

## Dietary shifts and fledging success in breeding Tawny Owls *Strix aluco*

Joop C. van Veen & David A. Kirk

**Dietary shifts and fledging success in breeding Tawny Owls *Strix aluco*.** – We examined prey delivered to nesting Tawny Owls *Strix aluco* by video recording or direct observation for at least three nights weekly in two forests, one in Holland (three pairs of owls) and one in France (one pair). All owls nested in specially-designed nest boxes fitted with video-recorders. We analyzed prey taken over an 12-year period, totalling five incubation and eleven nestling periods between 1984-1995. Following hatching of the eggs, the percentage of small rodent prey declined from 91% to 66%. By contrast, medium to large-sized bird prey (40-200 g mass) increased (by 11 times) as did larger mammals such as lagomorphs, European Moles *Talpa europaea* and Brown Rats *Rattus norvegicus* combined (by 5.7 times). Frogs *Rana temporaria* increased (by 20 times), although in terms of nutrient and energy content they were 60% less profitable than Wood Mice *Apodemus sylvaticus*. During the incubation and nestling periods most prey weighed < 35 g (99% and 91%, respectively). We suggest that small prey, such as shrews and small birds, are underestimated by exclusively counting prey taken to the nest, as occurs in the Great Gray Owl *Strix nebulosa* and Barn Owl *Tyto alba*. There was a positive correlation between the percentage of rodents in the diet and number of young owls fledged; the reverse was true for the percentage of birds, although their mean mass was two times larger during the study than mean rodent mass. Although differences in diet between sexes were not found, large prey was invariably delivered by females, which were 38% heavier than males during the post-brooding phase. Dietary shifts in Tawny Owls after hatching are consistent with optimal foraging theory. Shifting in Tawny Owls to larger prey sizes than rodents after hatching and back to smaller prey types after nest failure as occurs in the Spotted Owl *Strix occidentalis* is evidence for the active selection of larger prey sizes with increasing brood demand. The positive correlation between rodents in the diet and fledging success and the preferential predation on rodents during incubation is evidence that they are the most profitable prey. Prey abundance and foraging behaviour were not investigated, but proximate explanations are discussed.

**Key words:** diet, rodents, birds, alternative prey, prey type, profitability, metabolizable energy, mean prey mass

Joop C. van Veen, Wageningen, Agricultural University, Ritzema Bosweg 32 A, NL-6703 AZ Wageningen, The Netherlands

Corresponding address: Drs J. C. van Veen, Zomezmetez 11, NL-8607 GX Sneek, The Netherlands, e-mail: vveenjl@wxs.nl

David A. Kirk, Aquila Applied Ecologists, C..P. 47, Wakefield, Québec, Canada J0X 3G0

and c/o National Wildlife Research Centre, Canadian Wildlife Service, 100 Gamelin Blvd., Hull, Québec, Canada K1A 0H3

## Introduction

Many bird species show a dietary shift between winter and summer. Is this a question of a more diverse availability of prey types in summer or of selection during breeding? Predators are often considered as opportunistic, but one has generally viewed them to have evolved a level of foraging above the random approach (MACARTHUR & PIANKA 1966; PYKE et al. 1977). Little *Athena noctua*, Tawny and Ural Owls *S. uralensis* are considered as generalists because they are year round residents and prey on a variety of prey types from earthworms and insects to medium sized birds and young lagomorphs. Pellet analyses suggest that the diet of these owls shift seasonally in winter feeding almost exclusively on small rodents (SOUTHERN 1954, 1969, DELMÉE et al. 1978, LUNDBERG 1976, ILLE 1992). In the breeding season the diversity of prey is usually larger than in winter, when several prey species hibernate (Gliridae, insects), live underground (Water Voles *Arvicola terrestris*, Earthworms *Lumbricus* spp) or had migrated as several bird prey species do.

We followed food habits of breeding Tawny Owls during several years in an attempt to find a clue to selection. We selected this owl because it is the most common medium-sized nocturnal avian predator of small vertebrates in many forest habitats in Europe (VOOUS and CAMERON 1988). This single-brooded, relatively long-lived 'K-strategist' and highly vocal owl resides year-round on territory. Consequently, it tends to feed on a wider range of prey species than other similar-sized Strigiformes e.g. Long-eared Owl *Asio otus* and it will use a wide range of nest sites (SOUTHERN 1970). These attributes may partly explain why the species is so abundant and widespread. For example, since 1875 the Tawny Owl has expanded its range northward in Eurasia (MIKKOLA 1983) and recently it has colonised new habitats, such as coastal dunes in The Netherlands (KONING 1980), spruce plantations in Britain (PETTY 1987) and urban areas (BEVEN 1965, WENDLAND 1980, GALEOTTI et al. 1991, GOSZCZYNSKI et al. 1993, JOHNSON 1993).

We video recorded food habits of nesting Tawny Owls during incubation, when brood demand is low. This changes soon after hatching into high demand in the nestling period. We assume that rodent densities stay rather constant over that short period. We were particularly interested in the relationship between brood demand and the proportion of alternative prey (other than small rodents). We expect that larger alter-

native prey would be taken to the nest, because they yield a greater energetic return, than small rodents. However, this is only the case if the costs of capturing large prey, is not disproportionately high to the costs required to capture the more abundant small rodent prey. Because food demand is higher during the nestling than incubation period, we predict a diminishing preference for small rodents after hatching and an increase of larger prey. Provided small rodent availability does not change significantly in that period, although the availability of larger prey may increase. If not enough large prey is available we predict switching to even less profitable prey than rodents as frogs, small birds, shrews or even beetles and earthworms. In case of nest failure we predict that the owls should switch back to rodents including the smaller prey types. This follows from the predictions of optimal foraging theory. The term "alternative prey" has nothing to do with game as was defined in the alternative prey hypothesis (APH) by HAGEN (1952) and LACK (1954). It only refers to switching to other prey types than staple prey, in case of Tawny Owls forest rodents and further to the synchrony of switching with low rodent abundance. The term is applied in a similar sense in some other studies, too (DROST et al. 1992, JEDRZEJEWSKI et al. 1994). Here we 1) describe the diet of incubation and nestling periods separately and compare prey composition and metabolizable energy (ME) contents of prey between 5 incubation and 11 nestling periods and 2) examine if food habits in Tawny Owls are consistent with optimal foraging. Proximate explanations, which may account for the observed patterns of prey deliveries and reproductive success, were difficult to assess and were beyond the scope of the study, but it shall be discussed.

## Study areas and methods

The investigation was executed from 1984-1995. Our study sites were near Utrecht in central Holland (c. 52° 2' N, 5° 25' E) and 80 km north of Dijon in France (47° 40' N, 4° 50' E). The territories of the Dutch owls consisted of mixed woodland (*Quercus*, *Fraxinus*, *Betula* spp.) and small pine (*Pinus sylvestris*) plantations surrounding dairy farms. These patches of woodland (> 50 ha) are surrounded by extensive meadows, which are inhabited by Little Owls. According to local farmers, the three Tawny Owl territories there have been occupied for at least over 50 years. From 1988 on we cooperated with a group of french naturalists organized in "La Choue" and conducted by Baudvin. The French study area is in a beech-oak timber forest (*Fagus sylvaticus*, *Quercus robur* and *Q. petraea*) which is part of the Châtillon State Forest (8,875 ha, excluding adjacent communal forest). We believe that this broadleaved forest matches a natural beech-oak forest at least as far as the predator prey relationship is concerned. A detailed description of the vegetation in this forest is in NICLOUX (1986). The Tawny Owl pair videorecorded nested in a shed attic at the edge of this forest. Van Veen has studied the Tawny Owl population in this forest (c. 60 nest boxes) 1989-1995 in cooperation with "La Choue" (Baudvin, Burgundy).

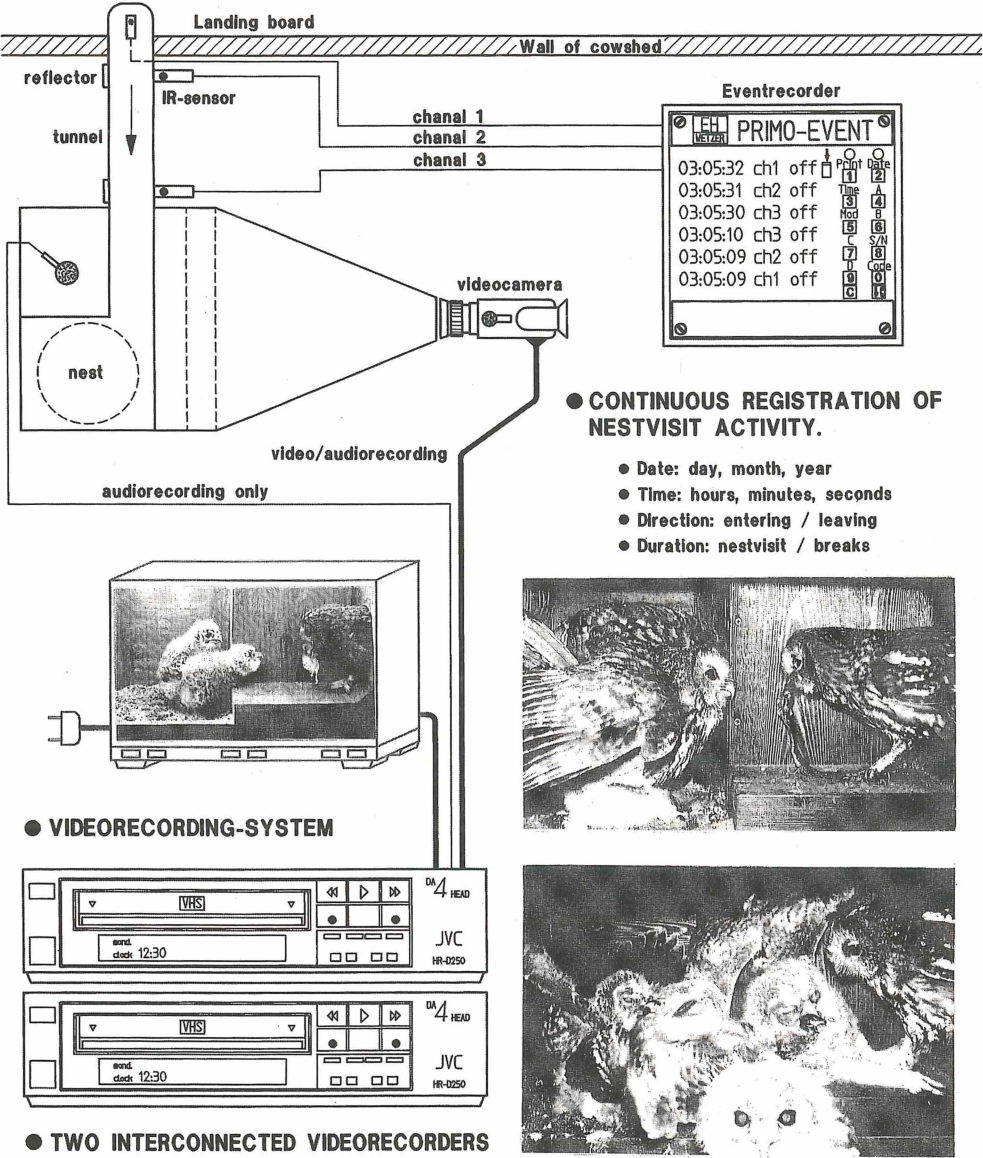


Fig. 1. Diagram of observation nestbox with video recording system and the visit registration equipment. Infrared sensor and reflector devices are connected with an eventrecorder for the registration of visit activity. Photographs: Hen owl with Yellow-necked Woodmouse, 1993 French nest (in monitor), male transferring a decapitated frog (bill to bill) to brooding female (upper right): Female had transferred a shrew to the third nestling of age. The fourth nestling did not yet took part in the competition for food. Both 1985 nest, a 5-brood was reduced to four.



Nest boxes fitted with videorecorders in Holland were erected in the attics of cowsheds. One advantage of these sites is that the background noise of cattle muffled sounds made by observers. Nest boxes were designed to encourage the male owl to transfer prey to the female inside the nestbox, by placing a platform beneath the nest and in front of a peep hole (Fig. 1). The latter was used for video-recording (Pal-VHS-system). Later the same platform was used by both parents to transfer prey to the nestlings. This arrangement was very successful and enabled us to identify of 97% of prey items. The method is described in detail in van VEEN & TEN BROEKE (1994). With the installation of an improved camera-system (Super-VHS) in 1993 we were also able to identify the sex (mass of male and female) of about 44% of the prey (from signs of lactation or pregnancy in Bank Voles *Clethrionomys glareolus* and Yellow-necked Mouse *Apodemus flavicollis* in the French study area).

Prey deliveries were recorded for at least three nights weekly either by video or direct observation. The increased light conditions implemented just before egg hatch were accepted by owls without any apparent ill effect. Between 1984-1989, incubating owls were habituated gradually to increased light conditions; from 1990 onwards diminished light conditions were used well before egg-laying while soon after egg-laying full light conditions were implemented. Six prey types were distinguished based on natural breaks of sizes as taken to the nest: shrew (c. 9 g), small bird (c. 18 g), small rodents (c. 20 g), frog (c. 30 g), "large" bird (c. 45 g - c. 200 g) and "large" mammal type (45 g - 150 g) (Tables 4, 8, 9, Fig. 2, 3). We calculated the geometric mean prey mass (MPM), metabolizable energy (ME) content of MPM and ME gain (ME in kJ per g prey mass) for each breeding pair per incubation and nestling period annually (Tables 5, 10, 12). In most cases mean adult prey mass could be used. However, because prey mass varies depending on whole prey, differing in age class, sex and year or partial prey differing in missing parts (eg. decapitated or hind parts), masses were adjusted accordingly. Table 1 shows the conversion factors we used to calculate the gross energy (GE) and the metabolizable energy (ME) in kJ. In Table 12 adult weights were used.

Prey masses were taken from GÓRECKI 1965 (shrews), GLUTZ & BAUER 1980, SYLVEN 1982 (frogs), BENNETT & HARVEY 1987 (birds) and WIJNANDTS 1984 (metabolizable energy coefficients and some prey masses). In France I (JvV) was able to weigh 1) surplus prey, including decapitated and hind parts of rodents, in nests during the early brooding phase in the Châtillon forest and 2) live-trap rodents (capture, mark and recapture method). Three sites were sampled (one ha in area) in spring and autumn annually in the Châtillon forest with 126 Longworth live traps baited with small balls of Dutch best quality of peanut butter and oats. Trapping was ended when at least 60 % was recaptured (totalling of 22,500 trap.nights in seven years). Traps were laid out in a grid of six lines and 21 rows; distance between traps was 10 m. We weigh a minimum of 20 adults per species trapped per sample site. Generally all unmarked individuals were weighed and always in a crash year (0-7 animals).





