

# Implications of temporal changes in forest dynamics on density, nest-site selection, diet and productivity of Tawny Owls *Strix aluco* in the Alps

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**Capsule** *In the areas studied, Tawny Owls showed extreme flexibility and opportunism, occupying most available vegetation types and elevations below the tree-line.*

**Aims** *To assess habitat relationships for the species so as to forecast the potential impact of habitat changes.*

**Methods** *We censused a total of 321 territories in 12 study areas covering the regional variation in elevation and the associated heterogeneity in vegetation types and landscape configurations.*

**Results** *The species occupied virtually all vegetation types and landscape configurations below the tree-line. Nests were mostly located on cliffs, but also in tree cavities, buildings, and stick nests of other raptors. Density varied from 12 to 60 territories/100 km<sup>2</sup> and mean nearest-neighbour distance from 0.7 to 1.8 km, depending on the availability of broadleaved woodland. Compared to availability, nests were nearer to cliffs and had higher richness of habitat edges and vegetation types, which positively affected chick production. Diet composition varied widely according to habitat and was mostly dominated by Edible Dormouse *Glis glis*, voles and mice.*

**Conclusion** *The conservation status of the species was satisfactory. Future habitat changes may favour an increase in density. Silvicultural practices encouraging more old trees with large cavities would further favour this opportunistic species.*

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TAWNY OWLS *STRIX ALUCO* ARE GENERALIST NOCTURNAL RAPTORS WIDELY DISTRIBUTED THROUGHOUT THE PALEARCTIC, WITH HIGHER ABUNDANCE IN THE TEMPERATE WOODLAND ZONE (PETTY & SAUROLA 1997). THOUGH OFTEN CONSIDERED A FOREST OWL, THEY HAVE SHOWN REMARKABLE ADAPTABILITY AND OPPORTUNISM, READILY COLONIZING URBAN HABITATS, FORESTRY PLANTATIONS AND INTENSIVELY CULTIVATED AREAS WITH FEW TREES (REDPATH 1995, PETTY & SAUROLA 1997). THE SPECIES HAS BEEN THE SUBJECT OF MANY INTENSIVE INVESTIGATIONS, MOSTLY FOCUSING ON DIET COMPOSITION AND THE RELATIONSHIP BETWEEN DENSITY, PRODUCTIVITY AND PREY AVAILABILITY (SOUTHERN 1970, DELMÉE ET AL. 1978, WENDLAND 1984, JęDRZEJEWSKI ET AL. 1996, PETTY & FAWKES 1997, PETTY 1999, GALEOTTI 2001). ONLY A FEW STUDIES HAVE FOCUSED ON HABITAT SELECTION AND MOST OF THEM WERE CONDUCTED IN URBAN AREAS OR INTENSIVE FARM-LAND (GALEOTTI 1990, HARDY 1992, REDPATH 1995, PETTY

1989). OVERALL, RESEARCH IN MOUNTAIN ENVIRONMENTS HAS BEEN VERY SPORADIC.

IN ITALY, THE SPECIES IS WIDELY DISTRIBUTED THROUGHOUT THE CENTRAL-NORTHERN PART OF THE PENINSULA (PETTY & SAUROLA 1997). APART FROM SCATTERED DATA ON DENSITY (SASCOR ET AL. 1999, VREZEC 2003) AND DIET (BOUVIER & BAYLE 1989), NO COMPREHENSIVE STUDIES HAVE BEEN PUBLISHED FOR ANY AREA OF THE ALPS, EITHER IN ITALY OR IN ADJACENT COUNTRIES. FURTHERMORE, ALPINE FORESTS ARE CURRENTLY IN A VERY DYNAMIC STATE. MUCH COPPICE-MANAGED WOODLAND IS RAPIDLY CONVERTING TO HIGH FOREST, WHILE LAND ABANDONMENT IS CAUSING PROGRESSIVE WOODLAND EXPANSION AT THE EXPENSE OF GRASSLAND (PEDRINI & SERGIO 2002, SERGIO ET AL. 2005), LEAVING AN URGENT NEED FOR STUDIES ON WOODLAND SPECIES SO AS TO FORECAST THE POTENTIAL FUTURE IMPACT OF SUCH LANDSCAPE CHANGES. HERE, WE REPORT DATA ON DENSITY, NEST-SITE SELECTION, DIET AND PRODUCTIVITY FOR 12 TAWNY OWL POPULATIONS OF THE CENTRAL-EASTERN ITALIAN ALPS.

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## STUDY AREAS

TAWNY OWLS WERE INTENSIVELY SURVEYED BETWEEN 2002 AND 2004 IN A 55 KM<sup>2</sup> STUDY AREA LOCATED ON MOUNT BALDO IN THE TRENTO REGION OF CENTRAL-EASTERN ITALIAN ALPS (FIG. 1). ELEVATION RANGED FROM 200 TO 1560 M ASL. THE LANDSCAPE WAS CHARACTERIZED BY FORESTED MOUNTAIN SLOPES INTERSPERSED WITH VINEYARDS AT LOWER ELEVATION AND MANAGED GRASSLAND AT MIDDLE ELEVATIONS. CLIFF AVAILABILITY WAS HIGH THROUGHOUT THE STUDY AREA. GIS ANALYSIS OF DATA FROM CEC (1993) REVEALED THAT 53% OF THE AREA WAS COVERED BY WOODLAND, 23% BY FARMLAND, 8% BY MANAGED GRASSLAND, 7% BY ALPINE MEADOWS ABOVE THE TREE-LINE, 7% BY SHRUB VEGETATION AND 2% BY URBAN AREAS. WITH INCREASING ELEVATION, WOODLAND TENDED TO BE DOMINATED BY *QUERCUS-TILIA-ACER* SPECIES, *FAGUS-ABIES* SPECIES AND *PICEA* SPECIES. IN WOODLAND AREAS, 75% WAS MANAGED AS COPPICE (MATTHEWS 1989), MOST OF WHICH WAS AT LOWER ELEVATION, AND 25% WAS HIGH FOREST, MOST OF WHICH WAS AT HIGHER ELEVATION. IN 2002 AND 2003, TAWNY OWLS WERE CENSUSED IN ANOTHER 11 QUADRATS OF 100 KM<sup>2</sup> SCATTERED THROUGHOUT THE TRENTO REGION (FIG. 1), AND SELECTED TO COVER THE REGIONAL VARIATION IN ELEVATION AND LANDSCAPE COMPOSITION.

## METHODS

TERRITORIAL PAIRS WERE CENSUSED BETWEEN OCTOBER AND FEBRUARY BY LISTENING TO SPONTANEOUS VOCALIZATIONS AND BY ELICITING TERRITORIAL CALLS BY BROADCASTING CONSPECIFIC VOCALIZATIONS WITH A PORTABLE TAPE-RECORDER (JęDRZEJEWSKI ET AL. 1996). IN EACH STUDY AREA, WE PLOTTED A NETWORK OF LISTENING STATIONS, LOCATED 300-500 M APART DEPENDING ON LOCAL TOPOGRAPHY AND ACOUSTICS, SO AS TO COVER THE WHOLE AREA. ALL PLOTS WERE SURVEYED AT LEAST THREE TIMES BETWEEN OCTOBER AND FEBRUARY AND A TERRITORY WAS DEFINED AS OCCUPIED IF TERRITORIAL CALLS WERE HEARD ON AT LEAST TWO VISITS WITH MORE THAN 30 DAYS IN BETWEEN.

