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BREEDING DENSITY AND ALTITUDINAL DISTRIBUTION OF THE URAL, TAWNY, AND BOREAL OWLS IN NORTH DINARIC ALPS (CENTRAL SLOVENIA)

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ABSTRACT.—Ural (*Strix uralensis*), Tawny (*Strix aluco*), and Boreal owl (*Aegolius funereus*) density and altitudinal distribution were determined using playback to census owls on Mt. Krim (North Dinaric Alps, central Slovenia). Survey points were selected proportionally by altitude according to the relief of the area (320–1060 masl). Density of Ural Owls was estimated to be 2.2 territories/10 km^2; high relative to published data from Europe, while densities of Tawny (4.0 territories/10 km^2) and Boreal owls (2.8 territories/10 km^2) were in the range or lower than other European data. The Tawny Owls were found at significantly lower altitudes (320–850 masl), while Boreal Owls were at higher altitudes (700–940 masl) than expected. I suggest that Ural Owl territories were located in suboptimal habitat for Tawny Owls. The segregation of these owls by altitude in temperate-zone, continuous-montane forests is either a consequence of competitive exclusion or predation. The similarity in altitudinal distribution between Tawny and Boreal owls was low, suggesting that Tawny Owl territories are not suitable habitat for Boreal Owls. At high altitudes, harsh conditions prevent the Tawny Owl from competing with the Ural Owl; an advantage for the Boreal Owl, which was capable of surviving harsh conditions within Ural Owl territories. Further studies are needed to determine competitive exclusion or predation interactions among these owls.

KEY WORDS: *Boreal Owl;* Aegolius funereus; *Tawny Owl;* Strix aluco; *Ural Owl;* Strix uralensis; *altitudinal distribution; density; Dinaric Alps; Slovenia.*

DENSIDAD DE ANIDAMIENTO Y DISTRIBUCIÓN ALTITUDINAL DE LOS BUHOS URAL, LEONADO Y BOREAL EN LOS ALPES DINARICOS DEL NORTE (ESLOVENIA CENTRAL)

RESUMEN.—La densidad y distribución altitudinal de los búhos ural (*Strix uralensis*), leonado (*Strix aluco*), y boreal (*Aegolius funereus* o búho de Tengmalm) se determinó usando play back para censar búhos en Mt. Krim (alpes dinaricos del norte, Eslovenia central). Los puntos de conteo fueron seleccionados proporcionalmente de acuerdo con el relieve del área (320–1060 msnm). La densidad de los búhos urales se estimo en 2.2 territorios/10 km^2; relativamente alta con respecto a datos publicados en Europa, mientras que la densidad de búhos leonados (4.0 territorios/10 km^2) y búhos boreales (2.8 territorios/10 km^2) estuvieron en el rango o por debajo de otros datos tomados en Europa. Los búhos leonados se encontraron en alturas significativamente mas bajas (320–850 msnm), mientras que los búhos boreales se encontraron altitudinalmente mas arriba (700–940 msnm) de lo esperado. Sugiero que los territorios del búho ural estaban localizados en hábitat suboptimo para búhos leonados. La segregación de estos búhos por altitud en un bosque montano continuo de zona templada es tanto una consecuencia de exclusión competitiva como de depredación. La similitud en la distribución altitudinal entre búhos leonados y boreales fue baja, sugiriendo que los territorios de búho leonado no proveen de hábitat adecuado a los búhos boreales. En elevadas altitudes, las duras condiciones impiden al búho leonado competir con el búho ural; una ventaja para el búho boreal, el cual fue capaz de sobrevivir a difíciles condiciones dentro de los territorios del búho ural. Se requiere de mayores estudios para determinar la exclusión competitiva o las interacciones de depredación entre estos búhos.

[Traducción de César Márquez]

Bird densities and their altitudinal distributions are influenced by habitat quality, competitive behavioral mechanisms, food supply, and availability of suitable nest sites (Gill 1995, Zabel et al. 1995, Newton 1998). For owls, defense of an exclusive hunting territory plays an important role; the size of the territory is

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often governed by owl mass and prey scarcity (Schoener 1968, Carbone and Gittleman 2002).