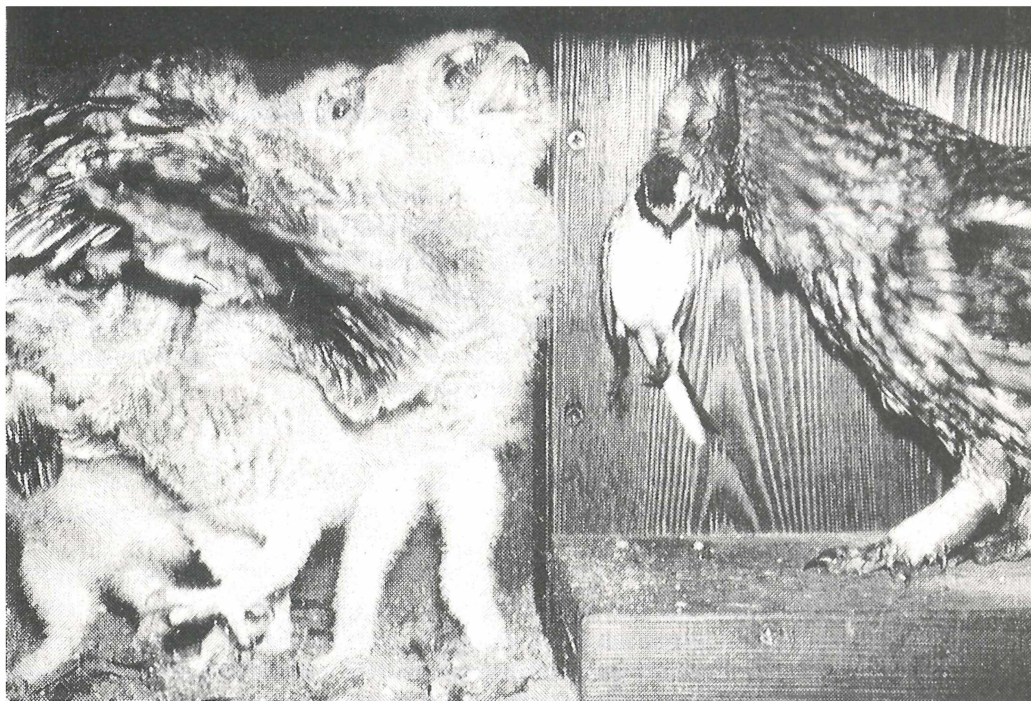
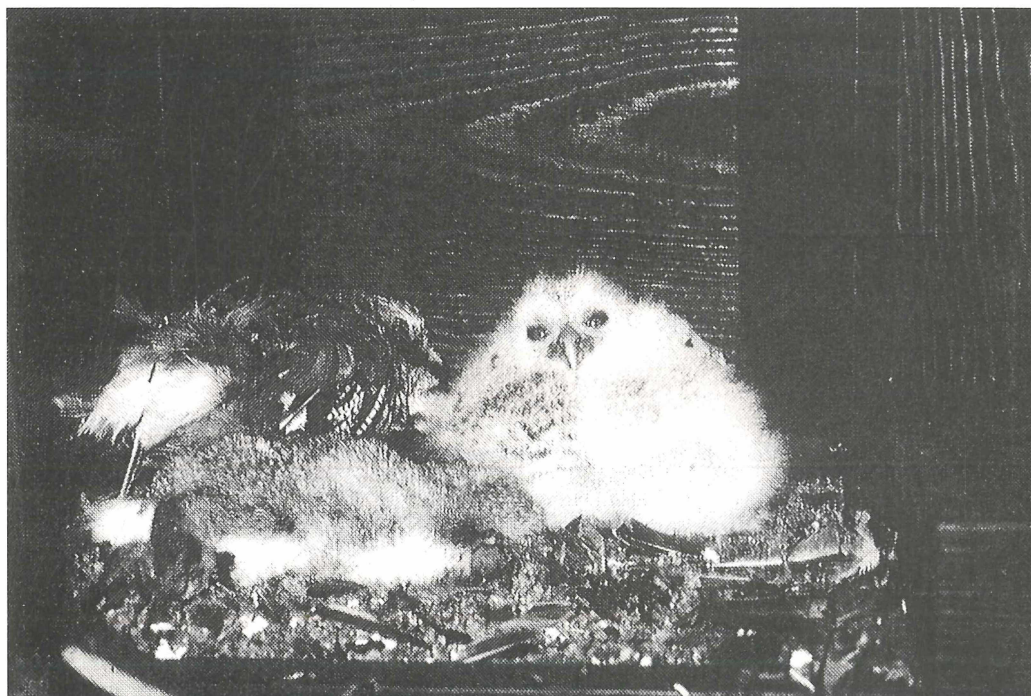


Fig. 3. Female and large prey types. Female entering with a European Blackbird (1985 nest, 5-brood was reduced to four)(upper). Remains of partially plucked rabbit and European Jay. Handling time of large prey depended on hunger of nestlings and hunter (1984, crash year, 3-brood was reduced to two).



We converted prey into "mouse units metabolizable energy" (MUME). These had a mass of 21.5 g (MU in g), a gross energy content (GE) of 160 kJ (MU in kJ) and a metabolizable energy (ME) content of 124.8 kJ. Using mouse units enabled us to compare kJME of 'other' prey with an equivalent quantity of mouse prey (Table 1). Moreover, it is equivalent to the nutrient composition of a Wood Mouse *Apodemus sylvaticus* (WIJNANDTS 1984). Invertebrate prey were not important components of the diet in either the Dutch or French study areas.

Tab. 1. Relationship between mass and metabolizable energy (ME) used for the calculation of energetic content of prey and metabolizable energy in mouse units (MUME).

Prey type	Body mass (g)	kJ/g fresh mass	GE <sup>1</sup> (kJ)	MEC <sup>2</sup>	ME <sup>3</sup> (kJ)
Mouse Unit (MU)	21.5	7.44	160	0.78	125
Shrew <i>Sorex araneus</i>	9.0	6.27	56	0.62	35
Bank vole <i>Clethrionomys glareolus</i>	18.0	7.74	139	0.68	95
Woodmouse <i>Apodemus sylvaticus</i>	20.0	8.0	160	0.79	126
Bird <i>Passer domesticus</i>	26.0	7.79	203	0.68	138
Frog/Toad <i>Rana</i> sp./ <i>Bufo</i> sp.	28.0	3.70	104	0.62	64
Lagomorph <i>Oryctogalus cuniculus</i>	175	7.61	1312	0.68	906

<sup>1</sup> Gross Energy value, <sup>2</sup> Metabolizable Energy Coefficient, WIJNANDTS 1984, <sup>3</sup> Metabolizable Energy value.

To assess diet during incubation, breeding behaviour was recorded for several days prior to egg-laying up until hatching of the first chick. We compared prey intake between incubation and nestling periods and standardized these among years. The

“standard” incubation period was from the date of laying the first egg until 30 days later. The nestling period began 31 days after the first egg was laid and ended on the night the first nestling fledged (‘Standard’ nestling period). However, for nestling period diets of 1984, 1985, 1986, and 1987, prey species may be included from a few days before the first chick hatched up until the last owlet fledged (Table 8). Means are presented  $\pm$  SE throughout this paper.

## Results

### Breeding events

#### Observed nests

In France two eggs (1993) and three eggs (1995) were laid and two fledglings were produced in both breeding seasons. Although the same Tawny Owl pair was observed in 1993 and 1995, only 1993 results could be used (Table 2). In 1995 the nest was disturbed on two consecutive evenings (day 17 and 18 of SNP) during the post brooding phase. The nest was evidently disturbed as could be read from the event recorder, probably by curious young people from the neighbourhood. We ended diet sampling on day 16, but in the early brooding phase the youngest sibling subsequently starved to death; by day 10 it weighed 55 g (first and second sibling were 140 g and 105 g resp.), by day thirteen 41 g (first and second sibling 185 g and 165 g resp.). At day 16 the apparently dead nestling laid for hours on the bottom of the nest and became dirty by trampling, breathing could not be detected as could be observed by the video recording. It had disappeared at least 6 hours of videorecording, after I left the nest. When I returned to the nest the next day it was gone. Probably fed to the remaining nestlings by the hen owl. The first nestling fledged at day 31, c. 30 g above mean fledging weight (1993 was an above average breeding year). In 1995 the first nestling at day 33, c. 45 g below mean fledging mass. (1995 was below average breeding year). Mean fledging mass was 345 g ( $n=88$ ) (VAN VEEN part 5; in prep.). The second nestlings weighted 325 g and 250 g at the end of SNP resp.

The breeding behaviour at the French and the Dutch study area was similar with respect to prey transfer behaviour, male/female communicative behaviour, sibling competition for food and nestling necrophagy, because the nestling was dead or nearly dead before it disappeared. Most probably it was fed to the other siblings by the hen owl as described by VAN VEEN (1994).

#### Brood reductions

During the breeding seasons of 1990 (5 fledglings), 1992 (3 fledglings) at the Dutch and 1993 at the French study area (2 fledglings) no brood reduction occurred, hence clutch size was apparently well adjusted to pre-laying prey availability, probably to the winter prey in the forest (Table 2).

Tab. 2. Breeding events of Tawny Owls.

Breeding events	Years									
	No broodreduction			One Egg or Nestling Reduction				2 Nestl Reduct		
	1990	1992	1993*	1995	1985	1993	1987	1984	1991	1986
Laying date	3 Feb	20 Feb	12 Mar	23 Feb	27 Feb	18 Jan	11 Mar	12 Mar	15 Feb	23 Feb
Clutch size	5	3	2	3	5	5	3	3	5	4
First hatchl.	4 Mar	22 Mar	13 Apr	25 Mar	29 Mar	17 Feb	11 Apr	11 Apr	18 Mar	27 Mar
No hatchl.	5	3	2	2	5	5	2 <sup>1</sup>	3	4 <sup>2</sup>	4
First fledgl.	8 Apr	1 May	15 May	4 May	4 May	23 Mar	14 May	22 May	26 Apr	30 Apr
No fledgl.	5	3	2	2	4	4	2	2	3	2
Age of death*	-	-	-	-	7	5	-1	9	10	14,15
Fledge time*	10	10	2	3	3	8	4	1	4	3

\* French site; + in days; <sup>1</sup> one egg chilled during incubation; <sup>2</sup> one nestling died some days after hatching.

However, in 1987 and 1995, one egg did not hatch, although the 1987 egg was later found to be fertile. We do not know why the eggs did not hatch, but we suspect that chilling was the cause. In 1985 (4 fledglings), 1993 (4 fledglings) and 1984 (2 fledglings) brood size was reduced by one during the nestling period. In only one year (1993) did this loss occur after the brooding phase.

In 1986 and 1991, two and three nestlings, respectively, died of starvation. The fate of individual nestlings is described elsewhere (VAN VEEN 1994).

In 1994 breeding failed almost completely because the male owl did not return to the nest during hatching. The female had to fend for her self and the three nestlings. A floater male was soon attracted by the soliciting calls of the female and arrived in the territory. After a week it approached the nest closely and often called many times from a tree at c. 25 m from the nest. No food seemed to be transferred. Later she herself was found dead, when the oldest nestling was 33 days old. After dissection by a veterinarian abnormal sings, probably of poisoning, were found: pale liver and kidneys. The remaining nestling was ringed and transferred to another Tawny Owl nest that was at a similar stage.

The mean duration of incubation and standard nestling periods (SNP) was  $30.1 \pm 1.1$  and  $36.6 \pm 3.7$  days respectively (range 29-31 days and 31-42 days respectively).

## Incubation period

### Eggs and hatching

In Holland during 11 nestling periods and France during 2 (1984-1995), 42 young were hatched from 45 eggs. We observed prey provisioning in six incubation periods (1990-1995) and excluded the 1993 and 1995 incubation period, because the pairs were not yet habituated to light conditions. Observation at full light conditions began on day 21 with pairs that were not habituated to light conditions (1985-1988), although recorded prey items were included in the prey list of SNP. However they were not used for calculations of annual diet, MPM and ME gain of SNP.

In a total of 82 nights of video-recording (about 55% of all nights of the incubation periods), 306 visits were made by the male owls. Of these visits, 187 (61%) were deliveries of prey, while the remainder were 'contact visits' without prey. Incubation breaks were excluded as "visits". Females returning from incubation or early brooding breaks (first 6 days of SNP) never brought prey with them. There was never an indication (prey transfer ritual cries) that prey was transferred to her near the nest in those phases of breeding. In the good rodent year 1990 (5-clutch/5-fledglings) the percentage of contact visits during incubation was highest over 50%.

Without exception, all observed prey deliveries during this study consisted of a single prey item ( $n=1398$  prey visits).



Tab. 3. Observed prey items of Tawny Owls during incubation period.

Prey categories (mass in g)	Years						Tot
	90	91	92	93	94	95*	
Amphibia: <i>Rana temporaria</i> (28)	-	1	-	-	-	1	2
Mammalia							
Soricidae: <i>Sorex araneus</i> (9)	1	1	-	-	-	2	4
Muridae: <i>Apodemus sylvaticus</i> (20)	24	18	21	12	20	12	107
Unidentified small murids (18)	-	1	1	-	-	-	2
Microtidae: <i>Clethrionomys glareolus</i> (18)	6	6	4	10	27	1	54
<i>Microtus agrestis</i> (23)	-	2	-	-	1	-	3
<i>Arvicola terrestris</i> (35)	1	-	-	-	-	-	1
Unidentified small microtid (18)	-	-	-	-	-	1	1
Lagomorph (150)	-	-	-	-	-	1	1
Aves							
Small birds: <i>Parus major</i> (17)	-	4	-	-	3	-	7
<i>Parus spec</i> (13)	-	1	-	-	-	-	1
<i>Passer domesticus</i> (25)	-	1	-	-	-	-	1
Unidentified small birds (18)	-	-	-	1	1	-	2
Large birds: <i>Turdus merula</i> (83)	-	1	-	-	-	1	2
<b>Total</b>	<b>32</b>	<b>36</b>	<b>26</b>	<b>23</b>	<b>53</b>	<b>18</b>	<b>188</b>

\* only 4 days of prey sampling (see text )

### Diet composition

Small rodents numerically comprised 92%, birds 6.4%, shrews 1% and frogs 0.6% of prey deliveries (Tables 3, 4). Four small rodent species and at least three avian species were recorded. Most bird prey was small and included Great Tits *Parus major* and a single House Sparrow *Passer domesticus* (mass 18 and 25 g, respectively).

By mass, mice (Muridae) were most important (60.2%) followed by Bank Voles (Microtidae) (31.5%); together these accounted for 92% of the diet (Fig. 1). Shrews (c. 9 g) were the smallest item and a young Water Vole *Arvicola terrestris* (c. 35 g) the largest. Two blackbirds were the only large prey delivered during the incubation period, thus 99% of the prey weighed < 35 g.

Tab. 4. Diet of tawny owls based on observed prey deliveries during standard incubation period.

Prey type categories	Percentage by number (N) and weight (W)									
	1990		1991		1992		1993		1994	
	5-clutch		5-clutch		3-clutch		5-clutch		4-clutch	
	N	W	N	W	N	W	N	W	N	W
Shrews	3.1	1.4	2.8	0.9	-	-	-	-	-	-
Frogs	-	-	2.9	3.7	-	-	-	-	-	-
Small rodents	93.8	92.3	74.3	74.4	100	100	95.7	92.7	92.5	93.7
Small birds -	-	-	17.1	12.1	-	-	4.3	7.3	7.5	6.3
Large birds	3.1	6.3	2.9	8.9	-	-	-	-	-	-
Ident.prey	32		34		25		23		53	
Unident. prey	-		1*		1*		-		-	
Obs. nights	13		15		19		11		24	

\* Partial small rodent item, mass roughly estimated for feeding rate.

