

**Nestling diet, juvenile dispersal, and adult habitat
selection of the Eagle owl *Bubo bubo* in the Swiss
Rhône valley**

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Zusammenfassung

1. Obwohl sich die Schweizer Uhu Population von ihrem Tiefststand zwischen den 1940er- und den 1990er-Jahren erholen konnte, gilt sie immer noch als gefährdet. Die Gründe für die langsame und teilweise erfolgreiche Wiederbesiedlung sind weitgehend unbekannt. Diese Studie behandelt in den Jahren 2002 und 2003 erfasste Daten zur Nestlingsnahrung, Jugend-Dispersion und Habitatwahl. Sie bildet den ersten Schritt zu einem besseren Verständnis der Gefährdungsursachen des Uhus.

2. *Ernährung der Nestlinge*: Die Nestlingsnahrung zweier Brutten konnte anhand von Video-Aufzeichnungen ermittelt werden. Säugetiere waren die wichtigste Beutekategorie (69% der Beutetiere, 61% der Biomasse). Vögel machten 28% der verfütterten Tiere und 35% der Biomasse aus. Fische waren von untergeordneter Bedeutung (4% und 5%). Siebenschläfer *Glis glis* waren ein sehr bedeutender Bestandteil der Nestlingsnahrung: An einem Nest machten sie 47% aller Beutetiere aus. Das durchschnittliche Gewicht der Beutestücke betrug rund 200 g. Gemittelt erhielt ein Nestling 185 g Nahrung pro Nacht. Dieser Wert entspricht Angaben aus Zoos. Offensichtlich litten die Nestlinge nicht an Nahrungsmangel.

3. *Jugend-Dispersion*: Die Dispersionswanderungen von acht Jungvögeln konnten mittels Radiotelemetrie verfolgt werden. Von einem Vogel konnten wir die Jugend-Dispersion bis zum Ende verfolgen. Drei Uhus starben während der Dispersion, drei zogen in südliche Gebiete der Alpen (Italien/ Frankreich) und einer blieb im Zentralwallis. Durchschnittlich begann die Dispersion am 1. Oktober. Die mittlere Länge aller verfolgten totalen Flugrouten lag bei 124 km (15 – 230 km). Hohe Bergketten stellten während der Jugend-Dispersion kein Hindernis dar. Diese Ergebnisse zeigen, dass ein genetischer Austausch mit anderen Populationen auch über Bergketten und grosse Distanzen möglich ist.

4. *Home range und Habitat-Selektion*: Mittels Radiotelemetrie konnte die Home range-Grösse und die Habitatwahl zweier adulter Weibchen untersucht werden. Die gesamthaft genutzte Fläche (100% minimum convex polygon) während annähernd einem Jahr betrug 29 km² und 22 km². Das 95% MCP war jedoch kleiner: 5 km² und 13 km². Verglichen mit anderen Studien sind diese Werte klein. Daraus kann man auf besonders ergiebige Lebensräume schliessen. Die Analyse der Habitatwahl zeigte, dass offene Landschaftstypen wie Grasflächen und Flächen mit höchstens lichter Vegetationsbedeckung bevorzugt genutzt wurden. Siedlungs- und Landwirtschaftsgebiet (mit Ausnahme von Grasflächen), besonders Obstplantagen und Äcker, wurden nur schwach genutzt. Unsere Daten lassen zudem vermuten, dass reich strukturierte Landschaften den Uhus Vorteile bieten.

5. Obwohl erst lückenhaft, lässt diese Studie annehmen, dass das Schweizer Rhonetal geeignete Bruthabitate mit ausreichender Nahrungsgrundlage für den Uhu bietet. Der sehr langsame Wiederbesiedlungs-Prozess kann möglicherweise durch anthropogene und die Populationsdynamik beeinflussende Faktoren erklärt werden.

Abstract

1. Although the Swiss Eagle owl population could slightly recover after having reached a very low level in the 1940s – 1990s, it still has to be regarded as vulnerable. The causes of this slow and partly successful recolonisation process are poorly understood. This study presents a synthesis of data obtained in 2002 and 2003 on nestling diet, juvenile dispersal and adult habitat selection. It is a first step towards a comprehensive understanding of Eagle owl conservation problems.

2. *Nestling diet*: To investigate nestling diet at two sites, an unbiased method (infrared video) was applied for the first time in this species. Mammals were the most important prey category (69% frequency, 61% biomass). Birds were represented with 28% frequency and 35% biomass. Fish were of minor importance (4% and 5%, respectively). Fat dormice *Glis glis* were very frequently delivered to the nest, making up 47% of prey frequency at one site. Mean individual biomass of prey items was around 200 g. The biomass brought averaged 185 g per nestling and night, which agrees with values observed from chick rearing in zoos. Apparently chicks did not suffer from lack of food.

3. *Juvenile dispersal*: Dispersal routes of 8 birds could be followed by radiotracking. From one individual we got data till first reproduction. 3 birds died during dispersal. 3 birds dispersed to the southern Alps (Italy/ France) and one stayed in Central Valais. On average, dispersal began on 1st of October. The mean flown distance was at least 124 km (range: 15 - 230 km). High mountain ridges did not hinder dispersal. Exchange of birds over so long distances and across the Alps indicates that gene flow occurs between different European populations.

4. *Home range and habitat selection*: Home range size and habitat selection of two adult females could be investigated by radiotracking. The overall home ranges (100% minimum convex polygon) during almost one year were 29 km² and 22 km², respectively. The 95% MCP were much smaller: 5 km² and 13 km², respectively. Compared with other studies these values are small, which suggests a highly productive habitat. Habitat selection analyses showed that open habitat types such as grassland and surfaces with only low vegetation cover were preferentially used, whereas settlements and agricultural areas, especially cropland and orchards, were neglected. Our results also show that highly structured landscapes could be advantageous for this raptor.

5. Although still fragmentary, this preliminary study suggests that the Upper Rhône valley offers suitable breeding habitats with sufficient trophic resources for the Eagle owl. Its very slow demographic recovery might possibly be due to anthropogenic factors negatively affecting population dynamics.

1. Introduction

1.1 Distribution and population trends

The Eagle owl has a very wide distribution, occurring across Europe, in North Africa and from subarctic to subtropical Asia (Glutz von Blotzheim & Bauer 1980; Mikkola 1983; Tucker & Heath 1994). The coaction of different factors such as direct persecution, general disturbances by human activity, collisions with aerial cables, cars and trains, electrocution and probably the application of biocides inflicted heavy casualties on the European Eagle owl *Bubo bubo* (Desfayes & G eroudet 1949; Olsson 1979; Mikkola 1983; Tucker & Heath 1994; Schmid et al. 2001). Although the species has recently recovered in some populations, about nearly two thirds of the populations for which trends are known are now in decline. For instance Russia, which harbours about 60% of the European population, has undergone a rapid, steady decline (Tucker & Heath 1994; Mebs & Scherzinger 2000).

In Switzerland, the Eagle owl was a widespread bird species until the middle of the 19th century. In the second half of the 19th century a clear population decrease became apparent (Richard 1923; Desfayes & G eroudet 1949). The last breeding pair was registered in 1886 in the Midland and in 1906 in Jura mountains (Daut 1921; Corti 1935, 1962; Guggisberg 1955 cited in L ups et al. (1978)). In the years 1972-1976, during data collection for the first Swiss ornithological atlas, presence of the Eagle owl could only be proved in the Alps with emphasis in the cantons of Ticino and Grisons. The population was assumed to consist of approximately 60 breeding pairs (Schifferli et al. 1980). About 15 years later, during the preparation of the second Swiss ornithological atlas, with an estimate of at least 120 breeding pairs, a definitely higher population size could be detected. More specifically, recolonisation processes in Valais, some parts of the Jura mountains, northern Midlands and along the northern edge of the Alps contributed to the increase (Arlettaz 1988; Mosimann-Kampe 1998; Schmid et al. 1998). From 1959 to 2002 at least 202 Eagle owls were released from captivity in Switzerland. This probably had a strong effect on the development of the Swiss Eagle owl population. Nevertheless this species has still to be regarded as vulnerable (Keller et al. 2001). Many sites with proved historical reproduction have not yet been recolonised. Also, some sites recolonised in the last 20 years have again been recently abandoned. This pattern of recolonisation – abandonment is well documented as regards the Valais population (Arlettaz, pers. comm.).

1.2 Aims of this study

The reasons for low population densities, high mortality and low fertility in Eagle owls in many parts of Europe are not really understood. To better understand the dynamics of the Swiss population, a long term study was launched in 2002 at the division of Conservation Biology at the University of Bern. Its goal is to gather objective information about resource exploitation patterns and risks affecting population dynamics. This diploma work presents the first results of this research program.

1.2.1 Nestling diet

Food provisioning to chicks can generally be seen as a possibly limiting factor affecting reproductive success and population dynamics. In *Bubo bubo*, during the reproductive period, the male has to deliver sufficient amounts of food to the juveniles, and to the female that does not hunt from the onset of incubation until several weeks after hatching (Glutz von Blotzheim & Bauer 1980; Mikkola 1983). Quantitative analyses of diet during this period could give information on the nutritional state of nestlings. Food composition of Eagle owls is well known thanks to numerous studies (Richard 1923; Desfayes & Géroutet 1949; Desfayes 1951; Bezzel & Lechner 1968; Wagner & Springer 1970; Ceska 1978; Orsini 1985; Bayle 1987a; Bayle et al. 1987; Arlettaz 1988; Darolova 1990; Martinez et al. 1992; Wadewitz & Nicolai 1993; Bayle 1994; Dalbeck 1996; Rathgeber & Bayle 1997; Cekoni-Hutter 1998; Leditznig 1999; Dalbeck 2000; Serrano 2000; Leditznig et al. 2001; Martinez & Zuberogoitia 2001; Marchesi et al. 2002a; Marchesi et al. 2002b; Penteriani et al. 2002; Dalbeck 2003; Penteriani et al. 2003). They are all based on the analysis of pellets and prey remains. With this method quantitative estimations of consumed biomass can hardly be made. Furthermore, the only systematic analysis of diet in Valais was carried out in 1949 at one single eyrie. This means that the actual food composition in this part of the Alps is poorly known. Thus we filmed two eyries in order to investigate nestling diet, both as regards prey spectrum and supplied biomass. This represents the first attempt to use a video equipment to monitor the foraging behaviour of free-ranging Eagle owls during reproduction.

1.2.2 Juvenile dispersal

Juvenile dispersal can be defined as the movements of juvenile animals from their place of birth to their settling place (Berndt & Sternberg 1969). Dispersal is an important process for the recolonisation of potential Eagle owl habitats and for the replacement of

territorial owls which perish (Haller 1978; Olsson 1979; Glutz von Blotzheim & Bauer 1980). Interactions between populations depend primarily on juvenile dispersal, because once settled down, Eagle owls become fully sedentary (Mikkola 1983; Tucker & Heath 1994; Mebs & Scherzinger 2000). In several articles distances of juvenile dispersal are specified. They mostly base on findings of dead or injured ringed owls (Desfayes 1951; Glutz von Blotzheim & Bauer 1980; Mebs & Scherzinger 2000). However, Leditznig (1999) studied dispersal of 6 juveniles in Lower Austria on the foothills of the Alps by means of radiotracking and could detect an average total dispersal distance of 222 km. Haller (1978) assumed that deep valleys of the Central Alps could canalise juvenile dispersal. This would have strong effects on the way recolonisation and also interactions between populations proceed. The main aim of this part of my diploma work was to estimate dispersal distances so as to evaluate the possibility of interactions with other Eagle owl populations.

1.2.3 Home range and habitat selection

In order to understand the mechanisms involved in resource exploitation, clear knowledge of habitat selection is required. Some studies from all over Europe have already characterised the habitat used by the Eagle owl. They either described the surrounding area of nest sites, the principal habitat of identified prey items or relied on direct optical observations (Loos 1906; Wagner & Springer 1970; Frey 1973; Haller 1978; Martinez et al. 1992; Bayle 1994; Buzzi & Tavernier 2002; Penteriani et al. submitted). Leditznig (1999, 2001) was so far the only one that investigated land use of Eagle owls by radiotracking. In order to determine home range size and the relevant habitat types and structures for the Eagle owls in Valais, we followed two radiotagged adult females at night. The composition of the used habitat within a bird's home range was compared to the overall available habitat.

