Density, diet and productivity of Long-eared Owls *Asio otus* in the Italian Alps: the importance of *Microtus* voles

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Capsule *Relatively large populations, feeding predominantly upon voles, were present at higher elevations.*

Aims *To determine the density, productivity and diet composition of Long-eared Owls breeding at higher elevations.*

Methods *Population census and breeding biology were investigated, and dietary analysis performed for 32 Long-eared Owl territories that were occupied over a six-year period (2000–05), in a 155 km² study area located in the Noce Valley of the central-eastern Italian Alps.*

Results *Territories were mainly situated at the edge of large pine forests, near large patches of grassland and/or open-structured apple orchards, at elevations ranging between 540 and 1210 m. Density varied between 10 and 15 pairs/100 km². Mean intraspecific nest spacing averaged 1727 m and territories were either solitary or clumped in loose aggregations of one to five pairs. Mean laying date was 27 March and the mean number of fledged young was 0.95 and 2.13 per territorial and successful pair, respectively. Adults and nestlings were preyed upon by Eagle Owls Bubo bubo and Common Buzzards Buteo buteo, both of them abundant in the study area. Diet was dominated by Common Voles Microtus arvalis, complemented by Apodemus mice and thrushes. Annual variations in owl density, productivity and diet breadth varied in parallel with the occurrence of Common Voles in the diet, suggesting that the owls responded numerically to the availability of their main prey. This confirms earlier analyses on other European populations, but without the marked three- to four-year cycles observed in such areas.*

Conclusion *The conservation status of the species in these Alpine habitats seemed currently satisfactory. However, the unregulated use of rodenticides in apple orchards and the loss of open habitats associated with land abandonment may represent long-term threats for the species in these habitats.*

Long-eared Owls *Asio otus* are medium-sized, nocturnal raptors typical of open or semi-open landscapes (Mikkola 1983, Cramp 1985), where they usually nest in woodland patches and forage in nearby open areas (Holt 1997, Henrioux 2000). The diet of Long-eared Owls is frequently dominated by small mammals of the subfamily Arvicolinae (Marti 1976, Mikkola 1983, Cramp 1985, Bertolino *et al.* 2001), whose availability may locally determine the fluctuations and breeding performance of the owls (Village 1981, Korpimäki & Norrdahl 1991, Korpimäki 1992). Long-eared Owls have suffered recent declines in many areas of Europe, probably in association with the intensification of agricultural practices and the consequent decline of small mammal prey (Auschwanden *et al.* 2005).

To date, most studies of Long-eared Owls have been biased towards analyses of diet composition, especially during the non-breeding period, when the habit of communal roosting makes the collection of large pellet-samples relatively easy (Nilsson 1981, Korpimäki 1992, Tome 1994). Investigations of breeding density, nest spacing, diet composition and breeding success have been scarce and mainly conducted in northern-central Europe (Village 1981, Korpimäki 1992, Tome 1997, 2003a, 2003b). Furthermore, most studies have been conducted in lowland areas, despite the fact that Long-eared Owls have been reported to nest at relatively high elevations (Glue & Nilsson 1997).

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Finally, in northern-central Europe, variations in Long-eared Owl density and productivity parallel the cycles of their main vole prey, individuals nomadically tracking the spatio-temporal vole peaks (Village 1981, Korpimäki & Norrdahl 1991, Korpimäki 1992). However, the existence of such rodent cycles has been little investigated in southern Europe (Mackin-Rogalska & Nabaglo 1990), and different cycles may generate different predator-prey dynamics. In summary, the species has been the object of much investigation, but there have been few comprehensive studies at high elevation and in southern latitudes.

In Italy, Long-eared Owls are widespread in the north, while the distribution appears more patchy in the central-southern part of the peninsula (Meschini & Frugis 1993). However, quantitative information is very scarce, mostly composed of analyses of winter diet and strongly biased towards intensively cultivated lowlands (Galeotti *et al.* 1997, Riga & Capizzi 1999, Bertolino *et al.* 2001). Here, we report data on density, productivity and diet composition of a population studied for six years in a mountainous environment of the central-eastern Italian Alps. We tested whether owl density and productivity were related to vole abundance, as estimated by vole occurrence in the owls' diet.