Diet parameters.

Mean prey mass (MPM) averaged 21.5 ± SE 0.7 g during the incubation period and ranged between 20.5 and about 22 g (Table 5). ME content of MPM was 125 ± SE 7.9 kJ (equivalent to 1.08 MUME) and varied little between 121 kJME (0.97 MUME) and 114 kJME (1.27 MUME). The highest value was found in 1990 (137 kJME)(5-clutch/ 5 fledglings) and is comparable with 1992 (130 kJME) an intermediate year (3-clutch/ 3 fledglings). This was a direct result of the proportion of murids in the diet (93.8% and 95.7% by number resp.)(Table 4). These forest rodents produce the highest ME gain (kJ/g prey mass) of all prey items recorded (6.32 kJME/g) (Table 1). No data were available from the incubation period (1993, 1995) at the French study site, because owls were not habituated to the artificial light conditions at the start of nesting.

Tab. 5. Mean prey mass (MPM), ME content of MPM and ME gain of observed prey of Tawny Owls during incubation periods (n = 170).

MPM (g)	MPM ME content		ME Gain kJ.g <sup>-1</sup>	No obs items	Clutch size hatchlings (year)
	kJ	MU			
23.0	128	1.04	5.59	17	3 (95)*
22.7	137	1.10	6.05	32	5 (90)
21.9	114	0.91	5.21	36	5 (91)
21.4	130	1.05	6.12	27	3 (92)
21.1	123	0.99	5.83	22	5 (93)
20.5	121	0.97	5.88	53	4 (94)
21.5	125	1.00	5.82	mean	
0.7	7.9	0.11	0.32	SE	

\* Not included in mean (see text)

### Feeding rates

The mean observed prey visit rate of the five incubation periods was 2.5 per night with a MPM of 21.5 g for an average clutch size of 4.4 eggs. This equals a gross intake of 52.7 g/day (307 kJME/day, 2.5 MUME/day). A visit rate of 2.2 per day was registered by the event recorder at the French nest site. However a percentage of 7% contact visits was estimated from the last days of incubation and the early brooding phase. The mean prey visit rate was calculated c. 2.0 per day. The calculated feeding rate was estimated c. 52.6 g/day (318 kJME, 2.55 MUME/day). The calculated energy content of MPM at the French site was, about 6% higher than at the Dutch study area (Table 5). This was attributed to the large proportion of Yellow-necked Mouse mass in the diet. This species does not occur in Holland and is much heavier than a Wood Mouse c. 21 g versus c. 27 g (Table 6).

Tab. 6. Observed prey items of Tawny Owls during nestling period.

Prey categories (mean mass)	Years											
	84	85	86	87	90	91	92	93	94	95	93 <sup>1</sup>	Tot.
Invertebrata: <i>Insecta</i> (1.5)	-	-	-	-	-	-	-	-	1	-	1	2
Amphibia:												
<i>Rana temporaria</i> (28)	24	28	22	1	3	12	13	6	11	5	-	125
<i>Bufo spec</i> (60)	-	-	-	-	-	-	-	-	-	-	2	2
Mammalia												
Soricidae:												
<i>Sorex araneus</i> (9)	2	1	9	3	3	-	-	4	1	1	-	24
<i>Crocidura russula</i> (11)	-	-	-	-	-	-	-	-	-	-	1	1
<i>Neomys fodiens</i> (15)	-	-	-	-	1	-	-	-	-	-	-	1
Unidentified shrews	-	-	-	-	-	-	-	-	1	-	-	1
Talpidae:												
<i>Talpa europaea</i> (85)	-	-	-	1	-	-	-	-	-	-	-	1
Muridae:												
<i>Apodemus sylvaticus</i> (20)	17	70	45	51	72	38	123	95	12	28	1	552
<i>A. flavicollis</i> (27)	-	-	-	-	-	-	-	-	-	-	81	81
<i>Mus musculus</i> (20)	1	31	-	-	1	-	3	1	1	-	-	38
<i>Rattus norvegicus</i> (80)	-	-	1	-	4	4	-	1	3	3	1	17
Unidentified small murids	-	-	-	-	-	1	-	-	1	2	-	4
Microtidae:												
<i>Clethrionomys glareolus</i> (18)	9	8	5	4	15	15	9	24	1	8	27	125
<i>Microtus agrest/arvalis</i> (23)	-	-	-	-	-	3	-	-	-	-	-	3
<i>Arvicola terrestris</i> (35)	-	-	-	-	1	-	-	-	-	-	-	1
Gliridae:												
<i>Eliomys quercinus</i> (65)	-	-	-	-	-	-	-	-	-	-	2	2
<i>Muscardinus avellanarius</i> (22)	-	-	-	-	-	-	-	-	-	-	5	5
Lagomorphs (100)	4	3	1	-	-	8	1	2	1	-	-	20
Aves	49	8	13	5	5	38	20	14	9	3	3	167
Owlets (necrophagy)	1	1	2	-	-	1	-	1	3	-	-	9
Completely unident. items	7	8	6	3	-	2	4	-	-	-	-	30
Total	114	158	104	68	105	122	173	148	45	50	124	1211

<sup>1</sup> The French study area

Tab. 7. Observed birds taken to Tawny Owl nests during nestling periods.

Species (mass in g)	Years											
	84	85	86	87	90	91	92	93	94	95	931	Tot
Great Tit <i>Parus major</i> (17)	2	2	2	-	-	8	7	-	-	-	-	21
Chaffinch <i>Fringilla coelebs</i> (21)	7	-	2	-	2	-	1	4	1	-	-	17
House Sparrow <i>Passer domesticus</i> (25)	11	-	1	-	-	3	-	-	-	2	2	19
Tit <i>Parus</i> spp (13)	1	-	-	-	1	5	-	-	-	-	-	7
White Wagtail <i>Motacilla alba</i> (18)	1	3	1	-	-	-	-	-	-	-	-	5
European Robin <i>Erithacus rubecula</i> (16)	-	-	1	-	-	3	-	-	-	-	-	4
<i>Phylloscopus</i> spec. (8.5)	3	-	-	-	-	-	-	-	-	-	-	3
Tree Sparrow <i>Passer montanus</i> (22)	1	-	-	-	-	-	-	-	1	-	-	2
Duncock <i>Prunella modularis</i> (17)	1	-	-	-	-	1	-	-	-	-	-	2
Blue Tit <i>Parus caeruleus</i> (11)	-	-	-	-	-	2	-	-	-	-	-	2
Greenfinch <i>Chloris chloris</i> (27)	-	-	-	-	-	-	-	1	-	-	-	1
Garden Warbler <i>Sylvia borin</i> (24)	1	-	-	-	-	-	-	-	-	-	-	1
Linnet <i>Carduelis cannabina</i> (18)	1	-	-	-	-	-	-	-	-	-	-	1
Winter Wren <i>Troglodytes troglodytes</i> (9)	1	-	-	-	-	-	-	-	-	-	-	1
Unidentified small birds	-	-	4	1	-	4	1	2	-	-	-	12

	84	85	86	87	90	91	92	93	94	95	931	Tot
European Blackbird <i>Turdus merula</i> (83)	12	3	-	3	-	5	2	5	2	1	1	34
Thrush <i>Turdus</i> spec. (65)	-	-	1	1	2	3	3	1	2	-	-	13
Starling <i>Sturnus vulgaris</i> (71)	2	-	-	-	-	-	-	1	-	-	-	3
Black-billed Magpie <i>Pica pica</i> (190)	1	-	-	-	-	-	-	-	1	-	-	2
European Jay <i>Garrulus glandarius</i> (153)	2	-	-	-	-	-	-	-	-	-	-	2
Dove spp. <i>Streptopelia</i> spec. (170)	1	-	-	-	-	-	-	-	-	-	-	1
Woodpigeon <i>Columba palumbus</i> (150)	-	-	1	-	-	-	-	-	-	-	-	1
Unidentified large birds	1	-	-	-	-	4	6	-	2	-	-	13
Total	49	8	13	5	5	38	20	14	9	3	3	167

1 French nest

## Nestling period

### Hatchlings and fledglings

Although data were available for 14 nestling periods, only 11 of these could be used for diet analyses. Two nests soon failed after hatching and one was probably disturbed by young people, although the two nestlings fledged successfully. In two seasons (1988, 1989) supplementary food was provided at three other active nests during expected poor years. While simulating peak food conditions we hoped to induce maximum growth rate, which was not yet known at that time. We excluded these years from the analyses, too. During the remaining nestling periods, 42 hatchlings and 32 fledglings were produced. In 246 nights of observations 1202 prey deliveries were recorded: 62% of total number of nights (395) of the Standard Nestling Periods (Tables 6, 7). Most prey were identified to species; the few unidentified items were generally very small parts of prey (SNP:  $N = 10$ , 1%). For all observed items in the whole study it was c. 3 % ( $N = 34$ ) (Table 6).

### Diet composition

At the Dutch study area small mammals numerically comprised c. 75%, birds 14.5% and amphibians (frogs) 11 % during the nestling periods and c. 97 %, 1.5 % and 1.5 % for the French study area respectively (Tables 6, 7). The single European Blackbird and the House Sparrow taken to the French nest two days and one day respectively before hatching, were most probably occasional items during hunting increase at hatching. These prey were included to the prey list, but excluded from the calculations for the diet, MPM, ME gain and feeding rate during SNP.

Prey biomass ranged from c. 8.5 g. (Chiffchaff *Phylloscopus collybita*) to c. 150 g (young lagomorphs and large birds), excluding two insects. Considering their apparent importance to Tawny Owls in other studies it was surprising that no invertebrate prey were recorded between 1984 to 1993 and no earthworms at all. Indeed only two insects were identified over 1,000 prey items in the Dutch study area. About 90.5 % of the observed prey weighed less than 35 g. At the French study area biomass varied between a shrew (c. 10 g) to a young rat and a European Blackbird (c. 60 g and 80 g resp), excluding a single beetle (c. 2 g). Under forest conditions even more prey (c. 98%) weighed less than 35 g (Table 6).

Altogether, 14 mammal species were observed (10 spec in the Dutch and 7 in the French study area (Table 6). The most abundant were Muridae (c. 60 %; mostly Wood Mice), followed by Microtidae (11 %; Bank Voles). Both are typically species of the forest floor. Shrews (often *Sorex araneus*), European moles *Talpa europaea*, young Water Voles and young Brown Rats were rarely taken. Young rats and young lagomorphs were brought to nests only at the end of the nestling period, when demand was greatest. All large prey (40 g - 150 g) were delivered by the 30 % heavier



female. BAUDVIN & DESSOLIN (1992) recorded body weight change in Burgundy forests during the breeding cycle. I (JvV) was not sure that the female herself had caught them, because many prey were transferred from male to female far from the nest out of reach for accurately recording.

### French nest

Only seven mammal species were observed on 27 of the 31 nights (87%) of the Standard Nestling Period of 1993 (Table 6). The diet comprised mainly of small rodents (97 % by number), mostly rodents of the forest floor (89 %): Murids c. 63 % (mostly Yellow-necked Mice c. 98 % of all murids and some Wood Mice and a single young rat), microtids exclusively Bank Voles 26 % of all mice and 2 species of glirids typical arboreal prey (c. 7%) and further a shrew, two toads and a beetle most probably *Rhizotrogus sositialis*. Glirids do not occur in Holland (Garden Dormouse *Eliomys quercinus* are about three times heavier than Bank Voles, Hazel Dormouse *Muscardinus avellanarius* as heavy as a Woodmouse (22 g). Although some surplus prey was available in the early brooding phase, the switch to larger prey, however, began from day 14 on of SNP. The glirids in particular originated from an other more arboreal niche, than the other prey types that forage on the forest floor (rodents, shrews, the toads and Blackbirds) (Table 6). This increase in diversity and supposed foraging in different niches of prey, mirrored probably the growing hunting effort while brood demand gathered volume.

### Staple prey taken

One would assume that the Tawny Owls at the border of the Châtillon Forest would hunt in the forest rather than in meadow habitats surrounding the border of the forest. That open area was favoured by foraging Barn Owls. (Incidentally, young were successfully raised by Barn Owls in the same observation nest box in the previous year and later years). At least three findings support the assumption that these owls hunted in the forest. First, we often saw the male flying towards the forest and generally heard it calling from this area prior to arrival at the nest with prey. Second, c. 98 % of small rodent prey delivered to the nest were forest species and c. 90 % of the prey were caught in live-traps in the forest (Yellow-necked Mice and Bank Voles). At the three regular trap sites in the forest I trapped over the last 6 years mainly Yellow-necked Mice (c. 80 %), including some Wood Mice and Bank Voles (c. 22,500 trap.nights). Only in a single year at a single trap site I trapped some arboreal mice, some young Fat Dormice *Glis glis*. Second Tawny Owls nesting in the centre of the forest had diets with similar proportions of rodent species as trapped. While examining these Tawny Owl nests (1990, 1991, 1993, 1995) during early brooding periods, we found surplus prey in similar proportions with little variations to those live trapped in the same year.

During early brooding only a few small alternative prey (c. 8 %) as shrews and tits were recorded and no remains of large items (> 40 g) were observed. This was also observed in Holland. Surplus prey was found up to 10 days after hatching, quickly disappearing after a week.

In the 1993 surplus prey sample collected in the centre of the forest, proportions of Yellow-necked Mice, Bank Voles and Wood Mice, were 90.7 %, 8.0 % and 1.3 % (n = 150, MPM = 28.6 g) versus 73 %, 22.4% and 4.6 % in the live trapped sample of 1993 (n = 152, 2268 trap.nights, mean mass of trapped rodents 28.1 g).

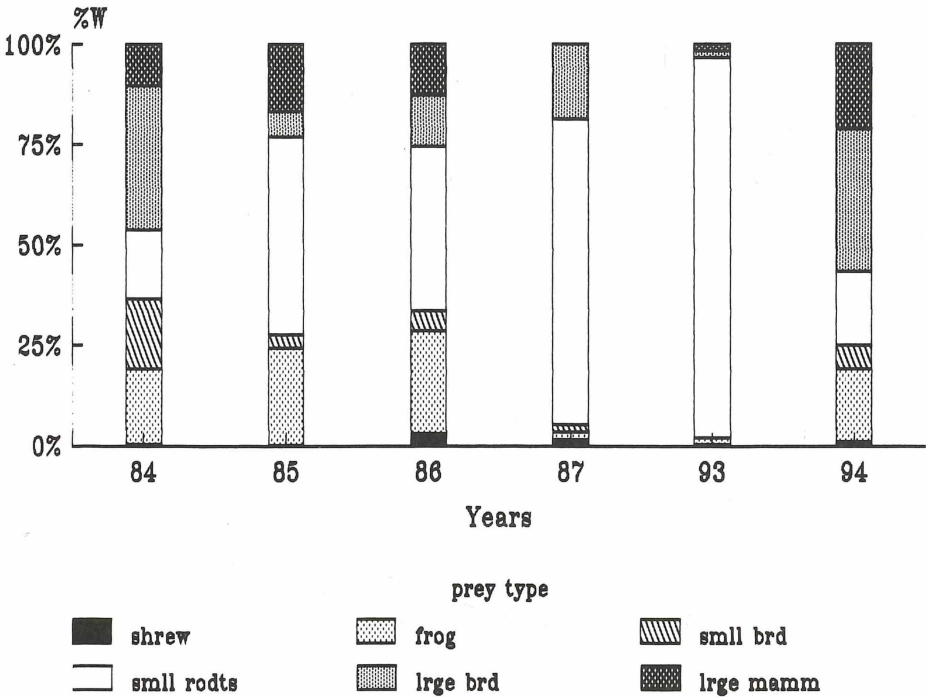


Fig. 4. Food habits during nestling periods. Annual contribution by mass of prey types to diet (1984-1987, Dutch nests, 1993 French nest, 1994 Dutch nest, male died during hatching). See Table 8 and 9 for proportions by number.

