THE JOURNAL OF RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 50 SEPTEMBER 2016 NO. 3

J. Raptor Res. 50(3):241–253

REPRODUCTIVE SUCCESS OF EURASIAN EAGLE-OWLS IN WETLAND AND NON-WETLAND HABITATS OF WEST-CENTRAL KOREA

DONG-MAN SHIN AND JEONG-CHIL YOO[1]

Korea Institute of Ornithology and Department of Biology, Kyung Hee University, Seoul 02447 Korea

ABSTRACT.—The breeding success of raptors is strongly affected by food supply. We examined the reproductive success of Eurasian Eagle-Owls (*Bubo bubo*) and assessed the effects of landscape and diet on reproductive success at 44 nest sites in wetland and non-wetland (mostly agricultural lands, forests, and human settlements) habitats in west-central Korea. We found that eagle-owl reproductive success was significantly higher in wetland than in non-wetland habitats (mean of 1.9 vs. 1.3 fledglings per breeding pair, respectively). Although the average number of fledglings per successful pair was similar in the two habitats (2.0 vs. 1.8), the average numbers of fledglings per hatchling (0.9 vs. 0.7) and per egg (0.8 vs. 0.5) were both higher in wetland habitats. Further, for the wetland habitats, birds (mostly Anatidae, Columbidae, and Phasianidae) were the most important prey group by both number and biomass (67% and 84%, respectively) in the breeding period. However, in non-wetland habitats, both mammals (59% by number) and birds (67% by biomass) were important prey in the breeding period. The amount of Phasianidae in the diet (by biomass) and the date of the onset of egg-laying were positively and negatively (respectively) significant determinants of the number of fledglings per egg, whereas the percentage of wetland in the habitat was the only significant determinant for the number of fledglings per hatchling.

KEY WORDS: *Eurasian Eagle-Owl*; Bubo bubo; *diet*; *prey availability*; *reproductive success*; *wetland habitat*.

ÉXITO REPRODUCTIVO DE *BUBO BUBO* EN HÁBITATS DE HUMEDALES Y NO HUMEDALES EN EL CENTRO OESTE DE COREA

RESUMEN.—El éxito reproductivo de las aves rapaces está afectado fuertemente por la disponibilidad de alimento. Estudiamos el éxito reproductivo de *Bubo bubo* y evaluamos los efectos del paisaje y la dieta en su éxito reproductor en 44 sitios de cría en hábitats de humedales y de no humedales (principalmente tierras agrícolas, bosques y asentamientos humanos) en el centro oeste de Corea. Encontramos que el éxito reproductor de *B. bubo* fue significativamente mayor en hábitats de humedales que en no humedales (media de 1.9 versus 1.3 volantones por pareja reproductiva, respectivamente). Aunque el número promedio de volantones por pareja exitosa fue similar en los dos tipos de hábitat (2.0 versus 1.8), los promedios de volantones por pollo eclosionado (0.9 versus 0.7) y por huevo (0.8 versus 0.5) fueron ambos mayores en hábitats de humedales. Además, para los hábitats de humedales, las aves (principalmente Anatidae, Columbidae y Phasianidae) fueron el grupo más importante de presas tanto por la cantidad como por la biomasa (67% y 84%, respectivamente) en la época reproductiva. Sin embargo, en los hábitats de no humedales, tanto los mamíferos (59% en cantidad) como las aves (67% en biomasa) fueron presas importantes en la época reproductiva. La cantidad de Phasianidae en la dieta (en términos de biomasa) y la fecha de inicio de la puesta de huevos fueron determinantes significativos del número de volantones por huevo de forma positiva y negativa (respectivamente), mientras que el porcentaje de humedales en el hábitat fue el único determinante significativo con respecto al número de volantones por pollo eclosionado.
[Traducción del equipo editorial]

[1] Email address: jcyoo@khu.ac.kr

In the population dynamics of territorial and solitary breeding species such as Eurasian Eagle-Owls (*Bubo bubo*), the reproductive success rate, distribution, population density, and diet are affected by land-cover types surrounding a nest site and the heterogeneous distribution of resources within the landscape (Penteriani et al. 2004, Bionda and Brambilla 2011). In addition, the diet tends typically to be dominated by the most abundant prey of the preferred size (Jaksić and Braker 1983, Korpimäki and Marti 1995, Marchesi et al. 2002, Zárybnická et al. 2009, Pérez-Garíca et al. 2012), and diet composition may reflect temporal and spatial variation in prey availability. Prey abundance and availability are the most important factors influencing variation in reproductive output of raptors (Whitfield et al. 2009).

A nocturnal, large, top predator, the Eurasian Eagle-Owl has been reported in a variety of habitat types (see Jaksić and Marti 1981, Martínez and Zuberogoitia 2001, Marchesi et al. 2002, Penteriani et al. 2004, Shin et al. 2013). However, few studies have focused on the fecundity, diet, and behavior of eagle-owls in wetland habitats (Alivizatos et al. 2005, Penteriani et al. 2012, Shin et al. 2013).

In a prior study, we reported the diet of wetland-dependent eagle-owls on the west-central Korea, Sihwa Reclaimed Area (SRA). Owls there fed mostly on avian prey such as ducks, Ring-necked Pheasants (*Phasianus colchicus*) and Oriental Turtle-Doves (*Streptopelia orientalis*; Shin et al. 2013). The mean weight of prey (MWP) was also remarkably heavier than that of eagle-owls living far from wetlands, which resulted from differences in food abundance, diet composition, and mass of potential prey (Shin et al. 2013). We here compare the reproductive success rates of eagle-owls in wetland and non-wetland habitats (i.e., forests, agricultural lands, and human settlements) during the breeding season, and assess the influence of landscape and diet on reproductive success.

METHODS

Study Areas. We studied eagle-owls at two study areas along the west-central coast of Korea: (1) wetlands located along the SRA (ca. 360 km^2; 37°4′–37°17′N, 126°34′–126°50′E) and (2) non-wetland areas located on the coastal area from Paju City and Gimpo City to Ganghwa District (PGG; ca. 810 km^2; 37°36′–37°49′N, 126°21′–126°51′E; Fig. 1). For the SRA, the marshes and open areas created after 1987 were widely distributed throughout the habitat (K-water 2009); elevation ranges from 28–146 masl, with gentle slopes (Shin et al. 2013). The PGG was composed of different landscapes: Paju and Gimpo were cultivated and urbanized, with intense human activity, whereas Ganghwa was characterized by hills (range = 42–468 masl; Shin et al. 2013).

Landscape Assessment. The landscapes around nest sites were classified following Shin et al. (2013). Based on Arirang 2 satellite images from the Ministry of Environment of Korea (Ministry of Environment of Korea 2009), we plotted a circle with a 1-km radius centered on each nest, and extracted the proportional areas of seven land-cover categories (fallow lands, agricultural lands, forests, water bodies, wetlands, human settlements, and grasslands) using ArcGIS 9.3 (ESRI 2008). We also measured: (1) nearest neighbor distance between nests (NND); (2) altitude above sea level (ASL); (3) distance to a paved road; (4) distance to an occupied residence; and (5) distance to an open area (DOA).

Diet and Reproduction. We examined 44 eagle-owl territories: 19 in SRA and 25 in PGG (Paju: 7, Gimpo: 11, Ganghwa: 7; Fig. 1). In the period from September 2010 to August 2012, we searched for nests using a combination of methods: passive listening for vocalizations, playing of conspecific calls and listening for responses, observing individuals at dusk, and visiting areas around historical nests (for more details, see Shin et al. 2013). To minimize disturbances, we visited nests once per week during the breeding season, starting with incubation.