IN THE MOUNT BALDO INTENSIVE STUDY AREA, WE PUT MAXIMUM EFFORT INTO TRYING TO LOCATE NESTS OF ALL PAIRS. ONCE AN OCCUPIED TERRITORY WAS FOUND, IT WAS REPEATEDLY VISITED AT NIGHT TO OBSERVE PREY DELIVERIES AT THE NEST, AND DURING THE DAY TO CHECK POTENTIAL NEST-SITES ON TREES, CLIFFS OR BUILDINGS. IF NO NEST WAS FOUND, WE CHECKED THE TERRITORY DURING JUNE AND JULY TO LISTEN FOR PERSISTENT FOOD-BEGGING CALLS OF THE FLEDGED YOUNG (SOUTHERN 1970, WENDLAND 1984, RANAZZI ET AL. 2000). IF NO SUCH CALLS WERE HEARD IN AT LEAST THREE SUCCESSIVE VISITS MORE THAN 40 DAYS APART, THE PAIR WAS ASSUMED TO HAVE FAILED. 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. MARCHESI. PELLETS AND REMAINS WERE POOLED ASSUMING THE MINIMUM NUMBER OF PREY-INDIVIDUALS, SO AS TO MINIMIZE BIASES ASSOCIATED WITH EACH METHOD (MARCHESI ET AL. 2002).

## GIS and statistical analysis

WE EMPLOYED LOGISTIC REGRESSION (TABACHNICK & FIDELL 1996) WITH A STEPWISE PROCEDURE TO ANALYSE THE ENVIRONMENTAL FACTORS (APPENDIX) DISCRIMINATING BETWEEN THE 33 OWL TERRITORIES (I.E. ONE RANDOMLY CHOSEN NEST USED WITHIN EACH TERRITORY) CENSUSED IN THE BALDO AREA AND 33 LOCATIONS RANDOMLY PLOTTED WITHIN THE BALDO AREA. ALL RANDOM LOCATIONS WERE GENERATED BY MEANS OF THE EXTENSION ANIMAL MOVEMENT OF THE GIS SOFTWARE ARCVIEW 3.2 (HOOGE & EICHENLAUB 1997). BECAUSE TAWNY OWLS IN OUR AREA NEST IN CLIFFS, TREES AND BUILDINGS (SEE RESULTS), RANDOM LOCATIONS WERE PLOTTED IN EQUAL PROPORTIONS ON SIMILAR STRUCTURES. THE LATTER WERE ALSO VISITED IN THE FIELD AND RETAINED AS RANDOM LOCATIONS ONLY IF JUDGED TO BE POTENTIALLY SUITABLE FOR NESTING OWLS, BASED ON FAMILIARITY WITH THE SPECIES IN THE REGION. IN ADDITION, BECAUSE TAWNY OWLS ARE TERRITORIAL AND SOLITARY NESTERS, THE MINIMUM NEAREST-NEIGHBOUR DISTANCE (NND) AMONG RANDOM LOCATIONS WAS SET TO BE THE SAME AS THE MINIMUM NND AMONG OWL TERRITORIES. FINALLY, RANDOM LOCATIONS WERE PLOTTED ONLY IN THE SAME RANGE OF ELEVATIONS RECORDED FOR OWL TERRITORIES.

THE VARIABLES (APPENDIX 1) WERE MEASURED IN THE FIELD, BY ACCESSING GIS LAND-USE MAPS (CEC 1993, SERVIZIO FORESTE 1999) OR BY DIGITIZING 1-M-RESOLUTION, AERIAL COLOUR PHOTOGRAPHS (COURTESY OF PROVINCIA AUTONOMA DI TRENTO, PERMIT IGM N.278 OF 30 JUNE 2000). THE VARIABLES WERE CHOSEN TO MEASURE: (1) THE CHARACTERISTICS OF THE NEST-SITE AND ITS IMMEDIATE SURROUNDINGS (WITHIN A RADIUS OF 100 M); (2) THE DISTANCE TO POTENTIAL HUNTING GROUNDS OR TO SOURCES OF HUMAN DISTURBANCE; AND (3) HABITAT STRUCTURE AND COMPOSITION WITHIN 330 M OF THE NEST, WHICH IS ROUGHLY HALF THE NND IN OUR POPULATION. TO REDUCE COLLINEARITY AND THE NUMBER OF VARIABLES PRESENTED TO LOGISTIC MODELS, WE EMPLOYED THE METHOD OF VARIABLE REDUCTION PROPOSED BY GREEN (1979) AND COMMONLY EMPLOYED IN HABITAT SELECTION STUDIES (SERGIO & BOGLIANI 2000, SERGIO ET AL. 2003A). IN THIS METHOD, PAIRS OF INTER-CORRELATED VARIABLES ( $r > 0.6$ ) ARE CONSIDERED AS ESTIMATES OF A SINGLE UNDERLYING FACTOR. ONLY THE ONE LIKELY TO BE PERCEIVED AS MORE IMPORTANT BY THE STUDY ORGANISM IS RETAINED FOR ANALYSIS. OF THE REMAINING

VARIABLES, ONLY THOSE FOR WHICH HIGH UNIVARIATE DIFFERENCES ( $P < 0.1$ ) WERE DETECTED BETWEEN NEST-SITES AND RANDOM LOCATIONS WERE INCLUDED IN MULTIVARIATE ANALYSES. THE LOGISTIC MODEL WAS VALIDATED BY APPLYING IT ON 30 OWL TERRITORIES AND 30 RANDOM LOCATIONS FROM THE RUMO STUDY AREA AND ITS SURROUNDINGS, I.E. THE FARTHEST FROM THE BALDO PLOT (FIG. 1).

TO GAIN A DEEPER UNDERSTANDING OF OWL HABITAT QUALITY AND TO TEST WHETHER THE OBSERVED HABITAT CHOICES WERE ADAPTIVE (SERGIO ET AL. 2003A, 2003B), WE USED MULTIPLE REGRESSION (SOKAL & ROHLF 1981) TO RELATE BREEDING SUCCESS (MEAN NUMBER OF FLEDGED YOUNG AVERAGED ACROSS YEARS FOR EACH TERRITORY) TO THE VARIABLES PRESENTED TO THE PREVIOUS HABITAT SELECTION MODELS. WE ADDED TO THE SET OF EXPLANATORY VARIABLES A FACTOR VARIABLE WITH TWO LEVELS (1 = TERRITORY DOMINATED BY COPPICE-MANAGED WOODLAND; 2 = TERRITORY DOMINATED BY HIGH FOREST); THIS WAS CONSIDERED AS A POTENTIAL DETERMINANT OF BREEDING SUCCESS, AND ALSO TESTED THE POTENTIAL IMPACT ON OWL PRODUCTIVITY OF THE ONGOING CONVERSION OF COPPICE WOODLAND TO HIGH FOREST.