The proportions of the video recorded diet at the French site did not show a preference for the heavier Yellow-necked mouse: c. 71 % Yellow-necked, probably including some Wood Mice and 29 % Bank Voles versus 77.6% and 22.4 % live trapped in 1993 resp. This difference may depend on the foraging habitat at the edge of the Châtillon Forest as compared to the centre. An other difference was that the diet of

the video recorded nest covers the whole of the nestling period and not the early days of brooding which are more similar to the samples of trapped rodents. In general the proportions of rodents in the diet roughly reflected the proportions found during live trapping, differences were hard to assess conclusively, because there were considerable differences between rodent densities of territories. Besides it was difficult to assess the vulnerability of rodent species (sizes and sexes within species) in the forest. Finely the proportion of small prey eaten at the spot of catch could not be estimated. These aspects were beyond the scope of the investigation.

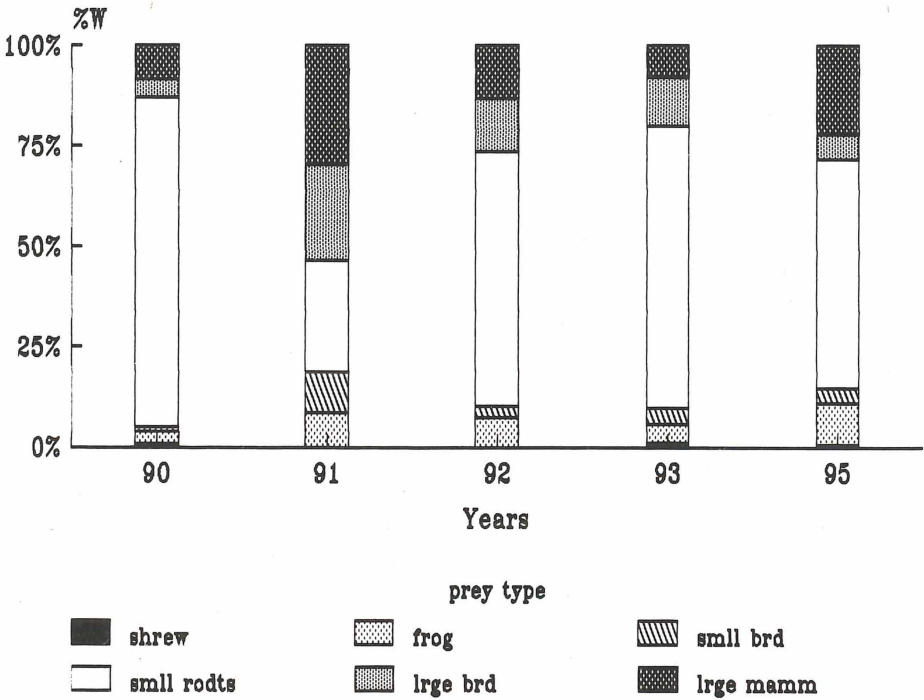


Fig. 5. Food habits during nestling periods of Tawny Owls. Annual contribution by mass of prey types to the diet (Dutch nests). See Table 9 for proportions by number.

Small and large birds

In total we counted 167 bird prey items in the Dutch area, the nine owlets that starved to death excluded (Table 6, 7). Of these, 98 were small (< 45 g; at least a 14 species) and 69 large items (between 48-200 g; at least a 8 species). The mean mass of small birds was 18.5 g and they had a ME energy content of 99 kJ equivalent to 0.79 MUME (about 80% of a net mouse unit). The mean mass of large birds was 70 g and these had

a ME energy content of 370 kJ, 2.96 MUME (nearly three net mouse units). Mean mass of small bird prey varied little annually, because most deliveries were one of three regular species. However, the mean mass of large bird prey varied annually considerably, because owls occasionally caught very large birds: the minimum was 50 g with a ME energy content of 240 kJ (nearly two net mouse units: 1.92 MUME), while the maximum was 107 g, 567 kJME (4.54 MUME).

The most frequently observed small species were tits *Parus* spp. with Great Tits comprising 19%, Chaffinches *Fringilla coelebs* and House Sparrows were equally frequent (10%). *Turdus* spp. were the most frequent medium-sized to large birds (28%), the European Blackbird *Turdus merula* being most frequently recorded (Table 7). Adults, fledglings and nestlings were all taken. As soon as migrants arrived in the study area they were vulnerable to owl predation (e.g. White Wagtail *Motacilla alba* and Chiffchaff) as is true elsewhere in Europe (e.g. SOUTHERN 1954, DELMÉE et al. 1979, JEDRZEJEWSKI et al. 1994).

#### Ephemeral prey

Generally, frogs were delivered during mild nights, often during or soon after rainy spells. Probably this had happened when eruptive migrations took place and rodent prey went into hide. Toads were not observed in the Dutch study area, but were observed twice during rainy spells at the French one. Seldom a beetle, no earthworms were ever taken to the nest (Table 6).

#### Diet and breeding success.

Productivity was highest in 1990 (five fledglings), when small rodents contributed 82.7% and large prey only for 12.8% to the diet. In the years 1985, 1990 and 1993 productivity was high with four, five and four young were fledged, respectively. There was a significant correlation between the percentage of rodents in the diet and the number of young fledged in each year (Spearman Rank Correlation Coefficient  $r_s = 0.7438$ ,  $n = 9$ ,  $P = 0.0216$ ). A similar correlation was recorded for three other populations in a ten year study in Burgundy (BAUDVIN 1991).

By contrast, there was a negative correlation between the percentage of birds, the most frequent alternative prey, in the diet and number of young fledged ( $r_s = -0.658$ ,  $P = 0.0539$ ). In the years when rodents predominated no brood reduction was observed (1990 and 1992 when there were five and three young, respectively). However, in years when birds were a more important dietary component, brood reduction occurred. When the diet was composed of 7.3% birds (1993), one chick died and whereas when it was 21% birds (1991), two chicks died, despite the highest MPM (40.8 g) observed during the study.

# MPM and MPM parameters

In poor years (1984, 1986, 1987 and 1995) when only two fledglings were reared, MPM was variable (c. 34 g, 26 g, 22 g and 24 g respectively), caused by variable proportions of alternative prey (averaged 52 % by mass  $\pm$  26 % SE). The MPM value of c. 34 g was from the "crash year" (1984), when one hatchling died shortly after hatching and the two remaining nestlings begged continuously for food during the longest standard nestling period recorded in the whole study (42 days). The highest MPM was recorded in 1991 when one young died soon after hatching, while another died at an age of 10 days, leaving three nestlings to fledge. This MPM value was attributed to a high proportion of large prey (53 % by mass, Tables 8, 9). MPM averaged 30.16 g  $\pm$  5.55 g, and ranged from 22.64 g to 40.80 g during nestling periods (Table 10). MPM of the video recorded diet in France (1993) (c. 28.0 g, n = 130 items) was similar to the average MPM of the Dutch study area (30.16  $\pm$  5.5 g), although the proportion of large alternative prey was low. This was attributed to Yellow-necked Mice. This species does not occur in Holland and is heavier than the Woodmouse, exclusively occurring in Holland (c. 21 g). Similar values of MPM of surplus prey, were found during the early brooding phase in the nest boxes in the forest (1993: MPM = 28.4 g, n = 150; 1991: MPM = 23.8, n = 108; 1990: MPM = 31.4 g n = 47).

Tab. 8. Food habits of Tawny Owls during nestling period. Annual proportions of prey types in diet, reflecting number of types taken to the nest. See Fig. 3 and 4 for return by mass.

Prey types	Percentage by number				
	1984 2-fledg	1985 4-fledg	1986 2-fledg	1987 2-fledg	1993* 2-fledlg
Shrews	1.9	0.8	9.8	4.4	0.7
Frogs	23.3	23.8	23.9	1.5	1.5
Small rodents	26.2	66.2	52.1	85.1	95.6
Small birds	27.2	4.2	7.6	3.0	0.0
Large birds	18.5	2.5	3.3	6.0	0.7
Large mammals	2.9	2.5	3.3	0.0	0.7
Ident prey	102	118	92	67	136
Uniden prey	6	8	5	3	0
Obs nights	32	29	22	22	26

\* French nest in at border of vast broadleaved forest

Mean mass of video recorded items was calculated from mean values acquired from the surplus prey sample of 1993 (whole items: Yellow-necked Mouse: 29.6 g, Bank Vole: 19.6 g, Wood Mouse: 22.4 g,  $n=152$ ). Interestingly nearly half (48%) of the prey in the 1993 forest sample were partial items. 29 items were decapitated Yellow-necked Mice (18.0 g per item), four were decapitated Bank Voles (11.3 g), 19 hindparts of Yellow-necked Mice (10 g) and four of Bank Voles (6.3 g). This percentage was much lower at the video recorded 1993 French nest site (c. 13 %).

Tab. 9. Food habits of Tawny Owls during nestling periods. Annual proportions of prey types, reflecting number of types taken to nest. See Fig. 4 for annual return by mass.

Prey types	Years, brood size and percentage by number					
	1990 5-fled	1991 3-fled	1992 3-fled	1993 4-fled	1994 <sup>1</sup> 1-fled	1995 2-fled
Shrews	2.9	0.0	0.0	2.7	0.7	4.5
Frogs	2.9	10.1	7.7	4.0	25.0	10.0
Small rodents	85.6	48.7	80.5	81.4	34.1	76.0
Small birds	1.9	20.2	4.2	4.6	11.4	4.0
Large birds	1.9	10.9	7.1	6.0	15.9	2.0
Large mammals	4.8	9.2	0.6	1.3	9.1	6.0
Ident prey	104	118	173	133	44	55
Unide prey	1	1	4	3	1	0
Obs nights	18	17	20	23	26	11

<sup>1</sup> Dutch nest, male died during hatching

ME content and ME gain. The mean ME content of MPM was  $154 \pm 26$  kJ (1.23 MUME) and varied between 126 kJME (1.0 MUME) and 212 kJME (1.7 MUME) (Table 10). The average ME gain ( $5.32 \pm 0.43$  kJ per g prey) was about 17 % less than that of a Wood Mouse (6.32 kJME). As expected there was a highly significant positive correlation between the proportion of small rodents in the diet and the ME gain ( $r_s = 0.817$ ,  $P = 0.0072$ ) (Table 1).

The highest ME gain was found when rodents comprised 76.2% of the diet (1987). On the other hand a low ME gain was recorded when there was a high proportion of

alternative prey: in 1984 (typical crash year, lowest value), 1985 and 1986, when proportion of rodents was low (17.1%, 49.2% and 40.9% rodents in the diet, respectively) and frogs high (18.8%, 24.2% and 23.9%, respectively; Tables 8,9, 10). The ME gain of a frog is about 35% less than that of a Wood Mouse (Table 1).  
French nest site. The ME content of MPM (161 kJME or 1.29 MUME) was slightly greater than the mean of the Dutch study area (154 kJME) attributed to the relative high proportion of Yellow-necked Mice by mass in the diet (Tables 9, 10).  
ME content in both the French (BAUDVIN & DESSOLIN 1987, Burgundy) and in the Swiss study (JUILLARD in BAUDVIN & DESSOLIN 1987) (139 kJME and 135 kJME resp.) acquired by photo-registration during post brooding, was within the range found in Holland (Table 10). Both the French and the Swiss diets represents intermediate rodent years (3.3 and 2.5 fledglings per brood resp.) (Fig. 4, 5).

Tab. 10. Mean prey mass (MPM), ME content of MPM and ME gain of observed prey of Tawny Owl during nestling period (n = 1,179 identified items).

MPM g	MPM <u>ME contents</u>		ME Gain kJg <sup>-1</sup>	No obs items	Brd.size fledgls (year)
	kJ	MU			
40.80	212	1.69	5.18	120	3 (91)
38.57	189	1.51	4.89	45	1 (94) <sup>+</sup>
34.73	164	1.31	4.72	107	2 (84) <sup>#</sup>
29.96	168	1.35	5.62	169	3 (92)
29.36	166	1.33	5.66	148	4 (93)
27.43	130	1.04	4.75	150	4 (85)
27.21	153	1.23	5.63	105	5 (90)
27.16	148	1.18	5.45	50	2 (95)
26.59	159	1.28	5.99	124	2 (93) <sup>*</sup>
26.13	126	1.01	4.82	98	2 (86)
22.64	133	1.06	5.87	63	2 (87)
30.16	154	1.27	5.32	mean	
5.55	36	0.20	0.47	SE	

<sup>+</sup> Catastrophic year, <sup>#</sup> crasch year, <sup>\*</sup> French nest



Feeding rates

As expected after hatching feeding rates increased in relation to brood size: in two, three, four and five broods with 2.36 (5.91 MUME/dy), 3.35 (8.93 MUME/dy), 4.5 (11.02 MUME/dy) and 4.41 (10.74 MUME/dy) times, respectively, the mean rate of incubation periods (2.5 MUME/dy). Switching contributed at least 20% by weight to the food, but it could not always prevent nestling mortality (Fig. 3, 6).

v. Ginkel 1990, 5 - brood

visits/day

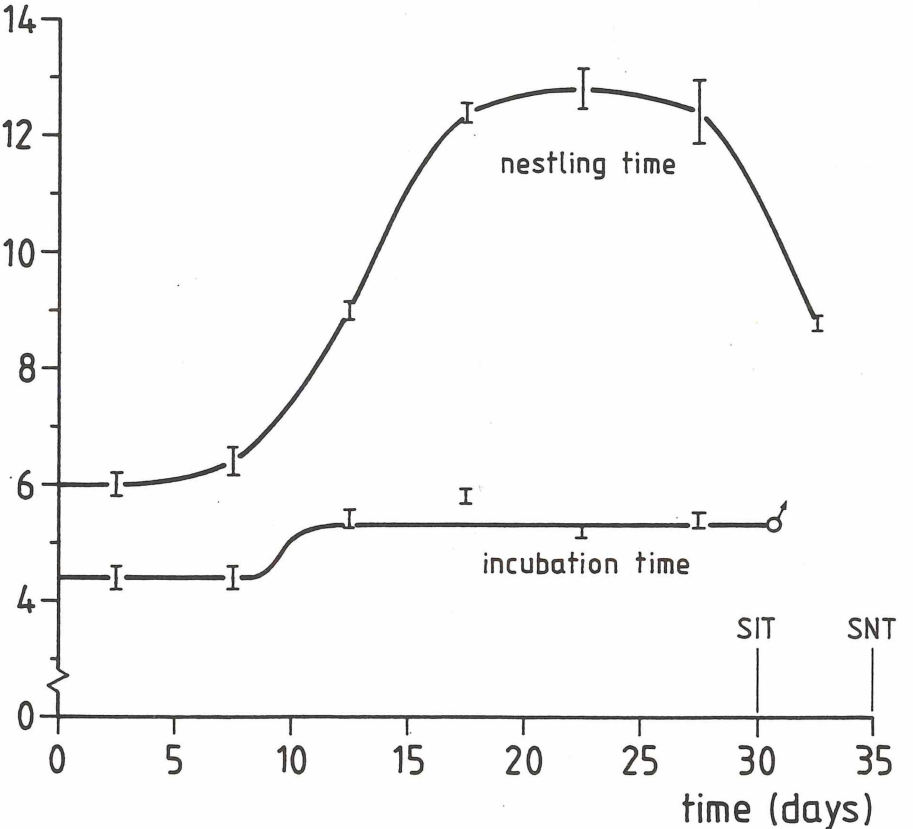


Fig. 6. Change in feeding rate of a 5-brood between incubation and nestling periods in a good rodent year (1990 nest Dutch nest, no brood reduction). See Fig. 5 and Table 9 for diet by mass and number respectively.