We examined laying date and clutch size. We estimated hatching date by back-calculating based on the feather development of nestlings (Penteriani et al. 2005), and estimated laying date by subtracting 35 d, the mean incubation period, from the hatching date (Cramp 1985, Penteriani 1996, Dalbeck and Heg 2006). We expressed laying dates in days since 15 December (1 = 15 December), because that was the earliest laying date. To record clutch size, we climbed to the nests during incubation. When replacement clutches (two each for SRA and PGG) were recorded, we used the date of the first clutch as the laying date.

We calculated reproductive breeding success at the two study areas using multiple parameters, i.e., the number of fledglings (1) per territorial pair, (2) per breeding pair, (3) per hatchling, (4) per egg laid, and (5) per successful pair. We defined a territorial pair as one that established and defended

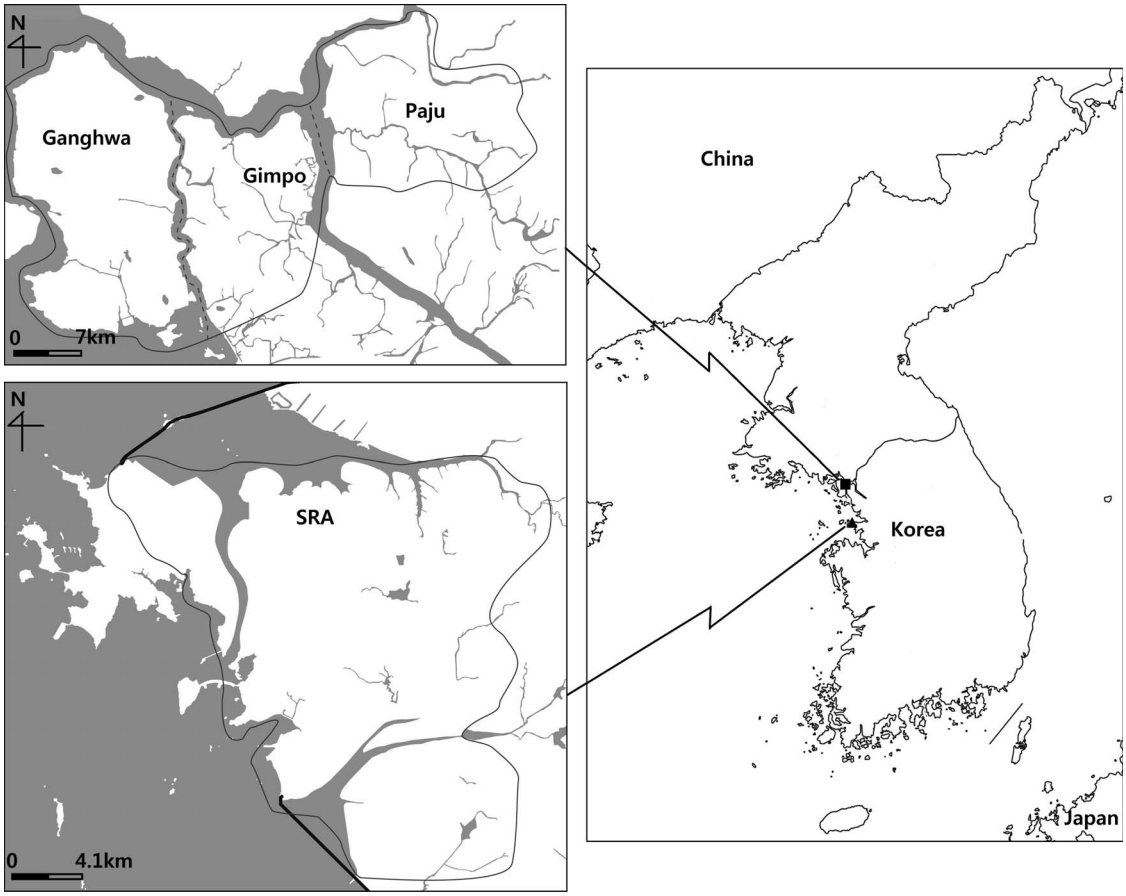


Figure 1. Study areas in west-central Korea, where landscape, diet, and reproductive rate of Eurasian Eagle-Owls were studied, September 2010–August 2012. ■ PGG (Paju City, Gimpo City and Ganghwa District); ▲ SRA (Sihwa Reclaimed Area).

a territory. Pairs that moved away >300 m from their nest sites in the next breeding season were also considered to maintain a separate territory. We defined a breeding pair as one that laid at least one egg and a successful pair as one that fledged at least one young. An occupied nest site was defined as one where a territorial pair was present during the breeding season, and nesting success was calculated as the percentage of territorial pairs that successfully fledged at least one young. Because eagle-owl young may leave the nests on the ground when they are ca. 1 mo old, we visited all nest sites as well as areas around the nests until the young were 8 wk old to record brood size at fledging.

To assess diet and its effects on reproductive output, we collected pellets and prey remains (1035 in SRA and 1977 in PGG) at nests, feeding sites, and roosting places, once or twice per month during the entire study period and every time we visited a nest during the breeding season. We identified prey items at the species level using published literature (Takada and Kanochi 2004, Yoon et al. 2004, Abe 2007, Won and Kim 2012). We determined the minimum number of prey items of each type for each collection event (Marti 1987, Bosè and Guidali 2001, Marchesi et al. 2002, Penteriani et al. 2005, Shin et al. 2013). We calculated the percent biomass and percent frequency of prey items for each territory by pooling all the years together (Smith et al. 1999). Biomass data for each prey species were based on mean body weight in Won (1981), Yoon et al. (2004), Song and Song (2005), Hume (2006), and in our measurements.

The various prey items that made up >3% of the diet pooled over the entire study area by number or by mass were classified at the family level: Anatidae, Ardeidae, Columbidae, Corvidae, Phasianidae, Leporidae, Muridae, and other prey (insects, crustaceans, reptiles, and actinopterygians). Other avian and mammalian prey items with three were grouped together as other birds and other mammals, respectively. Trace prey items made up 0.01% (Jaksić and Marti 1984).

The differences in diets between the two habitats were compared using diet composition, MWP, and Shannon–Wiener diversity index (H'). Because diet composition may vary seasonally for raptors (Bosè and Guidali 2001, Forsman et al. 2001, Marchesi et al. 2002), we used only diet data collected during the breeding season (from 15 December to 31 August in our study area) to describe diet and to assess the relationship of diet with reproductive rates.

Statistical Analyses. We used discriminant function analysis (DFA; Sokal and Rohlf 1995) to ascertain whether nest sites could be correctly classified into their original habitat types (wetland or non-wetland habitats). The difference in diet composition between the two habitats was compared by χ^2-test, based on the occurrence frequency of the categorized prey items. To avoid potential biases caused by the effect of sample size on diet indices (Smith et al. 1999), we excluded territories with fewer than 20 identified prey items from statistical analyses. In addition, territories affected by human disturbances such as amateur photographers or herb pickers were excluded from our analyses of the factors (landscape and diet) that may affect the reproductive output. Prior to analyses, percentage data were arcsine-transformed for normalization and variables related to MWP in the nonbreeding period were standardized as Z-scores to remove variation between years. Univariate comparisons of land-cover categories, nest location characteristics, dietary parameters and breeding estimates between the two different habitats were analyzed using t-tests, or Mann–Whitney U-tests when the data did not meet normality requirements or variances were not homogeneous after transformation. Associations of the independent variables with breeding success were analyzed using Pearson correlation. To examine factors affecting the reproductive success of eagle-owls, we used the landscape, nest location, onset of egg-laying, and diet variables as independent variable factors in a stepwise multiple linear regression (SMLR), with entry and removal criteria set at probability of $F \leq 0.05$ and ≥ 0.10, respectively. To avoid pseudoreplication, we averaged the value of reproductive success for the two study years for each territory (Marchesi et al. 2002). Significance was determined at $P < 0.05$. PASW Statistics 18.0 for Windows (SPSS Korea Datasolution Inc. 2009) was used for statistical analyses. Data are expressed as means ± SD.