FINALLY, TO INVESTIGATE THE OWL HABITAT RELATIONSHIPS AT A LARGER SPATIAL SCALE, WE CORRELATED OWL DENSITY IN EACH OF THE 12 STUDY AREAS WITH THE FOLLOWING VARIABLES: MEAN ELEVATION OF THE STUDY AREA (CALCULATED WITH A GIS, BASED ON A 10-M-RESOLUTION DIGITAL ELEVATION MODEL);

RUGGEDNESS INDEX (NUMBER OF CONTOUR LINES CROSSED BY TWO 1-KM NORTH-SOUTH AND EAST-WEST TRANSECTS, AVERAGED ACROSS THE WHOLE STUDY AREA); THE PERCENTAGE OF THE AREA COVERED BY URBAN AREAS, FARMLAND, GRASSLAND, WATER, SHRUB VEGETATION, ROCKY OUTCROPS, BROADLEAVED FORESTS, CONIFER FORESTS, MIXED BROADLEAVED AND CONIFER FORESTS, TOTAL WOODLAND, WOODLAND MANAGED AS COPPICE, AND WOODLAND MANAGED AS HIGH FOREST; AND THE SHANNON INDEX OF HABITAT DIVERSITY (KREBS 1998).

REGULARITY OF NEST SPACING WAS ASSESSED BY MEANS OF THE  $G$ -STATISTIC (BROWN 1975), CALCULATED AS THE RATIO OF THE GEOMETRIC TO THE ARITHMETIC MEAN OF THE SQUARED NNDs. THE INDEX RANGES FROM 0 TO 1 AND VALUES ABOVE 0.65 INDICATE A REGULAR DISPERSION OF NEST-SITES. IN ALL ANALYSES, MEANS ARE GIVEN  $\pm 1$  SE, TESTS ARE TWO-TAILED, AND STATISTICAL SIGNIFICANCE WAS SET AT  $\alpha \leq 0.05$ . WHEN MULTIPLE TESTS WERE PERFORMED ON THE SAME DATA SET, THE SEQUENTIAL BONFERRONI CORRECTION WAS USED TO ADJUST THE SIGNIFICANCE LEVEL.

## RESULTS

### Density, nest dispersion and productivity

WE CENSUSED 33 OWL TERRITORIES IN THE BALDO AREA, CORRESPONDING TO A DENSITY OF 60 PAIRS/100 KM<sup>2</sup> (TABLE



**Figure 1.** Location of 12 Tawny Owl study areas in the Trento region (depicted in grey in the inset) of the central-eastern Italian Alps. Each point represents the baricentre of a 100 km<sup>2</sup> quadrat. 1, Baldo study area; 2, Lavacchio; 3, Varagna; 4, Vallarsa; 5, Sarca Valley; 6, Calliano; 7, Caldonazzo; 8, Bleggio; 9, Molveno; 10, Adige Valley; 11, Noce Valley; 12, Rumo.



**Table 1.** Density, nest dispersion and productivity of a Tawny Owl population in the Mount Baldo study area (central-eastern Italian Alps, 2002–2004).

Variable	Year			Grand mean
	2002	2003	2004	
Density (territories/100 km <sup>2</sup> )	60.0	60.0	60.0	60.0
Mean NND (m)	684.9 ± 67.3	694.1 ± 67.9	653.4 ± 55.4	677.5 ± 36.5
G-test	0.692	0.687	0.696	0.692
No. nests checked for reproduction	20	24	9	53 <sup>a</sup>
Mean no. fledged young/territorial pair <sup>b</sup>	1.90 ± 0.28 (20)	1.17 ± 0.26 (24)	1.44 ± 0.38 (9)	1.49 ± 0.17 (53)
Mean no. fledged young/successful pair <sup>b</sup>	2.38 ± 0.22 (16)	1.87 ± 0.29 (15)	1.63 ± 0.37 (8)	2.03 ± 0.17 (39)
Successful pairs (%)	80.0	62.5	88.9	73.6

<sup>a</sup>Total number of nests checked. <sup>b</sup>The variations in sample size among the three years of study reflect sampling effort and not the breeding effort of the population.

**Table 2.** Density and nest spacing of Tawny Owls in 12 study areas of the Trento region (central-eastern Italian Alps, 2002–2003).

Study area	No. of territories	Mean territory elevation (m)	Density (territories/100 km <sup>2</sup> )	Mean NND (m)	Range of NNDs	G-test
Baldo	33	710.3 ± 37.3	60.0	677.5 ± 36.5	360–1912	0.69
Lavacchio	49	968.0 ± 96.9	49.0	1001.0 ± 109.0	550–1730	0.81
Varagna	60	1110.0 ± 62.5	60.0	766.0 ± 50.9	390–1020	0.87
Vallarsa	23	772.0 ± 53.2	23.0	1397.3 ± 186.8	490–2910	0.63
Sarca Valley	28	690.9 ± 35.0	28.0	1179.1 ± 153.3	520–1610	0.68
Calliano	15	725.0 ± 75.4	15.0	2056.0 ± 160.0	1460–2860	0.90
Caldonazzo	12	780.8 ± 68.3	29.0	1181.7 ± 162.1	490–2250	0.67
Bleggio	26	928.5 ± 73.4	12.0	1736.2 ± 254.2	870–4070	0.65
Molveno	15	865.0 ± 50.9	26.0	1145.0 ± 138.9	450–1730	0.71
Adige Valley	29	681.8 ± 43.1	15.0	1267.3 ± 119.6	450–3220	0.60
Noce Valley	13	768.2 ± 31.2	13.0	1272.1 ± 178.2	390–4210	0.38
Rumo	18	888.0 ± 70.1	18.0	1842.0 ± 220.8	820–2870	0.76
Grand mean	321	795.9 ± 17.2	27.8	1207.9 ± 52.0	360–4210	0.70

**1). THERE WAS NO VARIATION AMONG YEARS IN MEAN NND (ANOVA ON VARIABLE LOG<sub>F</sub>-TRANSFORMED,  $F_{2,93} = 0.62$ ,  $P = 0.94$ ; TABLE 1). IN THE OTHER STUDY AREAS, DENSITY VARIED BETWEEN 12 AND 60 TERRITORIES/100 KM<sup>2</sup> (TABLE 2). THERE WAS SIGNIFICANT VARIATION AMONG AREAS IN MEAN NND (ANOVA ON LOG<sub>F</sub>-TRANSFORMED VARIABLE:  $F_{11,309} = 8.22$ ,  $P = 0.0009$ ), WHICH RANGED BETWEEN 678 AND 2056 M (TABLE 2). THE G-STATISTIC INDICATED A REGULAR OR NEARLY REGULAR DISPERSION OF TERRITORIES IN TEN OF THE 12 AREAS.**

IN THE MOUNT BALDO PLOT, THE MEAN LAYING DATE WAS 1 APRIL (RANGE: 2 MARCH–16 APRIL; SE = 2 DAYS;  $N = 33$ ). THIS DOES NOT INCLUDE A POSSIBLE REPLACEMENT CLUTCH LAID ON 8 JUNE (ONE CHICK FLEDGED). THERE WAS NO VARIATION AMONG YEARS IN MEDIAN NUMBER OF YOUNG FLEDGED PER TERRITORIAL OR SUCCESSFUL PAIR (KRUSKAL-WALLIS TEST,  $\chi^2_2 < 4.42$ ,  $P > 0.11$ ), OR IN THE PERCENTAGE OF TERRITORIAL PAIRS WHICH SUCCESSFULLY RAISED AT LEAST ONE CHICK TO FLEDGING ( $\chi^2_2 = 3.15$ ,  $P = 0.21$ ) (TABLE 1).

