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 KM² 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 SILVESTIS* 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 (MARCHESE ET AL. 2002B, 2006, MARCHESE & 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 AGRISTIS* 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 $P \leq 0.05$.

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 KM², AVERAGING 13 PAIRS/100 KM² (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 ($F_{3,114} = 0.54$, $P = 0.74$). 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						Grand mean (n)
	2000	2001	2002	2003	2004	2005	
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)

^aNumber of territories/100 km². ^bMean 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 ($\chi^2_3 = 4.77$, $P = 0.45$), OR AS MEAN NUMBER OF FLEDGED YOUNG PER TERRITORIAL PAIR ($F_{3,79} = 1.67$, $P = 0.15$) OR PER SUCCESSFUL PAIR ($F_{3,32} = 1.11$, $P = 0.38$).

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 ($I_s = -0.83$, $P = 0.04$, FIG. 1C) AND WAS UNRELATED TO THE OTHER PREY CATEGORIES ($I_s \leq 0.60$, $P \geq 0.21$). BOTH OWL DENSITY AND ANNUAL PRODUCTIVITY WERE POSITIVELY RELATED TO THE OCCURRENCE OF COMMON VOLES IN THE DIET ($I_s = 0.75$, $P = 0.08$ AND $I_s = 0.94$, $P = 0.005$, RESPECTIVELY, FIG. 1A, 1B). THE RELATIONSHIP WITH THE OTHER PREY CATEGORIES WAS NOT SIGNIFICANT ($I_s \leq 0.66$, $P \geq 0.16$). AS A RESULT, DENSITY AND PRODUCTIVITY DECLINED WITH INCREASING DIET BREADTH ($I_s = -0.99$, $P = 0.0003$ AND $I_s = -0.94$, $P = 0.005$, 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
<i>Microtus arvalis</i>	1069	67.74	63.73
<i>Apodemus</i> sp.	168	10.65	8.39
<i>Microtus terricola</i>	140	8.87	5.54
<i>Microtus</i> spp.	44	2.79	2.61
<i>Microtus nivalis</i>	3	0.19	0.23
<i>Clethrionomys glareolus</i>	2	0.13	0.12
<i>Crocidura</i> spp.	1	0.06	0.02
<i>Sorex minutus</i>	1	0.06	0.01
<i>Sorex araneus</i>	7	0.44	0.14
<i>Musccardinus avellanarius</i>	4	0.25	0.20
<i>Glis glis</i>	1	0.06	0.30
Unidentified Bat	3	0.19	0.17
Birds	120	7.60	18.48
<i>Turdus</i> spp.	39	2.47	7.72
<i>Turdus merula</i>	16	1.01	3.06
<i>Turdus pilaris</i>	15	0.95	3.66
<i>Turdus viscivorus</i>	4	0.25	1.10
<i>Turdus philomelos</i>	3	0.19	0.51
Fringillidae	14	0.89	0.62
<i>Carduelis carduelis</i>	2	0.13	0.07
<i>Carduelis cannabina</i>	1	0.06	0.04
<i>Carduelis chloris</i>	1	0.06	0.07
<i>Fringilla coelebs</i>	1	0.06	0.05
Paridae	3	0.19	0.09
<i>Parus major</i>	1	0.06	0.04
<i>Passer domesticus</i>	1	0.06	0.06
<i>Passer montanus</i>	2	0.13	0.10
<i>Sturnus vulgaris</i>	2	0.13	0.36
<i>Dendrocopos major</i>	1	0.06	0.18
<i>Jynx torquilla</i>	1	0.06	0.08
<i>Phoenicurus phoenicurus</i>	1	0.06	0.04
Sylvidae	1	0.06	0.04
Unidentified bird	11	0.70	0.61
Insects	14	0.89	0.03
<i>Melolontha melolontha</i>	1	0.06	0.00
<i>Gryllotalpa gryllotalpa</i>	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 (3) 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)	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)

^aNumber of territories/100 km². ^bMean of 13 years of study. ^cMedian of the overall range of densities. ^dMean of four years of study. ^eMean of the mean NND of two loose colonies of seven pairs each. ^fMean of two years of study. ^gMean of six years of study. Source of data: ¹Korpimäki (1992), ²Village (1981), ³Tome (1997, 2003a), ⁴Birrer (2003), ⁵Galeotti et al. (2000), ⁶this study, ⁷Bull et al. (1989), ⁸Craig & Trost (1979), ⁹Marks (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, DIRNBÖCK 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 (LAILOLO ET AL. 2004, MARCHESI & SERGIO 2005, SERGIO ET AL. 2005, 2006).