2. Material and methods

2.1 Study area

The nests of the Eagle owls were found between Visp (7.9°E, 46.3°N; 650 m a.s.l.) and Villeneuve (6.9°E, 46.4°N; 380 m a.s.l.) in the Swiss Rhône valley. This 1-6 km wide plain, flanked with scarps and rock faces, is characterised by intensive agriculture and dense human settlement. Roads, railways, and canalised rivers fragment the plain. The slopes on each valley side rise up to more than 3000 m altitude in places. In 2003, the annual average temperature in the Swiss Rhône valley was 10.7° C, whilst precipitation amounted to 509 mm (MeteoSwiss), but note that some dispersing juveniles left the core of the study area towards other parts of Switzerland, Italy and France. I shortly describe the three sites where I studied nestling diet (sites B and C) and/ or habitat selection (sites A and C). Precise locations are not given to keep confidentiality.

Site A:

This site was situated in the western part of the study area (Chablais). There the plain consists mostly of monotonous cropland, interspersed with small wood fragments. The mountainsides are covered with dense forests, sometimes interrupted with rock faces which may reach the valley bottom.

Site B:

The landscape around this site is characterized by intensive agriculture, especially orchards. Several small gravel-pit lakes (maximum 15 ha area) are also present. Woodlands occur only on the adjacent slopes, whilst vineyards and rock faces abound.

Site C

At this site in Central Valais the bottom of the valley is strongly influenced by human activities including orchards, settlements and recreational facilities. A system of small gravel-pit lakes (maximum 11 ha area) is a conspicuous element of the landscape. On the south-exposed mountainside wide areas are covered with vineyards. On the north-exposed foothill apricot orchards, forests and human settlements occur. There are several rock faces along the foothills.

2.2 Radiotagging and basics of radiotracking

In 2002 and 2003 19 juvenile Eagle owls from 7 different nest sites (8 different broods) have been radio-tagged 5-6 weeks after hatching. In September 2002 we could tag an adult female which had been caught in a fishnet at a pisciculture. The owls were equipped with conventional transmitters (9 g, lifespan of 18 months, Holohil Systems Ltd., Ontario, Canada) with an activity sensor (pulse rate varying according to bird body position). Signal detection ranged from some hundred metres to more than 20 km, depending on the topography and the relative position above the ground of the tagged owl and the receiver antenna. Both in 2002 and 2003, two juveniles additionally got an ARGOS satellite transmitter (30-40 g, Microwave Telemetry Inc., Columbia, MD, USA; Northstar, Science and Technology, Baltimore, MD, USA). After an emitting period of 8 h the satellite tags switched off for either 32 h or 36 h. The transmitters were fixed with a self-made back-pack harness consisting of a nylon cord, muffled in a hose of Teflon.

Bearings were achieved with a radiotracking receiver (Australis 26k, Titley Electronics, Australia), coupled with a three-element hand-held Yaggi antenna (Titley Electronics, Australia) or an omnidirectional car-roof aerial (Hotline HL-M881H). To localise a tagged bird, I applied two techniques. First I relied on the homing-in technique (White & Garrott 1990). Because I did not want to disturb the bird, I tried to locate it optically from a distance. I systematically scanned the environment in the direction of the radio-signal emission with a light amplifier (Leica Big 25, Leica Geosystem AG, 9435 Heerbrugg, CH) and a powerful torch. I could frequently spot the light-reflecting eyes of the owl at distances greater than 200 m. Once a bird detected, I could estimated azimuth with a compass (Recta DP6, Recta AG, 2501 Biel, CH), as well as its distance from my position (GPS-receiver, Garmin eTrex Vista, Garmin International Inc. Olatha, USA) with the help of a laser binocular distance meter (Leica Geovid 7x42, Leica Geosystem AG, 9435 Heerbrugg, CH). Locations of the bird and observer were reported on a 1:25000 scaled map (Swiss Topo). Second I used the triangulation method with bearings taken from three different places (White & Garrott 1990). Locations were again recorded on a 1:25000 map. These triangulations could only be achieved when a bird remained immobile, which was assessed through the signal pulse rate. The localisations were classified according to their estimated accuracy: maximum precision consisted mostly of visual observations (class 1); the other classes (2 – 4) referred to bearings (Table 1). Between 8-20 minutes were required to reach a class 2 localisation with 3 bearings.

Table 1: Localisation points were divided into 4 classes of accuracy.

Class	Radius of the circle	Method
1	<10 m	visual
2	<50 m	triangulation
3	>50 m	triangulation
4	>100 m	triangulation

2.3 Nestling diet

Food provisioned to chicks was investigated at two eyries (B and C) using infrared video sets (Videotronic, CCD-7012P, Neumünster, Germany) coupled with infrared light sources (WF-I/LED80-230, Videor Technical E. Hartig GmbH, Rödermark, Germany). The cameras were placed in weatherproof protective boxes. Camera and light were fixed on 15 cm long metal bars which were screwed directly onto the rock about 10 m (Site C) and 30 m (Site B) away from the nest site, respectively, depending on the structure of the rocks and ledge. The events filmed at the nest were recorded continuously with a video recorder (Sanyo, SRT 7168P, Osaka, Japan) positioned on an easily accessible place above or below the rock face in a tool shed. I used standard 240min video tapes, on which I could register about 480min (8h) of activity per tape and night. Video picture focus was controlled daily with a small portable TV monitor (Sony, GV-D800, Tokyo, Japan). At site C power supply came from the grid to which we had access in a family house above the rock face. At site B it was supplied by a fuel generator (Honda EU 101, Tokyo, Japan). With the content of the fuel tank (2.3 l) the system was actuated 10-11h. Both systems were switched on and off automatically (digital clock timer, Mini Digi, Steffen). At site B, we filmed from 7.5.2003 (circa 5 weeks after hatching) to 17.6.2003. At site C, from 16.5.2003 (about 3 weeks after hatching) to 29.6.2003. Video recordings began around sunset (about 21h). At both sites there were two juveniles at the beginning of the recording sessions. The juveniles at site C left the niche on 24.6.2003. At site B the recordings were abandoned at date of death of the last juvenile bird on 18.6.2003. Altogether I got analysable material from 36 nights at site C and 40 nights at site B. Due to technical problems with the generator I got recordings of less than 6h during 7 nights at site B. To analyse the film material I used the same video recorder as for the recordings. I was fast-forwarding the tapes till an adult owl arrived at the nest. I noted the time of its

arrival and tried to identify prey items down to species level on the basis of different reference guides (Reichholf 1983; Görner & Hackethal 1988; Pedrolì et al. 1991; Hausser 1995; Snow & Perrins 1998; Richarz 2003). To estimate prey type biomass I used the average of the values of the reference guides cited above and those by Wagner (Wagner & Springer 1970) and Wadewitz (Wadewitz & Nicolai 1993). Data on rainfall stemmed from the MeteoSwiss station at Sion airport (46.13°N/7.20°E). All nights with a minimum of 6h of filming were included in the analysis of the phenology of food provisioning. I divided the nights in 9 periods of 1h each, beginning at dusk (around 21h) and ending at dawn (around 5h30). For each period I calculated the averaged number of prey items provisioned to the chicks. Data about time of sundown I got from a JavaScript on Internet (Brodbeck 2004).

2.4 Juvenile dispersal

As a result of regular monitoring, departure of the juveniles from the parent's territory could be asserted precisely (\pm one day). Dispersing Eagle owls were tracked as tightly as possible, using triangulation. Localisations at all accuracy levels were used for estimating dispersal routes. We tracked birds from a car with the help of an omnidirectional antenna installed on car roof. Twice, we hired an airplane equipped with a specially designed antenna and a signal amplifier. Flight distances were calculated from topographic maps and the software SwissMap 50 (SwissTopo, Wabern, Switzerland). The birds tagged with satellite transmitters were radio-monitored automatically about every other day.

2.5 Home range and habitat selection

2.5.1 Home ranges

We carried out home range and habitat selection analysis in the two adult territorial females of sites A and C (see above). Bird A was tagged in September 2002 when it was found in a pisciculture; it did not breed in 2003. Female C was tagged in 2002 as juvenile at site B. In November 2002, after dispersal, it settled down and reproduced in 2003 at site C. For both owls two seasonal and one global home ranges were calculated (Table 2). Home ranges were in most cases estimated with a 95% minimum convex polygon (MCP; i.e. 5% of the points, those most external within home range, were excluded; Harris et al. 1990; White & Garrott 1990) with ArcView GIS (ArcView GIS 3.3, 1992-2002, Environmental Systems Research Institute, Inc.) and Swiss Map 50. However, 100% polygon was also used to evaluate the globally used area during the whole study time. In this case

roost locations were included. They were always lying within home ranges. Home range size for the two winter and summer seasons were calculated with localisation data of all accuracy levels.

Table 2. Data sets for home range (MCP) estimations for two radio tracked birds in winter (2002–03), summer (2003) and globally. See text for more details.

Bird	Period		N of bearings (100% MCP)	N of bearings (95% MCP)	N of nights with bearings
A	winter	03.10.02 - 01.04.03	-	106	33
	summer	14.05.03 - 29.08.03	-	148	15
	global	03.10.02 - 28.08.03	268	-	48
C	winter	28.11.02 - 11.03.03	-	108	47
	summer	12.05.03 - 27.08.03	-	125	17
	global	28.11.02 - 10.09.03	253	-	67

2.5.2 Habitat selection

Bearings for habitat selection analysis were collected from 20.5.2003 to 28.8.2003. Each of the two females was tracked during one complete night per week during 15 weeks. A bearing prior to dusk enabled me to locate birds' daily roosts. In order to avoid temporal auto-correlation and to achieve data independency, bearings were taken every 30 minutes from dusk to dawn. As long as the bird stayed within a 50 m radius from roost, bearings were not recorded. Only bearings with accuracy levels 1 and 2 were used. I got such localisations during 12 nights (n = 131 bearings) for bird A and 9 nights (n = 89 bearings) for bird C. Bird A did not leave the roost cliff on 3 nights and bird C on 6 nights. Two 95% MCP were drawn from these locations, one for each female. To compare habitat use with habitat availability, a number of random points corresponding to the number of bearings obtained were chosen from inside each home range. Random points falling in a water area were replaced by a close position on land. MCP calculations and random point selection were achieved with a GIS. Habitat mapping and description within a 50 m radius around both bearing locations and random points was carried out in September and October 2003. Exact positioning was achieved with a GPS receiver whilst circle boundaries were estimated with a range finder (Leica Geovid 7x42). Within the 50 m radius circle I estimated the proportion of various habitat types, the length of linear structures and the number of punctual elements (Table 3). As regards cultivated land, habitat characterisation at that time of the year when the bird was lingering in a given plot was accomplished

after discussing with farmers. Each random point was randomly linked to the date of a bearing; habitat around it was characterised for that time of the year. Our habitat classification is based on Delarze et al. (1999). Univariate tests were carried out with all categories (# 1 – 23), compositional analysis only with area-expressing variables (# 1 – 16). At site A categories # 1 and # 9 were not represented. They were thus not included in the analyses.

Table 3: Categories used for habitat analyses. Area-expressing variables were measured in m² and then converted into percentages prior to running analyses. Percentages of the various habitat features at a given location summed up to 100%. Linear structures were measured in m, for punctual elements the number was indicated.