In the Dinaric Alps (western Balkan Peninsula) the ecology of Ural (*Strix uralensis*), Tawny (*Strix aluco*), and Boreal owls (*Aegolius funereus*) is poorly known. Density and some breeding habits of Ural Owls are documented for Slovenia (Mihelič et al. 2000), but only anecdotal data are available from other parts of the region (Kralj 1997). For the Tawny and Boreal owls, only distribution is known. Prior to this paper, the altitudinal distribution of owls from Dinaric Alps were based on several incidental observations (Tome 1996, Mihelič et al. 2000).

In this paper, I present data on density and altitudinal distribution of the Ural, Tawny, and Boreal owls from the north part of Dinaric Alps. Of particular value are data on the Ural and Boreal owls, because the study area is at the southern limit of their distribution and is disjunct from the main European population; both species are glacial relics.

STUDY AREA

The field work was done on Mt. Krim (14°25′55″E, 45°58′15″N) in a study area covering 140 km², 10 km south of Ljubljana (central Slovenia), between 1997 and 2000. Mt. Krim is a medium-high mountain (290–1107 masl) with a widely extended plateau. Most of the study area is north facing and is within the Dinaric zoogeographical region (Mršić 1997), part of the north Dinaric Alps.

Clearings or nonforest areas, both natural and manmade, represent 25% of the study area. They are small and dispersed, mostly around the settlements. The mixed forest is widespread (75%), belonging to the association of Dinaric beech forest with fir (*Omphalodo-Fagetum* s. lat.) appearing in different subassociations. The most frequent subassociation is *Omphalodo-Fagetum asaretosum europaei* (syn. *Abieti-Fagetum dinaricum clematidetosum*; for descriptions see Puncer 1980). Dominant tree species are silver fir (*Abies alba*), Norway spruce (*Picea abies*), and beech (*Fagus sylvatica*). Most of the trees in the forest have trunk diameter >30 cm. (Furlan 1988, Slovenian Forest Service unpubl.)

METHODS

To estimate owl density and altitudinal distribution, 41 survey points were selected from the base to the top of Mt. Krim. Survey points were selected proportionally by altitude. Density was estimated in the breeding season 1998 only, but the data for altitudinal distribution were collected between 1997 and 2000. Survey points were located about 1000 m apart, a distance recommended by Holmberg (1979) and Zuberogoitia and Campos (1998). The detection of owls was enhanced by using call playback (Forsman 1983, Redpath 1994, Zuberogoitia and Campos 1998, Appleby et al. 1999). Recordings of male territorial calls of Ural, Tawny, and Boreal owls were used (Roché and Mebs 1989). Surveys were conducted from dusk to approximately midnight during the spring and summer, up to three times per month. Playbacks were broadcast for 10 min, followed by a 5-min listening period, at each survey point; a sampling interval suggested to be adequate for detecting most owls that are occupying a territory (Zuberogoitia and Campos 1998). On a specific survey night, only one species' call was used during broadcast sampling.

I estimated human detection of the playback in forest habitat with the equipment used in the survey at a distance of ca. 500 m. This distance was used to define the effective survey area (0.78 km²) around each survey point. I assumed that each response at a point represented an occupied territory. The presence of two owl territories at one point count was recorded only if two males were detected at the same time. Spontaneous calling owls, that were estimated to be outside (>500 m from point) the survey area, were excluded from further analysis.

Crude density was estimated as the sum of all survey areas at all altitudes divided by the number of detected owl territories. Because territory-size data were not obtained, only approximations of ecological density were possible. Ecological densities (the number per unit of habitat space; Odum 1971) were calculated from survey areas within the lowest and the highest recorded altitude for species; only forest-covered areas were used in the analysis. Similar approaches to approximate owl densities were employed by Penteriani and Pinchera (1990) and Diller and Thome (1999).

The owl altitudinal distribution was presented as a relative abundance index. This standardized relative abundance was calculated as number of owl territories per survey point in a 100 m altitudinal interval per year. I defined altitudinal range with 50% of all detected owl territories as the center of altitudinal distribution for each species. Disproportionate use of a particular altitude by each owl species was tested with Mann-Whitney *U*-test (Sokal and Rohlf 1995) comparing the altitudinal distribution of all survey areas with the altitudinal distribution of survey areas with occupied owl territories. A similarity index of altitudinal distribution between three owl species was calculated using the MacNaughton-Wolf similarity index as suggested by Mikkola (1983) and Korpimäki (1986).