STUDY AREA

Long-eared Owls were surveyed between 2000 and 2005 in a 155 km^2 study area located in the Noce Valley of the central-eastern Italian Alps. Elevation ranged from 490 to 1730 m asl. The landscape was characterized by forested mountain slopes, interspersed with apple orchards at lower elevation and managed grassland at higher elevations: 45% of the area was covered by woodland, 40% by apple orchards, 7% by managed grassland, 5% by urban areas and 2% by waterbodies (GIS analysis, CEC 1993). With increasing elevation, forests were dominated by Scots Pine *Pinus silvestris* and European Beech *Fagus sylvatica*. The apple orchards had an open grid structure, with distances of 2–6 m among trees, which makes their interior accessible to Long-eared Owls for hunting, as verified by direct observation of the owls.

METHODS

Data collection

Territorial pairs were censused by listening to spontaneous vocalizations and by eliciting territorial calls by broadcasting conspecific vocalizations with a portable tape-recorder (Korpimäki 1992). Most surveys were conducted in the four hours after sunset or before sunrise, when the owls are most vocal. To reach adequate coverage, we plotted a network of listening stations, located 200–400 m apart depending on local topography and acoustics, so as to cover the whole area. Each station was visited a minimum of three times each year during the pre-incubation period (January–March) and a territory was classified as occupied if vocally defended by a male on at least two of the three visits. Because the area was the subject of intensive surveys on all owl species, typical of both woodland or open country (Marchesi *et al.* 2002b, 2006, Marchesi & Sergio 2005), coverage was thorough and it is unlikely that territorial pairs were missed even in unexpected sites (e.g. forest interior).

Once a territory was identified as occupied, we tried to locate the nest. However, in the initial years of the study it became clear that many nests were extremely well hidden and inconspicuous, and in some cases fledglings were observed where no nest had been previously found despite a pronounced field effort (Rodríguez *et al.* 2006). Therefore, to assess breeding output, territories were repeatedly visited during April–June to listen for the persistent food-begging calls of fledged young. These leave the nest when about three weeks old to 'branch' in nearby trees, and in the following two or three weeks are extremely easy to detect and count, their calls being easily audible from up to 500 m away (Mikkola 1983, Marks 1986, Korpimäki & Norrdahl 1991). If no such calls were heard in at least three successive visits distanced more than 50 days apart, the pair was assumed to have failed. Breeding output was recorded as the mean number of 'branchers' per territorial or per successful pair (i.e. a pair that raised at least one chick to the branching stage) and as the percentage of successful pairs.

Hatching date was estimated by backdating from the feather development of nestlings observed in the nest or at the branching stage, by reference to information contained in Mikkola (1983) and Cramp (1985), and by intensive observations conducted at five nests. The date of incubation commencement was estimated by subtracting 29 days, the median incubation period (Village 1981, Cramp 1985, Tome 1997), from hatching date.

Because nests could not be found in some cases, measures of nest spacing were calculated using the barycentre of the locations of all the branchers of a brood (at the branching stage the young are typically close together in the immediate proximity of their original nest). For pairs that did not produce fledglings, nest spacing was calculated using the barycentre of the observations of the territorial adults.

Pellets and prey remains found under nests and roost sites were collected during each visit (March–July). Prey were identified to genus or species level by comparison with the private reference collection of L.M. (Cles, Italy). Pellets and remains were pooled assuming the minimum number of prey individuals, so as to minimize biases associated with each method (Marchesi *et al.* 2002a). Mice of the genus *Apodemus* could not be identified to species level and were thus pooled in a single *Apodemus* spp. category. Prey mass was calculated by reference to information given by Macdonald & Barrett (1993) and Snow & Perrins (1998).