RESULTS

Landscape and Nest Location Variables. We found significant differences between the two habitat types for seven variables (DFA; $\chi^2 = 81.851$, canonical correlation = 0.942, $n = 43$, $P < 0.001$). All the nest sites in both SRA and PGG were accurately classified. The percentage of wetlands was higher in SRA, whereas the percentages of agricultural lands, forests, human settlements, and grasslands were higher in PGG (Table 1). However, the percentages of fallow lands and water bodies did not differ significantly between the two habitats (Table 1). Nests of the SRA, compared to those of the PGG, were farther from occupied houses and paved roads, nearer to open areas and located at a lower elevation (Table 1). NND did not differ between the two habitats.

Nest Sites and Reproductive Success. In 2011, 34 nests were occupied ($n = 12$ for SRA, $n = 22$ for PGG), whereas in 2012, six of those were not occupied, another seven nest sites were found, and two pairs moved away ca. 400 m and 1600 m from their previous nest sites within their own territories ($n = 17$ for SRA, $n = 20$ for PGG in 2012). Of the 43 occupied nests, eight ($n = 3$ for SRA, $n = 5$ for PGG) had pairs that did not lay any eggs during the two breeding seasons. Clutch size, brood size at hatching, and the number of hatchlings per egg did not differ between the two study areas (Table 2). Additionally, laying date ranged from mid-December to early March and did not significantly differ between SRA and PGG (Table 2).

Wetland-dependent eagle-owls had higher reproductive rates than non-wetland eagle-owls, using several measures of reproduction. Nesting success was 1.7 times higher in wetland habitat, and most measures of reproductive success varied between the two habitats (Table 3). SRA owls fledged more hatchlings than PGG owls (Table 3); the number of fledglings per egg was 1.6 times higher in SRA (Table 3). The number of fledglings per breeding pair of SRA was 1.5 times higher than that of PGG

Table 1. Characteristics of landscape surrounding 43 Eurasian Eagle-Owl nest sites in wetland (Sihwa Reclaimed Area) and non-wetland populations (Paju City, Gimpo City, and Ganghwa District) of west-central Korea during the period of September 2010–August 2012. Percentage data of land-cover types were analyzed within a radius of 1 km around the nest (see methods for details) and were arcsine-transformed to compare the means between the two study areas. At one nest site in the wetland study area that was first discovered after fledging, we measured only nearest neighbor distance. *n* in parenthesis is number of nest sites, and $P < 0.05$ was considered significant. Bold type indicates statistical significance. Values are represented as mean ± SD.

LANDSCAPE CHARACTERISTIC	WETLAND	NON–WETLAND	STATISTIC[a]	*P*
Fallow land (%)	6.1 ± 11.2 (18)	3.7 ± 4.5 (25)	−0.994	0.326
Agricultural land (%)	17.3 ± 12.2 (18)	32.9 ± 19.2 (25)	−2.905	**0.004**
Forest (%)	14.9 ± 12.1 (18)	33.6 ± 24.2 (25)	−2.880	**0.004**
Water body (%)	8.3 ± 12.0 (18)	8.0 ± 13.2 (25)	−0.072	0.943
Wetland (%)	49.6 ± 21.3 (18)	1.6 ± 2.8 (25)	−5.623	**<0.001**
Human settlement (%)	2.9 ± 2.0 (18)	17.5 ± 10.4 (25)	−4.727	**<0.001**
Grassland (%)	0.8 ± 1.6 (18)	2.8 ± 3.8 (25)	−2.825	**0.005**
Nearest neighbor distance between nests (m)	2280.3 ± 1241.7 (18)	3445.8 ± 2177.0 (24)	−3.863	0.093
Distance from a paved road (m)	744.2 ± 770.9 (18)	115.6 ± 131.7 (24)	−3.863	**<0.001**
Distance from an occupied house (m)	409.9 ± 410.3 (18)	110.2 ± 148.4 (24)	−3.279	**0.001**
Distance from an open area (m)	15.8 ± 32.7 (18)	189.2 ± 145.7 (24)	−4.449	**<0.001**
Altitude above sea level (m)	19.7 ± 10.8 (18)	65.4 ± 38.3 (24)	−4.754	**<0.001**

[a] *z*-value (Mann–Whitney *U*-test), except for fallow land and water body, which are *t*-value (*t*-test).

(Table 3). However, the number of fledglings per successful pair did not differ.

Diet. Pellets and prey remains contributed 76% and 24%, respectively, to the total sample of prey items (Table 4). For pellets, mammalian prey were more frequent than avian prey; however, among prey remains, avian prey were overwhelmingly more frequent than mammalian prey (Table 4). During the breeding period, diet composition significantly varied between the two habitats ($\chi^2 = 308.524$, $P < 0.001$; Table 5). For the SRA eagle-owls, birds were the most important prey group in terms of both number and mass (Table 5). The most important bird family groups were Anatidae, Columbidae, and Phasianidae, making up >52% by number and 75% by mass. Waterbirds such as Chinese Spot-billed Ducks (*Anas zonorhyncha*), Mallards (*A. platyrhynchos*), egrets (*Egretta* spp. and *Bubulcus ibis*), and Common Coots (*Fulica atra*) contributed greatly to the biomass of the owl diet at SRA (47%). Muridae, including brown rats (*Rattus norvegicus*), black-striped field mice (*Apodemus agrarius*), and voles (*Clethrionomys* spp.), were detected quite frequently in the SRA, but their frequency of occurrence and

Table 2. Breeding parameters for Eurasian Eagle-Owls in wetland (Sihwa Reclaimed Area) and non-wetland populations (Paju City, Gimpo City, and Ganghwa District) of west-central Korea, September 2010 to August 2012. Percentage data were arcsine-transformed. *P*-value indicates the significance of the difference between the two study areas. *n* in parenthesis refers to number of samples.

	WETLAND (*n*)		NON–WETLAND (*n*)			
BREEDING PARAMETER	MEAN ± SD	RANGE	MEAN ± SD	RANGE	STATISTIC[a]	*P*
First egg-laying date[bc]	25.6 ± 19.1 (23)	3–81	29.3 ± 10.1 (28)	4–44	−1.052	NS
Clutch size[d]	2.5 ± 0.6 (23)	1–3	2.7 ± 0.7 (28)	1–4	1.066	NS
Brood size at hatch[d]	2.00 ± 0.6 (18)	1–3	2.0 ± 1.1 (25)	0–4	−0.522	NS
Number of hatchlings per egg[d]	0.8 ± 0.2 (18)	0.5–1	0.8 ± 0.4 (25)	0–1	−0.396	NS

[a] *t*-value (*t*-test), except for first egg-laying date, which is *z*-value (Mann–Whitney *U*-test);
[b] 1–15 December;
[c] first clutch;
[d] replaced clutch;
NS not significant.