RESULTS

In 1998, 343 survey points were completed in 25 nights. Seven Ural Owl, 13 Tawny Owl, and nine Boreal Owl territories were found on 41 survey areas. Crude densities of Ural, Tawny, and Boreal owls were estimated at 2.2, 4.0, and 2.8 territories/10 km² respectively. Estimated ecological density was measurably higher only in the Boreal Owl (Table 1).

In years 1997–2000, 582 survey points were done during 50 nights. Twenty occupied territories of Ural, 23 of Tawny, and 17 of Boreal owls were recorded. The Ural Owl occurred over the greatest

Table 1. Estimated crude and ecological densities of three owl species in 1998 on Mt. Krim. Crude density is the sum of all survey areas divided by the number of detected owl territories (see Methods). Ecological density is the number of owl territories per unit of habitat space (calculated on the basis of sample area).

	Ural Owl	Tawny Owl	Boreal Owl
Crude density (territory/10 km^2)	2.2	4.0	2.8
Ecological density (territory/10 km^2)	2.8	5.6	6.9
Sample area (km^2)	25.1	23.0	13.0

span in altitudinal distribution (410–1060 masl; Fig. 1). The Tawny Owl was found at significant lower elevations, while Boreal Owls occurred at higher altitudes (Table 2, Fig. 1). The greatest similarity regarding altitudinal distribution was found between Ural and Boreal owls, and the least similarity was found between the distribution of the Tawny and Boreal owls (Table 3).

DISCUSSION

Ural Owl Density. Density of Ural Owls in North Dinaric Alps (including Mt. Krim) is high relative to other parts of Europe (Table 4). I suggest three possible explanations for these differences. First, different census methods may be responsible; we counted singing males, while active nests were counted in some other studies. With the playback technique, it is impossible to distinguish between breeding and nonbreeding pairs or even nonmated, but territorial individuals. Pairs can occupy a territory even if they do not breed (Saurola 1989). The proportion of Ural Owl pairs that actually lay eggs varies between 12 and 87% (Pietiäinen 1988).

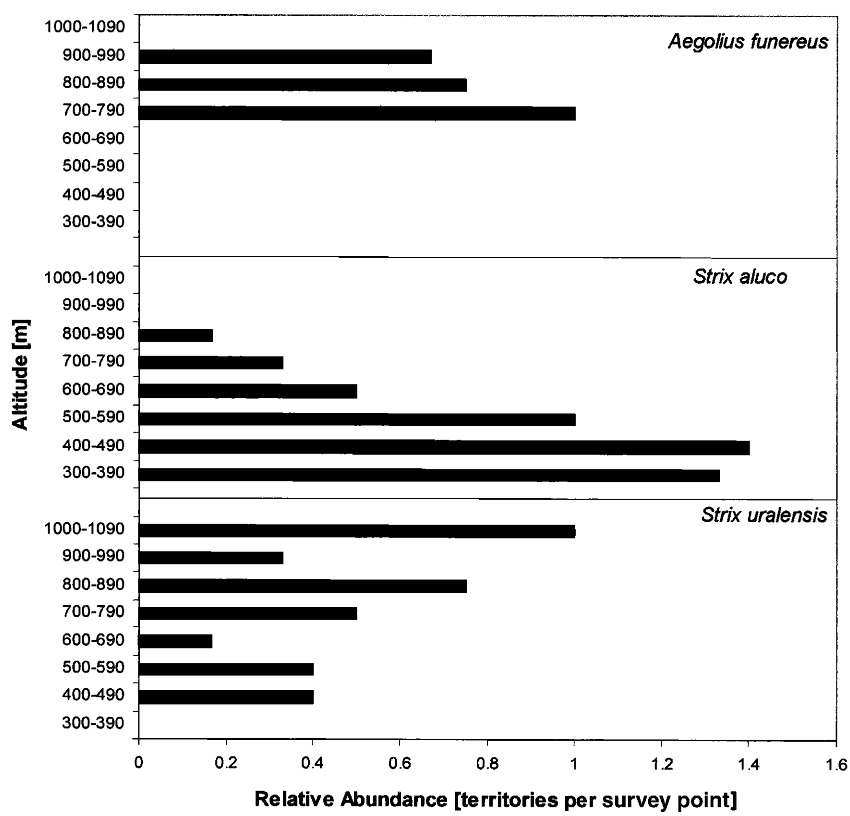

Figure 1. Altitudinal distribution of Ural ($N = 20$), Tawny ($N = 23$), and Boreal owl ($N = 17$) on Mt. Krim. Relative abundance was calculated as the number of owl territories per survey point in each 100 m altitudinal interval per year.