### Nest-site selection

OVERALL, WE FOUND 44 NESTS USED AT LEAST ONCE FOR LAYING IN THE BALDO AREA. OF THESE, 28 WERE IN CLIFF HOLES, NINE IN CAVITIES OF OLD TREES (EIGHT OF THESE IN SWEET CHESTNUT *CASTANEA SATIVA*), FOUR IN BUILDINGS, TWO IN TREE-HOLES ORIGINALLY EXCAVATED BY BLACK WOODPECKERS *DRYOCOPUS MARTIUS*, AND ONE IN A STICK NEST ORIGINALLY BUILT BY COMMON BUZZARDS *BUTEO BUTEO*. ALL CLIFF NESTS WERE IN THE LOWER PORTION OF THE CLIFF, AT OR BELOW THE TREE CANOPY LEVEL, AND WERE USUALLY HIDDEN BY IVY *HEDERA HELIX* GROWING ON THE CLIFF FACE.

OF THE VARIABLES PRESENTED TO THE LOGISTIC REGRESSION DISCRIMINATING BETWEEN OWL NESTS AND RANDOM SITES (TABLE 3), TWO ENTERED THE FINAL MODEL: DISTANCE TO CLIFF ( $B = -0.16 \pm 0.05$ , WALD = 12.23,  $P = 0.0001$ ) AND INTERSPERSION INDEX ( $B = 0.20 \pm 0.09$ , WALD = 5.14,  $P = 0.023$ ;  $B$  FOR CONSTANT =  $1.86 \pm 1.05$ ). THE MODEL

**Table 3.** Environmental variables (mean  $\pm$  1 se) measured at 33 Tawny Owl nests and at 33 random locations (Mount Baldo, central-eastern Italian Alps).

Variable	Nest-sites	Random locations
Elevation (m) <sup>a</sup> *	710.3 $\pm$ 37.3	839.1 $\pm$ 47.6
% slope <sup>a</sup> **	48.2 $\pm$ 4.2	30.6 $\pm$ 3.44
Ruggedness index <sup>a†</sup>	39.3 $\pm$ 3.0	32.0 $\pm$ 2.7
NND (m) <sup>a</sup>	646.4 $\pm$ 54.2	699.1 $\pm$ 28.3
Distance to cliff (m) <sup>b</sup> ***	277.2 $\pm$ 49.4	634.6 $\pm$ 53.6
Distance to tree cavity (m) <sup>b</sup>	1329.7 $\pm$ 169.9	1400.9 $\pm$ 155.1
Distance to grassland (m) <sup>b</sup>	131.2 $\pm$ 28.9	124.2 $\pm$ 30.6
Distance to coppice (m)	134.6 $\pm$ 45.4	130.6 $\pm$ 24.6
Distance to high forest (m)	692.1 $\pm$ 110.2	538.5 $\pm$ 92.6
Distance to dirt road (m) <sup>b</sup>	147.3 $\pm$ 19.8	123.6 $\pm$ 23.3
Distance to road (m) <sup>b</sup>	535.5 $\pm$ 82.7	388.2 $\pm$ 64.7
Distance to building (m) <sup>a</sup>	313.9 $\pm$ 50.6	256.4 $\pm$ 39.5
Cliff length (m)*	335.2 $\pm$ 81.4	101.5 $\pm$ 65.0
Isolated trees <sup>b</sup>	9.6 $\pm$ 1.3	7.7 $\pm$ 1.3
Edge length (m) <sup>b</sup>	1664.6 $\pm$ 199.3	1170.6 $\pm$ 144.8
Open interspersion index <sup>b</sup>	4.2 $\pm$ 0.6	3.1 $\pm$ 0.4
Interspersion index ***	8.0 $\pm$ 0.8	5.1 $\pm$ 0.5
% coppice woodland <sup>c</sup>	51.7 $\pm$ 6.3	36.4 $\pm$ 6.2
% Beech coppice <sup>c</sup>	7.9 $\pm$ 3.0	13.1 $\pm$ 4.9
% high forest <sup>c</sup>	18.2 $\pm$ 4.4	18.7 $\pm$ 5.0
% broadleaved high forest <sup>c</sup>	0.9 $\pm$ 0.5	0.9 $\pm$ 0.9
% conifer high forest <sup>c</sup>	15.3 $\pm$ 4.4	17.5 $\pm$ 5.0
% broadleaved woodland <sup>c</sup>	54.6 $\pm$ 6.3	37.7 $\pm$ 6.2
% total woodland <sup>c</sup>	69.9 $\pm$ 3.9	55.2 $\pm$ 5.8
% urban areas <sup>c</sup>	3.7 $\pm$ 2.5	3.2 $\pm$ 1.0
% grassland <sup>c</sup> *	21.8 $\pm$ 3.0	39.2 $\pm$ 5.2
% farmland <sup>c</sup>	1.5 $\pm$ 0.7	1.3 $\pm$ 0.5
% rocky <sup>c</sup> **	3.2 $\pm$ 1.0	1.1 $\pm$ 0.7
Habitat diversity	0.57 $\pm$ 0.20	0.55 $\pm$ 0.20

Univariate differences between the two samples were tested by means of *t*-tests: † 0.05 < *P* < 0.1; \**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.001. Variables in italic were presented to the logistic regression model after variable reduction (see Methods). <sup>a</sup> *t*-Test carried out on the variable log<sub>e</sub>-transformed; <sup>b</sup> *t*-test carried out on the variable square-root transformed; <sup>c</sup> *t*-test carried out on the variable transformed in the arcsine square root of the proportion.

**CORRECTLY RECLASSIFIED 82% OF THE OWL NESTS AND 79% OF THE RANDOM LOCATIONS (80% OVERALL). WHEN VALIDATED ON THE INDEPENDENT DATA SET, THE MODEL CORRECTLY CLASSIFIED 83% OF 30 OWL NESTS AND 87% OF 30 RANDOM LOCATIONS.**

#### Correlates of productivity and density

**IN A MULTIPLE REGRESSION, THE ONLY PREDICTOR OF THE MEAN PRODUCTIVITY OF A TERRITORY WAS THE INTERSPERSION INDEX ( $B = 0.11 \pm 0.01$ ,  $T = 2.27$ ,  $P = 0.032$ ,  $R^2 = 0.18$ ). DENSITY IN THE 12 STUDY POPULATIONS WAS POSITIVELY RELATED TO THE EXTENT OF BROADLEAVED WOODLAND IN EACH AREA ( $\beta_1 = 0.78$ ,  $P = 0.048$ ). ALL OTHER RELATIONSHIPS WERE NOT SIGNIFICANT AFTER THE BONFERRONI CORRECTION.**

#### Diet

**TO DESCRIBE VARIATIONS IN DIET COMPOSITION DURING THE BREEDING PERIOD (MARCH-JULY), WE ASSIGNED TERRITORIES TO**

**FOUR MAIN HABITAT CATEGORIES: (1) COPPICE-MANAGED WOODLAND (DOMINATED MAINLY BY BEECH OR A MIXTURE OF PUBESCENT OAK *QUERCUS PUBESCENS*, EUROPEAN HOPHORNBEAM *OSTRYA CARPINIFOLIA* AND FLOWERING ASH *FRAXINUS ORNUS*); (2) BROADLEAVED HIGH FOREST (MOSTLY BEECH-DOMINATED); (3) MIXED HIGH FOREST (MOSTLY COMPOSED OF BEECH AND SPRUCE); AND (4) URBAN. THE DIET WAS DOMINATED BY (1) EDIBLE DORMOUSE *GLIS GLIS* IN COPPICE-WOODLAND; (2) MICE, VOLES, EDIBLE DORMOUSE AND VARIOUS BIRD SPECIES IN BROADLEAVED HIGH FOREST; (3) EDIBLE DORMOUSE, VOLES, MICE, SQUIRRELS AND VARIOUS BIRD SPECIES (ESPECIALLY *TURDUS* SPP.) IN MIXED HIGH FOREST; AND (4) SPARROWS, FINCHES AND PIGEONS IN URBAN AREAS (TABLE 4).**

