-tailed Sea-Eagle and 1 Golden Eagle) are nests originally built by Imperial Eagles.

We used a PCA to evaluate how nest trees and nest habitat of each species could be similar while Imperial Eagle nests differed among forest regions. This analysis showed the similarity of Imperial Eagle nests in Naurzum forest with White-tailed Sea-Eagle and Golden Eagle nests throughout the Zapovednik, but also the divergence among Imperial Eagle habitat use in the three forest regions (Fig. 2). Total variance explained by the first two principal components ranged from 50–60% for each year.

NEST DIMENSIONS AND POSITION IN TREE

Although nesting habitat was similar for Imperial, Golden, and White-tailed Sea-Eagles, characteristics of the nests each species built were different (1998: Wilk's lambda = 0.26, $F_{8,20}$ = 7.3, $P < 0.001$; 1999: Wilk's lambda = 0.23, $F_{8,16}$ = 6.7, $P < 0.001$; 2000: Wilk's lambda = 0.30, $F_{16,60}$ = 3.1, $P < 0.001$; Table 2). There were significant pairwise differences between nests of Imperial and White-tailed Sea-Eagles in

every year of the study, and in 2000 there were also differences between Imperial and Golden Eagle nests. A separate DFA confirmed that the addition of Golden Eagles did not mask similarities between the nests of Imperial and White-tailed Sea-Eagles in 2000 (Wilk's lambda = 0.44, $F_{8,28}$ = 4.51, $P = 0.001$). The two characteristics that had high discriminatory power (i.e., high loadings) in each year of our study, the longest and shortest diameters of the nest, were both related to how the eagles built nests. Other less important variables were more closely related to where the nest was positioned, rather than to how it was built.

The significance of the distinction between characteristics associated with nest dimensions versus those associated with nest position became apparent when we considered Imperial Eagle nests in the three regions of the Zapovednik (Table 2). Imperial Eagle nests in different regions were significantly different in each year of the study (1998: Wilk's lambda = 0.16, $F_{16,24}$ = 2.2, $P = 0.04$; 1999: Wilk's lambda = 0.06, $F_{16,20}$ = 3.7, $P < 0.01$; 2000: Wilk's lambda = 0.06, $F_{16,40}$ = 8.1, $P < 0.001$). Imperial Eagle nests in Sip-sin forest were different from those in both Naurzum and Tersec forests in all years of the study, and in 2000 nests in Naurzum and Tersec also were different. The two variables with the highest positive or negative loadings in each year (position of the nest in the tree, and distance from the nest to the top of the tree) were associated with nest position rather than nest dimensions.

NEST LOCATION

Imperial Eagle nests were generally closer to the edge of Naurzum forest than White-tailed Sea-Eagle nests, although the range of distances to forest edge often overlapped considerably (Fig. 3). Golden Eagles also nested more toward the interior of the forest, although we were unable to test this trend statistically. In some cases Imperial Eagles nested in isolated trees at or outside the forest edge that we defined. This was never the case for either of the other tree-nesting species. However, the median and minimum distances from sea-eagle nests to the forest edge decreased in each successive year of the study.

TERRITORIALITY

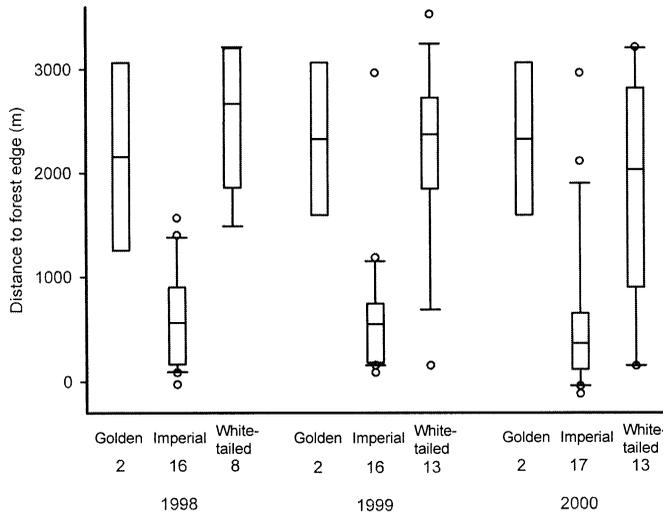Within the Naurzum forest, eagle nests were not spaced randomly in any year of our study.