Table 3. Mean reproductive success of Eurasian Eagle-Owls in wetland (Sihwa Reclaimed Area) and non-wetland populations (Paju City, Gimpo City, and Ganghwa District) of west-central Korea during the period of September 2010–August 2012. Percentage data were arcsine-transformed. Territories affected by human disturbances (e.g., amateur photographer, herb picker) were excluded from the analysis (see methods for details). *P*-value indicates the significance of the difference of breeding outputs between the two study areas, and significant difference is in bold type. *n* in parenthesis refers to numbers of sample.

	WETLAND (*n*)		NON–WETLAND (*n*)			
REPRODUCTIVE RATE	MEAN ± SD	RANGE	MEAN ± SD	RANGE	STATISTIC[a]	*P*
Nesting success (%)[b]	71.4 (21)		43.2 (37)			
Mean number of fledglings per territorial pair	1.4 ± 1.0 (21)	0–3	0.8 ± 1.0 (36)	0–3	−2.233	**0.030**
Mean number of fledglings per breeding pair (pair that laid eggs)	1.9 ± 0.7 (16)	0–3	1.3 ± 1.0 (23)	0–3	−1.982	**0.048**
Mean number of fledglings per successful pair	2.0 ± 0.5 (15)	1–3	1.8 ± 0.7 (16)	1–3	−0.870	0.392
Mean number of fledglings per hatchling	0.9 ± 0.3 (16)	0–1	0.7 ± 0.4 (20)	0–1	−2.801	**0.005**
Mean number of fledglings per egg	0.8 ± 0.3 (16)	0–1	0.5 ± 0.4 (23)	0–1	−2.253	**0.030**

[a] *t*-value (*t*-test), except for number of fledglings per breeding pair and number of fledglings per hatchling, which are *z*-value (Mann–Whitney *U*-test);
[b] percentage of territorial pairs that successfully fledged at least one young.

Table 4. Diet composition of the Eurasian Eagle-Owl in west-central Korea (September 2010–August 2012), analyzed by pellets and prey remains. Taxonomic groups with <3% of number or biomass of prey items were included in the categories "Other mammals" and "Other birds," respectively. tr = trace (<0.01%). Number of each species (*n*), frequency of each species (F), and biomass of prey (B) in the diet are shown. *n* in parenthesis refers to sample size.

	PELLETS			PREY REMAINS			POOLED		
TAXONOMIC GROUP	*n*	%F	%B	*n*	%F	%B	*n*	%F	%B
Birds (total)	**850**	**34.4**	**59.7**	**668**	**85.1**	**90.5**	**1518**	**47.0**	**72.4**
Anatidae	92	3.8	15.0	171	21.8	40.0	263	8.1	25.2
Ardeidae	48	2.0	4.1	45	5.7	5.6	93	2.9	4.7
Columbidae	94	3.8	17.7	122	15.5	26.8	673	20.8	15.5
Corvidae	478	19.5	18.7	195	24.8	11.0	107	3.3	2.3
Phasianidae	63	2.6	2.3	44	5.6	2.2	216	6.7	21.5
Other birds[a]	75	2.7	1.9	91	11.7	4.9	166	5.2	3.1
Mammals (total)	**1565**	**63.9**	**40.1**	**117**	**14.9**	**9.4**	**1682**	**52.0**	**27.5**
Leporidae	23	0.9	8.5	10	1.3	5.3	33	1.0	7.2
Muridae	1495	61.1	28.4	99	12.6	3.4	1594	49.3	18.1
Other mammals[b]	47	1.9	3.2	8	1.0	0.7	55	1.7	2.2
Insects[c]	**21**	**0.9**	**tr**				**21**	**0.6**	**tr**
Crustaceans[d]	**9**	**0.4**	**tr**				**9**	**0.3**	**tr**
Actinopterygians[e]	**1**	**tr**	**tr**				**1**	**tr**	**tr**
Reptiles[f]	**1**	**tr**	**tr**				**1**	**tr**	**tr**
Total prey items	**2447**	**100**	**100**	**785**	**100**	**100**	**3232**	**100**	**100**

[a] Accipitridae (*n* = 4), Caprimulgidae (*n* = 1), Cuculidae (*n* = 3), Coracidae (*n* = 2), Emberizidae (*n* = 1), Falconidae (*n* = 14), Laridae (*n* = 1), Motacillidae (*n* = 2), Oriolidae (*n* = 1), Phalacrocoracidae (*n* = 2), Picidae (*n* = 3), Podicipedidae (*n* = 1), Pycnonotidae (*n* = 17), Rallidae (*n* = 22), Scolopacidae (*n* = 5), Strigidae (*n* = 40), Threskiornithidae (*n* = 1), Turdidae (*n* = 15), Zosteropidae (*n* = 1), unidentified birds (*n* = 30);
[b] Canidae (*n* = 1), Erinaceidae (*n* = 1), Felidae (*n* = 2), Mustelidae (*n* = 22), Sciuridae (*n* = 6), Soricidae (*n* = 17), Talpidae (*n* = 6);
[c] Acrididae (*n* = 5), Carabidae (*n* = 7), Curculionidae (*n* = 2), Lucanidae (*n* = 6), Mantidae (*n* = 1);
[d] Leucosiidae (*n* = 7), Sesarmidae (*n* = 2);
[e] Cyprinidae (*n* = 1);
[f] Colubridae (*n* = 1).

Table 5. Spatial variations of the Eurasian Eagle-Owl diet in the breeding and nonbreeding periods in wetland (Sihwa Reclaimed Area) and non-wetland populations (Paju City, Gimpo City, and Ganghwa District) of west-central Korea, September 2010–August 2012. Number of each species (n), frequency of each species (F), and biomass of prey (B) in the diet are shown. Taxonomic groups with <3% of number or biomass of prey items were included in the categories "Other mammals" and "Other birds," respectively. tr = trace (<0.01%). Territories with $n < 20$ prey items were excluded from analyses of the difference between the two habitats. n in parenthesis refers to sample size.

	Breeding Period[a]						Nonbreeding Period[b]					
	Wetland			Non-wetland			Wetland			Non-wetland		
Taxonomic Group	n	%F	%B	n	%F	%B	n	%F	%B	n	%F	%B
Birds (total)	537	66.6	84.4	794	41.1	66.7	65	44.8	79.5	122	34.8	54.5
Anatidae	156	19.4	41.9	87	4.5	16.1	14	9.7	33.2	6	1.7	7.3
Ardeidae	25	3.1	3.3	54	2.8	5.3	6	4.1	7.5	8	2.3	5.7
Columbidae	174	21.6	11.2	400	20.7	18.1	25	17.2	14.3	74	21.1	18.7
Corvidae	25	3.1	1.5	69	3.6	2.8	3	2.1	1.6	10	2.8	2.3
Phasianidae	90	11.2	22.3	104	5.4	21.8	7	4.8	14.7	15	4.3	19.4
Other birds	67	8.3	4	80	4.5	2.6	10	7	8.2	9	2.7	1.1
Mammals (total)	**253**	**31.4**	**15.5**	**1129**	**58.5**	**33.3**	**78**	**53.8**	**20.4**	**222**	**63.2**	**45.4**
Leporidae	14	1.7	8.5	14	0.7	6				5	1.4	11.9
Muridae	223	27.7	5.5	1086	56.3	24.8	73	50.3	18.6	212	60.4	29.8
Other mammals	16	1.9	1.4	29	1.6	2.5	5	3.5	1.9	5	1.4	3.7
Insects	**10**	**1.2**	**tr**	**6**	**0.3**	**tr**				**5**	**1.4**	**tr**
Crustaceans	**5**	**0.6**	**tr**				**2**	**1.4**	**tr**	**2**	**0.6**	**tr**
Actinopterygians				**1**	**0.1**	**0.1**						
Reptiles	**1**	**0.1**	**tr**									
Total prey items	**806**	**100**	**100**	**1930**	**100**	**100**	**145**	**100**	**100**	**351**	**100**	**100**

[a] 15 December to 31 August;
[b] 1 September to 31 December.

biomass (31% and 16%, respectively) were lower than those of birds. In contrast, both birds and mammals were important components of the owl diet at the PGG. Mammals were 1.4 times more frequent than birds (Table 4), but avian prey contributed twice as much to the overall biomass (Table 5).