#### DISCUSSION

**OUR REGIONAL-SCALE RESULTS CONFIRMED THE REMARKABLE FLEXIBILITY AND OPPORTUNISM PREVIOUSLY REPORTED FOR THE SPECIES AT A LARGER, CONTINENTAL SCALE (PETTY & SAUROLA**

**Table 4.** Diet of Tawny Owls ( $n = 29$  sampled territories) on Mount Baldo (central-eastern Italian Alps) according to four main habitat types.

Prey category	Coppice woodland			Broadleaved high forest			Mixed high forest			Urban areas			
	<i>n</i>	% <i>n</i>	% <i>w</i>	<i>n</i>	% <i>n</i>	% <i>w</i>	<i>n</i>	% <i>n</i>	% <i>w</i>	<i>n</i>	% <i>n</i>	% <i>w</i>	
<b>Mammals</b>	<b>185</b>	<b>85.7</b>	<b>94.1</b>	<b>178</b>	<b>82.0</b>	<b>84.3</b>	<b>220</b>	<b>73.8</b>	<b>82.0</b>	<b>71</b>	<b>12.8</b>	<b>33.8</b>	
Edible Dormouse <i>Glis glis</i>	95	44.0	81.2	10	4.6	23.4	25	8.4	30.0	8	1.4	4.8	
Apodemus spp.	56	25.9	7.1	132	60.8	45.8	50	16.8	8.9	37	6.7	3.3	
Bank Vole <i>Clethrionomys glareolus</i>	28	13.0	4.8	14	6.5	6.6	47	15.8	11.2	0	0.0	0.0	
Common Dormouse <i>Muscardinus avellanarius</i>	0	0.0	0.0	10	4.6	3.9	27	9.1	5.4	0	0.0	0.0	
Brown Rat <i>Rattus norvegicus</i>	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	14	2.5	24.9	
Unidentified Microtinae	6	2.8	1.0	5	2.3	2.3	40	13.4	9.6	0	0.0	0.0	
Garden Dormouse <i>Eliomys quercinus</i>	0	0.0	0.0	0	0.0	0.0	10	3.4	7.6	0	0.0	0.0	
Red Squirrel <i>Sciurus vulgaris</i>	0	0.0	0.0	0	0.0	0.0	2	0.7	5.3	0	0.0	0.0	
Other mammals <sup>a</sup>	0	0.0	0.0	7	3.2	2.3	19	6.4	3.4	12	2.2	0.7	
<b>Birds</b>	<b>23</b>	<b>10.6</b>	<b>5.9</b>	<b>28</b>	<b>12.9</b>	<b>15.6</b>	<b>45</b>	<b>15.1</b>	<b>18.3</b>	<b>475</b>	<b>85.7</b>	<b>66.2</b>	
House Sparrow <i>Passer domesticus</i>	3	1.2	0.5	0	0.0	0.0	0	0.0	0.0	92	16.6	11.1	
Chaffinch <i>Fringilla coelebs</i>	6	2.8	0.8	7	3.2	2.6	4	1.3	0.7	69	12.5	6.6	
Unidentified Passeriformes	4	1.9	0.5	3	1.4	1.0	21	7.1	3.7	64	11.6	5.7	
European Greenfinch <i>Carduelis chloris</i>	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	51	9.2	6.6	
European Goldfinch <i>Carduelis carduelis</i>	1	0.5	0.1	2	0.9	0.6	0	0.0	0.0	43	7.8	3.1	
Common Blackbird <i>Turdus merula</i>	3	1.4	1.8	0	0.0	0.0	2	0.7	1.7	19	3.4	8.1	
Mistle Thrush <i>Turdus viscivorus</i>	0	0.0	0.0	0	0.0	0.0	8	2.7	8.0	0	0.0	0.0	
Unidentified Turdidae	0	0.0	0.0	4	1.8	7.1	2	0.7	1.8	3	0.5	1.4	
Rock Pigeon <i>Columba livia</i>	0	0.0	0.0	0	0.0	0.0	0	0.0	0.0	7	1.3	8.5	
Other birds <sup>b</sup>	6	2.8	2.1	12	5.5	4.3	8	2.7	2.2	127	22.9	15.1	
<b>Invertebrates</b>	<b>8</b>	<b>3.7</b>	<b>0.0</b>	<b>11</b>	<b>5.0</b>	<b>0.1</b>	<b>33</b>	<b>11.0</b>	<b>0.2</b>	<b>8</b>	<b>1.4</b>	<b>0.0</b>	
Melolontha <i>melolontha</i>	0	0.0	0.0	0	0.0	0.0	32	10.7	0.2	0	0.0	0.0	
Other invertebrates <sup>c</sup>	8	3.7	0.0	11	5.1	0.1	1	0.3	0.0	8	1.4	0.0	
<b>Total</b>	<b>216</b>			<b>217</b>			<b>298</b>			<b>554</b>			
<b>Mean prey mass ± se (n)<sup>d</sup></b>		<b>73.1 ± 3.8 (216)</b>			<b>26.6 ± 1.9 (217)</b>			<b>37.7 ± 2.6 (298)</b>			<b>40.3 ± 2.9 (554)</b>		