Statistical analysis

The degree of regularity of nest dispersion was estimated by means of the *G*-statistic (Brown 1975), calculated as the ratio between the geometric and arithmetic mean of the squared distances between neighbouring pairs (nearest-neighbour distances, NNDs) and varying between 0 and 1. Values close to 1 (>0.65) indicate a regular dispersion of nest-sites (Brown 1975). Diet breadth was estimated through the Shannon index (Krebs 1998).

To explore the relationship between owl density or productivity and the availability of their main prey, we used the annual occurrence of the two main prey categories in the diet of the owl (*Microtus agrestis* and *Apodemus* spp.) as an indirect estimate of their availability in the field. This was justified by three previous studies that demonstrated a tight relationship between the occurrence of such main prey species in the diet of the owl and the field abundance of such prey species, as estimated by trapping (Village 1981, Korpimäki & Norrdahl 1991, Korpimäki 1992, Tome 2003b). However, because this assumption was not locally tested, the results of these analyses should be treated with caution.

Differences in mean values were analysed by using one-way ANOVAs (Sokal & Rohlf 1981). To meet the assumptions of normality of parametric tests, variables were logarithmically, square-root, or arcsin-square-root transformed as necessary (Sokal & Rohlf 1981). We used non-parametric tests (Siegel & Castellan 1988) when no satisfactory transformation was found. Probability values were adjusted by means of the sequential Bonferroni's correction when carrying out multiple tests on the same data set (Rice 1989). All means are given ±1 se, all tests are two-tailed, and significance was set at $P \le 0.05$.

RESULTS

Nest-sites, density and nest spacing

Thirty-two occupied territories were censused for a cumulative total of 120 times over the six-year period of the study. Their mean elevation was 803 ± 31 m asl (range 540–1210 m). Territories could be classified according to four broad habitat configurations, which significantly differed from each other in mean elevation ($F_{3,28}$ = 10.0, P < 0.0001): (a) woodland edges bordering large patches of apple orchards (68.8% of 32 territories, mean elevation 725 ± 27 m); (b) woodland edges bordering large patches of managed grassland (21.9%, mean elevation 1007 ± 44 m); (c) woodland edges bordering a mosaic of grassland fields and apple orchards (6.3%, mean elevation 840 ± 130 m); and (d) forest interior. The latter category was represented by a single territory located at 1030 m asl in a forest of European Larch *Larix decidua*, more than 1 km from the nearest open areas. The diet of this pair was dominated by Common Voles *Microtus arvalis*, suggesting that the adults regularly foraged at least 1 km away from the nest in the surrounding open habitat. When excluding this territory from the above analysis, the difference in elevation among the other three territory categories was significant ($F_{2,28}$ = 14.0, P < 0.0001).

In 32 cases we were able to find the nest used for laying: 26 of them were on Scots Pines, three on Norway Spruce *Picea abies*, two on European Black Pine *Pinus nigra* and one on a European Larch. All these 32 clutches were laid in stick nests originally built by Eurasian Sparrowhawks *Accipiter nisus* (21 cases), Hooded Crows *Corvus corone* (three cases), Common Buzzards *Buteo buteo* (two cases) or by an unidentified avian species (six cases).

Density varied between 10 and 15 pairs/100 km^2, averaging 13 pairs/100 km^2 (Table 1). There appeared to be a regular alternation of high density and low density years (Table 1), but there was no evidence of the three- to four-year population cycles reported for northern latitudes (Korpimäki & Norrdahl 1991, Korpimäki 1992).