FIGURE 3. Distance from occupied Golden Eagle, Imperial Eagle, and White-tailed Sea-Eagle nests to the edge of the Naurzum forest at the Naurzum Zapovednik, Kazakhstan. Data shown are median, quartiles, 10th and 90th percentiles, and outliers. *P*-values from a Mann-Whitney *U*-test between Imperial and White-tailed Sea-Eagle nests were all <0.004. Sample sizes appear below species names.

White-tailed Sea-Eagles there nested closer to conspecifics, closer to other species, and closer to nests of any species of eagle than did Imperial Eagles (Table 3). Minimum internest distances between heterospecifics was always less than between conspecifics, indicating that intraspecific interactions among eagles were not the same as interspecific interactions. In the whole Zapoved-

nik, Imperial Eagles consistently had greater minimum and average nearest-neighbor distances than did White-tailed Sea-Eagles and Golden Eagles (Table 3, Fig. 4). This trend remained statistically significant whether or not Golden Eagles were included in the comparison (*t*-tests for the Imperial Eagle–White-tailed Sea-Eagle comparison of means were significant in each

TABLE 3. Mean ± SD and minimum nearest-neighbor distances, conspecific nearest-neighbor distances, and heterospecific nearest-neighbor distances of occupied Imperial and White-tailed Sea-Eagle nests at the Naurzum Zapovednik, Kazakhstan. Means and statistical tests are only for nests in the Naurzum forest. Minima are for nests from all three regions of the Zapovednik. Sample sizes are in parentheses.

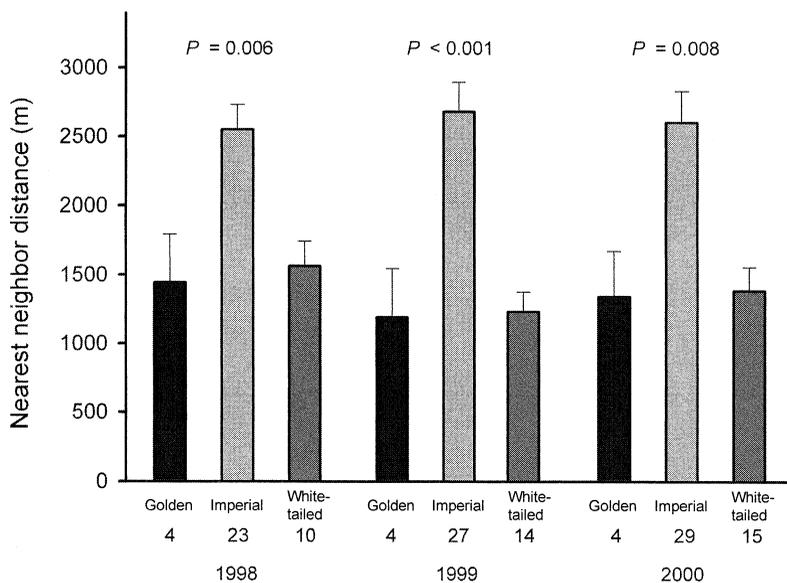|	Nearest-neighbor distance (m)				
	Imperial Eagle		White-tailed Sea-Eagle		
Year	Mean	Min.	Mean	Min.	*t*
All eagle species					
1998	2456 ± 631 (11)	791	1574 ± 575 (7)	732	3.0**
1999	2848 ± 1183 (14)	431	1268 ± 562 (11)	431	4.4***
2000	2235 ± 1190 (16)	367	1428 ± 703 (12)	367	2.1*
Conspecifics					
1998	2924 ± 1090 (9)	1676	2757 ± 2053 (7)	1509	0.2
1999	3605 ± 1267 (12)	1574	1489 ± 631 (8)	857	4.4***
2000	3240 ± 1218 (13)	1439	2082 ± 727 (10)	915	2.7*
Heterospecifics					
1998	3857 ± 1830 (16)	791	1850 ± 833 (8)	732	3.7**
1999	3667 ± 2209 (16)	431	1790 ± 747 (13)	431	3.2**
2000	2801 ± 2174 (17)	367	1636 ± 753 (13)	367	2.1*

* *P* < 0.05; ** *P* < 0.01, *** *P* < 0.001.

FIGURE 4.   Mean ± SE nearest-neighbor distances from occupied nests of Imperial Eagles, Golden Eagles, and White-tailed Sea-Eagles to the nearest territory occupied by any of these species at the Naurzum Zapovednik, Kazakhstan. Samples sizes appear below species names; P-values are from an ANOVA comparing distances among species.

year: 1998: $t_{31} = 3.0$, $P < 0.01$; 1999: $t_{39} = 5.1$, $P < 0.001$; 2000: $t_{42} = 3.5$, $P = 0.001$; sample sizes are those in Fig. 4).