Prey samples were collected at 11 territories dominated by coppice woodland vegetation, eight dominated by broadleaved high forest, eight dominated by mixed high forest, and at two urban territories. Only prey groups accounting for more than 5% by number or weight in at least one habitat category are shown. *n* = Number of items; % *n* = % by number; % *w* = % by live weight. <sup>a</sup>Includes: Common Shrew *Sorex araneus* (in order of habitat, respectively: *n* = 0, *n* = 1, *n* = 7, *n* = 0); Pygmy Shrew *Sorex minutus* (0, 2, 0, 0); Alpine Shrew *Sorex alpinus* (0, 0, 6, 0); Soricidae spp. (0, 2, 3, 0); Common Mole *Talpa europaea* (0, 1, 3, 0); Chiroptera spp. (0, 0, 0, 4); House Mouse *Mus musculus* (0, 1, 0, 2); Muridae spp. (0, 0, 0, 6). <sup>b</sup>Includes: Common Quail *Coturnix coturnix* (0, 0, 0, 1); Eurasian Scops Owl *Otus scops* (1, 0, 0, 0); Tengmalm's Owl *Aegolius funereus* (1, 0, 0, 0); Common Swift *Apus apus* (0, 0, 0, 7); Eurasian Wryneck *Jynx torquilla* (0, 0, 0, 1); Barn Swallow *Hirundo rustica* (0, 0, 0, 1); Eurasian Crag Martin *Ptyonoprogne rupestris* (0, 0, 0, 3); House Martin *Delichon urbicum* (0, 0, 0, 5); Pied Wagtail *Motacilla alba* (1, 4, 0, 23); Grey Wagtail *Motacilla cinerea* (0, 0, 0, 6); European Robin *Erithacus rubecula* (0, 0, 0, 8); Common Redstart *Phoenicurus phoenicurus* (0, 0, 0, 2); Song Thrush *Turdus philomelos* (1, 0, 2, 3); Blackcap *Sylvia atricapilla* (0, 0, 0, 3); Sylviidae spp. (0, 1, 0, 0); Common Chiffchaff *Phylloscopus collybita* (0, 0, 0, 1); Crested Tit *Lophophanes cristatus* (0, 0, 4, 0); Blue Tit *Cyanistes caeruleus* (0, 0, 0, 3); Great Tit *Parus major* (0, 0, 0, 11); Paridae spp. (0, 5, 0, 11); Wood Nuthatch *Sitta europea* (0, 0, 0, 1); Red-backed Shrike *Lanius collurio* (0, 0, 0, 1); Common Starling *Sturnus vulgaris* (0, 0, 0, 8); Eurasian Tree Sparrow *Passer montanus* (0, 0, 0, 6); Atlantic Canary *Serinus canaria* (0, 0, 0, 1); European Serin *Serinus serinus* (0, 0, 0, 2); Common Bullfinch *Phyrrula phyrrula* (0, 0, 2, 0); Hawfinch *Coccothraustes coccothraustes* (0, 1, 0, 1); Fringillidae spp. (2, 1, 0, 18). <sup>c</sup>Includes: Euscorpions spp. (4, 0, 0, 0); Coleoptera spp. (3, 7, 0, 8); Anoplotes stercorosus (0, 1, 0, 0); Scarabaeidae spp. (0, 0, 1, 0); Orthoptera spp. (1, 0, 0, 0). <sup>d</sup>Mean mass of all the prey items in each sample (measured in g).

**1997, GALEOTTI 2001). IN THE ALPS, TAWNY OWLS OCCURRED OVER AN EXTREMELY BROAD RANGE OF ELEVATIONS (TABLE 2), FROM THE VALLEY FLOORS UP TO THE LIMIT OF THE TREE-LINE, CORRESPONDING TO A MULTITUDE OF LANDSCAPE, MICROCLIMATE AND VEGETATION TYPES. THE ABILITY TO USE A WIDE ARRAY OF NEST STRUCTURES (CLIFFS, TREES, BUILDINGS, ETC.) FURTHER FAVOURED THE COLONIZATION OF MOST OF THE HABITATS AVAILABLE IN THE REGION, FROM URBAN AREAS TO FRAGMENTED WOODLANDS OR CONTINUOUS FORESTS VARYING IN FLORISTIC COMPOSITION AND MANAGEMENT. FURTHERMORE, THE PRONOUNCED**

**HABITAT-RELATED VARIATION IN DIET COMPOSITION HIGHLIGHTED THE OPPORTUNISTIC FORAGING TACTIC OF THIS OWL, CAPABLE OF EXPLOITING A WIDE SPECTRUM OF PREY, RANGING FROM GROUND-DWELLING SPECIES SUCH AS VOLES AND MICE, TO ARBOREAL SPECIES SUCH AS EDIBLE DORMOUSE AND SOME BIRDS.**

**COMPARED TO RANDOM LOCATIONS, TAWNY OWLS SELECTED SITES: (1) NEARER TO CLIFFS, WHICH MAY PROVIDE ABUNDANT NEST-SITES WITH DIFFICULT ACCESS TO MAMMALIAN PREDATORS (INCLUDING HUMANS; SERGIO ET AL. 2003A, 2005); AND (2) WITH HIGHER RICHNESS OF HABITAT TYPES AND ECOTONES. THE**



LATTER RESULT IS TO BE EXPECTED FOR VARIOUS REASONS: (A) TAWNY OWLS ARE A 'SIT-AND-WAIT' PREDATOR OFTEN EXPLOITING HABITAT EDGES (SOUTHERN & LOWE 1968, HARDY 1992, REDPATH 1995); (B) THE OWL DIET USUALLY VARIES SEASONALLY, BEING DOMINATED IN DIFFERENT PERIODS BY PREY TYPES ASSOCIATED WITH DIFFERENT HABITATS (SOUTHERN & LOWE 1968, WENDLAND 1984, GALEOTTI 2001); AND (C) PREY ABUNDANCE AND DIET COMPOSITION MAY VARY RADICALLY BETWEEN YEARS WITHIN EACH TERRITORY, WHICH IS USUALLY OCCUPIED FOR LIFE (SOUTHERN & LOWE 1968, PETTY & SAUROLA 1997).

LONG-TERM AND ALL-YEAR-ROUND MAINTENANCE OF AN ALL-PURPOSE TERRITORY MAY PROMOTE SELECTION OF A STRUCTURALLY DIVERSE FORAGING AREA, ALLOWING FOR RAPID PREY/HABITAT SWITCHING AMONG SEASONS AND YEARS, AS ORIGINALLY POINTED OUT BY SOUTHERN & LOWE (1968; PETTY 1989). IN TURN, THIS MAY EXPLAIN WHY TERRITORIES WITH HIGHER RICHNESS OF VEGETATION TYPES AND BOUNDARIES ALSO ENJOYED HIGHER PRODUCTIVITY, WHICH FURTHER SUGGESTS THAT THE OBSERVED CHOICES WERE ADAPTIVE, AND THAT SUCH A SELECTED FEATURE WAS A COMPONENT OF TERRITORY QUALITY FOR THE OWLS. A SIMILAR PREFERENCE FOR DIVERSE AREAS RICH IN EDGES HAS BEEN REPORTED FOR OTHER GENERALIST RAPTORS (AUSTIN ET AL. 1996, MARTÍNEZ & ZUBEROGOITIA 2004, SERGIO ET AL. 2005). FINALLY, THE FACT THAT TAWNY OWLS RESPONDED MORE TO THE STRUCTURE OF THE LOCAL LANDSCAPE (I.E. AVAILABILITY OF HABITAT EDGES) THAN TO ITS COMPOSITION (FORMAN 1995) MAY FURTHER EXPLAIN THE SUCCESSFUL COLONIZATION BY THE SPECIES OF SO MANY HABITAT TYPES, WHICH MAKES TAWNY OWLS PROBABLY THE MOST UBIQUITOUS RAPTORS OF THE ALPS. HOWEVER, DESPITE SUCH

FLEXIBILITY IN INDIVIDUAL HABITAT CHOICES, AT THE POPULATION LEVEL DENSITY WAS POSITIVELY RELATED TO THE AVAILABILITY OF BROADLEAVED WOODLAND, WHICH FURTHER CONFIRMS THE LARGE-SCALE LINK OF THIS SPECIES WITH SUCH MACROHABITAT, AS PREVIOUSLY QUALITATIVELY REPORTED AT A CONTINENTAL SCALE (PETTY & SAUROLA 1997).