Overall, NND varied between 270 and 6570 m and did not vary significantly among years ($F_{5,114}$ = 0.54, P = 0.74). In all years, the *G*-statistic was well below the

Table 1. *Density, nest spacing and productivity of a Long-eared Owl population in the Noce Valley, central-eastern Italian Alps (2000–05).*

Variable	Year 2000	2001	2002	2003	2004	2005	Grand mean (n)
Density[a]	14.8 (23)	11.0 (17)	14.8 (23)	11.6 (18)	15.5 (24)	9.7 (15)	12.9 [b]
NND (m)	1670 ± 252 (23)	878 ± 421 (17)	2008 ± 326 (23)	1827 ± 369 (18)	1577 ± 261 (24)	1332 ± 252 (15)	1727 ± 128 (120)
G-statistic	0.48	0.38	0.26	0.36	0.20	0.36	0.34[b]
Breeding success (n)	55.6 (18)	33.3 (12)	30.0 (10)	45.5 (11)	57.1 (21)	30.8 (13)	44.7 (85)
Mean no. fledged young per territorial pair (n)	1.17 ± 0.29 (18)	0.58 ± 0.26 (12)	0.60 ± 0.34 (10)	1.00 ± 0.43 (11)	1.43 ± 0.30 (21)	0.46 ± 0.22 (13)	0.95 ± 0.13 (85)
Mean no. fledged young per successful pair (n)	2.10 ± 0.28 (10)	1.75 ± 0.25 (4)	2.00 ± 0.58 (3)	2.20 ± 0.58 (5)	2.50 ± 0.19 (12)	1.50 ± 0.29 (4)	2.13 ± 0.14 (38)

[a]Number of territories/100 km^2. [b]Mean of the four years of research

cut-point value of 0.65 (Table 1), indicating that nest dispersion was not regular: territories were either solitary and well spaced or clumped in loose aggregations of two to five pairs (mean 2.9 ± 0.3).

Phenology and productivity

Long-eared Owls were observed all year round at some territories. However, observations were non-systematic and whether a portion of the population migrated elsewhere in winter is open to question. No communal roosts have been observed in the region. Mean date of incubation commencement was 27 March (se = ±4.1 days, n = 20; earliest date 20 February, latest date 26 April). Productivity did not vary significantly among years (Table 1), whether measured as breeding success ($\chi^2_5 = 4.77$, $P = 0.45$), or as mean number of fledged young per territorial pair ($F_{5,79} = 1.67$, $P = 0.15$) or per successful pair ($F_{5,32} = 1.11$, $P = 0.38$).

Among the ascertained causes of mortality, four nestlings were preyed upon by Common Buzzards and 14 adults and one fledgling were found among the prey remains collected at Eagle Owl *Bubo bubo* nests (out of a total of 1106 Eagle Owl prey items).

Diet composition in the breeding period

The diet was strongly dominated by *Microtus* voles, which altogether accounted for 80% of the diet by number and 72% by mass (Table 2). The Common Vole accounted for 68% and 64% of the diet by number and by mass, respectively. The main alternative prey categories were mice of the genus *Apodemus*, which accounted for 11% and 8% of the diet by number and by mass, respectively, and birds of the family Turdidae, which collectively accounted for 5% and 15% of the diet by number and by mass, respectively (Table 2). Mean prey mass was 28.8 ± 0.4 g (n = 1578 prey items).

Diet composition and annual variations in density and productivity

For the following analyses, we used the percentage occurrence by mass of the three main prey categories: Common Vole, wood mice and thrushes. Analyses using prey occurrence by number gave identical results. The Shannon index of diet diversity declined with increasing occurrence of Common Voles in the diet ($r_s = -0.83$, $P = 0.04$, Fig. 1c) and was unrelated to the other prey categories ($r_s \leq 0.60$, $P \geq 0.21$). Both owl density and annual productivity were positively related to the occurrence of Common Voles in the diet ($r_s = 0.75$, $P = 0.08$ and $r_s = 0.94$, $P = 0.005$, respectively, Fig. 1a, 1b). The relationship with the other prey categories was not significant ($r_s \leq 0.66$, $P \geq 0.16$). As a result, density and productivity declined with increasing diet breadth ($r_s = -0.99$, $P = 0.0003$ and $r_s = -0.94$, $P = 0.005$, respectively).