MWP was 1.7 times greater at SRA than at PGG during the breeding period (SRA: 473.8 ± 498.9 g, PGG: 276.6 ± 365.9 g; Mann–Whitney U-test, $z = -11.036$, $n = 2513$, $P < 0.001$). H' was also significantly higher in SRA (SRA: 2.1 ± 0.4, PGG: 1.7 ± 0.5; t-test, $t = -3.555$, $n = 35$, $P = 0.001$). Eagle-owls in the SRA wetland area captured more diverse prey, but MWP of avian prey that they hunted was 2.6 times greater than that of mammalian prey (Fig. 2).

Association of Landscape Variables, Nest Location, and Diet with Reproductive Rate. Percent wetland was the only landscape variable positively associated with the reproductive success of eagle-owls (Table 6, Fig. 3A). As the proportion of wetland area increased, there were also increases in the number of fledglings per hatchling and per egg. Of nest location characteristic variables, NND was negatively correlated with the number of fledglings per breeding pair and hatchling, and DOA was negatively associated with the number of fledglings per hatchling (Table 6). MWP and H' were positively associated with both the number of fledglings per breeding pair (Fig. 3B) and per egg (Fig. 3C, Table 6). The percentage of Anatidae (by number) in the diet was positively correlated with the number of fledglings per hatchling; similarly, the percentage of Phasianidae (by number) in the diet was positively correlated with the number of fledglings per breeding pair and per egg (Table 6). The number of fledglings per successful pair was not significantly associated with any of the independent variables.

A SMLR revealed that H', percent biomass for "other family" and NND were significant determinants of the number of fledglings per breeding pair, whereas percent wetland was the only significant determinant of the number of fledglings per hatchling (Table 7). The percent of Phasianidae in the diet (by number) and date of the onset of egg-

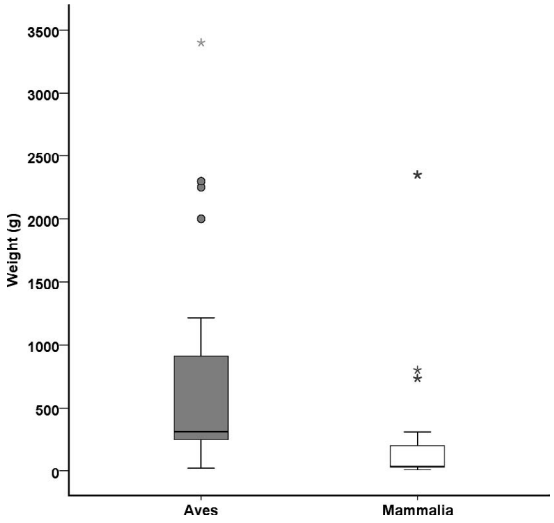


Figure 2. Biomass contribution of avian and mammalian prey in the Eurasian Eagle-Owl diet in the breeding period in the wetland population (Shihwa Reclaimed Area) of west-central Korea (September 2010–August 2012). Aves: $\bar{X} = 608.2 \pm 446.7$ g, $n = 537$, Mammalia: $\bar{X} = 237.1 \pm 529.4$ g, $n = 253$ (Mann–Whitney U-test: $z = -18.895$, $P < 0.001$). The box includes the middle 50% of the distribution of prey weights, with the bold central line within the box indicating the median of the data. The top and bottom of the box represent the 75th and 25th percentile of the data, respectively. The vertical lines outside the box show the upper and lower deciles. Circles and asterisks represent outliers and extreme values, respectively.

laying were significant determinants of the number of fledglings per egg (Table 7). A significant predictor of the number of fledglings per successful pair was not detected in the pooled samples. Overall, the predictive power of a multiple linear regression was highest for reproductive rate in terms of the number of fledglings per breeding pair, accounting for >47% of the variation.

DISCUSSION

Reproductive success of eagle-owls in wetland-dominated habitats in Korea (2.0 young per successful pair) was slightly lower than that of owls studied in Spain (2.3 young per successful pair, Beneyto and Borau 1996) but similar to or higher than reproductive success in Germany (2.1 young per successful pair, Dalbeck and Heg 2006), Austria (2.0 young per successful pair, Frey 1992), France (1.9 young per successful pair, Cochet 1985; 1.8 young per successful pair, Penteriani et al. 2002), and Sweden (1.6 young per successful pair, Olsson 1979).

High breeding success of eagle-owls in Mediterranean habitats was related to high local abundance of rabbits (*Oryctolagus cuniculus*), their primary local prey (Donázar 1990, Penteriani et al. 2002, Pérez-García et al. 2012). Our results suggest that the large and abundant prey in wetlands (i.e., waterbirds) might be a driver of the differences in breeding success between the wetland and non-wetland populations. Actually, wetland-dependent waterbirds formed almost half of biomass delivered to owl nests. This result is not consistent with a widespread premise that the eagle-owls feed primarily on mammals (Martínez and Zuberogoitia 2001, Marchesi et al. 2002, Penteriani et al. 2002, König and Weick 2008). However, our findings are consistent with an eagle-owl diet study at the Amvrakikos wetland in Greece, where birds made up 62% of prey by biomass and 20% by number (Alivizatos et al. 2005). The avian predominance is likely linked to the proximity or prevalence of wetlands and the low availability of rats due to the distance to villages. This may result in a higher predation on birds and a more diverse diet (Marchesi et al. 2002, Penteriani et al. 2004, Shin et al. 2013).

Generally, a decline in abundance of a preferred prey species causes both an increase in dietary breadth and a decline in reproductive success (Steenhof and Kochert 1988, Korpimäki 1992, Marchesi et al. 2002). Alternative prey is sometimes less accessible or has lower biomass (Korpimäki 1986, Steenhof and Kochert 1988, Zárybnická et al. 2009). For the SRA, decreasing predation on Muridae (mainly brown rat and black-striped field mouse) was associated with increasing predation on birds, and dietary diversity indices (H') increased. Nevertheless, the low Muridae availability did not necessarily result in lower reproductive rates. Although eagle-owls of the wetland-dominated SRA captured more diverse prey types than those of the PGG, they produced more fledglings and had higher breeding success rates (the number of fledglings per hatchling and per egg). Due to the spatial proximity to wetlands and open areas, they were able to hunt profitable and high-energy prey, e.g., ducks and Ring-necked Pheasants. As an SMLR analysis showed, the percentage of Phasianidae (by biomass) in the diet was one of the significant determinants influencing the number of fledglings per breeding pair. A greater MWP might be an

Table 6. Correlation of the landscape, nest location, and diet variables with the reproductive success of Eurasian Eagle-Owls in west-central Korea, September 2010–August 2012, analyzed by Pearson correlation analysis. Dietary data in the breeding period were pooled among years, and breeding data were averaged across the two study years for each territory. Percentage data were arcsine-transformed. Territories with $n < 20$ prey items and affected by human disturbances (e.g., amateur photographer, herb picker) were excluded from the analysis (see Methods for details). *n* in parenthesis refers to sample size.