IN CONCLUSION, TWO FEATURES OF OUR POPULATION DIFFER FROM MOST PREVIOUS STUDIES ON THIS SPECIES. FIRST, TO OUR KNOWLEDGE, THIS IS THE FIRST POPULATION STUDIED THAT HAS SUCH A HIGH FREQUENCY OF CLIFF NESTING. THIS MAY HAVE BEEN PROMOTED BY (1) THE LOW AVAILABILITY OF MATURE TREES WITH SUITABLE CAVITIES, AND (2) THE WIDESPREAD PERSECUTION OF RAPTORS AT THE NEST WHICH OCCURRED IN THE ALPS UNTIL RELATIVELY RECENTLY. AS WELL AS BEING WIDELY AVAILABLE IN THE ALPINE LANDSCAPE, CLIFFS ARE LIKELY TO BE LESS ACCESSIBLE TO HUMANS THAN NESTS IN TREES OR BUILDINGS. SIMILAR DYNAMICS HAVE BEEN REPORTED FOR OTHER ALPINE RAPTORS (SERGIO ET AL. 2003A, 2005). SECOND, APART FROM A PREVIOUS STUDY IN THE WESTERN ALPS (BOUVIER & BAYLE 1989), THIS IS THE FIRST POPULATION STUDIED THAT HAS A DIET DOMINATED BY EDIBLE DORMOUSE. THIS SPECIES IS EXTREMELY ABUNDANT IN THE BROADLEAVED WOODLAND OF THE ALPS AND MAY REPRESENT AN IDEAL PREY GIVEN ITS RELATIVELY LARGE BODY WEIGHT AND EXTREMELY PERSISTENT NOCTURNAL VOCALIZATIONS, WHICH PROBABLY MAKE IT AN EASY TARGET FOR A NIGHT PREDATOR EMPLOYING AUDITORY CUES. FURTHERMORE, EDIBLE DORMOUSE IS MORE ABUNDANT IN COPPICE-MANAGED WOODLAND THAN IN OTHER FOREST TYPES (UNPUBL. DATA), WHICH EXPLAINS ITS HIGHER OCCURRENCE IN THE DIET OF PAIRS OCCUPYING TERRITORIES DOMINATED BY COPPICE WOODLAND (TABLE 4). THIS

**Table 5.** Density, nearest-neighbour distance (NND) and productivity of some Tawny Owl populations in mountainous areas of Europe (1980s and 1990s). Only study areas of more than 30 km<sup>2</sup> are included, as smaller plots were demonstrated to yield inflated estimates of density (Galeotti 2001).

Area	Year	Territories/ 100 km <sup>2</sup> (n)	NND (m) (n)	Breeding success <sup>a</sup> (%)	Young fledged (n)		Source
					per territorial pair	per successful pair	
Kielder Forest, England	1981–1987	64.4 (58) <sup>b</sup>	890 (30)	30–96	1.63 (210)	–	Petty 1989, Petty & Fawkes 1997
Bizkaia, Spain	1993–1996	72.6 (1704)	–	–	–	–	Zuberogoitia & Martínez Climont 2000
Mt. Krim, Dinaric Alps, Slovenia	1997–2000	40.0 (23)	–	–	–	–	Vrezec 2003
Sirente-Velino, Apennines, Italy	1987–1988	40.2 (49)	–	–	–	–	Penteriani & Pinchera 1990
Central Alps, Italy	1990s	45.0 (18)	–	–	–	–	P. Galeotti & R. Sacchi, unpubl. data in Galeotti (1990)
Mount Corvo, Alps, Italy	1997–1998	22.4 (17)	1550 (17)	–	–	–	Sascor et al. 1999
Mount Baldo, Alps, Italy	2002–2004	60.0 (33)	710 (33)	74	1.49 (53)	2.03 (39)	This study
Trento region, Alps, Italy <sup>c</sup>	2002–2004	27.8 (321) <sup>c</sup>	796 (321) <sup>c</sup>	–	–	–	This study

<sup>a</sup>Percentage of territorial pairs raising at least one chick to fledging age. <sup>b</sup>Cumulative number of territories occupied at least once during a seven-year period. <sup>c</sup>Based on the cumulated sample from 12 study areas (see Table 2).

CONFIRMS THE WELL-DEMONSTRATED PREFERENTIAL EXPLOITATION OF THE MOST AVAILABLE AND PROFITABLE PREY BY THIS OPPORTUNISTIC SPECIES (SOUTHERN 1970, DELMÉE ET AL. 1978, WENDLAND 1984, JĘDRZEJEWSKI ET AL. 1996, PETTY 1999).

### Conservation implications

THE CONSERVATION STATUS OF THESE POPULATIONS IS SATISFACTORY. POPULATIONS SEEM STABLE, BASED ON MORE THAN 30 TERRITORIES KNOWN TO BE CONTINUOUSLY OCCUPIED FOR THE PAST TEN YEARS. DENSITY WAS IN THE RANGE OF VALUES REPORTED FOR OTHER MOUNTAINOUS AREAS OF EUROPE (TABLE 5) AND PRODUCTIVITY WAS COMPARABLE TO PREVIOUSLY REPORTED ESTIMATES (SOUTHERN 1970, WENDLAND 1984, PETTY 1989, JĘDRZEJEWSKI ET AL. 1996, RANAZZI ET AL. 2000). THE ONGOING CONVERSION OF MUCH COPPICE WOODLAND TO HIGH FOREST IS LIKELY TO BE BENEFICIAL FOR TAWNY OWLS, WHILE THE PROGRESSIVE WOODLAND EXPANSION ASSOCIATED WITH LAND ABANDONMENT MAY FURTHER FAVOUR THE SPECIES. SILVICULTURAL PRACTICES ALLOWING HIGHER AVAILABILITY OF EDGE HABITATS AND OF MATURE OR DEAD TREES WITH LARGE CAVITIES WOULD ADDITIONALLY BENEFIT THIS OPPORTUNISTIC OWL.

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### REFERENCES

Austin, G.E., Thomas, C.J., Houston, D.C. & Thompson, B.A. 1996. Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a Geographical Information System and remote sensing. *J. Appl. Ecol.* **33**: 1541–1550.

Bouvier, M. & Bayle, P. 1989. Le regime alimentaire de la Chouette hulotte *Strix aluco* dans le sud des Alpes francaises. *Bièvre* **10**: 1–22.

Brown, D. 1975. A test of randomness of nest spacing. *Wildfowl* **26**: 102–103.

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, Bruxelles, Belgium.

Delmée, E., Dachy, P. & Simon, P. 1978. Quinze annees d'observations sur la reproduction d'une population forestiere de Chouettes hulottes (*Strix aluco*). *Le Gerfaut* **68**: 590–650.

Forman, R.T.T. 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge.

Galeotti, P. 1990. Territorial behaviour and habitat selection in an urban population of the tawny owl *Strix aluco* L. *Boll. Zool.* **57**: 59–66.

Galeotti, P. 2001. *Strix aluco* Tawny Owl. *BWP Update* **3**: 1–34.

Green, R.H. 1979. *Sampling Design and Statistical Methods for Environmental Biologists*. John Wiley & Sons, New York.

Hardy, A.R. 1992. Habitat use by farmland Tawny Owls *Strix aluco*. In Galbraith, C.A., Taylor, I.R. & Percival, S. (eds) *The Ecology and Conservation of European Owls*: 55–63. Joint Nature Conservation Committee, Peterborough.

Hooge, P.N. & Eichenlaub, B. 1997. *Movement. Animal Movement Extension to ArcView ver. 1.1*. Alaska Biological Science Center, US Geological Survey, Anchorage.

Jeźdrzejewski, W., Jeźdrzejewska, B., Szymura, A. & Zub, K. 1996. Tawny owl (*Strix aluco*) predation in a pristine deciduous forest (Białowieża National Park, Poland). *J. Anim. Ecol.* **65**: 105–120.

