

Tyto alba Barn Owl

Du. Kerkuil FR. Effraie des clochers GE. Schleiereule It. Barbagianni RU. Сипуха
Sp. Lechuza común Sw. Tornuggla Cz. Sovy palene P. Coruja-das-torres
Po. Plomykowki H. Gyöngybagoly

Strix alba Scopoli, 1769

Polytypic. Subspecies taxonomy based on morphology. Nominate *alba* (Scopoli, 1769), Algeria, Balearic Islands, Egypt, England, France, Ireland, Italy, Libya, Morocco, Scotland, Sicily, Spain, Tunisia; *guttata* (Brehm, 1831), Austria, Balkan republics, Czech Republic, Denmark, Germany, Netherlands, Poland, Slovenia, Sweden; hybrid zone *alba guttata*, Belgium, France, Germany, Luxemburg, Switzerland; *ernesti* (Kleinschmidt, 1901), Corsica and Sardinia; *erlangeri* (Sclater, 1921), Arabia, Egypt, Iraq, Iran, Israel, Palestine, Crete, Cyprus; *affinis* (Blyth, 1826), Africa, southern Egypt; *schultzei* (Hartert, 1900), Madeira and Porto Santo; *gracilliostris* (Hartert, 1905), Canary Islands; *detorta* (Hartert, 1913), Cape Verde Islands. Extralimital: c. 28 further races worldwide and c. 6 further species.

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Summary. This Update provides more detailed information on several topics covered by the previous version published in 1985 and also develops new research aspects. Loss of habitat and suitable nest-sites, traffic, and poison are main factors causing a decline in most European countries. Food supply has been shown to have a major effect on population size, survival prospects, and breeding biology. Survival also decreases with increasing latitude. British owls differ in several respects from those on the continent. They more frequently breed in trees, hunt during the day, produce fewer second broods (that are also smaller than first broods), their clutch size decreases instead of increases with season, and site/mate fidelity is greater. Owls have been shown to preferentially prey on 10–40 g small mammals. Using telemetry, home-range varies from 90 to 465 ha. Courtship starts in winter and birds can copulate up to 70 times a day. Polyandry is more frequent than polygyny. Feeding rate is on average 3 prey items per nestling per day. Experimental research has been conducted on physiology (energetics), on nestling growth under varying environmental conditions, and on the trade-off faced by parents between current and future reproduction. Field experiments showed that siblings negotiate vocally among each other over priority of access to impending food resources, and that degree of spotting of female plumage reflects the offsprings' ability to resist parasites. Finally, in Switzerland, males displaying a reddish brown plumage produced more offspring, and fed their brood at a higher rate than lighter-coloured individuals. Cross-fostering experiments were useful to determine the genetics of variation in plumage coloration and spottiness.

Evolution of *Tyto alba*. (New section)

SYSTEMATICS. Systematic studies of Strigiformes based on mitochondrial 12S rDNA (Mindell *et al.* 1997, Miranda *et al.* 1997), protein-coding cytochrome oxidase subunit I (Miranda *et al.* 1997), mitochondrial cytochrome *b* (Wink and Heidrich 1999), DNA–DNA

hybridization (Sibley *et al.* 1988), egg-white proteins (Sibley and Ahlquist 1972), and multi-locus protein electrophoresis (Randi *et al.* 1991) all place Tytonidae family as sister lineage of Strigidae family. In Tytonidae, number of chromosomes $2n = 92$ and in Strigidae $2n = 82$. All acrocentric with no clear distinction between

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micro- and macro-chromosomes (Belterman and De Boer 1984). Systematics within Tytonidae unclear, as no molecular analyses have yet been performed.