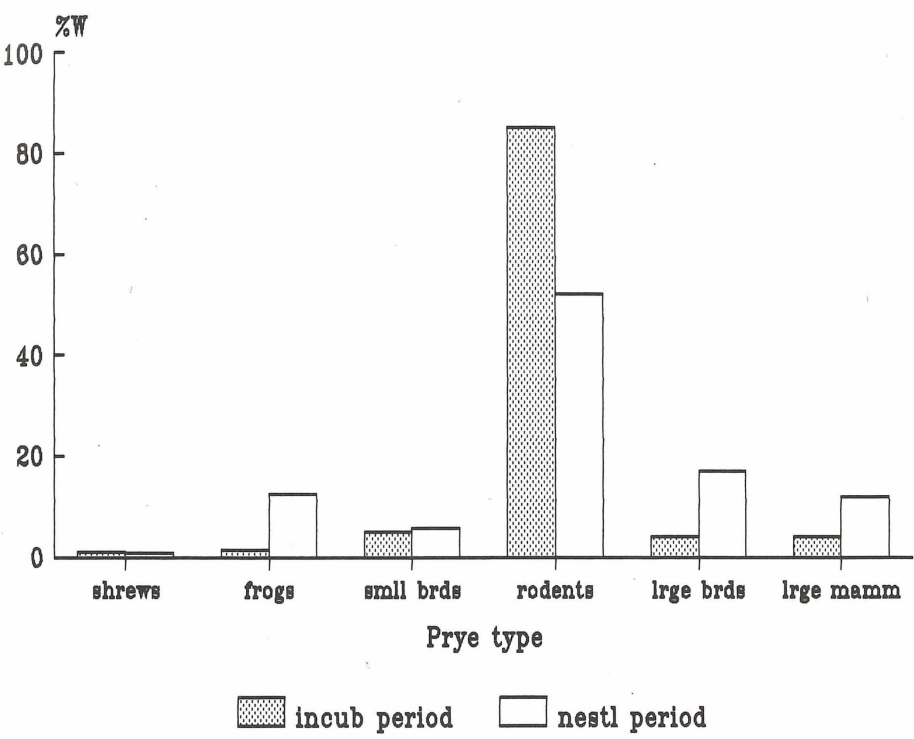


Fig. 7. Dietary shift at the Dutch study area. Contribution of prey types by mass, mirrors the return (in g) of foraging for prey types. See Table 11 for proportions by number.

Dietary shift

Shift to larger prey

There was a dramatic change in diet in the Dutch area following hatching: small rodents decreased from 91.1 % to 66.3 % by number (Table 11, Fig. 7). The proportion of all other prey increased (by 1.4-20 times), although small birds increased by only 1.4 times, frogs increased by 20 times. After hatching the proportion of large prey increased considerably; large birds (40-200 g) by 11 times and large mammals (young lagomorphs, young rats and moles; 50-200 g) by 5.7 times. In the French oak-beech forest this was less dramatic, although a shift was recorded in the post brooding phase, from day 14 of nestling period on.

MPM (21.5 g) and ME content of it (125 kJME, 1.08 MUME) increased after hatching by 40% and 23% respectively (Tables 5, 10). The smaller increase of metabolizable

energy contents of MPM was mainly caused by the high water content of the frog prey and to a lesser extend by birds (Table 1). The range of variation of MPM increased from 2.2 g during incubation to 18.2 g in the nestling periods, that is, 8.3 times. Such changes to larger prey types are not unexpected by optimal foraging.

Tab. 11. Dietary shift after hatching in Tawny Owls at the Dutch studea area. Fragmented forest habitat near human habitation rich in alternative prey. See Fig. 6.

Prey type	Incubation period % N	Nestling period % N	<u>NT</u> IT
Shrews	1.2	2.5	2.08
Frogs	0.6	12.0	20.0
Small rodents	91.1	66.3	0.73
Small birds	6.5	9.3	1.43
Large birds	0.6	6.7	11.17
Lagom, moles, rats	0.6	3.4	5.67
Small prey 35 g	99.5%	90.5%	0.91
MPM in g	21.5	29.8	1.39
Range MPM (g)	2.20	18.16	8.25

Discussion

Ultimate explanations

The discussion is divided in two parts. In the first part we attempt to explain foodhabits by an evolutionary approach. The second one concerns the direct responses of owls to their environment.

Prey abundance in particular staple prey of owls fluctuate dramatically from year to year. Fledging success is usually positively correlated with rodent abundance in spring. Nocturnal predators have evolved different breeding strategies to exploit these fluctuations. For example 1) by pursuing breeding grounds with high rodent densities (nomadism) e.g. of common voles *Microtus arvalis* by Short-eared Owls *Asio flammeus*,

Long-eared Owls *A. otus* (KORPIMÄKI & NORRDAHL 1992), 2) by being sedentary (resident strategy), sticking to scarce nest sites and exploit rodent fluctuations with alternative prey resources e.g. forest owls as Ural (LUNDBERG 1979, SAUROLA 1989b) and Tawny Owls (SOUTHERN 1970, DELMÉE et al. 1978, WENDLAND 1972) as well as Little Owls (EXO 1983, ROMANOWSKI 1988, FINCK 1989) or 3) a mixed strategy Tengmalm's Owl: males usually sedentary, female often nomadic in Central Europe (KORPIMÄKI et al. 1987, KORPIMÄKI & LAGERSTRÖM 1988, KORPIMÄKI & NORRDAHL 1989, KORPIMÄKI 1992, SCHWERDTFEGGER 1992).

#### Increase of large prey

In the Dutch study area we demonstrated a considerable increase in feeding rates after hatching and found a highly significant difference in the proportion of small prey, compared to large prey between the incubation and nestling periods ( $\chi^2 = 1395$ ,  $P < 0.0001$ ). During incubation over 90 % was rodent prey, while some large alternative prey was available (resident medium sized birds as European Blackbirds, Jays, Blackbilled Magpies, and medium sized mammals: some moles and rats) as well as small prey (resident birds: e.g. Tit spp, two Sparrow spp., Chaffinches, Green Finches). This indicates that incubation demand was adjusted to prevailing small rodent prey type and that clutch size was adjusted to prelaying rodent abundance (SOUTHERN 1970).

After hatching the demand of broods increases and as predicted we found a diminishing preference for the rodent prey type (Table 3, Fig. 4, 5). This was already noted by Southern in 1969 by three methods pellet analysis, surplus prey in the early nestling period and direct observation in red floodlight. However in forest habitats the diversity and abundance of alternative prey is restricted compared to the fragmented forest habitats near dairy farms and small villages. Curiously DELMÉE et al. 1979 found hardly any bird prey in a mixed forest during their fifteen year study and GOSZCZYNSKI et al. 1993 demonstrated a range of habitat related diets.

#### Variation rodents in diet

Second we observed a significant positive correlation between rodents in the diet and fledging success, which was earlier recorded for the Tawny Owl (Finland: LINKOLA & MYLLYMÄKI 1969; Uk: SOUTHERN 1970; Belgium: DELMÉE et al. 1979; Germany: WENDLAND 1984, France, BAUDVIN 1991). More over we found a significant correlation between the proportion rodents in the diet and ME gain per g prey delivered.

Such a positive correlation between rodents and fledging success was found in the Ural Owl, too (KORPIMÄKI & SULKAVA 1987, PIETÄINEN 1989, SAUROLA 1989b).

In Burgundy the diet of broods that fledge 4 up to 7 owlets consisted of 80 % up to over 90% (by number) of small rodents, leaving a small proportion of less than 20 % to 10 % for alternative prey. It is highly improbable that there is always a lack of alternative prey in good rodent years, on the contrary abundance is usually high.

We found a similar fledging success of 4 and 5 fledglings (1985, 1990, 1993) with an average proportion of 82.7 % rodents in the diet and a proportion of large prey of 12.8 % (Tables 8, 9).

But in 2-broods the proportion of rodents averaged c. 40 % and BAUDVIN (1991) found about 35 % in the other forests in Burgundy.

An intermediate value of c. 65 % of rodents was found for broods that fledge three owlets as recorded in Burgundy (BAUDVIN 1991). A similar relationship with forest voles was found in Ural Owls (PIETIÄINEN 1989, SAUROLA 1989). It seems unlikely, too, that in good vole years the availability of alternative prey in Fenno-Scandinavia was lower than in poor ones (HAGEN 1952).

This indicates that the proportion of small rodents consumed are preferred and had the greatest benefit-to-cost ratio as compared to alternative prey. In other words the proportion of rodents determines fledging success not only in resident owl species as Ural, Tawny and Little Owl and Barn Owls (SCHÖNFELD & GIRBIG 1975, MULLER 1992), but in all owl species feeding on small mammals (KORPIMÄKI & NORRDAHL 1987, KOPIMÄKI & NORRDAHL 1991).

#### Alternative prey and fledging success

We found a negative correlation between bird prey and number of fledglings, despite mean bird mass was on average about two times higher (c. 47 g, c. 2.00 MUME, c. 250 kJME) than mean small rodent prey (21.5 g, 125 kJME, 1.00 MUME). This indicates that birds provide less energetic return than rodent prey type do. More over large bird prey renders less energy return to brood growth, probably caused by the amount of digestible remains often found in the nest caused by incomplete plucking. Besides a proportion of large bird prey was often consumed by the female during plucking. We were not able to estimate this proportion. Under poor conditions this may be greater than under favourable ones. The same was found in large prey as rabbits. Rodent prey could already be swallowed whole by owlets within 7 days of age, small decapitated birds (< 45 g) about a week before fledging.

Second we observed that alternative prey could not prevent brood reduction, in spite of an increase of MPM and an increase of feeding rate. This suggests that a certain proportion of rodents in the diet should be met for a certain fledging success. However, a minimal proportion of rodents (35 %) are necessary for fledging two and some times even one owlet (SOUTHERN 1970, DELMÉE et al. 1978, WALLIN 1988). Such a small proportion of rodents in the diet can open up a great variety of opportunities to meet a low brood demand by several types of alternative prey. This is probably often considered as nonselective hunting, what is probably true within a poor season. But not in good or peak rodent years.

Broods that under went reduction could prevent nest failure to ultimately fledge one owlet (WALLIN 1988, n = 63 nests, in this study two owlets). Energetically reduction

of broods is inefficient, indicating that clutch size adjustment to prevailing rodent density is an efficient strategy in reproduction. This adjustment is observed in both Tawny, Ural Owls (SOUTHERN 1970, SAUROLA 1989, PIETIÄINEN & KOLONEN 1993) and Little Owls (EXO 1983, FINCK 1989).

#### Significance alternative prey

The large proportion of alternative prey enables owls with the resident strategy to successfully fledge a limited number of young (2 or some times even one) with only 35 % of rodents in the diet. Probably this strategy enables them to reproduce in poor rodent habitats, too e.g. urban parks (WENDLAND 1980, GOSZCZYNSKI et al. 1993). A similar breeding under poor rodent conditions is observed in the Ural Owl (SAUROLA 1989a) and the Little Owl (JUILLARD 1984). But do young that fledge small broods have equal chances to survive as owlets that fledge large broods? Tawny Owls that became independent in autumns without beech mast and acorns have little chances to survive their first year of life, because the rodents suffer than from severe winter mortality. But the reverse is the case in mast and acorn years. As soon as abundant tree fruit, rich in energy and nutrients, had fallen rodents start to reproduce and minimally suffer from winter mortality (SOUTHERN 1970, JEDRZEJEWSKI et al. 1994, pers obs in Châtillon Forest).

#### Rodents and recruitment

The positive correlation we found between fledging success and small rodents suggests a higher recruitment probability for owls originating from large broods than from small ones. WALLIN (1988) recorded for large broods (4 and 5 fledglings) a two times higher recruitment probability (c. 0.4 recruits/brood,  $n = 74$ ) than for 2-broods and single broods (0.2 recruits/brood,  $n = 165$  and  $n = 63$  resp.). An intermediate value was found for 3-broods (c. 0.3 recruits/brood,  $n = 158$ ). Dispersion distance is also positively correlated with rodent density in the autumn of becoming independent (WALLIN 1988). This finely explains the significance of the different proportions of rodent and alternative prey in the diet for fitness in Tawny Owls.

#### Prey type selection

It is generally recorded that shifts did not occur in good and peak rodent years (Southern 1970, DELMÉE et al. 1979, WENDLAND 1984). However, dietary shifts between winter and summer have recently been demonstrated in several resident owl species, as Ural, Tawny and Little Owl (SOUTHERN 1969, LUNDBERG 1976; KORPIMÄKI & HUHTALA 1986; JEDRZEJEWSKI et al. 1994, ILLE 1992) and a shift back after nest failure to non-breeding diet in Northern Spotted Owl (BARROWS 1987).

Similarly we found a highly significant difference in diet between incubation and nestling periods, while it was evident that several resident alternative prey species were available during incubation. This supports the hypothesis of selective predation

on larger prey by breeding pairs in contrast with the opposite trend in nonbreeding and incubating pairs. The winter diet of Tawny Owls consisted mainly of small rodents (90 % by number) (SOUTHERN 1969, JEDRZEJEWSKI et al. 1994). The observed significant shift away from the larger alternative prey back to the smaller types after nest failure and the 90 % choice of small rodent type during incubation is consistent with the preferential predation of most profitable prey during low demand.

### Alternative prey options

Unquestionably availability of prey types as staple prey versus several alternative prey and between alternative prey types (insect and earthworm type c. 1.5 g, shrew type 9 g, small bird or frog types 20 to 30 g and large bird type averaging 70 g) is an important factor in determining the diet of resident owls. Some prey types are only available later in the season as the ephemeral frogs, swarming beetles and small birds that had returned from migration. Glirids appear after hibernation (March/April) and young rabbits emerge even later in the season (April/May). Water voles became more vulnerable when reproduction starts (March/April) and when they increase foraging above ground. We believe that this increases the options, but do not change the inherited foraging strategy. In peak rodent years they stick to the staple prey, although alternative prey is abundant. Under poor rodent conditions they hunt for more alternative prey, even when they are less abundant too.