Krebs, C.J. 1998. *Ecological Methodology*. Harper Collins, New York.

Marchesi, L., Pedrini, P. & Sergio, F. 2002. Biases associated with diet study methods in the Eurasian Eagle Owl. *J. Raptor Res.* **36**: 11–16.

Martínez, J.A. & Zuberogoitia, I. 2004. Habitat preferences for Long-eared Owls *Asio otus* and Little Owls *Athene noctua* in semi-rural environments at three spatial scales. *Bird Study* **51**: 163–169.

Matthews, J.D. 1989. *Silvicultural Systems*. Oxford University Press, Oxford.

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.

Penteriani, V. & Pinchera, F. 1990. Censimento di una popolazione di Alocco, *Strix aluco*, in un massiccio montuoso dell'Appennino centrale (Abruzzo). *Riv. Ital. Orn.* **60**: 20–28.

Petty, S.J. 1989. Productivity and density of tawny owls *Strix aluco* in relation to the structure of a spruce forest in Britain. *Ann. Zool. Fenn.* **26**: 227–233.

Petty, S.J. 1999. Diet of tawny owls (*Strix aluco*) in relation to field vole (*Microtus agrestis*) abundance in a conifer forest of northern England. *J. Zool.* **248**: 451–465.

Petty, S.J. & Fawkes, B.L. 1997. Clutch size variation in Tawny Owls (*Strix aluco*) from adjacent valley systems: can this be used as a surrogate to investigate temporal and spatial variations in vole density? In Duncan, J.R., Johnson, D.H. & Nivholls, T.H. (eds) *Biology and Conservation of Owls of the Northern Hemisphere*: 315–324. USDA Forest Service, St. Paul, USA.

Petty, S.J. & Sauro, P. 1997. Tawny Owl *Strix aluco*. In Hage-meijer, W.J.M. & Blair, M.J. (eds) *The EBCC Atlas of European Breeding Birds, Their Distribution and Abundance*: 420–421. T & AD Poyser, London.

Ranazzi, L., Manganaro, A. & Salvati, L. 2000. The breeding success of Tawny Owls (*Strix aluco*) in a Mediterranean area: a long-term study in urban Rome. *J. Raptor Res.* **34**: 322–326.

Redpath, S.M. 1995. Habitat fragmentation and the individual: tawny owls *Strix aluco* in woodland patches. *J. Anim. Ecol.* **64**: 652–661.

Sascor, R., Maistri, R. & Noselli, S. 1999. Densità e preferenze ambientali di alcune specie di Strigiformi nel Parco Naturale Monte Corno/Alto Adige. *Avocetta* **23**: 100.

Sergio, F. & Bogliani, G. 2000. Hobby Falco subbuteo nest-site selection and productivity in relation to intensive agriculture and forestry. *J. Wildl. Manage.* **64**: 637–646.

Sergio, F., Pedrini, P. & Marchesi, L. 2003a. Adaptive selection of foraging and nesting habitat by black kites (*Milvus migrans*) and its implications for conservation: a multi-scale approach. *Biol. Conserv.* **112**: 351–362.

Sergio, F., Pedrini, P. & Marchesi, L. 2003b. Spatio-temporal shifts in gradients of habitat quality for an opportunist avian predator. *Ecography* **26**: 243–255.



- Sergio, F., Scandolaro, C., Marchesi, L., Pedrini, P. & Pentieri, V.** 2005. Effect of agro-forestry and landscape changes on common buzzards (*Buteo buteo*) in the Alps: implications for conservation. *Anim. Conserv.* **8**: 17–25.
- Servizio Foreste** 1999. Carta Fisionomica della Copertura Forestale in Trentino. Provincia Autonoma di Trento, Trento, Italy.
- Sokal, R.R. & Rohlf, F.J.** 1981. *Biometry*. W. H. Freeman, New York, USA.
- Southern, H.N.** 1970. The natural control of a population of Tawny owls (*Strix aluco*). *J. Zool.* **162**: 197–285.
- Southern, H.N. & Lowe, V.P.W.** 1968. The pattern of distribution of prey and predation in Tawny owl territories. *J. Anim. Ecol.* **37**: 75–97.
- Tabachnick, B.G. & Fidell, L.S.** 1996. *Using Multivariate Statistics*. HarperCollins, New York.
- Vrezec, A.** 2003. Breeding density and altitudinal distribution of the Ural, Tawny, and Boreal Owls in North Dinaric Alps (central Slovenia). *J. Raptor Res.* **37**: 55–62.
- Wendland, V.** 1984. The influence of prey fluctuations on the breeding success of the Tawny Owl *Strix aluco*. *Ibis* **126**: 284–295.
- Zuberogitia, I. & Martínez Climent, J.A.** 2000. Methods for surveying Tawny Owl *Strix aluco* populations in large areas. *Biota* **1**: 137–146.

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## APPENDIX

Environmental variables measured at Tawny Owl nests and random locations.

Variable	Description
Elevation (m)	Elevation of the nest above sea level
% slope	Percentage slope within 100 m of the nest
Ruggedness index	Number of contour lines crossed by two N–S and W–E transects of 660 m
NND (m)	Distance to the nearest Tawny Owl territory
Distance to cliff (m)	Distance to the nearest cliff
Distance to tree cavity (m)	Distance to the nearest tree with potentially suitable nesting cavities
Distance to grassland (m)	Distance to the nearest grassland field
Distance to coppice (m)	Distance to the nearest patch of coppice-managed woodland
Distance to high forest (m)	Distance to the nearest patch of woodland managed as high forest
Distance to building (m)	Distance to the nearest building
Distance to dirt road (m)	Distance to the nearest dirt road
Distance to road (m)	Distance to the nearest paved road
Distance to building (m)	Distance to the nearest inhabited building
Cliff length (m)	Length of cliff fronts within a radius of 330 m
Isolated trees	Number of isolated trees within a radius of 330 m
Edge length (m)	Length of edges between woodland and grassland
Open interspersed index	Number of boundaries between woodland and grassland crossed by two N–S and W–E transects of 660 m
Interspersed index	Number of habitat boundaries crossed by two N–S and W–E transects of 660 m
% coppice woodland	Percentage extent of coppice-managed woodland within a radius of 330 m
% Beech coppice	Percentage extent of coppice-managed woodland dominated by Beech within a radius of 330 m
% high forest	Percentage extent of woodland managed as high forest within a radius of 330 m
% broadleaved high forest	Percentage extent of broadleaved high forest within a radius of 330 m
% conifer high forest	Percentage extent of conifer high forest within a radius of 330 m
% broadleaved woodland	Percentage extent of broadleaved woodland within a radius of 330 m
% total woodland	Percentage extent of any woodland type within a radius of 330 m
% urban areas	Percentage extent of urban areas within a radius of 330 m
% grassland	Percentage extent of grassland within a radius of 330 m
% farmland	Percentage extent of intensive farmland within a radius of 330 m
% rocky	Percentage extent of rocky outcrops and arid-sparse vegetation within a radius of 330 m
Habitat diversity	Shannon index <sup>a</sup> of habitat diversity (Krebs 1998)

<sup>a</sup>Calculated as:  $\sum(p \log_e p)$ , where  $p$  is the proportion of each habitat type.