DISCUSSION

Long-eared Owls typically nested near the edge of large forests and foraged in nearby expanses of open areas, where they foraged for their main prey, microtine voles. The human-induced fragmentation of woodland has

Table 2. *Diet composition of Long-eared Owls in the central-eastern Italian Alps (2000–05).*

Species	n	Per cent by number	Per cent by mass
Mammals	*1444*	*91.51*	*81.49*
Microtus arvalis	*1069*	*67.74*	*63.73*
Apodemus sp.	*168*	*10.65*	*8.39*
Microtus terricola	*140*	*8.87*	*5.54*
Microtus spp.	*44*	*2.79*	*2.61*
Microtus nivalis	*3*	*0.19*	*0.23*
Clethrionomis glareolus	*2*	*0.13*	*0.12*
Crocidura spp.	*1*	*0.06*	*0.02*
Sorex minutus	*1*	*0.06*	*0.01*
Sorex araneus	*7*	*0.44*	*0.14*
Muscardinus avellanarius	*4*	*0.25*	*0.20*
Glis glis	*1*	*0.06*	*0.30*
Unidentified Bat	*3*	*0.19*	*0.17*
Birds	*120*	*7.60*	*18.48*
Turdus spp.	*39*	*2.47*	*7.72*
Turdus merula	*16*	*1.01*	*3.06*
Turdus pilaris	*15*	*0.95*	*3.66*
Turdus viscivorus	*4*	*0.25*	*1.10*
Turdus philomelos	*3*	*0.19*	*0.51*
Fringillidae	*14*	*0.89*	*0.62*
Carduelis carduelis	*2*	*0.13*	*0.07*
Carduelis cannabina	*1*	*0.06*	*0.04*
Carduelis chloris	*1*	*0.06*	*0.07*
Fringilla coelebs	*1*	*0.06*	*0.05*
Paridae	*3*	*0.19*	*0.09*
Parus major	*1*	*0.06*	*0.04*
Passer domesticus	*1*	*0.06*	*0.06*
Passer montanus	*2*	*0.13*	*0.10*
Sturnus vulgaris	*2*	*0.13*	*0.36*
Dendrocopos major	*1*	*0.06*	*0.18*
Jynx torquilla	*1*	*0.06*	*0.08*
Phoenicurus phoenicurus	*1*	*0.06*	*0.04*
Sylvidae	*1*	*0.06*	*0.04*
Unidentified bird	*11*	*0.70*	*0.61*
Insects	*14*	*0.89*	*0.03*
Melolontha melolonta	*1*	*0.06*	*0.00*
Gryllotalpa gryllotalpa	*11*	*0.70*	*0.02*
Coleoptera	*2*	*0.13*	*0.00*
Total	*1578*		

resulted in widespread availability of patches of open habitats suitable for Long-eared Owl foraging. The open structure of apple orchards has probably further increased the overall landscape suitability for this species. Thus the Long-eared Owl population in our study area appears highly reliant upon the habitat mosaic produced by current agro-forestry practices.

The dependence of Long-eared Owls on *Microtus* voles confirms numerous earlier studies and reviews (Marti 1976, Mikkola 1983, Cramp 1985, Riga & Capizzi 1999, Tome 2003b) and makes this species one