For example in a forest habitat in Burgundy under intermediate conditions of fledging success (3.33 fledglings per brood) three nests were photo-registered in the post brooding phase. During rainy spells it is assumed that almost no prey is accessible, except ephemeral frogs and earthworms. These types were indeed taken to the nest during long rainy spells. (Tawny Owls catching earthworms under rainy conditions has been described by MACDONALD 1976). More of the larger frog prey (8.1 % by number of the diet,  $n = 37$ ) were taken than earthworms (3.3 %,  $n = 15$ ). (BAUDVIN & DESSOLIN 1987). In the Dutch study area frogs were usually delivered during mild rainy nights, too, no earthworms were ever observed. This indicates that climatic conditions can severely limit prey choice. There were 2.5 times more large prey (c. 30 g) taken to the nest than small (c. 2 g) during high brood demand and this is consistent with optimal foraging. These options of prey types seem not to influence the foraging strategy.

A comparable example. Observations concern the whole post brooding phase under very low conditions of fledging success: 1.6 fledglings/brood, 3 nests had undergone brood reduction out of the 7 observed ones with two nestlings. Under these apparent very poor conditions the proportion of larger prey types was greater than the very small prey types. Larger alternative types 36.6 % by number (frogs 17.5 %, shrews 16.0 %, small birds 3.1 %) and 24.2 % smallest ones (insects 23.8 %, earthworms 0.4 %) were photo-registered ( $n = 813$ ) (DE BOE 1992). This is consistent with optimal foraging.



This is evidence, although circumstantial, that options of alternative prey choice do not ware off the strategy of maximizing prey delivery.

#### Minimizing costs of transportation

The diet, as recorded at nests, is influenced by central place foraging itself. It is almost certain that we under estimated the proportion of small prey (shrews 10 g and birds 18 g) taken to the nest or probably did not even record even smaller prey types (earthworms, insects). LIBOIS (1984) and BULL et al.(1989) demonstrated that male Barn Owls *Tyto alba* and Great Grey Owls *Strix nebulosa* respectively maximized return for their expenditure of hunting energy by consuming a significant proportion of small prey at the spot of catch and carrying larger prey to the nest.

We observed, that the largest prey types as young rabbits, young rats and large birds, were usually delivered during postbrooding phase. This foraging behaviour is consistent with optimal foraging (central place foraging). Similar selection of larger prey was found in an experimental set up. Barn Owls caught larger rats (80 g - 100 g) when breeding than in nonbreeding conditions (average 60 g) (ILLE 1991). A similar selection for size was recorded in free living Barn Owls (COLVIN & MCLEAN 1986).

It was noted (JEDRZEJEWSKI et al. 1994) that European Blackbirds were significantly more caught than expected, but no relationship to breeding was given. We suspect that the foraging behaviour on the forest floor increases its vulnerability.

#### Unprofitable prey

Catching and carrying considerable amounts of very small prey as insects and earthworms to broods in resident owl species, tempts to raise the question of the limits to size (mass) taken to the nest ? Theory postulates that unprofitable prey (energy and nutrient content) should be avoided at any time (PYKE et al. 1977) (up to 24 % in Tawny Owls, DE BOE 1991; up to 84 % in the Little Owl, JUILLARD 1984). We calculated a percentage of 24.6 % of insects, including 0.4 %earthworms in the diet of those Tawny Owls. Such a proportion of very small prey in the post-brooding period suggests very poor conditions. MPM was estimated a 17 g (121 nights, 796 photo-registered identified items, 7 nests, three seasons). We calculated MPM ( $1.77 \pm 0.48$  g SE) and feeding rate for the Little Owl (  $89.8 \pm 15.5$  g per day) during post brooding ( photo-registered prey: 8,474 items; 8 nests, several seasons. JUILLARD 1984). The conditions were very poor, fledging success 1.8 fledgling per brood (1978-1980). The ration of prey taken to the nest per day is equivalent to c. 4.5 mouse units in g and equals a calculated prey visit rate of 4.5 per night versus an observed ten times higher visit rate (50,76 "15.5 prey visits per night). It is no wonder that the observed population became almost completely extinct. At some time a threshold of unprofitable foraging must have been crossed. We believe that Little Owls can reproduce/survive temporarily low densities of rodents, if sufficient profitable alternative prey is available. It is likely that both the staple and the large alternative prey has been decreasing

in Central Europe after 1945 (MADON 1933, UTTENDÖRFER 1939, ILLE 1992, LECOMPTE 1994).

### Conclusion

The findings of this study are consistent with optimal foraging (central place) theories for 1) the post hatching dietary shift to larger prey and 2) the preference for small rodents during relatively low demand in winter and during incubation, although limited alternative prey is available as compared to the summer period and 3) the positive correlation of rodent prey and fledging success in this study affirm the diet findings of other authors. Rodents appeared to provide the greatest benefit-to-cost ratio as compared to alternative prey, because during peak years hardly any alternative prey was taken to the nest, although their abundance was most probable. We consider the shift back to the smaller winter prey type as found in the Spotted Owl and the choice to carry most large prey to the nest (LIBOIS 1984, BULL et al. 1989) as support for the active selection of larger prey types.

### Proximate explanations

Although some observations are very difficult to assess conclusively as direct responses, other support the explanation of food habits in owls feeding on small rodents.

### Rodent fluctuations

A relationship between an increase of primary production associated with rodent food is hard to establish for voles e.g. in northern regions (PIETIÄINEN 1989). But for rodents in broad-leaved forests, as Wood Mice and to a lesser extend voles (Bank Voles), beech mast and acorn production initiates an increase of these rodents soon after the fall. After a winter rest reproduction is resumed in early March and densities can increase to peak values at the end of the summer depending on the fruit production (SMITH 1966, SOUTHERN 1970, JEDRZEJEWSKI et al. 1994, pers obs). For the Tawny Owl the spring density is a good predictor for the quality of the breeding season. A short fall of tree fruit production in the autumn can cause a severe winter mortality (crash in rodent density). The production of mast (tree fruit) is a complex interaction between the physiology of trees and climate. More over rodent density is influenced by predator-prey interactions itself (KORPIMÄKI & NORRDAHL 1989). In fact rodent fluctuations are rather unpredictable. Autumn density is vital for fledglings when they become independent and start to disperse. Similarly spring abundance of Field Voles in coniferous forests are good predictors for Ural Owl breeding season quality and crashes seem also to be rather unpredictable (SAUROLA 1989b, PIETIÄINEN 1989).

### Range variations of rodents

I measured annual density of rodents in the Châtillon forest over 10 years and found a variation between less than a rodent per ha after the winter crash 1987/88 (1890 trap.nights) up to almost 200 per ha in a peak year 1991 (945 trap.nights). The gregarious Common Vole can have often greater fluctuations e.g. as found in the Saale Valley (Germany) some tents per ha up to over some thousands per ha in a peak year (SCHÖNFELD et al. 1977). These observations demonstrate the different ranges of variation in the fluctuations of open and forested habitat. The greater amplitude of voles at open habitat may explain why the costly mode of foraging on the wing (e.g. in nomadism) could have been evolved.

### Fledging success and rodents

In the two resident species Tawny and Ural Owls 80% of the variation of number of fledglings per brood is explained by clutch size variation. In turn clutch size variation is significantly correlated with rodent abundance in a sense pooling together poor, intermediate and good rodent years (LINKOLA & MYLLYMÄKI 1969, SOUTHERN 1970, Korpimäki & Sulkava 1987, Pietiäinen 1989). This is a functional response to exploit fluctuating prey resources. The high abundance as well as its foraging behaviour of rodents on the forest floor contributed to the profitability of these prey. Such a prey behaviour facilitates catching by a sit and wait hunting mode. The great increase of feeding rates found in this study demonstrates that large numbers of rodents were channelled to reproduction.

We believe that Little Owls also regulate their clutch size according to Common Vole availability. In good vole years they tend to lay larger clutches (c. 5 eggs) and lay earlier than usually (Ullrich 1980, Finck 1989). But for obvious reasons one had not found the evidence for this clutch size adjustment (Gaszmann & Bäumer 1993, Gaszmann et al. 1994). All studies of Little Owl concerning a k-factor analysis have been executed after the disappearance of the dramatic fluctuations of the Common Vole between 1945 and 1960 in Central Europe (Exo 1987, Knötzsch 1988). The significant increase of mean clutch size from west to east in Central Europe (Exo 1987) had to be interpreted by an increasing vole abundance eastward related to less intensive agricultural practice. As Kloppe (1970) had suspected earlier.

Little Owls can easily produce large clutches (7 to 8 eggs), in response to prelaying ad libitum feeding, when reared in a cage (Robiller & Robiller 1986). Such large clutches were also found in the field in peak vole years before 1945 (Collinge 1922, 1923, Uttendörfer 1939, Schön et al. 1991: p.154).

Under good prey conditions as prevailed up to the beginning of this century in England the Little Owl dispersed after a staggering introduction from two small populations in the surroundings of London over the whole of England within about ten years. However either breeding nor Field Vole density data of the dispersion period were published. This colonising performance suggests larger dispersion dis-

tances associated with higher vole availability (WITHERBY & TICEHURST 1908) than recorded now a days (KÄMPFER & LEDERER 1988, SCHÖN et al. 1991, GASZMANN & BÄUMER 1993).

#### Hunting and alternative prey

During a rodent low of less than one rodent per ha, as I found in Châtillon Forest (1989), alternative prey were the only food source for the winter. If such conditions coincide with a severe winter with snow, a high mortality up to about 50 % of the breeding population can occur (SOUTHERN 1970). This happened also in other resident owls (Ural and Little, including Barn Owls). But a resident owl populations will recover within about three years from such events (SOUTHERN 1970, EXO 1983, KNÖTZSCH 1988). However, in habitats where staple prey and alternative prey availability is impoverished, owl populations cannot recover by local recruitment (JUILLARD 1984, EXO 1987). Winter decrease can only be compensated for by immigration, if there exists richer breeding area's elsewhere. (DE BRUYN 1994).

It is tempting to associate hunting experience and fledging success in Tawny and Ural Owl. Both species are capable to breed in their first year of life. This only occurred when rodent density is high as found in good and peak years. This indicate that hunting for rodents has been acquired before becoming independent. However first year owls are unable to breed successfully in poor years, when a large a proportion (c. 65 % by number) of alternative prey is involved. Only third year of age and older Tawny and Ural Owls breed successfully in poor years (SAUROLA 1989, WALLIN 1988). Tawny Owl offspring production increased asymptotically with age, which was statistically reliable in both sexes (WALLIN 1988). The effect was greatest in males the hunters. In both sexes it takes three years to acquire the full breeding capability. This suggests that a process of experience is involved. And we believe that the mayor component in the process is hunting experience for alternative prey and familiarity with local hunting conditions (niches of alternative prey).

This idea was supported by the finding in the Little Owl, that territorial size and quality is poor in inexperienced males as compared to experienced ones (FINCK 1989, FINCK 1993).

#### Pellet analysis Tawny Owl

In order to compare my calculated diet parameters with other diets, I calculated MPM, ME content of MPM and ME gain per g prey for several diet studies. Usually a diet is assessed by means of a pellet analysis. However finding Tawny Owl pellets away from nest sites is extremely difficult. Sample sizes are often to small for comparisons between poor and good years (RUPRECHT & SZWAGRZAK 1987, BOUVIER & BAYLE 1989, KIRK 1992) and within seasons (SOUTHERN 1954, JEDRZEJEWSKI et al. 1994). In forests with considerable ground vegetation like the Châtillon forest, it is almost impossible to find pellets at a regular basis. SOUTHERN (1954), however, found that Tawny Owls

generally cast one of the two pellets daily prior to roosting and championed in finding pellets on a regular basis. But owls frequently change their daily roost sites within seasons, making pellet stations very hard to find. Only in exceptional cases do individual owls use regular pellet stations (WENDLAND 1972, KIRK 1992). Nest remains usually show the food habits of a small breeding population and remains of nestling period predominate.

Tab. 12. Mean prey mass (MPM) en metabolizable energy of prey calculated from diet analysis, based on pellets and prey remains collected in and around Tawny Owl nests, during short-term (\*) and long-term investigations in Europe (N = 17,011).

MPM (g)	MPM <u>ME content</u>		ME gain kJ.g <sup>-1</sup>	n items	No yrs collect	Source year (country)	
	kJ	MU					
47.1	245	1.97	5.21	2743	*	KORPIMÄKI 1986	(SF)
39.9	212	1.70	5.31	1158	9	KONING 1980	(NL)
34.2	170	1.37	4.97	647	*	NILSSON 1984	(S)
29.4	156	1.25	5.31	1382	18	WEBER 1973	(D)
29.3	153	1.23	5.22	3903	12	SCHNURRE 1975	(D)
24.7	130	1.04	5.26	480	*	RUPRECHT & S 1987	(PL)
23.5	119	0.95	5.06	3221	9	KÄLLANDER 1977	(S)
20.4	117	0.94	5.73	381	*	CONTOLI & S 1978	(I)
20.4	108	0.86	5.29	3096	15	DELMÉE et al. 1979	(B)
29.9	157	1.26	5.24	-	-	mean	
8.6	44	0.35	0.20	-	-	± SE	

Prey remains bias

While prey remains at nests are easy to collect, they do not necessarily provide a reliable picture of the diet of individual nests. However, they are usually the main information source for food habits in owls, if one samples several nests (Table 12). Yet sampling prey remains at individual nests is subject to numerous biases. First, individual female owls vary in their behaviour of cleaning the nest site (VAN VEEN pers obs, LUNDBERG 1976). Second, the proportion of partial prey items varies from year

to year (e.g. decapitated prey and hind parts taken to the nest, this study) and is difficult to identify, when essential parts as skulls are missing (BAUDVIN and DESSOLIN 1987, DE BOE 1992). Third, a percentage of rodent skulls (which depends on species and age involved) is digested by the nestlings (RACZYNSKI & RUPRECHT 1974, LOWE 1980). BAUDVIN and DESSOLIN (1987) found a considerable difference between photo-registered prey deliveries and prey later recovered from nests during the post-brooding phase: for Yellow-necked Mice about 70% were recovered, Bank Voles 50% and frogs 39%. Therefore, it is difficult to estimate prey provisioning quantitatively during breeding for owls as LUNDBERG (1976) attempted for the Ural Owl. Nevertheless many nests in diet studies resulting in large numbers of prey reduces this bias and give a reliable picture between annual food habits and generally over the years, even in some quantitative aspects of MPM. I (JvV) only used diets containing a minimum of insects and earthworms for the comparison (Table 12).