#	Habitat category	measurement unit
1	Pond	area
2	River	area
3	Megaforbiae	area
4	Grassland	area
5	Woodland	area
6	Small forest ¹	area
7	Park	area
8	Shrubbery/ hedgerow	area
9	Vineyard/ tree nursery	area
10	Corn	area
11	Vegetables/ beets/ potatoes	area
12	Bare cropland	area
13	Asphalted	area
14	Area with slight vegetation cover ²	area
15	Single building ³	area
16	Settlement ⁴	area
17	Edge of woodland	linear
18	Low voltage power line	linear
19	High voltage power line	linear
20	Fruit trees	punctual
21	Single trees ⁵	punctual
22	Wooden power pole (low voltage)	punctual
23	Steel/ concrete power poles (high voltage)	punctual

¹: < 1 ha area

²: not asphalted areas with no or slight vegetation cover such as gravel pit, field path or detritus

³: single building or few buildings more than 50 m apart

⁴: at least two buildings closer than 50 m from one another

⁵: tree: trunk diameter > 10 cm

2.6 Statistical analysis

Univariate comparisons comprised Mann-Whitney U, Kruskal-Wallis and Wilcoxon signed rank tests. Correlation tests were Spearman Rank Correlation tests. Significance level was set at $p = 0.05$. Statistical analyses were run with the program JMP4 (SAS Institute Inc. 2001, Cary, NC, USA). Compositional analysis was performed for habitat selection analyses, with the two individuals treated separately. The original data set was randomized with 1000 iterations using an add-in tool programmed in MS Excel before running the analysis (Compositional Analysis software V4.1., Smith Ecology Ltd., 2003, Monmouthshire, Wales, UK). Zero values were replaced by 0.001, i.e. a value smaller than the smallest recorded nonzero proportion obtained from the used data (Aebischer et al. 1993b). As I carried out separate analyses for the two birds I treated each single locations as the sampling unit, which differs from the approach by Aebischer, for whom the sample unit was an individual (Aebischer & Robertson 1992; Aebischer et al. 1993a; Aebischer et al. 1993b).

3. Results

3.1 Nestling diet

We could film the eyrie at site B during a total of 299h (40 nights, average 7.2h per night) and at site C during 295h (36 nights, 8.2h per night). 95% (site B) and 96% (site C) of prey items could be identified from videos. For various reasons it was often impossible to classify prey down to species level (see Table 4).

3.1.1 Food composition

Altogether, mammals made up 60% of the estimated biomass, birds 35% and fish 5%. The total percentage of fat dormice was 21% of total biomass. Birds as large as rock dove or carrion crow reached 24% (Table 4). About half of the prey consisted of medium to largesized vertebrates. Table 4 provides information about intersite variation.

Site B

Mammals made up 57.7% of the total estimated prey biomass (11950 g) and 66.7% of prey frequency ($n = 57$), followed by birds (41% biomass, 31.6% frequency) and fish (1.3% and 1.8%, respectively). Note that two Leporidae made up one third of the overall provisioned biomass, pigeons and crows 18.5% and 12.6%, respectively, fat dormice 11.5% (Table 4). In frequency terms, Arvicolidae (*Arvicola* or *Microtus*) represented 35.1% and fat dormice 19.3%. The mean (\pm sd) weight of prey items was 209 g (\pm 378), the median 125 g. The mean body mass of birds (273 g) was higher than that of mammals (181 g).

Side C

At this site, 63.2% of the overall provisioned prey biomass (14405 g) and 70.3% of the total item frequency ($n = 74$) were mammals. Birds represented 28.4% of biomass and 24.3% frequency whilst fish contributed 8.3% and 5.4%, respectively. In terms of biomass, fat dormice predominated (30.4%, even 36.2% if prey similar to fat dormice are included). They were followed by the single rabbit and corvid-like birds (both 13.9%) (Table 4). As regards prey item frequency fat dormice came first with 47.3%. If fat dormice, garden dormice and dormice-like prey were pooled, this category even achieved 59.5%. Birds similar to thrushes reached 12.2% of frequency. The mean (\pm sd) body mass of prey items amounted to 195 g (\pm 262), the median was 125 g. The weight of mammals averaged 175 g, the weight of birds 228 g.

Table 4: Prey provisioned to nestlings at eyries B and C (frequency and estimated biomass). Biomass of prey items that could not be identified down to species level was estimated from data on closely related species.

Prey category	Reference species	Estimated mass (g)	Frequency (n)			Frequency (%)			Biomass (%)		
			Site B	Site C	B+C	Site B	Site C	B+C	Site B	Site C	B+C
Unclassified			3	3	6						
Total (classified)			57	74	131						
Mammals			38	52	90	66.7	70.3	68.5	57.7	63.2	60.5
European hedgehog	<i>Erinaceus europaeus</i>	1050		1	1		1.4	0.7		7.3	3.6
Rabbit	<i>Oryctolagus cuniculus</i>	2000		1	1		1.4	0.7		13.9	6.9
Rest of hare	<i>Lepus europaeus</i>	1500	1		1	1.8		0.9	12.6		6.3
Leporidae sp.	<i>Lepus europaeus</i>	2500	1		1	1.8		0.9	20.9		10.5
Muridae sp.	<i>Microtus arvalis</i>	30	20	4	24	35.1	5.4	20.2	5.0	0.8	2.9
Similar Rattus sp.	<i>Rattus rattus</i>	175	4		4	7.0		3.5	5.9		2.9
Fat dormouse	<i>Glis glis</i>	125	11	35	46	19.3	47.3	33.3	11.5	30.4	20.9
Similar fat dormouse	<i>Glis glis</i>	125		2	2		2.7	1.4		1.7	0.9
Garden dormouse	<i>Eliomis quercinus</i>	85		6	6		8.1	4.1		3.5	1.8
Similar garden dormouse	<i>Eliomis quercinus</i>	85		1	1		1.4	0.7		0.6	0.3
Part of fox	<i>Vulpes vulpes</i>	500		1	1		1.4	0.7		3.5	1.7
Stoat	<i>Mustela erminea</i>	220	1		1	1.8		0.9	1.8		0.9
Similar Mustelidae sp.	<i>Mustela erminea</i>	220		1	1		1.4	0.7		1.5	0.8
Birds			18	18	36	31.6	24.3	28.0	41.0	28.4	34.7
Similar Pigeon sp.	<i>Columba livia</i>	315	7	1	8	12.3	1.4	6.8	18.5	2.2	10.3
Similar Jay	<i>Garrulus glandarius</i>	175	4	3	7	7.0	4.1	5.5	5.9	3.6	4.8
Magpie	<i>Pica pica</i>	215	1		1	1.8		0.9	1.8		0.9
Rest of Corvidae sp.	<i>Corvus corone</i>	400		1	1		1.4	0.7		2.8	1.4
Similar Corvidae sp.	<i>Corvus corone</i>	500	3	4	7	5.3	5.4	5.3	12.6	13.9	13.2
Similar Turdidae sp.	<i>Turdus merula</i>	95	3	9	12	5.3	12.2	8.7	2.4	5.9	4.2
Fish			1	4	5	1.8	5.4	3.6	1.3	8.3	4.8
35 cm long	<i>Salmo trutta</i>	300		4	4		5.4	2.7		8.3	4.2
20 cm long	<i>Salmo trutta</i>	150	1		1	1.8		0.9	1.3		0.6

3.1.2 Feeding patterns

Considering only nights with more than 6h of continuous video recording time we estimated that at both sites about two prey items were brought to the nest per night (Site B: mean (\pm sd) = 1.6 (\pm 1.3), median = 1.95; Site C: mean = 2.0 (\pm 1.4), median = 1.95). Corresponding biomass supplied averaged 348 g and 388 g per night at site B and C, respectively (medians: 171 g and 268 g, respectively; Table 5). Neither the number nor the biomass of prey delivered per night differed significantly between the two sites (Mann-Whitney U-test, $n_1 = 36$, $n_2 = 33$, $Z = -0.344$, $P = 0.731$ for biomass; $Z = -0.799$, $P = 0.424$ for frequency).

Table 5: Mean and median prey number and biomass delivered to the nest per night (n = 36 nights at site B, n = 33 nights at site C).

	Frequency (n)		Biomass (g)	
	Site B	Site C	Site B	Site C
Mean	1.6	2.0	348	388
SD	1.1	1.4	500	437
Median	1.95	1.95	171	268

At both sites, no differences in the number of provisioning events between the single hours could be detected (Kruskal-Wallis test: site B: $\chi^2 = 5.4$, df = 8, P = 0.709; site C: $\chi^2 = 11.26$, df = 8, P = 0.187; Figure 1).

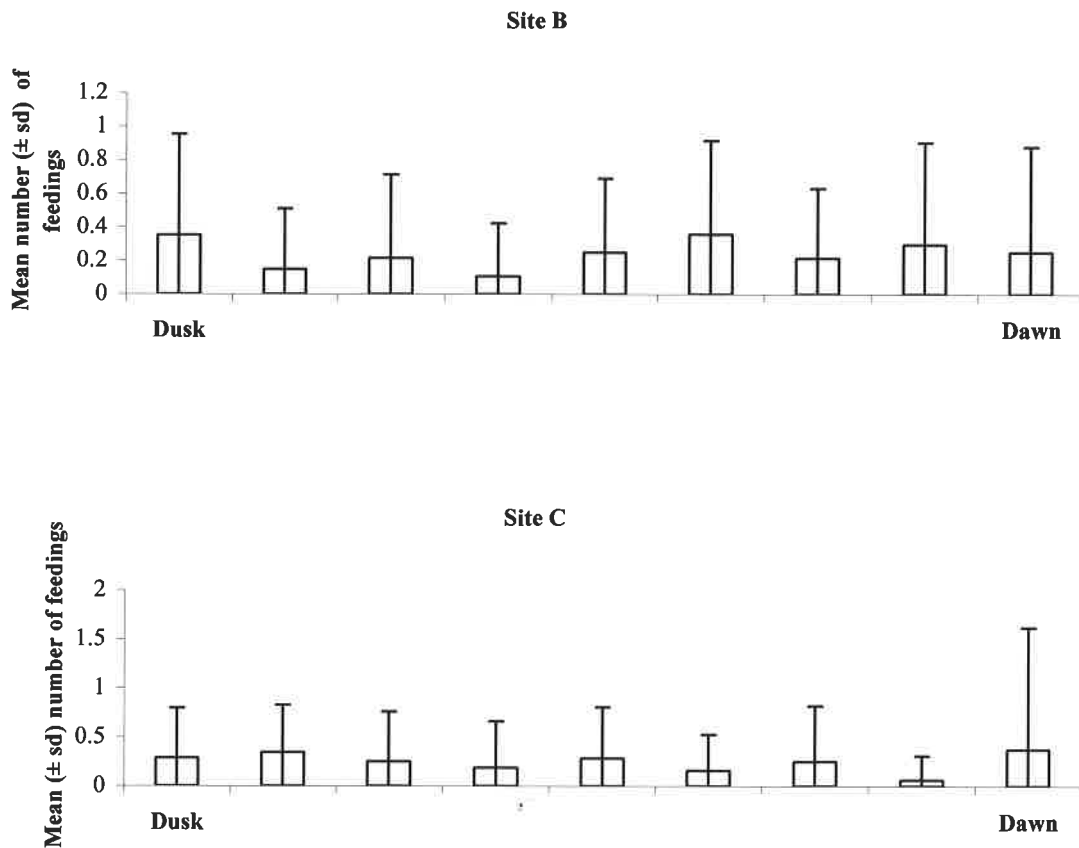


Figure 1: nightly feeding patterns at sites B and C with respect to time: mean (\pm sd) of feedings per hour