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REFERENCES

- Auschwanden, J., Birrer, S. & Jenni, L. 2005. Are ecological compensation areas attractive hunting sites for common kestrels (*Falco tinnunculus*) and long-eared owls (*Asio otus*)? *J. Ornithol.* **146**: 279–286.
- Bertolino, S., Ghiberti, E. & Perrone, A. 2001. Feeding ecology of the long-eared owl (*Asio otus*) in northern Italy: is it a dietary specialist? *Can. J. Zool.* **79**: 2192–2198.
- Birrer, S. 2003. Bestand und Bruterfolg der Waldohreule *Asio otus* im Luzerner Mittelland, 1989–1992. *Orn. Beob.* **90**: 189–200.
- Brown, D. 1975. A test of randomness of nest spacing. *Wildfowl* **26**: 102–103.
- Bull, E.L., Wright, A.L. & Henjum, M.G. 1989. Nesting and diet of Long-eared Owls in conifer forests, Oregon. *Condor* **91**: 908–912.
- CEC 1993. CORINE Land Cover – Guide Technique. Commission of the European Communities, Directorate-General – Environment, Nuclear Safety and Civil Protection. Office for Official Publications of the European Communities, Brussels.
- Cernusca, A., Tappeiner, U. & Bayfield, N. 1999. Land-use Changes in European Mountain Ecosystems. Blackwell, Berlin.
- Craig, T.H. & Trost, C.H. 1979. The biology and nesting density of breeding American Kestrels and Long-eared Owls on the Big Lost River, southwestern Idaho. *Wilson Bull.* **91**: 50–61.
- Cramp, S. 1985. *Birds of the Western Palearctic*, Vol. 4. Oxford University Press, Oxford.
- Dirnböck, T., Dullinger, S. & Grabherr, G. 2003. A regional impact assessment of climate and land-use change on alpine vegetation. *J. Biogeog.* **30**: 401–407.
- Galeotti, P., Tavecchia, G. & Bonetti, A. 1997. Home-range and habitat use of Long-eared Owls in open farmland (Po Plain, northern Italy), in relation to prey availability. *J. Wildl. Res.* **2**: 137–145.
- Galeotti, P., Tavecchia, G. & Bonetti, A. 2000. Parental defence in Long-eared Owls *Asio otus*: effects of breeding stage, parent sex and human persecution. *J. Avian Biol.* **31**: 431–440.
- Glue, D.G. & Nilsson, I.N. 1997. Long-eared Owl *Otus scops*. In Hagemeyer, W.J.M. & Blair, M.J. (eds.) *The EBCC Atlas of European Breeding Birds, their Distribution and Abundance*: 416–417. T & A D Poyser, London.
- Henrioux, F. 2000. Home range and habitat use by Long-eared Owl in northwestern Switzerland. *J. Raptor Res.* **34**: 93–101.
- Holt, D.W. 1997. The Long-eared Owl (*Asio otus*) and forest management: a review of the literature. *J. Raptor Res.* **31**: 175–186.
- Korpimäki, E. 1992. Diet composition, prey choice, and breeding success of Long-eared Owls: effects of multiannual fluctuations in food abundance. *Can. J. Zool.* **70**: 2373–2381.
- Korpimäki, E. & Norrdahl, K. 1991. Numerical and functional responses of kestrels, Short-eared Owls, and Long-eared Owls to vole densities. *Ecology* **72**: 814–826.
- Krebs, C.J. 1998. *Ecological Methodology*. HarperCollins, New York, USA.
- Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A. 2004. Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *J. Appl. Ecol.* **41**: 294–304.
- Macdonald, D. & Barrett, P. 1993. *Mammals of Britain and Europe*. HarperCollins, London.
- Mackin-Rogalska, R. & Nabaglio, L. 1990. Geographical variation in cyclic periodicity and synchrony in the Common vole, *Microtus arvalis*. *Oikos* **59**: 343–348.
- Marchesi, L. & Sergio, F. 2005. Distribution, density, diet and productivity of the Scops Owl *Otus scops* in the Italian Alps. *Ibis* **147**: 176–187.
- Marchesi, L., Pedrini, P. & Sergio, F. 2002a. Biases associated with diet study methods in the Eagle owl. *J. Raptor Res.* **36**: 11–16.
- Marchesi, L., Sergio, F. & Pedrini, P. 2002b. Costs and benefits of breeding in human-altered landscapes for the Eagle owl *Bubo bubo*. *Ibis* **144**: E164–E177.
- Marchesi, L., Sergio, F. & Pedrini, P. 2006. Density, nest-site selection, diet and productivity of the Tawny Owl *Strix aluco* in the Alps: implications of temporal changes in forest dynamics. *Bird Study* **53**: 310–318.
- Marks, J.S. 1986. Nest-site characteristics and reproductive success of Long-eared Owls in southwestern Idaho. *Wilson Bull.* **98**: 547–560.
- Marti, C.D. 1976. A review of prey selection by the Long-eared Owl. *Condor* **78**: 331–336.
- Meschini, E. & Frugis, S. 1993. *Atlante degli uccelli nidificanti in Italia*. Istituto Nazionale per la Fauna Selvatica, Ozzano dell'Emilia, Italy.
- Mikkola, H. 1983. *Owls of Europe*. T & A D Poyser, Calton.
- Nilsson, I.N. 1981. Seasonal changes in food of the Long-eared Owl in southern Sweden. *Ornis Scand.* **12**: 216–223.
- Pedrini, P. & Sergio, F. 2002. Regional conservation priorities for a large predator: golden eagles (*Aquila chrysaetos*) in the Alpine range. *Biol. Conserv.* **103**: 163–172.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution* **43**: 223–225.
- Riga, F. & Capizzi, D. 1999. Dietary habits of the Long-eared Owl *Asio otus* in the Italian peninsula. *Acta Ornithol.* **34**: 45–51.
- Rizzolli, F., Sergio, F., Marchesi, L. & Pedrini, P. 2005. Density, productivity, diet and population status of the Peregrine Falcon *Falco peregrinus* in the Italian Alps. *Bird Study* **52**: 188–192.
- Rodríguez, A., García, A.M., Cervera, F. & Palacios, V. 2006. Landscape and anti-predation determinants of nest-site selection, nest distribution and productivity in a Mediterranean population of Long-eared Owls *Asio otus*. *Ibis* **148**: 133–145.
- Sergio, F., Boto, A., Scandolara, C. & Bogliani, G. 2002. Density, nest-sites, diet, and productivity of Common Buzzards (*Buteo buteo*) in the Italian pre-Alps. *J. Raptor Res.* **36**: 24–32.
- Sergio, F., Marchesi, L. & Pedrini, P. 2003. Spatial refugia and the coexistence of a diurnal raptor with its intraguild owl predator. *J. Anim. Ecol.* **72**: 232–245.
- Sergio, F., Scandolara, C., Marchesi, L., Pedrini, P. &