#### Diets with invertebrates

We excluded studies conducted in the United Kingdom (Table 12), because of uncertainty about the number of earthworms (*Lumbricus* spp., *Alolobophora* spp.) prey. In a composite "national diet" for the Tawny Owl in Britain, YALDEN (1985) found that earthworms composed 18 % of the diet by mass. Earthworms are usually taken to the nest during prolonged periods of rain (BAUDVIN and DESSOLIN 1987). YALDEN (1985) attempted to calculate the biomass of earthworms and concluded that 1 g of sand and chaetae was equivalent to 10 g of earthworm. However, MPM might not be calculated as accurately for diets containing that amount of earthworms as those composed mainly of vertebrates and some arthropods. If earthworms are excluded, the MPM of Tawny Owls in SOUTHERN's (1970) study at Wytham Wood (Oxford, England) is close to the midpoint of the values in Table 10 (26.1 g, ME content 145 kJ equivalent to 1.16 MUME and ME gain of 5.56 kJME /g prey; n=9494), which is thus a slight overestimation.

#### Diets with a few invertebrates

Our findings are similar to those from several studies in continental Europe, where MPM ranged from 20.4 to 47.1, with an average of  $29.9 \pm 8.6$  g, equivalent to 1.26 MUME (157 kJME). The highest MPM (Finland) was attributed to the high proportion of Water Voles, some medium sized birds and lagomorphs. The next highest value (Holland dune area; Koning 1980) was mainly attributed to lagomorphs. The values we found during the incubation period are similar to those from DELMÉE et al. (1979) in Belgium and CONTOLI & SAMMURI (1978) in Italy where the proportion of birds were negligible; the lowest of the list and equals mean rodent weight. The mean value from all our nestling phases combined was similar ( $30.2 \pm 5.5$  g, equivalent to  $1.23 \pm 0.43$  MUME and  $154 \pm 26$  kJME) to the overall mean of all studies mentioned above ( $29.9 \pm 8.6$  g;  $1.26 \pm 0.35$  MUME and  $157 \pm 44$  kJME) or if exclusively the

longterm studies were considered ( $28.5 \pm 6.7$  g;  $150 \pm 36$  kJME), based on a mean of 12 years sampling and 12,760 identified prey items. This is close to our findings.

#### Sex differences in food habits

**Observed deliveries.** We were not able to investigate sex differences in diet during the postbrooding phase. It is possible that prey captured by the male, weighing:  $377$  g  $\pm 7.4$  SE, ( $n=29$ , BAUDVIN & DESSOLIN 1992), at post brooding, was transferred to the female (weighing  $523$  g  $\pm 8.6$ ,  $n = 109$ ) unobserved, before she delivered it to the nest. However, all large prey (adult European Blackbirds, young rats, young lagomorphs and a single European Mole) were delivered by the heavier female. Similar behaviour was recorded by infra-red photo-registration in the Little Owl, although reversed size dimorphism in this species is minimal (JULLARD 1984). This may indicate that this might be associated with plucking prey, too. A task exclusively executed by female owls. Males drop their food in the nest when young did not take them in the bill and the female is not at nest. Male owls were never recorded plucking prey at nest during our 12 years of observation.

During the 1994 breeding season the male did not return to the nest. At that time the female owl was brooding her hatchlings and she was forced to fend for herself and the brood. Only one nestling survived (Table 2). The mean prey size delivered by the female following male's disappearance was larger (MPM =  $38.6$  g) and had a higher net energy content ( $5.51$  MUME) than the mean value (MPM =  $30.2 \pm 5.6$  g,  $5.32 \pm 0.43$  MUME) of all nestling periods, when prey was taken by male and female together (Table 10). In this case larger prey could counterbalance the lower ME gain ( $4.89$  kJME per g prey) compared to average ME gain ( $5.32 \pm 0.43$  kJME) of all nestling periods. The female appeared to be able to increase prey size by over 25 % (by mass) and counter balanced the almost 10% lower ME gain per g prey of that diet. This foraging behaviour is consistent with optimal foraging.

#### Breeding home range and habitat

During the breeding season, the female Tawny Owl has a restricted home range. She may wait for prey to be brought to her by the male during courtship feeding as in the Ural Owl (LUNDBERG 1979,1980) and the Northern Spotted Owl *Strix occidentalis* (FORSMAN et al. 1984); in good years she may stop hunting altogether as observed in Spotted, Tawny and Ural Owls (WENDLAND 1972 a, LUNDBERG 1980, FORSMAN et al. 1984).

Moreover, habitat structure influences hunting behaviour between sexes. In continuous forests male interperch distances are slightly greater than in females, but in fragmented woodland males flew 40 % further per hour than its mates (REDPATH 1996). This might support the idea that males hunt further away from nest, at least they obtain longer areas traversed

In contrast, OVERSKAUG et al. (1995) found evidence that male Tawny Owls killed in road accidents preyed on larger prey than females. We suggest that because they are lighter and have lower energy costs for hunting, males can forage further from the nest than females (van Veen pers obs). It is well known that female Tawny and Little Owls confine their hunting in the neighbourhood of the nest during nestling time (GÉNOT & WILHELM 1994). In Tawny Owls this is related to nest defence and is positively correlated with brood size (WALLIN 1988). The different sexes could therefore hunt in different areas (even different habitats) and as a consequence catch different prey types; this may explain the findings of OVERSKAUG et al. (1995).

Analyses of stomach contents are rare, although sometimes very revealing (BIBER & SCHMID 1987, OVERSKAUG et al. 1995). To date sex differences in diet among owl species have only been reported for the Northern Pygmy Owl *Glaucidium gnoma californicum* from British Columbia based on stomach contents (EARHART & JOHNSON 1970).

Conclusion. There is circumstantial evidence that owls feeding on small rodents adjust their clutch size mainly to spring abundance of rodents. Even resident owls do so and again fledging success (number of fledglings per brood) and recruitment probability in these species is positively correlated with the rodent density. Rodent availability is crucial for owl conservation.

## Acknowledgements

We would like to thank Mr. J. W. Kroon, Prof. Dr. J. H. Koeman and Dr. W. Bongers for their interest and support during our investigations and the Wageningen Agricultural University (WAU) for placing their facilities at JvV's disposal. In addition JvV thanks the late Anton Bruyn for help in selecting the Dutch study area and the families Bieshaar, van Ginkel and Boerse for their hospitality at the farms. Thanks are due to technical assistant Zomer Bruyn (1984-86) who designed the observation nest box, all people of the technical services department Biotechnion Wageningen University and the students who participated in this study: Corian Sasse (1984), Karin Rood (1985), Marjanne Smith (1986), Eric Arnold (1986-87), Erik Kwinkelenberg (1988), Lodewijk Koster (1991), Marthe van Dongen (1992), Boris Berents (1991-94) and ir. Ellen ten Broeke (1988-92), Gerard Mijnhout (1993-95). Special appreciation is extended to the representatives of "La Choue" (Dijon Burgundy, France), Baudvin and Dessolin, for their cooperation in the study of owls, the foresters Guy Boisson and Paul Brossault, who supported the fieldwork so kindly in the Châtillon Forest and the Office National des Forêts for the permission to work in the Châtillon State Forest and the CRBPO for the banding permit, as well as to prof.dr. K. Vooüs for his comments on earlier drafts of the paper and to dr. H. Gaszmann for the translation of the title and summary into German.



## Zusammenfassung

Der Ausflugerfolg beim Waldkauz *Strix aluco* in Abhängigkeit von Veränderungen in der Nahrungszusammensetzung. – Die Zusammensetzung der Nestlingsnahrung beim Waldkauz *Strix aluco* wurde in zwei Waldgebieten, eines in Holland (3 Brutpaare), eines in Frankreich (ein Brutpaar) mit Hilfe von Videoaufnahmen, aber auch durch direkte Beobachtung, untersucht. Die Beobachtungen erfolgten während mindestens dreier Nächte pro Woche. Die Brutpaare nisteten in speziell konstruierten und mit Videokameras ausgerüsteten Nistkästen. Wir analysierten die Nahrungswahl über einen Zeitraum von 12 Jahren, Daten liegen aus fünf Bebrütungs- und elf Nestlingsphasen zwischen 1984 und 1995 vor.

Nach dem Schlupf der Jungvögel gingen die Anteile an kleinen Nagetieren von 91 % auf 66 % zurück. Im Gegensatz hierzu nahmen die Anteile mittelgrosser bis grosser Vögel (40-200g Körpermasse) um das Elffache zu, die Anteile grösserer Säugetiere wie zu.B. Hasenartige, Maulwürfe *Talpa europaea* und Wanderratten *Rattus norvegicus* um das 5,7 fache. Die Anteile an Grasfröschen *Rana temporaria* nahmen um das Zwanzigfache zu, obwohl sie im Hinblick auf Nährstoff- und Energiegehalt um 60% weniger profitabler sind als Waldmäuse *Apodemus sylvaticus*.

Das mittlere Gewicht der Beutetiere während der Bebrütungs- und Nestlingszeit betrug weniger als 35 g (99% bzw. 91 %). Wir vermuten, dass die Anteile kleiner Beutetiere wie Spitzmäuse und kleine Vögel, in den Beutetierlisten unterproportional vertreten sind, weil nur die Beutestücke gezählt wurden, die tatsächlich zum Nest gebracht wurden (und nicht von den Adulten an Ort und Stelle verzehrt wurden); diese Feststellung wurde auch bei Bartkauz *Strix nebulosa* und Schleiereule *Tyto alba* gemacht. Zwischen dem Anteil an Nagetieren und der Zahl ausgeflogener Jungvögel ergab sich eine positive Korrelation, dies bestätigte frühere Studien. Weiterhin ist es allgemein bekannt, dass sich jährliche Fluktuationen in der Häufigkeit der Nagetiere im Anteil an erbeuteten Nagetieren und im Bruterfolg niederschlagen; dies bestätigte sich auch im Wald von Châtillon. Jedoch kann aus verschiedenen Gründen die Häufigkeit der Nagetiere im Laufe der Brutsaison abnehmen: Hier ist es dann die "nächstbeste" Lösung, auf alternative Beute umzuschwenken, mit dem Ziel, die zum Nest gebrachte Energiemenge zu erhöhen. Sobald alternative Beute in den Beutelisten auftauchte, ergab sich ein negativer Effekt im Hinblick auf den Ausflugerfolg. Sogar wenn die mittlere Masse der alternativen Beute zwei Mal grösser war als die kleiner Nagetiere, war diese Beziehung negativ, wie bei der Vogelbeute nachgewiesen werden konnte.

Obwohl keine Unterschiede in der Ernährung zwischen den Geschlechtern des Waldkauzes gefunden wurden, wurden von den Weibchen, die in dieser Zeit um etwa 38 % schwerer sind als die Männchen, durchweg grössere Beutetiere eingetragen. Die Änderung der Nahrungszusammensetzung beim Waldkauz nach dem Schlupf der Jungvögel stehen in Übereinstimmung mit der Optimalitätstheorie. Der bei den Waldkäuzen zu beobachtende Wechsel hin zu grösseren Beutetieren als Nagetieren

nach dem Schlupf der Jungvögel und die "Rückkehr" wieder zu kleineren Beutetieren für den Fall erfolgloser Bruten wurde ebenfalls bei der gefleckte Waldkauz (Spotted Owl) *Strix occidentalis* ermittelt und ist ein Hinweis auf die aktive Wahl grösserer Beutetiere als Reaktion auf die grössere Nachfrage der Jungvögel.

Die positive Beziehung zwischen dem Anteil der Nagetiere und dem Ausflugerfolg sowie die Bevorzugung von Nagetieren während der Bebrütung der Eier ist ein Hinweis darauf, dass Nagetiere die profitabelsten Beutetiere sind. Die Häufigkeit der Beutetiere sowie das Nahrungssuchverhalten wurden nicht näher untersucht, es werden jedoch weitergehende Erläuterungen diskutiert.

## References

- BARROWS, C.W. (1987): Diet shifts in breeding and nonbreeding Spotted owls. *J. Raptor Res.* 21:95-976. – BAUDVIN, H. & J.-L. DESSOLIN (1987): A propos de la Chouette Hulotte, *Strix aluco*: réponses apportées et questions posées par les "nichoirs-photos". *Nos oiseaux* 39:129-134. – BAUDVIN, H. (1991): L'influence du régime alimentaire sur la reproduction des Chouettes hulottes, *Strix aluco*, dans les forêts bourguignonnes. JUILLARD, M. et al. (eds.) *Rapaces Nocturnes*. *Nos Oiseaux*, Prangins, CH, pp. 33-36. – BAUDVIN, H. & J.-L. DESSOLIN (1992): Analyse de la morphométrie de la Chouette Hulotte *Strix aluco* en Bourgogne. *Alauda* 60:93-104. – BENNETT P.M. & P.H. HARVEY (1987): Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool., Lond.* 213:327-363. – BEVEN, G. (1965): The food of Tawny Owls in London. *London Bird Rep.* 29:56-72. – BIBER, J.-P. & P. SCHMID (1987): Magenanalysen bei Greifvögeln (*Falconiformes*) und Eulen (*Strigiformes*) aus dem Kanton Bern. *Jahrb. Naturhist. Mus. Bern* 9:159-173. – BOE, J. DE. (1992): Recherche sur le régime alimentaire de la Chouette Hulotte, *Strix aluco*, par la méthode de la photographie sur pellicule infrarouge. M. JUILLARD et al. (eds.) *Rapaces nocturnes*. *Nos Oiseaux*, Prangins, CH, 93-107. – BOUVIER, M. & BAYLE, P. (1989): Le régime alimentaire de la Chouette Hulotte *Strix aluco*. dans la sud des Alpes Françaises. *Bièvre* 10:1-22. – BRUYN, de O. (1994): Population ecology and conservation of the Barn Owl *Tyto alba* in farmland habitats in Liemers and Achterhoek (The Netherlands). *Ardea* 82:1-109. – BULL, E.L., M.G. HENJUM & R.S. ROHWEDER (1989): Diet and optimal foraging of Great Gray Owls. *J. Wildl. Manage.* 53:47-50. – COLLINGE, W.E. (1922): The food and feeding habits of the Little Owl. *J. Min. Agric.* 28:1022-1031, 1133-1140. – COLLINGE, W.E. (1923): A local investigation of the food of the Little Owl. *J. Min. Agric.* 29:750-752. – COLVIN, B.A. & E.B. MCLEAN (1986): In TAYLOR 1994. – CONTOLI, L. & G. SAMMURI (1978): Predation on small mammals by Tawny Owl and comparison with Barn Owl in the Farma valley (central Italy). *Boll. Zool.* 45:323-335. – DELMÉE, E., P. DACHY & P. SIMON (1978): Quinze année d'observations sur la reproduction d'une population forestière de chouette hulottes, *Strix aluco*. *Le Gerfaut* 68:590-650. – DELMÉE, E., P. DACHY & P. SIMON (1979): Etude comparative du régime alimentaire d'une population forestière de Chouettes Hulottes (*Strix aluco*). *Gerfaut* 69:45-77. – DROST, C. A. & R.C. MACCLUSKEY (1992): Extirpation of alternative prey during a small rodent crash. *Oecologia* 92:301-304. – EARTHART, C.M. & N.K. JOHNSON (1970): Size dimorphism and food habits of North American owls. *Condor* 72:251-264. – EXO, K.-M. (1983): Habitat, Siedlungsdichte, und Brutbiologie einer