VARIABLE	REPRODUCTIVE RATE MEASURE			
	NFBP[a] ($n = 29$)	NFH[b] ($n = 27$)	NFE[c] ($n = 29$)	NFSP[d] ($n = 23$)
Wetlands	NS	0.484*	0.402*	NS
Distance from a nest to open area	NS	−0.407*	NS	NS
Nearest neighboring distance between nests	−0.439*	−0.445*	NS	NS
Mean weight of prey	0.466*	NS	0.421*	NS
Shannon–Wiener diversity index (H')	0.517**	NS	0.428*	NS
Percent number for Anatidae	NS	0.404*	NS	NS
Percent number for Phasianidae	0.470*	NS	0.503**	NS
Percent biomass for Phasianidae	0.507**	NS	0.480**	NS
Percent biomass for Columbidae	−0.372*	NS	−0.382*	NS
Percent biomass for Muridae	−0.374*	NS	NS	NS
Percent biomass for other family	−0.383*	NS	−0.442*	NS

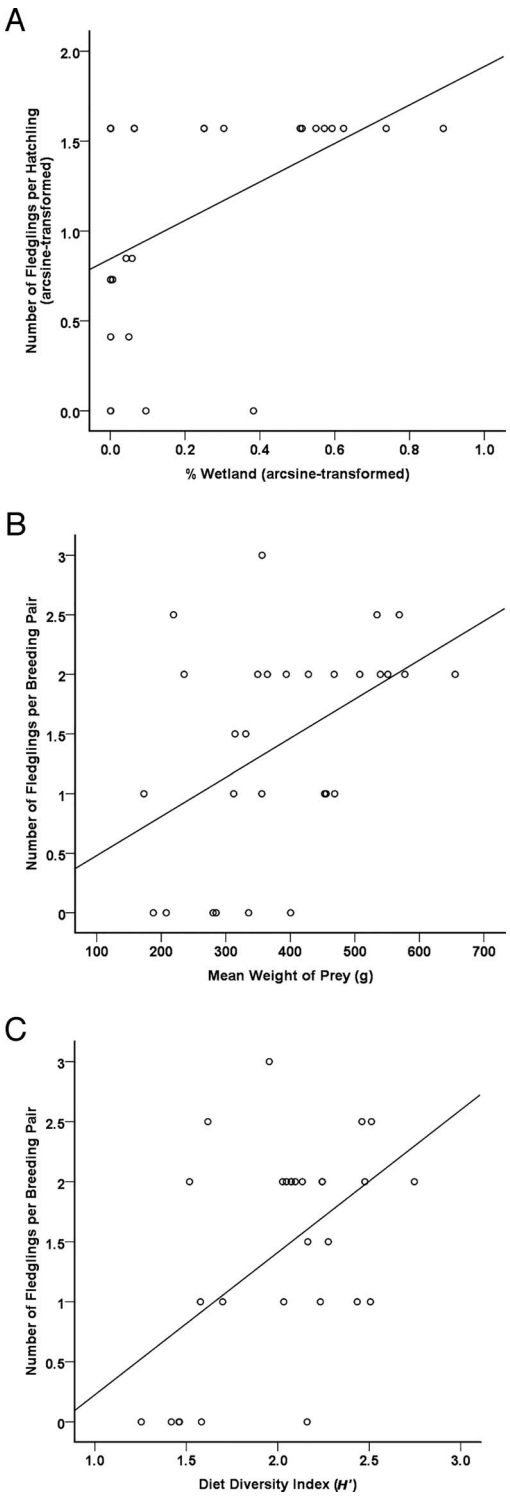
[a] Number of fledglings per breeding pair;
[b] number of fledglings per hatchling;
[c] number of fledglings per egg;
[d] number of fledglings per successful pair that fledged at least one young;
NS not significant;
* $P < 0.05$;
** $P < 0.01$.

important contributor to the higher reproductive success in wetland habitat.

The ecology of eagle-owls at SRA appears to be similar to that recorded in a France massif (Penteriani et al. 2002): the eagle-owls along the border had a higher reproductive output than those in the interior, although the former had a broader diet (D.M. Shin unpubl. data). With the highest degree of diversity and food-niche breadth value among owls (Herrera and Hiraldo 1976), eagle-owls can profitably focus on large mammals or medium- to large-sized birds. As Whitfield et al. (2009) discussed, a positive association between specialized diet and reproductive success can be expected when the spatial and temporal availability of specific profitable prey types is stable and predictable. The abundance, availability, and distribution of prey are probably more influential than individual foraging specialization in determining reproductive output (Whitfield et al. 2009).

When rabbit (preferred prey) abundance is low, eagle-owls usually capture alternative prey such as brown rats and hedgehogs (Hiraldo et al. 1976, Donázar 1988, Marchesi et al. 2002). The Korean hare (*Lepus coreanus*), the only lagomorph in west-central Korea, once ranged widely over most of Korea but has decreased in number and range because of excessive hunting and habitat loss/destruction (Won and Smith 1999). In our study areas, this species was extremely rare (Table 4, 5; Shin et al. 2013). Therefore, PGG eagle-owls probably focused on brown rats as a suitable substitute with medium size, high abundance, and year-round availability (Marchesi et al. 2002). Oriental Turtle-Doves and Ring-necked Pheasants also played a key role as another substitute prey and a second important food resource for them (Shin et al. 2013).

The breeding strategy of the PGG eagle-owls should be considered from the perspective of brood reduction (Lack 1947, Ricklefs 1965). These owls laid relatively large clutches, but lost a few recently hatched nestlings due to starvation and siblicide (73% of overall nestling mortality and 33% of all nestlings; D.M. Shin unpubl. data). This might be associated with lower MWP and result in a decrease in reproductive rates. It is possible they have adopted a brood-adjustment strategy to produce



the maximal brood size that can be raised while still balancing the energetic costs of brood-rearing (Mock and Forbes 1995, Wellicome 2000, Penteriani et al. 2010). There is, however, a need for further experimental research on the relationship between the decrease in MWP and brood reduction at PGG.

Diurnal raptors such as Northern Goshawks (*Accipiter gentilis*), Common Buzzards (*Buteo buteo*), and White-tailed Eagles (*Haliaeetus albicilla*) frequently hunt various birds in SRA in winter (K-water 2009). It is also possible that avian prey remains were overrepresented in the sample due to the abundance of their feathers and their longevity in the nest. Furthermore, annual and territorial variation in Eurasian Eagle-Owl diet is often attributed to spatial or temporal variation in prey abundance (Rusch et al. 1972, Pietiainen 1989, Hakkarainen and Korpimäki 1994, Steenhof et al. 1997). However, previous studies demonstrated that the use of pooled samples consisting of pellets and prey remains yielded a relatively close fit to diet composition assessed by direct observation (Simmons et al. 1991, Redpath et al. 2001, Marchesi et al 2002, Penteriani et al. 2005).