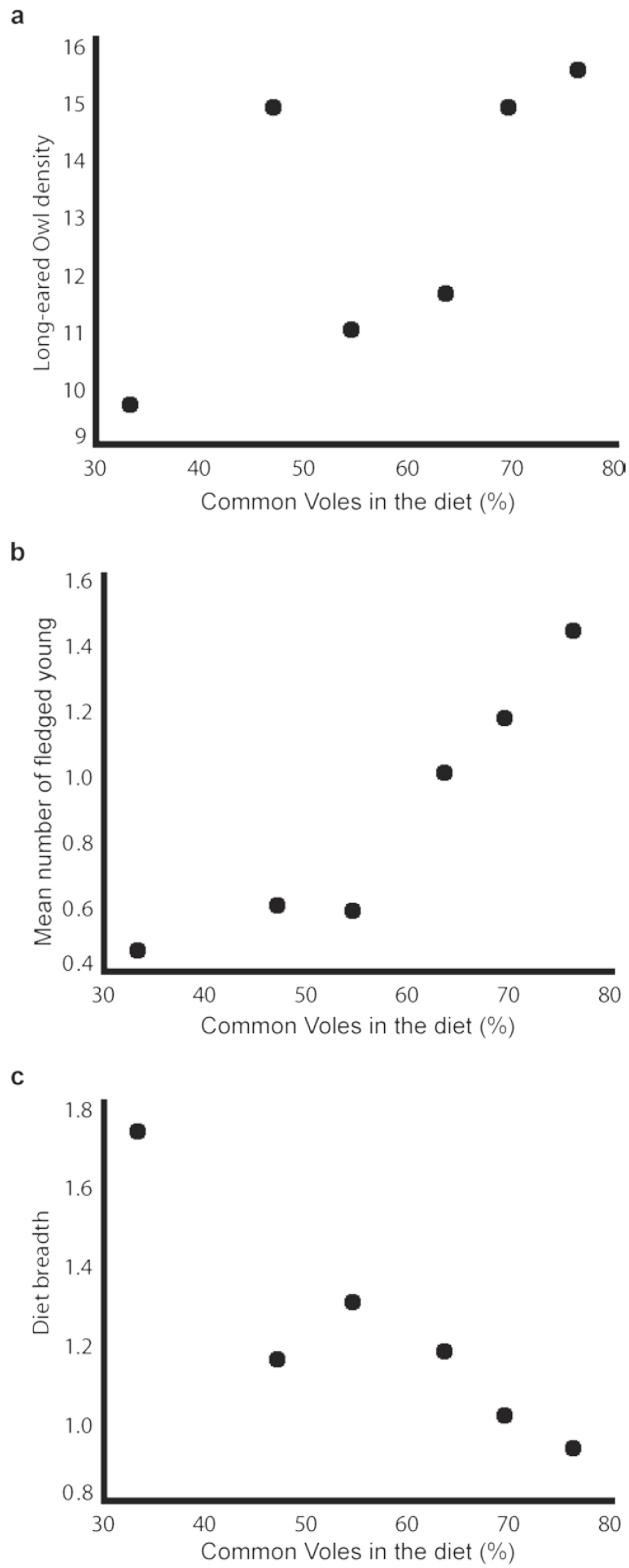

Figure 1. *Annual density (number of territories/100 km²) (a), productivity (b) and diet breadth (Shannon index of diversity, Krebs 1998) (c) in relation to the occurrence of Common Voles in the diet of a Long-eared Owl population in the central-eastern Italian Alps.*

of the most stenophagous raptors of the Alps (for comparison with other Alpine species, see Marchesi *et al.* 2002b, 2006, Pedrini & Sergio 2002, Sergio *et al.* 2002, 2003, Marchesi & Sergio 2005, Rizzolli *et al.* 2005). Given such restricted diet, it is probably no surprise that local owl density and productivity varied in parallel with the occurrence of Common Voles in the diet. In three previous studies, the annual occurrence of voles in the Long-eared Owl diet was tightly related to their field abundance (Village 1981, Korpimäki & Norrdahl 1991, Korpimäki 1992, Tome 2003b). Similarly in our area, Long-eared Owls showed a numerical response to the availability of their main prey. The fact that diet breadth depended solely on the incidence of Common Voles (and not on the occurrence of the other main prey categories) suggests that Common Voles were the preferred prey, and that other prey species were included in the diet when the preferred prey was less readily available (Korpimäki & Norrdahl 1991, Korpimäki 1992, Tome 1994, 2003b). Overall, such results seem to conform to the predator–prey dynamics observed at other sites, but without the marked three- to four-year cycles observed in such areas (Village 1981, Korpimäki & Norrdahl 1991, Korpimäki 1992, Tome 2003b). More in-depth investigations incorporating direct estimates of vole availability will be needed to confirm such patterns.