3.2 Juvenile dispersal

Altogether 19 juvenile birds from 8 different nests could be radio-tagged. All of them fledged, i.e. reached the age of two months. However, one radio transmitter failed during fledgling stage and 10 juveniles died between fledging and dispersal. Data about dispersal of the 8 remaining birds are shown in Table 6 and in Appendices 1-8. Mean date of first dispersal day was October 1st (median September 20th). The birds left their parents at ages varying between 21 and 29 weeks (mean: 24 weeks; median: 23 weeks). It was not possible to track birds continuously during the whole dispersal phase; knowledge about dispersal of some birds is thus fragmentary. Three birds died during dispersal, probably from starvation (# 1, 5, 8). Three individuals crossed the Alps towards Italy; two of them were lost (# 2, 7), one can still (March 2004) be tracked thanks to its satellite transmitter (# 8). One female bird was electrocuted in her second calendar year after having successfully raised two chicks (# 3). We lost track of the second remaining Eagle owl after 19 months because of battery exhaustion (# 4). From four birds we got at least 7 values about distances covered per night (# 4, 6, 7, 8; Table 7). Mean (\pm sd) individual distances amounted to 12.5 km (\pm 5.7). There were differences among the individuals: Bird 6 flew about 18 km per night while bird 8 only reached a value of 5 km. The maximal nightly distance (30 km) could be measured during dispersal of bird 4. Bird 6 probably reached even higher levels: it covered 90 km in three nights but daily details are missing. Distances between nesting place and the first site where the birds stayed for at least three weeks consecutively were between 5 and 90 km (Table 6). A few examples illustrate the dispersal potential of Eagle owls. Bird 6, one of the three individuals that went to Italy, settled down about 90 km away from its place of birth. After a wide-ranging migration (at least 230 km in about 18 days) bird 4 stayed for almost four months in a temporary home range of 44.5 km² (95% MCP from 211 localisations) only 5–17 km away from its birth place. At the end of March 2003 it left this area on the plain of the Rhône (550 m a.s.l.) and moved for at least one month to a side valley (1200 m - 1900 m a.s.l.). The bird was retrieved only in October 2003 in its initial territory on the plain where it stayed until the tag battery exhaustion (02.2004). Bird 3 covered a distance of at least 150 km till it occupied its reproduction site. On average, the total flown distances that could be followed amounted to at least 124 km (median 141 km), with a maximum value of about 230 km (Table 6). Final distances from birthplace were clearly smaller, which indicates some philopatric behaviour in some birds. Distance from the nest to the place where the birds settled down for at least three weeks (# 3, 4, 6) was 38.7 km.

Table 6: Dispersal data of 8 birds radiotagged as nestlings. Minimum total kilometrage during dispersal, final distance to birthplace and dispersal duration. All distances are measured in km.

Bird #	Approximate date of hatching	Beginning of dispersal	Age at first dispersal day (weeks)	Minimum total kilometrage¹	Final distance to birthplace	Dispersal duration (weeks)
1	04.04.02	end of August 2002	21	15	12.3	-
2	28.03.02	14.09.2002	24.5	53	-	-
3	27.03.02	15. or 16. 09.2002	24.5	150	21	11
4	01.05.02	19. or 20. 11.2002	29	230	5	2.5
5	17.04.02	12. or 13. 09.2002	21	85	62	-
6	24.04.03	25.09.2003	22	157	90	3
7	27.04.03	29.09.2003	22	173	-	-
8	24.04.03	12.11.2003	29	132	8	-

¹: sum of the nightly distances

Table 7: Mean distance covered per night in four birds with at least 7 values of single night movements available. All distances are given in km.

Bird #	N nights	Mean distance/ night	sd	Minimum	Maximum
4	11	14.8	8.4	5	30
6	9	17.9	10.4	2.5	30
7	7	12.5	7.6	5	24
8	8	4.6	1.6	2	7

In total, 12 overflights of mountain ranges with a minimum altitude of 2250 m could be recorded from 7 birds during dispersal. Two crosses even occurred above 3000 m altitude. No preference concerning direction of dispersal could be detected although chicks were all born along the axis of the profound Rhône valley. Juveniles often changed direction during dispersal, following mostly the major valley axes.

3.3 Home range and habitat selection

3.3.1 Home ranges

Female A:

The 95% MCP for winter and summer were almost identical: 12.7 km² and 12.6 km², respectively (Table 8). The globally used area added up to 21.7 km², showing the effect of few outlying points. The maximal distance between the roost and the most distant vertex of the corresponding polygon reached 4.0 km for the 95% MCP, and 5.5 km for the globally used area.

Female C

Home ranges for winter and summer showed almost identical values: 4.5 km² and 5 km², respectively. The globally used area amounted to 29.2 km². The maximal distance between roost and polygon extremities was 2.5 km for the 95% MCP. The longest distance was 7 km when the female engaged in a two-days long excursion in September (Table 8).

Table 8: Seasonal and global home ranges (km²) of two radio tracked females and maximal distances from the roost to the most distant vertex of the 95% MCP (km). The global home range for both seasons and roost locations pooled represents the 100% MCP.

		Winter	Summer	Global
Home range	Site A	12.7	12.6	21.7
	Site C	5.0	4.5	29.2
Maximum distance	Site A	4.0	3.5	5.5
	Site C	2.5	2.2	7.0

3.3.2 Habitat selection

Table 9 shows the results of the habitat selection analysis, with a ranking of area-expressing variables according to their decreasing relevance to the two females A and C (compositional analysis). Table 10 shows univariate statistical comparisons (Mann-Whitney U-test) of habitat variables between bearings and random points for both birds.

Female A

Grassland was the most favourite habitat of this bird, followed by woodland, Megaforbiae and areas with slight vegetation cover (Table 9). In contrast, cropland and settlement were the least used habitats. Considering univariate tests of area-expressing variables, Megaforbiae, woodland, small forest, areas with slight vegetation cover and shrubbery/ hedgerows showed significantly higher values at bearings than at random points; it was the contrary for corn and vegetables/ beets/ potatoes (Table 10). Regarding linear structures and punctual elements, edges of wood had higher values at bearings ($P < 0.0001$) whilst it was the contrary for low voltage power lines and wooden power poles ($P = 0.0312$ and 0.0172 , respectively), with the latter two correlating strongly ($r_s = 0.974$, $P < 0.0001$), alike high and mean voltage power lines vs. steel/ concrete power poles ($r_s = 0.709$, $P < 0.0001$). There were more different landscape elements according to Table 3 around actual bearing locations (mean = 5.3) than around random points (mean = 4.5) (Mann-Whitney U-test, $n_1 = 124$, $n_2 = 122$, $P = 0.0002$); however, Shannon–Wiener–Indices of diversity were $H_s = 1.73$ for bearings and $H_s = 1.91$ for random points.

Female C

This individual preferred slight vegetation cover, followed by grassland, Megaforbiae and shrubbery/ hedgerows. Settlements have the lowest level of usage (Table 9). Regarding univariate tests of area-expressing variables, areas with slight vegetation cover, Megaforbiae and small forests had higher values, while settlement, vegetables/ beets/ potatoes, single buildings, vineyard/ tree nursery and grassland had lower values at actual locations than at random points (Table 10). Considering linear structures and punctual elements, edge of wood and single trees had higher values around bearing locations than around random points ($P = 0.020$ and $P = 0.042$, respectively). This was also the case for high and mean voltage power lines and steel/ concrete power poles ($P = 0.007$ and $P = 0.043$, respectively), which are correlated ($r_s = 0.633$, $P < 0.0001$). Fruit trees were less represented at bearings than at random points ($P = 0.0007$). I could not detect a difference in the number of elements present in the circles around bearings and random points (mean = 6.7 and mean = 6.9 elements, respectively) (Mann-Whitney U-test, $p = 0.39$). Shannon–Wiener–Indices of diversity were $H_s = 2.21$ for bearings and $H_s = 2.17$ for random points.

Table 9: Results of a compositional analysis run for females A and C during the breeding season. Variables are ranked (from top to bottom) according to their decreasing relevance to the bird. Variables within lines did not differ among each other with respect to relevance.

Female A	Female C
Grassland	Area with slight vegetation cover
Woodland	Grassland
Megaforbiae	Megaforbiae
Area with slight vegetation cover	Shrubbery/ hedgerow
Shrubbery/ hedgerow	Asphalted
Asphalted	Small forest
Park	Building
Small forest	Bare cropland
Building	Park
River	Pond
Bare cropland	River
Settlement	Woodland
Corn	Vegetables/ beets/ potatoes
Vegetables/ beets/ potatoes	Vineyard/ tree nursery
	Corn
	Settlement

Table 10: Statistical comparisons (Mann-Whitney U-test, $n_1 = 124$, $n_2 = 122$ for female A; $n_1 = n_2 = 85$ for female C) of habitat variables at actual bearings (n_1) vs. random points (n_2) within breeding home range. P-values are indicated. +: over-used, -: under-used. Significant differences in bold. Variables below the horizontal line are linear structures and punctual elements.

	Female A		Female C	
Megaforbiae	0	+	0.009	+
Woodland	<.0001	+	0.551	-
Small forest	0.006	+	0.029	+
Area with slight vegetation cover	0.011	+	<.0001	+
Shrubbery/ hedgerow	0.026	+	0.306	+
Grassland	0.082	+	0.036	-
Bare cropland	0.997	+	0.092	+
River	0.791	-	0.495	-
Park	0.723	-	0.311	+
Asphalted	0.315	-	0.078	-
Single building	0.293	-	0.026	-
Settlement	0.054	-	0.0003	-
Vegetables/ beets/ potatoes	<.0001	-	0.011	-
Corn	<.0001	-	0.323	-
Pond			0.059	+
Vineyard/ tree nursery			0.035	-
Edge of wood	<.0001	+	0.020	+
Steel/ concrete power poles (high voltage)	0.325	+	0.043	+
Single trees	0.487	+	0.042	+
High voltage power line	1	+	0.007	+
Wooden power pole (low voltage)	0.017	-	0.421	-
Low voltage power line	0.031	-	0.412	-
Fruit trees	0.073	-	0.0007	-

4. Discussion

4.1 Nestling diet

Most studies about food composition of Eagle owls are based upon analysis of pellets and remains found around nest and/ or perch sites (Richard 1923; Desfayes & G eroudet 1949; Desfayes 1951; Bezzel & Lechner 1968; Wagner & Springer 1970; Orsini 1985; Bayle 1987a; Bayle et al. 1987; Arlettaz 1988; Darolova 1990; Martinez et al. 1992; Wadewitz & Nicolai 1993; Bayle 1994; Dalbeck 1996; Rathgeber & Bayle 1997; Cekoni-Hutter 1998; Leditznig 1999; Dalbeck 2000; Serrano 2000; Leditznig et al. 2001; Martinez & Zuberogoitia 2001; Marchesi et al. 2002a; Marchesi et al. 2002b; Penteriani et al. 2002; Dalbeck 2003; Penteriani et al. 2003). The advantage of the video technique we used is that it is unbiased contrary to other methods (Simmons et al. 1991; Bielefeldt et al. 1992; Marchesi et al. 2002a; Marchesi et al. 2002b). Also, video filming allows the collection of data on the actual biomass supplied as well as on feeding schedules. One disadvantage of the video technique is that it does not reach the same taxonomic precision as the study of prey remains. I often had problems to identify prey items because they were decapitated or plucked when delivered to the nest (Desfayes & G eroudet 1949; Desfayes 1951; Wagner & Springer 1970; Glutz von Blotzheim & Bauer 1980; M arz & Piechocki 1980; G orner 1987). Another technical problem occurred: we focused the lens for infrared conditions, which gave unsharp pictures at twilight. At site B the distance from camera to the nest site was 30 m, which rendered difficult the recognition of fine details. At site C, we could not film the entire niche. In addition some prey were delivered to the chicks before dusk and after dawn, outside our monitoring window. In these cases prey were taken from caches close to the eyrie where adults had stored them, a typical behaviour of the Eagle owl (Glutz von Blotzheim & Bauer 1980; M arz & Piechocki 1980; Mebs & Scherzinger 2000). Nevertheless I could identify at both sites about 95% of prey items at least down to the level of genus.