Conspecific nearest-neighbor distances of Imperial Eagle nests differed among the three regions of the Zapovednik (1998: $F_{2,15} = 7.5$, $P < 0.01$; 1999: $F_{2,18} = 4.3$, $P = 0.03$; 2000: $F_{2,20} = 4.2$, $P = 0.03$). However, the differences between the regions were of greater significance when nests in the northern and southern subregions of the Naurzum forest were considered separately (Fig. 1, Table 4).

In general, nearest-neighbor distances averaged less than conspecific nearest-neighbor distances for both Imperial and White-tailed Sea-Eagles. However, because nearest-neighbor dis-

tance at a nest may be the same as conspecific nearest-neighbor distance, and because we adjusted α for this comparison, this difference was only significant for Imperial Eagles in 2000 (P-values ranged from <0.01 to 0.19, adjusted α = 0.008).

STEPPE EAGLES

Steppe Eagles usually built nests directly on the ground or in a low juniper (*Juniperus sabina*) or spirea (*Spirea* spp.) bush on flat ground or a ridge. The two tree nests we found were structurally similar to Imperial Eagle nests, but were built in isolated trees in habitat typical for Steppe Eagles and located many kilometers from protected forest.

TABLE 4.   Conspecific nearest-neighbor distances (m) for Imperial Eagle nests in four regions of the Naurzum Zapovednik, Kazakhstan, during 1998–2000. P-value is for an among-region difference within years (ANOVA); different letters within a column indicate significant differences in a Student-Newman-Keuls multiple comparison. Sample sizes are in parentheses.

Region	1998	1999	2000
Sip-sin	4475 ± 686 A (4)	4157 ± 942 A (3)	4631 ± 1008 A (5)
North Naurzum	3548 ± 1094 A (5)	4551 ± 991 A (6)	4032 ± 1006 A (7)
South Naurzum	2143 ± 330 B (4)	2659 ± 636 B (6)	2314 ± 662 B (6)
Tersec	2266 ± 331 B (5)	2253 ± 546 B (6)	2734 ± 738 B (5)
P	<0.001	<0.001	<0.001

DISCUSSION

NEST TREES AND NESTING HABITAT

If interspecific competition was the primary mechanism underlying coexistence in the eagle community in northern Kazakhstan and suitable nesting habitat was a limiting resource, then all available nest habitat either should be monopolized by a single species or species should occupy distinct nesting habitats (niches). Instead, the nest-habitat variables we measured were often similar and sometimes identical for each of the three forest-dwelling species of eagles. Furthermore, we observed vacant nests and territories of each eagle species in which successful breeding had previously occurred, strongly suggesting that availability of nesting habitat and space for territories did not limit eagles. We suggest that interspecific competition for available nest sites may not be the dominant factor in determining habitats used for nesting.

This hypothesis is supported by observations in the previous 20 years (EAB, pers. obs.) that eagles often have successfully bred in sites originally occupied by other species. Similar behavior has been noted among falcons (Newton 1979), Golden and Bonelli's (*Hieraaetus fasciatus*) Eagles in Spain and Israel (Bahat 1989, Fernandez and Insausti 1990), and Red-tailed and Swainson's Hawks (*Buteo jamaicensis* and *B. swainsoni*) in North America (Rothfels and Lein 1983). However, in these cases occupation of a territory by a similar species usually incurred a breeding expense to the original inhabitants. In most cases when this occurred at the Naurzum Zapovednik, the pair that built the original nest successfully bred in another nearby site.

Nesting ecology of Steppe Eagles was clearly distinct from that of the three tree-nesting species but because these differences were so great, we considered it unlikely that nest habitats used by Steppe Eagles were influenced by current interspecific competition. Nesting habitat of Steppe Eagles in the Naurzum Zapovednik also was not different from that in regions where the other species of eagles were absent (Watson 1997). Thus, differential habitat use by Steppe Eagles and tree-nesting species suggests that interspecific competition for nest habitats played little role in their coexistence.