- Penteriani, V.** 2005. *Effect of agro-forestry and landscape changes on common buzzards (Buteo buteo) in the Alps: implications for conservation.* *Anim. Conserv.* **7**: 17–25.
- Sergio, F., Pedrini, P., Rizzolli, F & Marchesi, L.** 2006. *Adaptive range selection by golden eagles in a changing landscape.* *Biol. Conserv.* **133**: 32–41.
- Siegel, S. & Castellan, N.J.** 1988. *Nonparametric Statistics for The Behavioral Sciences.* McGraw Hill, New York.
- Snow, D.W. & Perrins, C.M.** 1998. *The Birds of the Western Palearctic: Concise Edition.* Oxford University Press, Oxford.
- Sokal, R.R. & Rohlf, F.J.** 1981. *Biometry.* WH Freeman, New York.
- Tome, D.** 1994. *Diet composition of the Long-eared Owl in central Slovenia: seasonal variation in prey use.* *J. Raptor Res.* **28**: 253–258.
- Tome, D.** 1997. *Breeding biology of the long-eared owl (Asio otus) in central Slovenia.* *Folia Zool.* **46**: 43–48.
- Tome, D.** 2003a. *Nest site selection and predation driven despotic distribution of breeding long-eared owls Asio otus.* *J. Avian Biol.* **34**: 150–154.
- Tome, D.** 2003b. *Functional response of the Long-eared Owl (Asio otus) to changing prey numbers: a 20-year study.* *Ornis Fenn.* **80**: 63–70.
- Village, A.** 1981. *The diet and breeding of Long-eared Owls in relation to vole numbers.* *Bird Study* **28**: 215–224.

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