Table 2. Altitudinal distribution of all survey areas compared to survey areas, where Ural Owls, Tawny Owls, and Boreal Owls were detected in years 1997–2000 on Mt. Krim. Data were compared with Mann-Whitney *U*-test.

	Median	Altitude (m) Minimum–Maximum	Center of Altitudinal Distribution[a]	*U*	*P*
All survey areas ($N = 4$)	710	320–1060	520–820		
Survey areas with Ural Owls ($N = 20$)	800	410–1060	650–840	271.0	>0.05
Survey areas with Tawny Owls ($N = 23$)	490	320–850	410–610	223.5	0.033
Survey areas with Boreal Owls ($N = 17$)	800	700–940	770–850	163.5	0.037

[a] Center of altitudinal distribution contains 50% of all detected owl territories.

For that reason density is herein presented as occupied territories and not as breeding pairs. Secondly, density in birds is a function of the size of the study area (Bezzel 1982). Areas with low densities of owls were considerably larger than my study area (Table 4). Finally, the amount of available food may be responsible. In Slovenia, a large part of Ural Owl's diet consists of fat dormouse (*Glis glis*) (Vrezec 2000b), while in other countries, voles (*Microtus* spp.) are the predominant prey species (Sladek 1961/62, Mikkola 1972, 1983, Jäderholm 1987, Korpimäki and Sulkava 1987, Glutz von Blotzheim and Bauer 1994, Czuchnowski 1997, Stürzer 1998, 1999). Fat dormouse is an abundant small mammal in Slovenian forests (Kryštufek 1991) and its mass is approximately four times as much as voles, that is 245 g compared to 64 g (Kryštufek 1991, Glutz von Blotzheim and Bauer 1994). Prey availability and prey body mass are important factors that inversely affect the size of a predator's territory (Schoener 1968, Zabel et al. 1995). One consequence of large territories is a relatively lower density of owls (LaHaye et al. 1997). Prey availability on Mt. Krim could result in small territories and may explain the observed high density of the Ural Owl. However, I have no data on fat dormouse density on Mt. Krim to support this suggestion.

Table 3. Similarity in altitudinal distribution between three owl species on Mt. Krim (MacNaughton-Wolf similarity index following Mikkola [1983] and Korpimäki [1986]).

	Ural Owl	Tawny Owl
Boreal Owl	0.65	0.17
Tawny Owl	0.42	

Tawny Owl Density. According to data from Europe (Table 4), density of Tawny Owls on Mt. Krim was low; perhaps, because of interspecific competition with the larger Ural Owls (Mikkola 1983, König et al. 1999, Vrezec 2000a). The Tawny Owl is lowland species in Slovenia (Tome 1996), and that was confirmed also on Mt. Krim (Fig. 1).

Boreal Owl Density. The Boreal Owl has a relatively small territory (König et al. 1999). Neighboring males can sometimes sing very close to each other without any aggressive interactions (König et al. 1999), so ecological densities can exceed 10 pairs/10 km^2 (Table 4). Three important factors that limit Boreal Owl density in forests were advanced by Locker and Flügge (1998): (1) presence of suitable nest tree holes of Black Woodpeckers (*Dryocopus martius*); (2) optimal foraging areas, large clearings or windfall areas; and (3) absence of the Tawny Owl, an important predator of Boreal Owls throughout Europe. In the area of Mt. Krim all factors are optimal, so high ecological densities are no surprise. Low crude density (Table 2) is the consequence of altitudinal limitations of the species' distribution, which was probably caused by the presence of Tawny Owls at lower altitudes.

Altitudinal Partitioning. The present study has shown that in North Dinaric Alps, competing owl species are segregated by altitude, an important factor in habitat selection for some species such as for Tawny and Boreal owls. The Ural Owl is the dominant species in the owl guild living in my study area, and its distribution is not restricted by

Table 4. Size of study areas and densities (pairs or territories/ 10km^2) of Ural, Tawny, and Boreal owls in Slovenia and Europe.