4.1.1 Food composition

All studies of Eagle owl diet mention a dominance of mammals as regards item frequency (Burnier & Hainard 1948; Desfayes & G eroudet 1949; Bezzel & Lechner 1968; Orsini 1985; Bayle 1987a; Darolova 1990; Martinez et al. 1992; Wadewitz & Nicolai 1993; Bayle 1994; Rathgeber & Bayle 1997; Cekoni-Hutter 1998; Serrano 2000; Leditznig et al. 2001; Marchesi et al. 2002a; Marchesi et al. 2002b; Penteriani et al. 2002; Dalbeck 2003). This is confirmed by our study. In biomass terms, however, birds often appear more

important than mammals (Desfayes 1949, biomass estimated a posteriori by myself; Bezzel & Lechner 1968; Wagner 1970; Leditznig et al. 2001). The contribution of dormice to diet in this study, especially fat dormouse *Glis glis*, is very high (frequency: 33.3%, biomass: 20.9%). Dalbeck (2000) noticed an East-West gradient in the contingent of Gliridae in the diet of Eagle owls in Europe with highest values in southern France. He emphasised Valais as the most eastern part of the Alps with notable amounts of dormice, referring to the study by Desfayes (1949, 8.7% of frequency with 6.1% *Glis glis*). Interestingly, at another Valais site at 2000 m elevation garden dormice *Eliomys quercinus* tended to be the principal resource (Burnier & Hainard 1948), whilst at another site in Valais (1750 m) Richard (1923) found at least 10 garden dormice in pellets and remains. High amounts of Gliridae in the diet of Eagle owls (23% frequency, 8.5% biomass) found in the central-eastern Alps in Italy (Trento), about 300 km east of Central Valais, contradict the cline suspected by Dalbeck (Marchesi et al. 2002a; Marchesi et al. 2002b). In Switzerland, fat dormice are limited to areas below 1500 m where they can reach densities up to 5 inds/ ha, while garden dormice can be found up to 2100 m altitude (Hausser 1995). No data about fat dormouse densities are available in Valais, but the species might be especially abundant in apricot orchards. Due to their body mass (ca. 125 g) and noisy habits, fat dormice might represent optimal prey for Eagle owls. According to previous studies Eagle owls can be regarded as food opportunists whose composition of diet depends largely on the relative abundance and accessibility (i.e. availability) of prey (Desfayes & G eroudet 1949; Hiraldo et al. 1976; Frey 1981; Mikkola 1983; Bayle et al. 1987; Arlettaz 1988; Arlettaz et al. 1990; Sulkava et al. 1991; Martinez et al. 1992; Mebs & Scherzinger 2000; Leditznig et al. 2001; Martinez & Zuberogitia 2001; Marchesi et al. 2002a; Marchesi et al. 2002b; Penteriani et al. 2002; Dalbeck 2003). Additionally, Dalbeck (2003) stresses that the feeding strategy during offspring rearing seems to be a compromise between the duration of searching for prey, the duration and costs of transfer flight of prey to the nest, and the mass of the item, according to the "optimal foraging" hypothesis (Krebs & Davies 1993). Fat dormice may represent the best option in this regard for the Eagle owls in some regions of the Upper Rh one valley. Dalbeck (2003) reached a similar conclusion as regards some Eagle owl pairs in Germany which fed heavily on *Microtus arvalis*. Richard (1923) and Wagner (1970) also reported a high proportion of small mammals. Overall, however, optimal foraging theory may explain why the presence of small mammals is anecdotal in Eagle owl's diet. A priori it seems evident that evolution has promoted mutual predator prey relationships in which predator's body size is in part an adaptive response to prey size. As regards small mammals, which partitioning must be an integrative part of owl guild structure. In this

respect, Eagle owls, due to their larger body size, ought to specialize upon medium-sized prey which are not exploited by other nocturnal, smaller sized raptors.

4.1.2 Feeding patterns

The average biomass delivered per night and nestling was very similar at both sites (about 185 g). The underlying variation shows, however, that biomass was not equally distributed between nights. At both sites, no delivery of prey was registered during several nights while in other nights high amounts of biomass were brought in form of big mammals. Ceska (1978) indicated an average food consumption of about 230 g for adult birds. In the Zoos of Zurich and Bern, Eagle owls are fed with 150 to 200 g biomass of prey daily (G. Hürlimann; M. Rosset, pers. comm.). Our figures for free-ranging birds are minimum values given that we may have missed some feedings before dusk and after dawn. It is thus very likely that our juveniles didn't suffer from food deprivation. The death of chicks at site B probably originated from a viral infection (*Hepatosplenitis infectiosa strigum*) which appears to be transmitted orally through the ingestion of pigeons (H. Frey, pers. comm.). We could see on the recordings that chicks refused the food provisioned by parents, a typical symptom of this infection (H. Frey, pers. comm.). Also other studies allude to diseases in Eagle owl (Langgemach et al. 2000; Stubbe & Stubbe 2000; Leditznig et al. 2001). Diseases possibly have a not negligible impact on population dynamics in Eagle owl. Although some studies ascertained that most prey is delivered to the nest around twilight (Frei 1969; Blondel & Badan 1976), we could not detect such patterns.

4.2 Juvenile dispersal

Some studies provide information about dispersal distance in juveniles based on recovery of ringed birds (Desfayes 1951; Olsson 1979; Glutz von Blotzheim & Bauer 1980; Mikkola 1983; Tucker & Heath 1994; Mebs & Scherzinger 2000). This does not allow the recognition of the exact flight routes of dispersing birds, contrary to the radiotracking method used here (Olsson 1979). Comparisons are therefore limited. Ringing-recapture data report distances of dispersal up to 80 km away from place of birth (Desfayes 1951; Olsson 1979; Glutz von Blotzheim & Bauer 1980), although some studies mention 200 and even 400 km (Glutz von Blotzheim & Bauer 1980; Tucker & Heath 1994), the latter figure concerning an individual released from captivity. Leditznig (1999), who studied

juvenile dispersal by means of radiotracking in Austria, reports mean total distances of 222 km, i.e. higher than ours (124 km). On average, Austrian birds finally settled down 84 km away from their place of birth (39 km in our study). In contrast daily stages of the Swiss birds were longer than in Austria (12.5 vs. 8.9 km). One of our birds showed small values as it starved 7 weeks after dispersal beginning. In both radiotracking studies in Austria and Switzerland (this study) the maximal detected distance flown in a single night was around 30 km although most nightly movements were clearly shorter. Considering a flight speed up to 60 km/h (pers. obs.), these distances appear quite short. This indicates that during dispersal movements the birds were scanning the region overflowed in search of good feeding grounds, although the presence of suitable roosting sites or even mates may also have played a role. This could partly explain why some of our radiotagged birds, after dispersal of about 100 km, returned back to an area they already knew. Olsson (1979) showed that old birds were found closer to the nest they were born than young ones. He assumed hence that either far-flying young died in distant areas or survived, gradually returning home. This would be supported by dispersal patterns in two of our birds. Haller (1978) supposed valleys to canalise dispersal movements. This was partly the case in this study since birds mostly followed valley axes although they left valleys several times and crossed mountain chains at high altitude. Our data on the initiation of dispersal agree with other studies: young leave their parents' territory from August to November (Olsson 1979; Marchesi 2002). Yet, in Austria, birds left their parents generally about one month later than the individuals in this study (Leditznig 1999). One major lesson of our investigation of dispersal is that gene flow among alpine and surrounding populations is potentially high; the Valais population might therefore be regarded as a non-isolated population belonging to a metapopulation whose limits are far beyond the Alpine massif. Through this radiotracking study we could also establish that mortality during juvenile dispersal is high since 38% of the young died during that phase. It adds up to 56% of the juveniles dying in their parents' territory, after they had started to fly. This sort of data upon population dynamics can hardly be collected with indirect methods such as ringing.

4.3 Home range and habitat selection

4.3.1 Home ranges

We found no difference in the area of winter and summer home ranges contrary to former descriptions (Glutz von Blotzheim & Bauer 1980; Leditznig 1999). Short temporary trips, partially to remote sites, explain why the global home range was clearly larger than the 95% polygon. Compared with most other estimations, our home range sizes are small (about 12.5 km² at site A and 5 km² at site C). Another radiotracking study reports 26-128 km² (Leditznig 1999). In 3 ♂♂, Leditznig (1999) could show a reduction of home range size during breeding to 23–26 km² which represented a small proportion of the total home range. For a female who had to feed the offspring by herself because the male died, Dalbeck (2002) detected 4.7 km as maximal distance to the nest. He assessed home ranges to be between 10 and 100 km² (Dalbeck et al. 1998). Mikkola (1983) points out that the average size of an Eagle owl's territory and its hunting range around the nest site mainly depends upon the amount of available prey in the area. Leditznig (1999) suspects that there is a negative correlation between food availability and home range size too. This suggests good feeding opportunities for the two Eagle owl pairs we investigated.

4.3.2 Habitat selection

Our analysis of habitat selection relied principally on observations of stationary, perched birds. We assumed that all bearings collected in that manner referred to hunting activity, although this may not hold true for all locations. Compositional analysis gives us a more sophisticated estimation of preferences of area-expressing habitat categories than univariate tests. The latter do not respect data independency because their percentages sum up to 100%. These differences may explain why for some habitat types (especially grassland) contradictory results were obtained with the two methods.

The clear preference for open habitat such as grassland and areas with slight vegetation cover detected in our two females agrees with many other studies (Wagner & Springer 1970; Glutz von Blotzheim & Bauer 1980; März & Piechocki 1980; Mikkola 1983; Bayle 1994; Leditznig 1999; Mebs & Scherzinger 2000). However, dense cropland and vineyard reached a very low ranking in our compositional analysis. One reason might be the low prey availability of these monocultures. Additionally, vegetation cover of more than 60-70 cm seriously hinders hunting (Leditznig 1999). Bare cropland was more used than the other types of farmland, except grassland. Yet, this habitat type was mostly

represented by recently mown cereal and maize fields, whose resources may have attracted potential prey, although the lack of hunting perches may reduce the attractiveness of this habitat to Eagle owls. Orchards, which can be seen as semi-open habitat, were clearly under-used. A striking difference between my analysis and many other studies of habitat selection in Eagle owls is the low level of usage of water habitats (Leditznig 1999; Leditznig et al. 2001; Buzzi & Tavernier 2002). This may be due to fauna-poor water habitats in Valais. Scrubland and hedgerows, a selected habitat at site C, concerned an area with a dense rabbit population. In south-eastern Spain, where rabbits made up over 80% of biomass, scrubland was an important habitat of Eagle owls (Martinez et al. 1992). Edges of wood were used over-proportionally by one of our two females. This may be due to the fact that Eagle owls spend a large part of their nightly activity sitting on elevated perches (Wagner & Springer 1970). Bird C very often used power poles as stands. In its home range the average number of available power poles was close to 1/ ha. In Leditznig's study (1999) the most used areas were meadowland and cropland interspersed with single trees or small groups of trees which were used as hunting perches. An over-use of single trees at site C was also evidenced. Yet, it could be noticed that habitat interfaces, such as edges of wood probably offer more feeding opportunities. Several authors described dense forests as unsuitable to Eagle owls (Haller 1978; Glutz von Blotzheim & Bauer 1980; März & Piechocki 1980; Mikkola 1983; Bayle 1994; Mebs & Scherzinger 2000; Leditznig et al. 2001; Penteriani et al. submitted). On the few occasions I could localise a bird in woodland, it was along forest tracks. Leditznig (1999) also reports commuting and suspects hunting along these paths. The two birds we tracked were both hunting in a landscape which was characterized by intensive agriculture, although agricultural habitats were little used. At site A, where huge areas are covered with monocultures, localisation points showed a higher number of habitat variables than the random points. At site C, diversity at random points was even higher than at localisation points at site A. The importance of highly structured territories was already highlighted in several other publications (Glutz von Blotzheim & Bauer 1980; März & Piechocki 1980; Mosimann-Kampe et al. 1998; Mebs & Scherzinger 2000). Over wide parts of their distribution ranges Eagle owls may well have lost extensive suitable foraging habitats throughout intensification of agricultural practices which have massively, negatively affected the landscape matrix that has become almost everywhere very monotonous.