In conclusion, wetland-dependent Eurasian Eagle-Owls had higher reproductive rates than non-wetland eagle-owls in west-central Korea. The wetland offered a variety of large and profitable prey and the focus on avian prey played an important role in their reproductive rate. An in-depth study may be required to better understand the nature of the relationship between wetland habitat and breeding success. Further studies are also needed to examine the effects on owl reproductive rate of a continuing decrease in wetland areas due to the conversion to rice paddy

←

Figure 3. Association of percent wetlands (A), mean weight of prey (B), and diet diversity index (C) in the breeding period with reproductive success, based on 43 Eurasian Eagle-Owl territories in west-central Korea, September 2010–August 2012. Dietary data were pooled among years and breeding data were averaged across the two study years for each territory. Percentage data were arcsine-transformed. n in parenthesis is sample size. The equations of 3A, 3B, and 3C are $y = 1.070x + 0.845$ ($r^2 = 0.234$, $n = 29$, $P = 0.010$), $y = 0.003x + 0.153$ ($r^2 = 0.218$, $n = 29$, $P = 0.011$), and $y = 1.186x - 0.960$ ($r^2 = 0.267$, $n = 29$, $P = 0.004$), respectively.

Table 7. Multivariate determinants influencing reproductive success of Eurasian Eagle-Owls in west-central Korea, September 2010–August 2012, analyzed by a stepwise multiple linear regression. Landscape and diet variables were entered as independent variables and each of the four measures of reproductive rate as dependent variable (only the final model is shown). Dietary data in the breeding period were pooled among years and breeding data were averaged across the two study years for each territory. Percentage data were arcsine-transformed. Territories with $n < 20$ prey items and affected by human disturbances (e.g., amateur photographers, herb pickers) were excluded from the analysis.

Dependent Variable	Predictor	Coefficient	Std. Error	Beta	t	P
Number of fledglings per breeding pair[a]	Constant	0.858	0.852		1.008	0.323
	Diet diversity (H')[b]	0.706	0.346	0.308	2.041	0.052
	Percent biomass for other family	−71.238	22.352	−0.462	−3.187	0.004
	NND[c]	0.000	0.000	−0.442	−2.855	0.009
Number of fledglings per hatchling[d]	Constant	0.845	0.142		5.970	<0.001
	Wetland	1.070	0.387	0.484	2.767	0.010
Number of fledglings per egg[e]	Constant	0.731	0.186		3.938	0.001
	Percent number for Phasianidae	4.802	1.263	0.606	3.803	0.001
	Onset of egg laying	−0.014	0.006	−0.382	−2.401	0.024
Number of fledglings per successful pair[f]	No variable retained in the model					

[a] $r^2 = 0.530$, $r^2_{adj} = 0.474$, SE = 0.655, $F = 8.153$, $P = 0.009$;
[b] Shannon–Wiener diversity index;
[c] nearest neighbor distance between nests;
[d] $r^2 = 0.234$, $r^2_{adj} = 0.204$, SE = 0.550, $F = 7.658$, $P = 0.010$;
[e] $r^2 = 0.388$, $r^2_{adj} = 0.341$, SE = 0.471, $F = 5.764$, $P = 0.024$.

cultivation fields, industrial complexes, and apartment complexes.

Acknowledgments

We thank the Korean Cultural Heritage Administration, Ganghwa District, Gimpo City, Ansan City, Paju City, and Hwaseong City for permission to conduct research (permit number KCHA Natural Heritage Division-461) and the Korean Ministry of Environment for providing support with GIS data. We are also very grateful to Da-Mi Jeong, Jong-In Choi, and Hyeon-Chil Shin for valuable help with fieldwork. Special thanks to Jari Valkama, Heimo Mikkola, and an anonymous referee for critical review of an earlier version of this report.

Literature Cited

Abe, H. 2007. Illustrated skulls of Japanese mammals. Hokkaido University Press, Sapporo, Japan (In Japanese).

Alivizatos, H., V. Goutner, and S. Zogaris. 2005. Contribution to the study of the diet of four owl species (Aves, Strigiformes) from mainland and island areas of Greece. *Belgian Journal of Zoology* 135:109–118.

Beneyto, A. and J.A. Borau. 1996. El búho real (*Bubo bubo*) en Cataluña (NE de España). Pages 477–483 *in* J. Muntaner and J. Mayol [Eds.], Biología y conservación de las rapaces mediterráneas. SEO, Madrid, Spain.

Bionda, R. and M. Brambilla. 2011. Rainfall and landscape features affect productivity in an alpine population of eagle owl *Bubo bubo*. *Journal of Ornithology* 153:167–171.

Bosè, M. and F. Guidali. 2001. Seasonal and geographic differences in the diet of the Barn Owl in an agro-ecosystem in northern Italy. *Journal of Raptor Research* 35:240–246.

Cochet, G. 1985. Données préliminaires sur le Hibou grand-duc *Bubo bubo* dans les Causseset les Cévennes. *Bièvre* 7:93–100.

Cramp, S. [Ed.]. 1985. The birds of the western Palearctic, Vol. IV. Oxford University Press, Oxford, U.K.

Dalbeck, L. and D. Heg. 2006. Reproductive success of a reintroduced population of eagle owls *Bubo bubo* in relation to habitat characteristics in the Eifel. *Ardea* 94:3–21.

Donázar, J.A. 1988. Selección del hábitat de nidificación por el Búho Real (*Bubo bubo*) en Navarra. *Ardeola* 35:233–245.

———. 1990. Geographic variation in clutch and brood size of the eagle owl *Bubo bubo* in the western Palearctic. *Journal of Ornithology* 131:439–443.

ESRI. 2008. ArcGIS 9.3. New York, NY U.S.A.

Forsman, E.D., I.A. Otto, S.G. Sovern, M. Taylor, D.W. Hays, H. Allen, S.L. Roberts, and D.E. Seaman. 2001.

Spatial and temporal variation in diets of Spotted Owls in Washington. *Journal of Raptor Research* 35:141–150.

FREY, H. 1992. Bestandsentwicklung und Jungenproduktion des Uhus (*Bubo bubo*) in Niedersterreich zwischen 1969 und 1991. *Egretta* 35:9–19.

HAKKARAINEN, H. AND E. KORPIMÄKI. 1996. Competitive and predatory interactions among raptors: an observational and experimental study. *Ecology* 77:1134–1142.

HERRERA, C.M. AND F. HIRALDO. 1976. Food-niche and trophic relationships among European owls. *Ornis Scandinavica* 7:29–41.

HIRALDO, F., F. PARREÑO, V. ANDRADA, AND F. AMORES. 1976. Variations in the food habits of the European Eagle Owl (*Bubo bubo*). *Doñana Acta Vertebrata* 3:137–156.

HUME, R. 2006. RSPB birds of Britain and Europe, Revised Ed. Dorling Kindersley, London, U.K.

JAKSIĆ, F.M. AND H.M. BRAKER. 1983. Food-niche relationships and guilds structure of diurnal birds of prey: competition versus opportunism. *Canadian Journal of Zoology* 61:2230–2241.

——— AND C.D. MARTI. 1981. Trophic ecology of *Athene* owls in Mediterranean-type ecosystems: a comparative analysis. *Canadian Journal of Zoology* 59:2331–2340.

——— AND ———. 1984. Comparative food habits of *Bubo* owls in Mediterranean-type ecosystems. *Condor* 86:288–296.

KÖNIG, C. AND J. WEICK. 2008. Owls of the world, Second Ed. Yale University Press, New York, NY U.S.A.

KORPIMÄKI, E. 1986. Seasonal changes in the food of the Tengmalm's Owl *Aegolius funereus* in western Finland. *Annales Zoologici Fennici* 23:339–344.