- niederrheinischen Steinkauzpopulation (*Athene noctua*). Ökol. Vögel 5:1-40. – EXO, K.-M. 1987. Das territorialverhalten des Steinkauzes - eine verhaltensökologische Studie mit Hilfe der Telemetrie. Ph.D. Thesis University of Cologne, Germany.
- FINCK, P. (1989): Variabilität des Territorialverhaltens des Steinkauzes (*Athene noctua*). Ph.D. Thesis University of Cologne, Germany. – FINCK, P. (1993): Territoriengrösse beim Steinkauz (*Athene noctua*): Einfluss der Dauer der Territorienbesetzung. J. Orn. 134:35-42. – FORSMAN, E.D., E.C. MESLOW & H.M. WIGHT (1984): Distribution and biology of the Spotted Owl in Oregon. Wild. Monogr. 87:1-64.
- GALEOTTI, P., F. MORIMANDO & C. VIOLANI (1991): Feeding ecology of Tawny Owls in urban habitats (northern Italy). Boll. Zool. 58:143-150. – GASZMANN, H. & B. BÄUMER (1993): Zur Populationsökologie des Steinkauzes (*Athene noctua*) in der westlichen Jülicher Börde. Erste Ergebnisse einer 15 jährigen Studie. Vogelwarte 37:130-143. – GASZMANN, H., B. BÄUMER & W. GLASNER (1994): Faktoren der Steuerung des Bruterfolges beim Steinkauz *Athene noctua*. Vogelwelt 115:3-13. – GÉNOT, J.C. & J.L. WILHELM (1994): Occupation and use of an area by the Little Owl (*Athene noctua*) on the edge of the Vosges du Nord (north-east France). Alauda 61:181-194. – GLUTZ VON BLOTZHEIM, U.N. & K.M. BAUER (eds.) (1980): Handbuch der Vögel Mitteleuropas. Bd 9. Akademische Verlagsgesellschaft, Wiesbaden. – GÓRECKI, A. (1965): Energy values of body in small mammals. Acta Theriologica X, 23:333-352. – GOSZCZYNSKI, J., P. JABLONSKI, G. LESINSKI & J. ROMANOWSKI (1993): Variation in diet of Tawny Owl *Strix aluco* L. along an urbanization gradient. Acta Ornithologica 27:113-123.
- HAGEN, Y. (1952): Quoted by KORPIMÄKI et al. 1990.
- ILLE, R. (1991): Preference of prey size and profitability in Barn Owls *Tyto alba guttata*. Behaviour 116:180-189. – ILLE, R. (1992): Zur Biologie und Ökologie des Steinkauzes (*Athene noctua*) im Marchfeld: Aktuelle Situation und mögliche Schutzmassnahmen. Ergetta 35:49-57.
- JEDRZEJEWSKI, W., JEDRZEJEWSKA, B., ZUB, K., RUPRECHT, A. & C. BYSTROWSKI (1994): Resource use by Tawny Owls *Strix aluco* in relation to rodent fluctuations in the Bialowieza National Park, Poland. J. Avian Biol. 25: 308-318. – JOHNSON, P.N. (1993): Prey selection and breeding ecology of urban and rural Tawny Owls. The Raptor 4:86-91. – JUILLARD, M. (1984): Eco-éthologie de la Chouette Chevêche, *Athene noctua* (Scop.), en Suisse. Nos Oiseaux, Prangins, CH. Ph.D thesis University of Neuchatel (CH). – JUILLARD, M. (1987): in BAUDVIN & DESSOLIN 1987.
- KÄLLANDER, H. (1977): Food of the Tawny Owl *Strix aluco* and the Long-eared Owl *Asio otus* - a comparison. Vår Fagelvärld 36:134-142. – KÄMPFER, A. & W. LEDERER (1988): Dismigration des Steinkauzes *Athene noctua* in Mittelwestfalen. Vogelwelt 109:155-164. – KIRK, D.A. (1992): Diet changes in breeding Tawny Owls (*Strix aluco*). J. Raptor Res. 26:239-242. – KLOMP, H. (1970): The determination of clutch size in birds: a review. Ardea 58:1-124. – KNÖTZSCH, G. (1988): Bestandsentwicklung einer Nistkasten-Population des Steinkauzes *Athene noctua* am Bodensee. Die Vogelwelt, 109:164-171. – KONING, F.J. (1980): in GLUTZ VON BLOTZHEIM & BAUER. – KORPIMÄKI, E. (1986): Niche relationships and life history tactics of three sympatric *Strix* owl species in Finland. Ornis Scan. 17:126-132. – KORPIMÄKI, E. (1992): Fluctuating food abundance determines the lifetime reproductive success of male Tengmalm's owls. J. An. Ecol. 61:103-111. – KORPIMÄKI, E. & K. HUHTALA (1986): Nest visit frequencies and activity patterns of Ural Owls *Strix uralensis*. Ornis Fenn. 63:42-46. – KORPIMÄKI, E., K. HUKTALA, & S. SULKAVA (1990): Does the year-to-year variation in the diet of Eagle and Ural Owls support the alternative prey hypothesis? Oikos 58:47-54. – KORPIMÄKI, E., M. LAGERSTRÖM & P. SAUROLA (1987): Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. Ornis Scan. 18:1-4. – KORPIMÄKI, E. & K. NORRDAHL (1989): Predation of Tengmalm's owls: numerical responses, functional responses

- and damping impact on population fluctuations of microtines. *Oikos* 54:154-164. – KORPIMÄKI, E. & K. NORRDAHL (1991): Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology* 72:814-826. – KORPIMÄKI, E. & S. SULKAVA (1987): Diet and breeding performance of Ural Owls *Strix uralensis* under fluctuating food conditions. *Ornis Fenn.* 64: 57-66.
- LACK, D. (1954): The natural regulation of animal numbers. Oxford Univ. Press, London, (UK).
- LECOMTE, P. (1994): Sur la piste de la chouette aux yeux d'or. *Le Courrier de la Nature* 147:23-27. – LIBOIS, R.M. (1984): Le régime alimentaire de la Chouette Effraie. Ph.D. Thesis. Univ. de Liège (B). – LINKOLA, P. & A. MYLLYMÄKI (1969): Der Einfluss der Kleinsäugerfluktuationen auf das Brüten einiger kleinsäugerfressender Vögel im südlichen Häme, Mittelfinnland 1952-1966. *Ornis Fenn.* 46:45-78. – LOWE, V.P.W. (1980): Variation in digestion of prey by the Tawny owl (*Strix aluco*). *J. Zool., Lond.* 192:283-293. – LUNDBERG, A. (1976): Breeding success and prey availability in a Ural Owl *Strix uralensis* PALL. population in central Sweden. *Zoon* 4:65-72. – LUNDBERG, A. (1979): Residency, Migration and a Compromise: Adaptations to Nest-Site Scarcity and Food Specialization in Three Fennoscandian Owl Species. *Oecologia (Berl)* 41:273-281. – LUNDBERG, A. (1980): Vocalizations and courtship feeding of the Ural Owl *Strix uralensis*. *Ornis Scan.* 11:65-70.
- MACARTHUR, R.H. & E.R. PIANKA (1966): On optimal use of a patchy environment. *Am. Naturalist* 100:603-609. – MACDONALD, D.W. (1976): Nocturnal observations of Tawny Owls *Strix aluco* preying upon earthworms. *Ibis* 118:579-580. – MADON, P. (1933): Les rapaces d'Europe, leur régime, leurs relations avec l'agriculture et la chasse. Toulon, France. – MIKKOLA, H. (1983): Owls of Europe. T. & A.D. Poyser, Calton, U.K. – MULLER, Y. (1991): Les secondes nichées chez la Chouette effraie, *Tyto alba*. JUILLARD et al. eds. Rapaces Nocturnes. Nos Oiseaux. Prangins, Ch, pp 173-188
- NICLOUX, C. (1986): Typologie des stations forestières dans la Forêt Domaniale de Chatillon sur Seine. Internal Report: École Nationale du Génie Rural et des Forêts, 54042 Nancy Cedex, France. – NILSSON, I.N. (1984): Prey weight, food overlap, and reproductive output of potentially competing Long-eared Owls and Tawny Owls. *Ornis Scand.* 15:176-182.
- OVERSKAUG, K., E. KRISTIANSEN & P. SUNDE (1995): Sex-specific diet analysis of the Tawny Owl (*Strix aluco*) in Norway. *J. Raptor Res.* 29:137-140.
- PETTY, S.J. (1987): Breeding of Tawny Owls *Strix aluco* in relation to their food supply in an upland forest. Pp. 167-179 in D.J. Hill (Ed.) Breeding and Management in Birds of Prey. University of Bristol, Bristol, U.K. – PIETIÄINEN, H. (1989): Seasonal and individual variation in the production of offspring in the Ural Owl *Strix uralensis*. *J. Anim. Ecol.* 58:905-920. – PIETIÄINEN, H. & H. KOLUNEN (1993): Female body condition and breeding of the Ural Owl *Strix uralensis*. *Functional Ecology* 7:726-735. – PYKE, G.M., H.R. PULLIAM & E.L. CHARNOV (1977): Optimal foraging: a selective review of theory and tests. *Quater. Rev. Biol.* 52:137-154.
- RACZYNSKI, J. & A.L. RUPRECHT (1974): The effect of digestion on the osteological composition of owl pellets. *Acta Ornithologica* 14:25-38. – REDPATH, S. M. (1996): Impact of habitat fragmentation on activity and hunting behaviour in the Tawny Owl, *Strix aluco*. *Behavioural Ecology* 6:410-415. – ROBILLER, F. & M. ROBILLER (1986): Ein Beitrag zur Brutbiologie des Steinkauzes (*Athene noctua*). *Beitr. Vogelkd.* 32:161-174. – ROMANOWSKI, J. (1988): Trophic ecology of *Asio otus* (L.) and *Athene noctua* (Scop.) in suburbs of Warsaw. *Pol. ecol. Stud.* 14:223-234. – RUPRECHT, A.L. & A. SZWAGRAK (1987): Zur Ernährung der Eulen im Westteil des Bialowieza-Urwaldes. *Ökol. Vögel* 9:89-96.

- SAUROLA, P. (1989a): Lifetime reproduction in birds. (Ed) I. NEWTON, Pp 327-345, Academic Press, Padstow. – SAUROLA, P. (1989b): Breeding strategy of the Ural Owls *Strix uralensis*. MEYBURG, B.-U & R. D. CHANCELLOR (eds). Raptors in the Modern World, WWGBP: Berlin, London & Paris. – SCHÖN, S., W. SCHERZINGER, K.-E. EXO & R. ILLE (1991): Der Steinkauz. Ziemsen Verlag, Wittenberg Lutherstadt. – SCHÖNFELD, M. & G. GIRBIG (1975): Beiträge zur Brutbiologie der Schleiereule, *Tyto alba*, unter besondere Berücksichtigung der Abhängigkeit von der Feldmausdichte. *Hercynia* 12:257-319. – SCHÖNFELD, M., G. GIRBIG & H. STURM (1977): Beiträge zur Populationsdynamik der Schleiereule, *Tyto alba*. *Hercynia* 14:303-351. – SCHNURRE, O. (1975): Ernährungsbiologische Studien an Schleiereule (*Tyto alba*) und Waldkauz (*Strix aluco*) im gleichen Lebensraum (Kloster Chorin Kr. Eberswalde). *Milu*, Leipzig 3:748-755. – SCHWERDTFEGER, O. (1992): The dispersion dynamics of Tengmalm's Owl (*Aegolius funereus*) in Central Europe. In MEYBURG, B.-U. & R. C. CHANCELLOR (eds), Raptors Today, (WWPB); Pica Press, London. – SMITH, M. (1966): Winter breeding in Wood Mice, *Apodemus sylvaticus*, and voles, *Clethrionomys glareolus* and *Microtus agrestis*, near Oxford. *J. Anim. Ecol.* 35:471-485. – SOUTHERN, H.N. (1954): Tawny owls and their prey. *Ibis* 96:384-410. – SOUTHERN, H.N. (1969): Prey taken by Tawny Owls during the breeding season. *Ibis* 111:293-299. – SOUTHERN, H.N. (1970): The natural control of a population of Tawny Owls (*Strix aluco*). *J. Zool., Lond.* 162:197-285. – SYLVEN, M. (1982): Reproduction and survival in Common Buzzards (*Buteo buteo*) illustrated by the seasonal allocation of energy expenses. Thesis, University of Lund, Sweden. TAYLOR, I. (1994): Barn Owls: Predator-prey relationships and conservation. Cambridge University Press, NY, USA.
- ULLRICH, B. (1980): Zur Populationsdynamik des Steinkauzes. *Vogelwarte* 30:179-198. – UTTENDÖRFER, O. (1939): Die Ernährung der deutschen Raubvögel und Eulen und ihre Bedeutung in der heimische Natur. Neumann- Neudamm, Berlin.
- VEEN, J.C. VAN & E.M. TEN BROEKE (1994): A silent method to record nesting events in hole-breeding Owls. MEYBURG, B.U. & R.D. CHANCELLOR (eds). Raptor conservation today. Pica Press; pp. 551-555. – VEEN, J.C. VAN (1994): Nestling necrophagy in Tawny Owls *Strix aluco*. MEYBURG, B.U. & R.D. CHANCELLOR (eds). Raptor conservation today. Pica Press; pp. 557-563. – VEEN, J.C. VAN (in prep): Prey rations of the Tawny Owl during incubation and nestling periods. – VOOUS, K.H. & A. CAMERON (1988): Owls of the Northern Hemisphere. Collins, London, U.K.
- WALLIN, K. (1988): Life history evolution and ecology in the Tawny Owl *Strix aluco*. Ph.D. Thesis, University of Göteborg, Sweden. – WEBER, B. (1973): Beitrag zur Kenntnis der Ernährung der Eulen in der Magdeburger Börde, im Gebiet zwischen Ohre und oberer Aller und in der Altmark. *Beitr. Vogelkd.*, Leipzig 19:363-375. – WENDLAND, V. (1972): 14jährige Beobachtungen zur Vermehrung des Waldkauzes (*Strix aluco* L.). *J. Orn.* 113:276-286. – WENDLAND, V. (1980): Der Waldkauz (*Strix aluco*) im gebauten Stadtgebiet von Berlin (West). *Beitr. Vogelkd.* 26:157-171. – WENDLAND, V. (1984): The influence of prey fluctuations on the breeding success of the Tawny Owl *Strix aluco*. *Ibis* 126:284-294. – WITHERBY, H.F. & N.F. TICEHURST (1908): The spread of the Little Owl from the chief centres of its introduction. *Brit. Birds* 1:335-342. – WIJNANDTS H. (1984): Ecological energetics of the Long-eared owl (*Asio otus*). *Ardea* 72:1-92. YALDEN, D.D. (1985): Dietary separation of owls of the Peak District. *Bird Study* 32:122-131.

# ZOBODAT - [www.zobodat.at](http://www.zobodat.at)

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Ökologie der Vögel. Verhalten Konstitution Umwelt](#)

Jahr/Year: 2000

Band/Volume: [22](#)

Autor(en)/Author(s): Veen Joop C. van, Kirk David A.

Artikel/Article: [Dietary shifts and fledging success in breeding Tawny Owls \*Strix aluco\* 237-281](#)