4.3.3 Diet versus habitat selection

When comparing the results from habitat selection analysis and food composition at site C, an apparent contradiction was found: the tracked female did mostly use open habitat. Woodland was not used preferentially and orchards were even avoided. These are typical habitats of fat dormice, one of the dominant prey delivered to the nest (Hausser 1995; Richarz 2003). However, it was the male who delivered most prey, the female staying most of the time in the nest cliff. This indicates that the two sexes differed in habitat selection and/ or predation strategies as suggested by Wagner (1970). Sex-specific adaptations to diverging prey sizes and therefore spectra may result from sexual dimorphism, the male being ca. 20% smaller than the female in *Bubo bubo* (Mebs & Scherzinger 2000). This could explain why so few hedgehogs and rabbits were present in the provisioned food despite both prey abundant in nest surroundings. Also, while tracked in winter and late summer, the same female was observed three times eating on rabbits and three times on hedgehogs. Alternatively, energetic constraints could also play a role. Males might be able to subdue hedgehogs or rabbits but may have problems to transport them from the hunting grounds on the plain to the nest which is situated 150 m higher up on the slope. Note that these two hypotheses are not mutually exclusive. As our video filming concerned the period when the mother stayed in the vicinity of the eyrie most of the time, our sample must be biased towards smaller prey items. This may possibly explain why other studies, even those carried out in Valais (Richard 1923; Desfayes & Géroutet 1949) mention so frequently hedgehogs in remains collected at and around breeding sites, contrary to our study. Further investigations are needed to understand whether males and females actually differ in their predatory strategies, and hence habitat preferences, or whether mere energetic constraints dictate the circumstances of prey provisioning to chicks.

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Literature

- Aebischer, N. J., V. Marcström, R. E. Kenward, and M. Karlbom. 1993a. Survival and habitat utilisation: A case for Compositional Analysis. Pages 343-353 in J.-P. Lebreton, and P. M. North, editors. *Marked individuals in the study of bird population*. Birkhäuser Verlag, Basel.
- Aebischer, N. J., and P. A. Robertson. 1992. Practical aspects of compositional analysis as applied to pheasant habitat utilization. Pages 285-296 in S. M. Swift, editor. *Wildlife Telemetry. Remote Monitoring and Tracking of Animals*. Ellis Horwood, Chichester.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993b. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**:1313-1325.
- Arlettaz, R. 1988. Statut du Hibou Grand-Duc, *Bubo bubo*, en Valais central. *Bulletin de la Murithienne* **106**:3-23.
- Arlettaz, R., G. Carron, J. Curchod, J. M. Fivat, J. Fournier, N. Jordan, J. Lehman, R. Lévêque, A. Lugon, P. A. Oggier, B. Posse, J. C. Praz, J. Trüb, A. Sierro, and O. Zuchuat. 1990. Déclin et retour du Hibou grand-duc, *Bubo bubo*, dans les Alpes valaisannes (sud-ouest de la Suisse): vers une explication causale? Pages 189-193 in M. Juillard, editor. *Rapaces Nocturnes. Nos Oiseaux*, Porrentruy.
- Bayle, P. 1987a. Découverte des restes d'un aigle de Bonelli *Hieraetus fasciatus* juvenile dans une aire de hibou grand-duc *Bubo bubo* en Provence. *Faune de Provence* **8**:49-53.
- Bayle, P. 1987b. Mise à jour des données concernant la répartition du Molosse de Cestoni *Tadarida teniotis* en Provence. *Faune de Provence* **8**:16-17.
- Bayle, P. 1994. Régime alimentaire du Grand-duc d'Europe *Bubo bubo* dans le parc national du Mercantour et ses environs (Alpes du Sud, France). *Les Oiseaux de Montagne, Actes du 32e colloque interregional d'ornithologie, Grenoble (France)*:147-175.
- Bayle, P., P. Orsini, and J. Boutin. 1987. Variations du régime alimentaire du Hibou grand-duc *Bubo bubo* en période de reproduction en Basse-Provence. *L'Oiseau et la Revue Française d'Ornithologie* **57**:23-31.
- Berndt, R., and H. Sternberg. 1969. Über Begriffe, Ursachen und Auswirkungen der Dispersion bei Vögeln. *Vogelwelt* **90**:41-53.

- Bezzel, E., and F. Lechner. 1968. Zur Ernährung eines südbayerischen Uhu-paares (*Bubo bubo*). *Ornithologische Mitteilungen* **20**:23-24.
- Bielefeldt, J., R. N. Rosenfield, and J. M. Papp. 1992. Unfounded assumption about the diet of the Cooper's Hawk. *Condor* **94**:427-436.
- Blondel, J., and O. Badan. 1976. La biologie du Hibou grand-duc en Provence. *Nos Oiseaux* **33**:189-219.
- Brodbeck, R. 2004. Astrollexikon - Javascript zu den Formeln. <http://lexikon.astronomie.info/zeitgleichung/sunscript.html>.
- Burnier, J., and R. Hainard. 1948. Le Grand-duc chez lui. *Nos Oiseaux* **19**:217-236.
- Buzzi, T., and G. Tavernier. 2002. Prospection, étude et suivi du Grand duc d'Europe *Bubo bubo* en Midi-Pyrénées 1999-2002.
- Cekoni-Hutter, B. M. 1998. Zur Verbreitung und Nahrungsökologie des Uhus (*Bubo b. bubo*) in Kärnten mit besonderer Berücksichtigung der Wechselbeziehung zum Wanderfalken (*Falco p. peregrinus*). Page 150. Institut für Parasitologie und Zoologie. Veterinärmedizinische Universität, Wien.
- Ceska, V. 1978. Nahrungsbedarf und Energiehaushalt bei verschiedenen Eulenarten im Jahresverlauf und Anwendung dieser Ergebnisse auf das Freiland. *Naturwissenschaftliche Fachbereiche. Friedrich-Alexander-Universität, Erlangen-Nürnberg*.
- Dalbeck, L. 1996. Die Bedeutung von Hausratte (*Rattus rattus*) und Wanderratte (*Rattus norvegicus*) für die Ernährung des Uhus in Eifel und Saarland. *Säugetierkundliche Informationen* **20**:155-162.
- Dalbeck, L. 2000. Schläfer (Rodentia: Gliridae) als Beute der Uhus - *Bubo bubo* - im nordwestlichen Mittelgebirgsraum. *Fauna Flora Rheinland-Pfalz* **9**:533-547.
- Dalbeck, L. 2003. Der Uhu *Bubo bubo* in Deutschland - autökologische Analysen an einer wieder angesiedelten Population - Resümee eines Artenschutzprojekts. Page 159. Zoologisches Forschungsinstitut & Museum Alexander König. Bonn, Bonn.
- Dalbeck, L., W. Bergerhausen, and O. Krischer. 1998. Telemetriestudie zur Orts- und Partnertreue beim Uhu *Bubo bubo*. *Die Vogelwelt* **119**:337-344.
- Dalbeck, L., and W. Breuer. 2001. Der Konflikt zwischen Klettersport und Naturschutz am Beispiel der Habitatansprüche des Uhus (*Bubo bubo*). *Natur und Landschaft* **76**:1-7.
- Darolova, A. 1990. Food composition in the Eagle-Owl (*Bubo-bubo*-Linnaeus, 1758) in small carpathians. *Biologia* **45**:831-840.
- Delarze, R., Y. Gonseth, and P. Galland 1999. Lebensräume der Schweiz, Thun.
- Desfayes, M. 1951. Nouvelles notes sur le Grand-duc. *Nos Oiseaux* **21**:121-126.

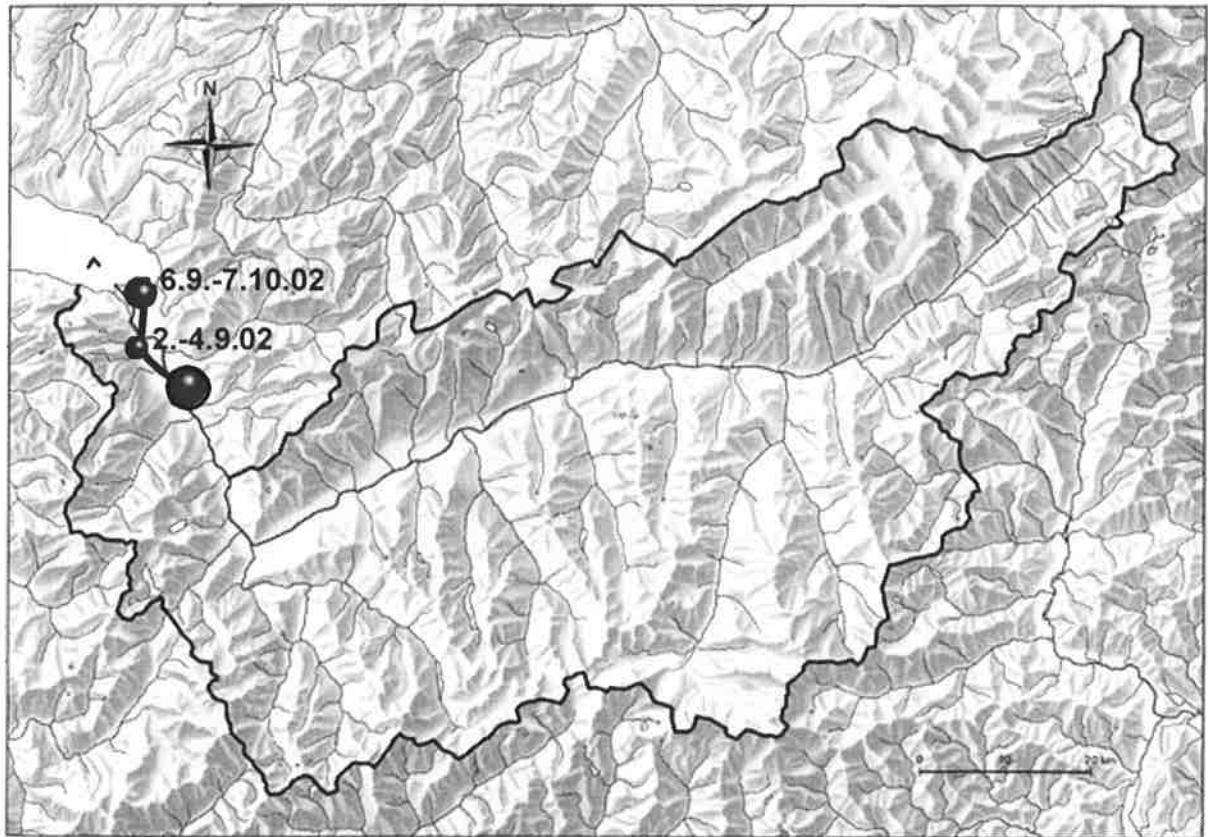
- Desfayes, M., and P. Géroutet. 1949. Notes sur le Grand-duc *Bubo bubo* (L.). Nos Oiseaux **20**:49-60.
- Frei, P. 1969. Beobachtungen zur Brut und Ernährungsbiologie des Uhus im Oberengadin. Zoologisches Institut. Universität Zürich, Zürich.
- Frey, H. 1973. Zur Ökologie niederösterreichischer Uhuspopulationen. Egretta **1/2**:1-68.
- Frey, H. 1981. Vorkommen und Gefährdung des Uhus in Mitteleuropa. Ökologie der Vögel **3**:293-299.
- Glutz von Blotzheim, U., and K. M. Bauer 1980. Handbuch der Vögel Mitteleuropas. Akademische Verlagsgesellschaft, Wiesbaden.
- Görner, M. 1987. Zur Ernährungsökologie des Uhus (*Bubo bubo*). Populationsökologie Greifvogel- und Eulenarten **1**:453-459.
- Görner, M., and H. Hackethal 1988. Säugetiere Europas. Ferdinand Enke Verlag, Deutscher Taschenbuch Verlag, Stuttgart, München.
- Haller, H. 1978. Zur Populationsökologie des Uhus *Bubo bubo* im Hochgebirge: Bestand, Bestandesentwicklung und Lebensraum in den Rätischen Alpen. Der Ornithologische Beobachter **75**:237-265.
- Harris, S., W. J. Cresswell, P. G. Forde, W. J. Trehwella, T. Woollard, and S. Wray. 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review **20**:97-123.
- Hausser, J., editor. 1995. Säugetiere der Schweiz. Birkhäuser, Basel.
- Hiraldo, F., F. F. Parreno, J. Andrada, and F. Amores. 1976. Variations in the food habits of the European Eagle Owl (*Bubo bubo*). Donana-Acta Vertebrata **3**:137-156.
- Keller, V., N. Zbinden, H. Schmid, and B. Volet 2001. Rote Liste der gefährdeten Brutvogelarten der Schweiz. Bundesamt für Umwelt, Wald und Landschaft, Bern.
- Krebs, J. R., and N. B. Davies 1993. An introduction to behavioural ecology. Blackwell Science Ltd., Oxford.
- Langgemach, T., P. Sömmer, A. Aue, U. Wittstatt, and O. Krone. 2000. Vergleichende Untersuchungen zu den Verlustursachen einheimischer Eulen in der Mark Brandenburg. Populationsökologie Greifvogel- und Eulenarten **4**:473-490.
- Leditznig, C. 1992. Telemetriestudie am Uhu (*Bubo bubo*) im niederösterreichischen Alpenvorland – Methodik und erste Ergebnisse. Egretta **35**:69-72.
- Leditznig, C. 1999. Zur Ökologie des Uhus im Südwesten Niederösterreichs und den donau nahen Gebieten des Mühlviertels. Nahrungs-, Habitat- und Aktivitätsanalysen auf Basis von radiotelemetrischen Untersuchungen. Page 200. Institut für Wildbiologie und Jagdwirtschaft. Universität für Bodenkultur, Wien.