	Ural Owl		Tawny Owl		Boreal Owl		
	Density[a]	Area (km^2)	Density[a]	Area (km^2)	Density[a]	Area (km^2)	Sources
This study	2.2	32.2	4.0	32.2	2.8	32.2	
Slovenia	2.0–5.0	13.0–15.7	0.7	210.0	—	—	Benussi and Genero 1995, Vogrin 1998, Mihelič et al. 2000
Germany	0.5–1.0	10.0	0.2–16.0	10.0–137.0	0.5–16.0	28.0–200.0	Glutz von Blotzheim and Bauer 1994, März 1995, Locker and Flügge 1998, Stürzer 1999, Mebs and Scherzinger 2000
Italy	—	—	4.0–11.0	16.0–122.0	—	—	Penteriani and Pinchera 1990, Galeotti 1994
Austria	—	—	9.0–25.0	25.0	—	—	Dvorak et al. 1993
Switzerland	—	—	4.8	21.0	1.2–4.5	15.0–150.0	Penteriani and Pinchera 1990, Augst 2000, Mebs and Scherzinger 2000
Spain	—	—	0.8–7.1	2384.0–11 317.0	—	—	Zuberogoitia and Campos 1998, Sanchez-Zapata and Calvo 1999
Great Britain	—	—	22.0	10.2	—	—	Hirons 1985
Denmark	—	—	4.0–20.0	53.2–65.0	—	—	Penteriani and Pinchera 1990, Grell 1998
Poland	3.0	60.0	0.8–6.0	250.0–485.0	—	—	Penteriani and Pinchera 1990, Czuchnowski 1997, Mebs and Scherzinger 2000
Finland	0.1–1.0	4800.0	2.0	104.3	1.0	104.3	Glutz von Blotzheim and Bauer 1994, Solonen 1996, Pietiäinen and Saurola 1997
Sweden	0.2–3.0	10.0–100.0	—	—	—	—	Hirons 1985, Glutz von Blotzheim and Bauer 1994
Estonia	0.2–0.3	10.0	—	—	—	—	Mikkola 1983
Belorus	0.4–0.9	140.0–760.0	—	—	—	—	Tischechkin and Ivanovsky 2000
Russia	24	25.0	—	—	—	—	Mikkola 1983

[a] Pairs or territories/10 km^2.

altitude (Mihelič et al. 2000). Studies from Scandinavia indicate keen interspecific competition between both *Strix* owls (Lundberg 1980, Korpimäki 1986). However, work from the more temperate climates of Central Europe, where the Ural Owl was reintroduced, did not report competition between Ural and Tawny owls (Stürzer 1998). It is possible, that in mild weather conditions, especially in lowlands, the Tawny Owl can coexist with the Ural Owl, while in more extreme conditions (northern limit of distribution or high altitudes), the Ural Owl out-competes the smaller Tawny Owl. Low breeding density of Tawny Owls at Mt. Krim, compared to other European countries (Table 4), could indicate, that the Ural Owl is a limiting factor. Evidence of regular breeding of the Tawny Owl at elevations over 1000 masl, where it is allopatric with Ural Owls, is needed.

The altitudes occupied by the Tawny Owl are unsuitable for Boreal Owls. At high altitudes, harsh conditions prevent the Tawny Owl from competing with the Ural Owl; an advantage for the Boreal Owl, which was capable of surviving harsh conditions within Ural Owl territories. Boreal Owls are able to breed in Ural Owl territories, although their density and breeding activity can be reduced (Hakkarainen and Korpimäki 1996). On the contrary, as shown with altitudinal segregation in this and some other studies from Central and Southern Europe (Pedrini 1982, Glutz von Blotzheim and Bauer 1994, Locker and Flügge 1998, Augst 2000), Tawny Owls seem to exclude Boreal Owls from their territories. Further studies are needed to examine the competitive and predation interactions among these two owls.

Few studies have dealt with the altitudinal distribution of owls. The present study showed that owl density or abundance can vary substantially according to altitude in some species (Fig. 1). Owl survey studies in areas with elevations ranging more than 500 m should record altitude. For accurate estimations of owl densities or abundance, all altitudes with suitable habitat should be surveyed. Normally, such surveys cover very large areas, which are impossible to search intensively. A sampling approach stratified by altitude should be used. Although the accuracy of density estimates based on broadcast sampling permit comparisons with other studies (Table 4), the reliability of this method should be tested more thoroughly to determine the relationship of resulting estimates to absolute population size.

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