Results from our study were novel in two ways. Firstly, they demonstrate that forested landscapes at higher elevations are capable of supporting important Long-eared Owl populations. These areas have been overlooked in the past because of the difficulty of finding nests and the absence of the communal roosts frequently observed in nearby lowlands (Mikkola 1983, Galeotti *et al.* 1997). This may have generated the false impression that the species is present only occasionally at higher elevation. Second, the owls were capable, albeit sporadically, of nesting in the woodland interior at considerable distances from patches of open habitats, confirming the results of an earlier American study (Bull *et al.* 1989). Even if such nests occurred with only low frequency, this should be kept in mind when planning population surveys of Long-eared Owls.

Overall, when compared to other populations in Europe and North America, the density and productivity of our study population were in the lower range (Table 3). Reasons for this are unclear and could include: (1) the frequent and poorly monitored use of rodenticides in apple orchards (pers. obs.), which may indirectly kill the owls through secondary poisoning and deplete prey availability; (2) the locally high density of potential predators and competitors, such as Eagle Owls, Common Buzzards and Tawny Owls *Strix aluco* (Marchesi *et al.* 2002b, 2006, Sergio *et al.* 2005); and (c) the lower productivity of high-elevation ecosystems, which may translate into lower prey abundance. The latter hypothesis seems unlikely given the high density and breeding success reported for some high-elevation Long-eared Owl populations studied in North America (Table 3).

Table 3. *Density, nearest neighbour distance (NND), and productivity of some Long-eared Owl populations. Only studies in areas of at least 10 km² were included.*

Country (area)	Period	Habitat	Elevation (m)	Density[a] (n)	NND (m (n))	Breeding success[c] (% (n))	Mean no. fledged young: per territorial pair (n)	Mean no. fledged young: per successful pair (n)
Finland (Alajoki)[1]	1977–89	Lowland	–	13.3 (8)[b]	–		1.6 (107)[b]	–
Scotland (Eskdalemuir)[2]	1976–79	Hills	200–540	14.5 (15)[c]	–	57 (58)	1.6 (58)	3.2 (33)
Slovenia (Ljubljansko b.)[3]	1984–93	Hills	300	17.0 (5)[d]	–	37 (75)	1.6 (75)	3.9 (28)
Switzerland[4] (Luzerner Mittelland)	1989–92	Hills	500–700	23.1 (16)[c]	–		–	2.2 (58)
Italy (Po Plain)[5]	1992–94	Lowland			626 (14)[e]	96 (51)	2.3 (51)	–
Italy (Alps)[6]	2000–05	Mountain	490–1730	12.9 (20)[f]	1727 (120)	45 (85)	1.0 (85)	2.1 (38)
Oregon, USA (La Grande)[7]	1987–88	Mountain	1070–1524	56.0 (30)[g]	–	56 (9)	–	3.0 (12)
Idaho, USA (Big Lost River)[8]	1975–76	Desert	1524	–	–	83 (18)	–	4.2 (18)
Idaho, USA (Snake River)[9]	1980–81	Desert	740–875	–	1480 (104)	41 (99)	1.5 (99)	1.7 (41)

[a]Number of territories/100 km². [b]Mean of 13 years of study. [c]Median of the overall range of densities. [d]Mean of four years of study. [e]Mean of the mean NND of two loose colonies of seven pairs each. [f]Mean of two years of study. [g]Mean of six years of study. Source of data: [1]Korpimäki (1992), [2]Village (1981), [3]Tome (1997, 2003a), [4]Birrer (2003), [5]Galeotti et al. (2000), [6]this study, [7]Bull et al. (1989), [8]Craig & Trost (1979), [9]Marks (1986).

In conclusion, the main potential threats to the Alpine population are likely to be the unregulated use of rodenticides and land abandonment, which is causing widespread woodland expansion in the whole Alpine chain, mainly at the expense of grassland habitats (Cernusca *et al.* 1999, Dirnbock *et al.* 2003). Subsidies to halt such land use changes would benefit the long-term persistence of Long-eared Owls, as well as of other species dependent on open habitats (Laiolo *et al.* 2004, Marchesi & Sergio 2005, Sergio *et al.* 2005, 2006).

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