- Leditznig, C., W. Leditznig, and H. Gossow. 2001. 15 Jahre Untersuchungen am Uhu (*Bubo bubo*) im Mostviertel Niederösterreichs - Stand und Entwicklungstendenzen. *Egretta* **44**:45-73.
- Loos, K. 1906. Der Uhu in Böhmen nebst einigen Notizen über die Verbreitung dieser Eule in einigen anderen Ländern, Saaz.
- Lüps, P., R. Hauri, H. Herren, H. Märki, and R. Ryser. 1978. Die Vogelwelt des Kantons Bern. *Orn. Beob.* **75**, supplement.
- Marchesi, L., P. Pedrini, and F. Sergio. 2002a. Biases associated with diet study methods in the eurasian Eagle-Owl. *J. Raptor Res.* **36**:11-16.
- Marchesi, L., F. Sergio, and P. Pedrini. 2002b. Costs and benefits of breeding in human altered landscapes for the eagle owl *Bubo bubo*. *Ibis* **144**:164-177.
- Martinez, J. A., and I. Zuberogoitia. 2001. The response of Eagle Owl (*Bubo bubo*) to an outbreak of the rabbit haemorrhagic disease. *Journal für Ornithologie* **142**:204-211.
- Martinez, J. E., M. A. Sanchez, D. Carmona, J. A. Sanchez, A. Ortuno, and R. Martinez. 1992. The ecology and conservation of the Eagle owl *Bubo bubo* in Murcia, south-east Spain. Pages 84-88 in C. A. Galbraith, I. R. Taylor, and S. Percival, editors. *The ecology and conservation of European owls*. UK Nature Conservation, No 5.
- März, R., and R. Piechocki 1980. Der Uhu *Bubo bubo*, Wittenberg Lutherstadt.
- Mebs, T., and W. Scherzinger 2000. *Die Eulen Europas*. Kosmos, Stuttgart.
- Mikkola, H. 1983. *Owls of Europe*. T & A D Poyser.
- Mosimann-Kampe, P., H. Haller, and R. Arlettaz. 1998. Verbreitung und Bestand des Uhus *Bubo bubo* in der Schweiz. *Der Ornithologische Beobachter* **95**:143-151.
- Olsson, V. 1979. Studies on a population of Eagle owls, *Bubo bubo* (L.) in Southeast Sweden. *Swedish Wildlife Research* **11**:3-93.
- Orsini, P. 1985. Le régime alimentaire du hibou Grand-duc *Bubo bubo* en Provence. *Alauda* **53**:11-28.
- Pedroli, J.-C., B. Zaugg, and A. Kirchhofer 1991. *Verbreitungsatlas der Fische und Rundmäuler der Schweiz*. Schweizerisches Zentrum für die kartographische Erfassung der Fauna, Neuchâtel.
- Penteriani, V., M. Ferrer, F. Sergio, M. Del Mar Delgado, and M. Gallardo. 2003. Habitat Heterogeneity affects diet composition: a case example with the Eagle owl. *J. Wildl. Manage.* **in press**.
- Penteriani, V., M. Gallardo, and M. Ferrer. submitted. Spatial heterogeneity and structure of bird populations: a case example with the Eagle owl. **submitted**

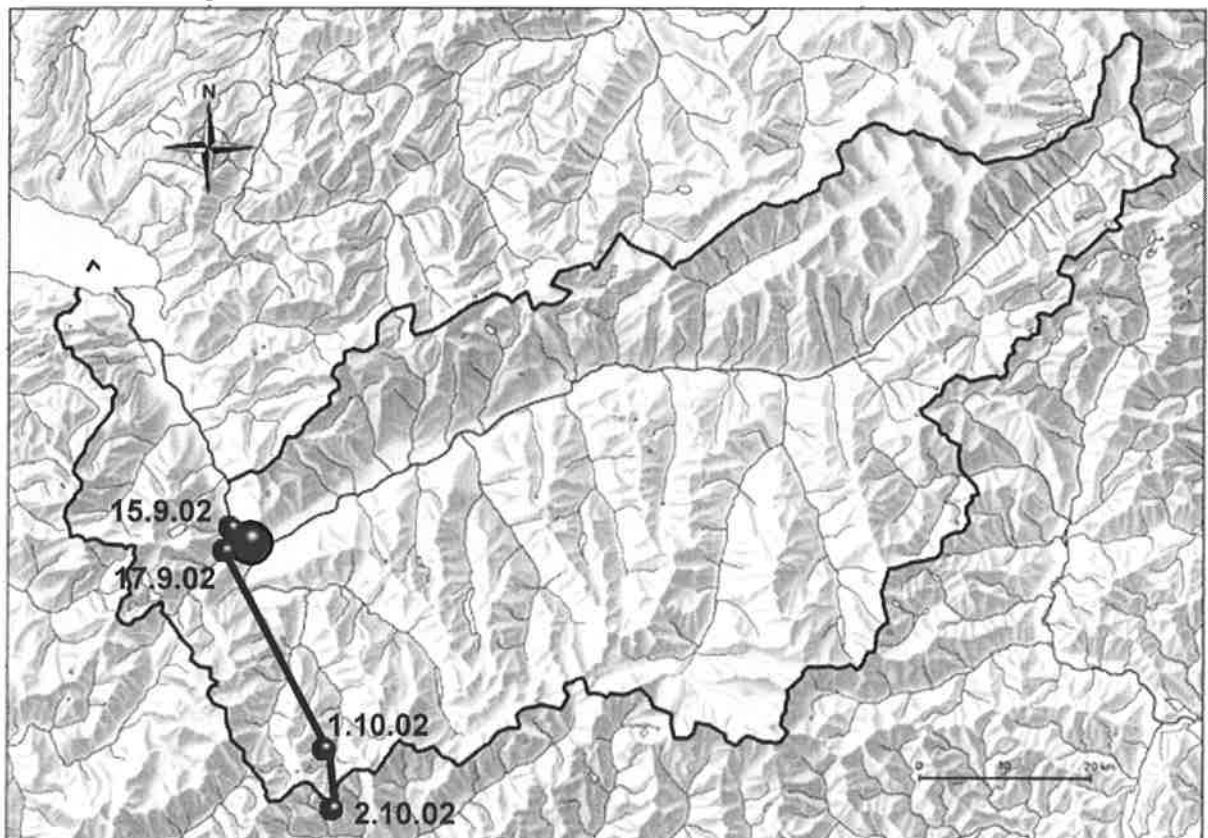
- Penteriani, V., M. Gallardo, and P. Roche. 2002. Landscape structure and food supply affect eagle owl (*Bubo bubo*) density and breeding performance: a case of intra-population heterogeneity. *J. Zool. Lond.* **257**:365-372.
- Rathgeber, C., and P. Bayle. 1997. Régime alimentaire du Grand-duc d'Europe *Bubo bubo*, en période de reproduction, dans la région de Menton (Alpes-Maritimes, France). *Alauda* **65**:351-356.
- Reichholf, J. 1983. Säugetiere. Mosaik Verlag, München.
- Richard, A. 1923. Le Grand-Duc dans les Alpes. *Nos Oiseaux* **6**:65-74.
- Richarz, K. 2003. Säugetiere. Verlag Eugen Ulmer, Stuttgart.
- Schifferli, A., P. Géroutet, and R. Winkler 1980. Verbreitungsatlas der Brutvögel der Schweiz, Sempach.
- Schmid, H., M. Burkhardt, V. Keller, and P. Knaus 2001. Die Entwicklung der Vogelwelt in der Schweiz. Schweizerische Vogelwarte, Sempach.
- Schmid, H., R. Luder, B. Naef-Daenzer, R. Graf, and N. Zbinden 1998. Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993-1996. Schweizerische Vogelwarte, Sempach.
- Serrano, D. 2000. Relationship between raptors and rabbits in diet of Eagle Owls in southwestern Europe: Competition removal or food stress? *Journal of Raptor Research* **34**:305-310.
- Simmons, R. E., D. M. Avery, and G. Avery. 1991. Biases in diets determined from pellets and remains: correction factors for a mammal and bird-eating raptor. *Journal of Raptor Research* **25**.
- Snow, D. W., and C. M. Perrins 1998. *The Birds of the Western Palearctic*. Oxford University Press, Oxford.
- Stubbe, M., and A. Stubbe. 2000. Populationsökologie von Greifvogel und Eulenarten. 4. Internationales Symposium "Populationsökologie von Greifvogel und Eulenarten". Gesellschaft für Wildtier- und Jagdforschung e.V.; Institut für Zoologie, Martin-Luther-Universität Halle-Wittenberg, Meisdorf/ Harz.
- Sulkava, S., E. Korpimäki, and K. Huhtala. 1991. Kleinsäugerzyklen und die Nahrungsökologie der Eulen in Finnland. *Populationsökologie Greifvogel- und Eulenarten* **2**:423-433.
- Tucker, G. M., and M. F. Heath 1994. *Birds in Europe: their conservation status*. BirdLife International, Cambridge.
- Wadewitz, M., and B. Nicolai. 1993. Nahrungswahl des Uhus *Bubo bubo* im nordöstlichen Harzvorland. *Ornithologische Jahresberichte des Museum Heineanum* **11**:91-106.

- Wagner, G., and M. Springer. 1970. Zur Ernährung des Uhus *Bubo bubo* im Oberengadin. *Der Ornithologische Beobachter* 67:77-94.
- White, G. C., and R. A. Garrott 1990. *Analysis of Wildlife Radio-Tracking Data*. Academic Press, Inc., San Diego.