NEST DIMENSIONS AND LOCATION

We expected that the types and locations of nests of tree-nesting eagles would differ among species if interspecific competition was a significant factor influencing this assemblage. Although nest types and locations were somewhat different, we found no evidence that nests were limiting or that competition excluded eagles from any type of nest sites. In fact, there were many unoccupied nest sites (often 1–3 per territory) and repeated instances where eagles successfully bred in nests originally built by another species.

If interspecific competition does not limit eagles in this landscape, then at higher densities they should occupy a greater range of habitats than at lower densities (Brown 1969, Fretwell and Lucas 1969, Wiens 1977). This was indeed the case for Imperial Eagles, the most numerous eagle species at the Zapovednik, which occupied the greatest range of nest and habitat types. Furthermore, it follows that if sea-eagles or Golden Eagles were at higher densities, they too might use a greater variety of nests and nest sites, as they do in other parts of their range. In support of this idea, as the number of pairs of breeding White-tailed Sea-Eagles has increased in recent years, they have used a greater variety of nests and nest sites (Katzner 2002).

TERRITORIALITY

If interspecific interactions were a significant influence on resource use by the tree-nesting species of eagles in the Naurzum Zapovednik, individuals should exclude heterospecifics as well as conspecifics from territories. Although in other areas eagles and other raptors exclude heterospecifics from their territories (Cheylan 1973, Newton 1979, Gerstell and Bednarz 1999), eagle territoriality at the Zapovednik was primarily intraspecific. The dichotomy between responses to conspecifics and to heterospecifics was most evident for Golden Eagles, whose minimum nearest-neighbor distance to other Golden Eagles was 12 km, but which tolerated nesting by other eagle species as close as 475 m (although this may be in part an artifact of a small sample size). Likewise, active Imperial Eagle nests always were >1.4 km apart, but conspecifics often nested within 1 km of an Imperial Eagle nest. Similarly, White-tailed Sea-Eagles never nested <900 m from a conspecific, but heterospecifics sometimes nested as close as 370 m. Given the similarity in their resource use, the extent to which eagles tolerated other species is surprising (Newton 1979, Schmutz et al. 1980, Rothfels

and Lein 1983, Burton et al. 1994, Gerstell and Bednarz 1999).

Territory size of Golden Eagles may be related to the availability of food. In Scotland, density of nesting Golden Eagles was inversely correlated with food availability during winter and early spring, when territories were established and defended most stringently (Watson et al. 1992, Watson 1997). Food limitation during northern Kazakhstan's long, harsh winter may explain why Golden Eagle density is similar to that in other low-density areas, such as Scotland and Europe (Tjernberg 1985, Watson 1997). This mechanism for nest spacing would depend only on early-season intraspecific interactions with other Golden Eagles and is independent of the presence of or competition with other species of eagles.

A hierarchical set of factors based on availability of nesting habitat and food resources may determine nest spacing patterns of Imperial Eagles. Availability of suitable nesting habitat is likely of primary importance for this species. Distances between Imperial Eagle nests are greater in regions surrounding the Naurzum Reserve where nesting habitat, consisting of clumps of trees, is widely dispersed (EAB, unpubl. data). Where nesting habitat is not limiting, such as within the Reserve, nest spacing is more likely a function of food availability and interaction with conspecifics. Imperial Eagles nested at highest densities in Tersec and south Naurzum forests, areas adjacent to exceptionally large colonies of steppe marmots and ground squirrels (Bragin 1989, Katzner 2002). They nested at lower densities in Sip-sin and north Naurzum forests, which had suitable nesting habitat but were farther from dense concentrations of prey. Thus, intraspecific behavior interacting with food availability appeared responsible for spacing of Imperial Eagle nests.

White-tailed Sea-Eagles did not occupy all potentially available nesting habitat. Therefore, it is difficult to decipher the mechanisms determining nest spacing in this species. However, patterns of nest spacing in the White-tailed Sea-Eagle population were not influenced by interspecific actions with other eagles. Thus, we expect that limits to nesting by this species are driven by intraspecific interactions similar to those that influence the other eagle species at the Naurzum Zapovednik.

Resource-based interspecific competition for breeding habitat and territories appeared unlikely determinants of the distribution and abundance of tree-nesting species of eagles at the Naurzum Zapovednik. Instead, intraspecific territoriality may be the critical mechanism that limited the breeding population size of each species of tree-nesting eagle. Steppe Eagles coexisted with tree-nesting species by using a divergent set of resources (i.e., ground nests). Although this interpretation of our data does not preclude the role of interspecific effects, we suggest that such processes are of secondary importance in enabling this unique community of endangered eagles to coexist.

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