———. 1992. Population dynamics of Fennoscandian owls in relation to wintering conditions and between-year fluctuations of food. Pages 1–10 *in* C.A. Galbraith, I.R. Taylor, and S. Percival [EDS.], The ecology and conservation of European owls. UK Nature Conservation, No. 5. Joint Nature Conservation Committee, Peterborough, U.K.

——— AND C.D. MARTI. 1995. Geographical trends in trophic characteristics of mammal-eating and bird-eating raptors in Europe and North America. *Auk* 112:1004–1023.

K-WATER. 2009. Management of biodiversity in Songsan Green-city. (In Korean.)

LACK, D. 1947.The significance of clutch-size. *Ibis* 89:302–352.

MARCHESI, L., F. SERGIO, AND P. PEDRINI. 2002. Costs and benefits of breeding in human-altered landscapes for the eagle owl *Bubo bubo*. *Ibis* 144:164–177.

MARTI, C.D. 1987. Raptor food habit studies. Pages 67–80 *in* B.A. Pendleton, B.A. Millsap, K.W. Cline, and D.M. Bird [EDS.], Raptor management techniques manual. National Wildlife Federation, Washington, DC U.S.A.

MARTÍNEZ, J.A. AND I. ZUBEROGOITIA. 2001. The response of the eagle owl (*Bubo bubo*) to an outbreak of the rabbit haemorrhagic disease. *Journal of Ornithology* 142:204–211.

MINISTRY OF ENVIRONMENT OF KOREA. 2009. Digital land cover map (medium classification). Gwacheon, Korea. http://egis.me.go.kr/ewebgis/webgis.jsp (last accessed 10 January 2013).

MOCK, D.W. AND L.S. FORBES. 1995. The evolution of parental optimism. *Trends in Ecology and Evolution* 10:130–134.

OLSSON, V. 1979. Studies on a population of eagle owls, *Bubo bubo* (L.), in southeast Sweden. *Viltrevy* 11:3–99.

PENTERIANI, V. 1996. The eagle owl. Calderini Edagricole, Bologna, Italy.

———, M.M. DELGADO, AND M. GALLARDO. 2002. Landscape structure and food supply affect eagle owl *Bubo bubo* density and breeding performance: a case of intra-population heterogeneity. *Journal of Zoology* 257:365–372.

———, ———, M. GALLARDO, AND M. FERRER. 2004. Spatial heterogeneity and structure of bird populations: a case example with the eagle owl. *Population Ecology* 46:185–192.

———, ———, J.M. PÉREZ-GARCÍA, F. BOTELLA, S. GARCÍA, J.A. SANCHEZ ZAPATA, M.L. ORTEGA, J.E. MARTÍNEZ, J.F. CALVO, J. ORTEGO, G. PENTERIANI, M. MELLETTI, I. KRUGERSBERG, AND O.M. TALAVERA. 2010. Sex allocation from an owl perspective: clutch order could determine brood sex to reduce sibling aggression in the eagle owl *Bubo bubo*. *Ornis Fennica* 87:135–143.

———, R. LOURENÇO, AND M.M. DELGADO. 2012. Eagle owls in Doñana: a conservation dilemma or not? *British Birds* 105:88–95.

———, F. SERGIO, M.M. DELGADO, M. GALLARDO, AND M. FERRER. 2005. Biases in population diet studies due to sampling in heterogeneous environments: a case study with the eagle owl. *Journal of Field Ornithology* 76:237–244.

PÉREZ-GARCÍA, J.M, J.A. SÁNCHEZ-ZAPATA, AND F. BOTELLA. 2012. Distribution and breeding performance of a high-density eagle owl *Bubo bubo* population in south-east Spain. *Bird Study* 59:22–28.

PIETIAINEN, H. 1989. Seasonal and individual variation in the production of offspring in the Ural Owl *Strix uralensis*. *Journal of Animal Ecology* 58:905–920.

REDPATH, S.M., R. CLARKE, M. MADDERS, AND S.J. THIRGOOD. 2001. Assessing raptor diet: comparing pellets, prey remains, and observational data at Hen Harrier nests. *Condor* 103:184–188.

RICKLEFS, R.E. 1965. Brood reduction in the Curve-billed Thrasher. *Condor* 67:505–510.

RUSCH, D.H., E.C. MESLOW, P.D. DOERR, AND L.B. KEITH. 1972. Response of Great Horned Owl populations to changing prey densities. *Journal of Wildlife Management* 36:282–296.

SHIN, D.M., J.C. YOO, AND D.M. JEONG. 2013. Spatial variation of Eurasian Eagle Owl diets in wetland and non-wetland habitats in west-central Korea. *Journal of Raptor Research* 47:400–409.

Simmons, R.E., D.M. Avery, and G. Avery. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *Journal of Raptor Research* 25:63–67.

Smith, R.B., M.Z. Peery, R.J. Gutiérrez, and W.S. Lahaye. 1999. The relationship between Spotted Owl diet and reproductive success in the San Bernardino Mountains, California. *Wilson Bull* 111:22–29.

Sokal, R.R. and F.J. Rohlf. 1995. Biometry, the principles and practice of statistics in biological research, Third Ed. W.H. Freeman and Co., New York, NY U.S.A.

Song, S.C. and S.K. Song. 2005. The complete guide to the birds of the Korean peninsula. Kimyoung Press, Seoul, Korea. (In Korean.)

SPSS Korea Datasolution Inc. 2009. PASW statistics 18.0. Korean Version. Seoul, Korea.

Steenhof, K. and M.N. Kochert. 1988. Dietary responses of three raptor species to changing prey densities in a natural environment. *Journal of Animal Ecology* 57:37–48.

———, ———, and T.L. McDonald. 1997. Interactive effects of prey and weather on Golden Eagle reproduction. *Journal of Animal Ecology* 66:350–362.

Takada, M. and T. Kanochi. 2004. The feathers of Japanese birds in full scale. Bunich Sogo Shuppan, Tokyo, Japan. (In Japanese.)

Wellicome, T.I. 2000. Effects of food on reproduction in Burrowing Owls (*Athene cunicularia*) during three stages of the breeding season. Ph.D. dissertation. University of Alberta, Alberta, Canada.

Whitfield, D.P., R. Reid, P.F. Haworth, M. Madders, M. Marquiss, R. Tingay, and A.H. Fielding. 2009. Diet specificity is not associated with increased reproductive performance of Golden Eagles *Aquila chrysaetos* in western Scotland. *Ibis* 151:255–264.

Won, C.M. and K.G. Smith. 1999. History and current status of mammals of the Korean peninsula. *Mammal Review* 29:3–33.

Won, P.O. 1981. An illustrated guide of Korean fauna and flora, Vol. 25. Fauna (Birds). Ministry of Culture and Education. Samhwa Books, Seoul, Korea. (In Korean.)

——— and H.J. Kim. 2012. The birds of Korea. Academy Press, Seoul, Korea (In Korean).

Yoon, M.H., S.H. Han, H.S. Oh, and J.K. Kim. 2004. The mammals of Korea. East Media Press, Seoul, Korea. (In Korean.)

Zárybnická, M., O. Sedláček, and E. Korpimäki. 2009. Do Tengmalm's Owls alter parental feeding effort under varying conditions of main prey availability? *Journal of Ornithology* 150:231–237.

Received 29 April 2015; accepted 29 September 2015
Associate Editor: Vincenzo Penteriani