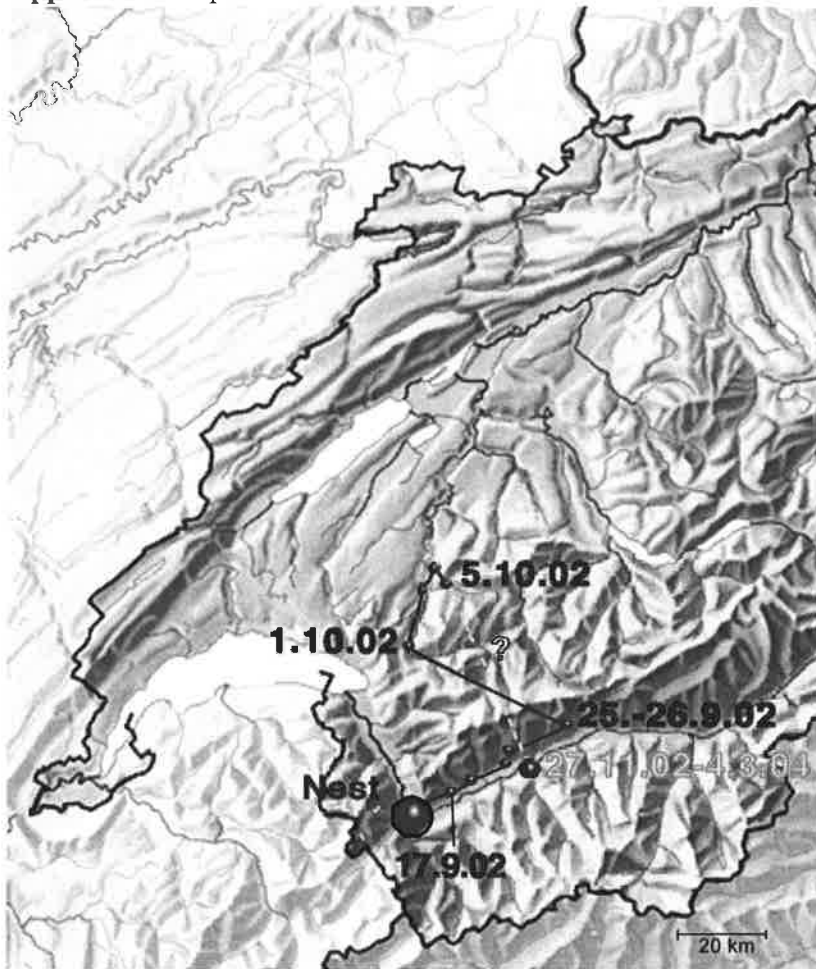
Appendix 1: Dispersal route of bird # 1



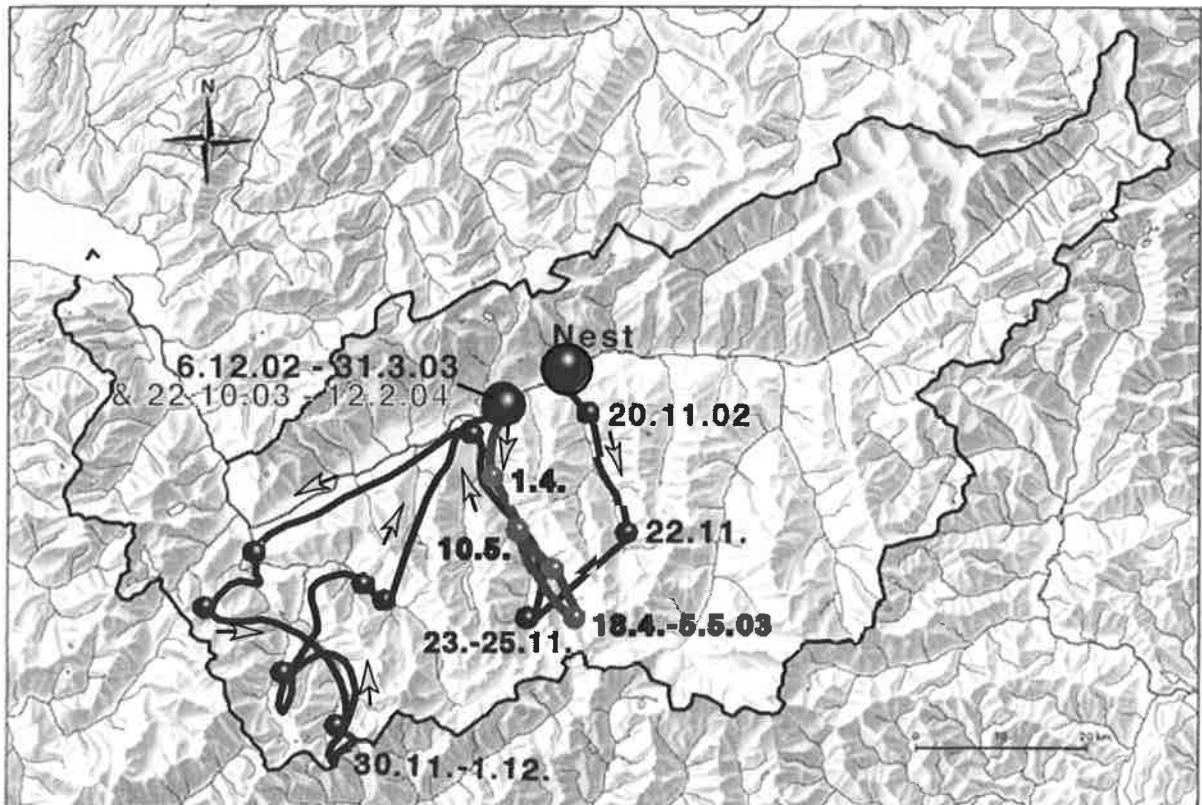
Appendix 2: Dispersal route of bird # 2



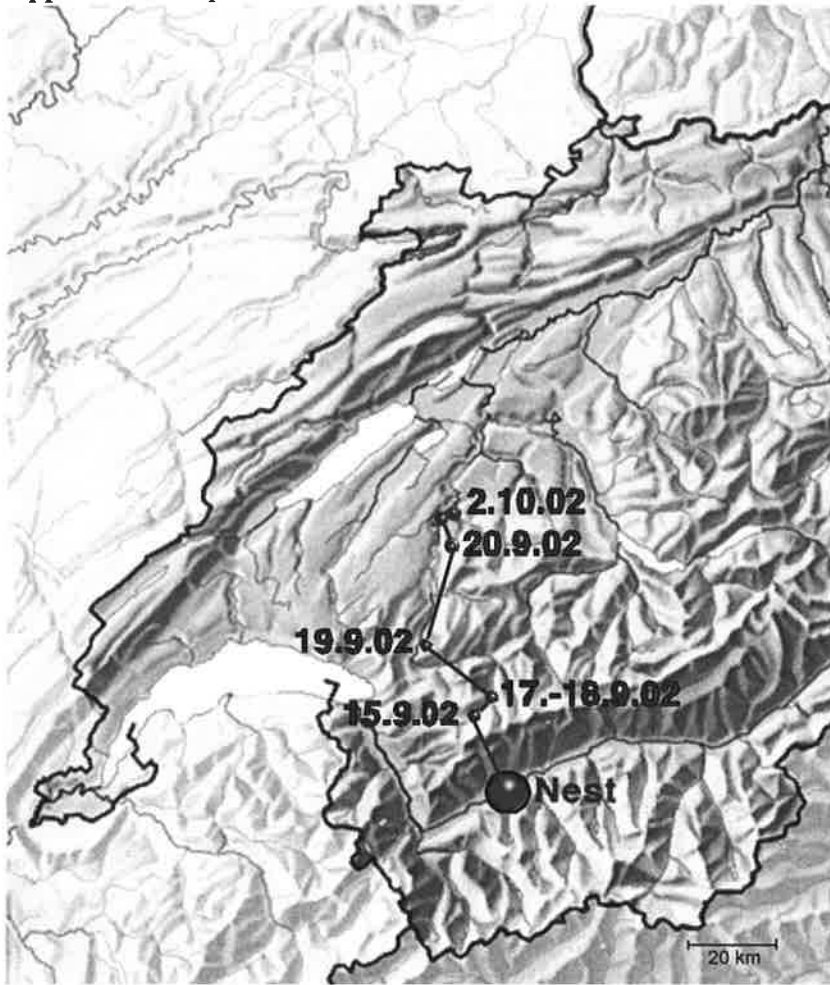
Appendix 3: Dispersal route of bird # 3



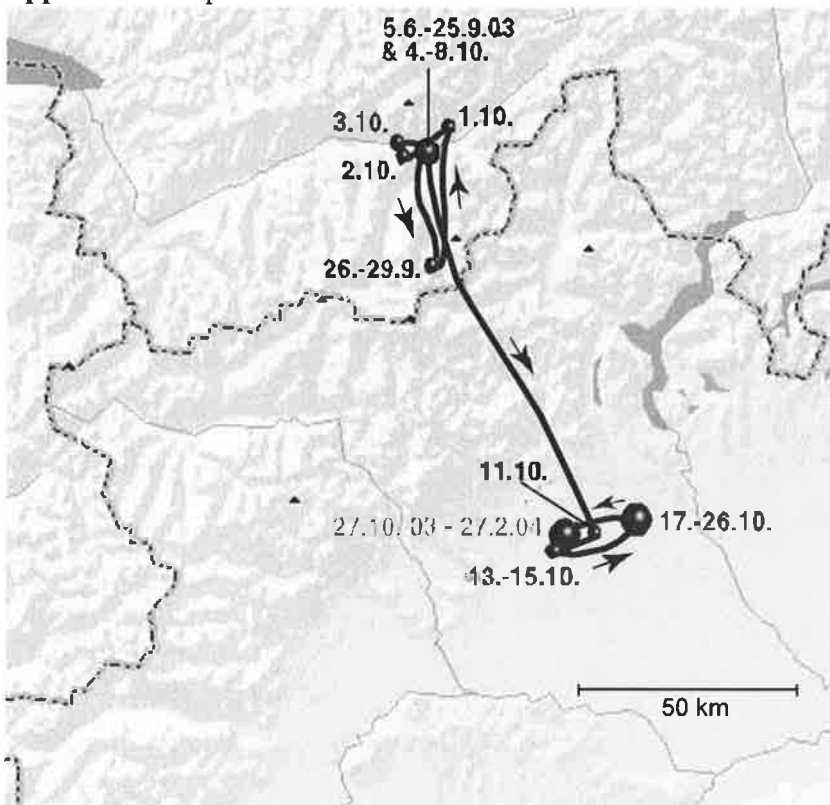
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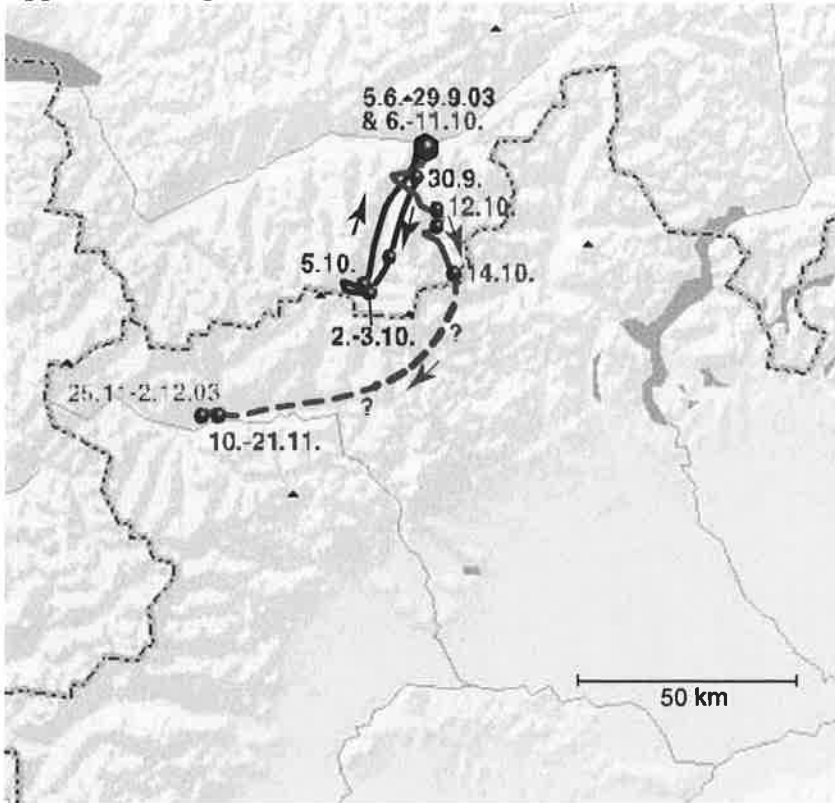
Appendix 5: Dispersal route of bird # 5



Appendix 6: Dispersal route of bird # 6



Appendix 7: Dispersal route of bird # 7



Appendix 8: Dispersal route of bird # 8