EVIDENCE FROM FOSSIL RECORDS. In Early Tertiary (Eocene and Oligocene) Barn Owls represented by several extinct subfamilies, while Strigidae known only since Early Miocene (Mourer-Chauviré 1987). Oldest known Tytonidae belong to genus *Necrobyas*, which is present from Late Eocene in France dated from c. 37 million years ago (m.y.a.) (Legendre and Lévêque 1997). So separation between Tytonidae and Strigidae dates at least from 37 m.y.a. Agreement between molecular and fossil records over this issue (Randí *et al.* 1991). Oldest occurrence of genus *Tyto* is from Middle Miocene (13–12.5 m.y.a.) in France (Mein 1990, Daams *et al.* 1999). Oldest species of genus *Tyto* is *T. sanctialbani* that was found in France. Second species *T. campiternae* has been found in Hungary from late Miocene (6.8–5 m.y.a.). In Early Pliocene (5–4 m.y.a.) three large forms, *T. sanctialbani*, *T. robusta*, and *T. gigantea*, evolved on Gargano archipelago in southern Italy in insular conditions where rodent and insectivore prey species were large (Ballmann 1973, 1976). Compared with recent European forms of *T. alba*, *Tyto gigantea* was up to 1.6 times larger (Ballmann 1976). Another large species, *Tyto balearica*, was present on the continent as well as on western Mediterranean islands at end of Pliocene, and survived as relict until Middle Pleistocene in Corsica (Salotti *et al.* 1997) and Sardinia (Lydekker 1891a, Louchart 2002). *T. melitensis* described by Lydekker (1891b) in Malta was not actually larger than recent species *T. alba* (Mourer-Chauviré *et al.* 1980, Mlikovsky 1998). *T. alba* has been reported during Pleistocene in Mallorca, Sardinia, Crete, and Karpathos (Mourer-Chauviré *et al.* 2002).

Field characters. Habitat. See *BWP* Vol. IV, pp. 432–4.

Distribution. (Additional material to *BWP* Vol. IV, p. 434) See Fig. 1.

Geographic division between *T. a. alba* and *T. a. guttata* is marked by 3°C January isotherm following British east coast, eastern border of France, across North Italy to Bulgaria (Osieck and Shawyer 1997).

Population. (Additional material to *BWP* Vol. IV, pp. 434–5)

In Europe, 110 000–210 000 breeding pairs. Since 1950, has become extinct in Malta, and decreased by >50% in 7 countries and by 20–50% in 13 others. Populations believed to have increased in only 1 of 16 countries (Tucker and Heath 1994). See Shawyer (1987) for review of decrease in population in British Isles from 1750 to 1979. In 1932, on average 8.13 pairs bred per

100 km² compared with 2.74 in 1982–5 (Shawyer 1987). Decrease in population size also recorded in shorter-term studies (1974–86) in Germany (Illner 1988). Strong decline in numbers can be prevented through intensive supply of nest-boxes. For instance, in Netherlands population flourished between 1976 and 1990 (de Jong 1991) and in Switzerland number of breeding pairs reached 42 per 100 km² (Kéry in Roulin 1999a). High densities can easily occur if nest-sites available and food supply good, since Barn Owls can sometimes be relatively gregarious. Shortest recorded inter-nest distances 4.5 m (Callion 1972), 65 m (Epple 1985), and 300 m (Kaus 1977). For 1800s, there are mentions of tens of Barn Owls occupying interconnected cottages and of dozen pairs breeding in single farmhouse (Shawyer 1994). Furthermore, in winter, Taylor (1994) observed resident males and females sharing roost with up to three yearlings. Also observed one female roosting alongside incubating female. Barn Owl also observed within roost of Long-eared Owls *Asio otus* (Henrioux 2000).

Snow cover had negative impact on French population (Muller 1989) but not on Scottish population (Taylor 1992). In contrast to rainfall and drought, fluctuation in abundance of field voles *Microtus agrestis* played significant role in Barn Owl population cycle in British Isles (Shawyer 1994), Germany (Kaus 1977, Schönfeld *et al.* 1977, Illner 1988), and Czech Republic (Poprach 1996). In Scotland, Taylor (1994) showed that voles and Barn Owls vary synchronously in numbers, with peaks occurring every 3 years. Therefore not surprising that change in population size was correlated with vole abundance and not with number of young fledged in previous year. Shaw (1994) reports that 72% of recruited yearling breeders had hatched in years when vole populations were increasing. Only 23% came from high vole years and 5% had hatched in low vole years. Across France, Germany, and Switzerland populations fluctuate in synchrony (Giraudoux *et al.* 1990). In Netherlands, population cycle of staple prey common vole (*M. arvalis*) is 3–4 years (de Bruijn 1979).

Survival. (Additional material to *BWP* Vol. IV, pp. 434–5)

In Germany, survival of nestlings ringed in August, September, and October lower than for nestlings ringed in May, June, and July (Bairlein 1985). Seasonal effect on survival expectancy, however, not verified in eastern France where nestlings from first and second annual broods recovered dead in first year of life at similar rate (8% vs. 10%) (Baudvin 1986). Mortality not randomly distributed through year. Most casualties occur in January and February in most European countries (Taylor 1994), except in Spain where peak was between August and

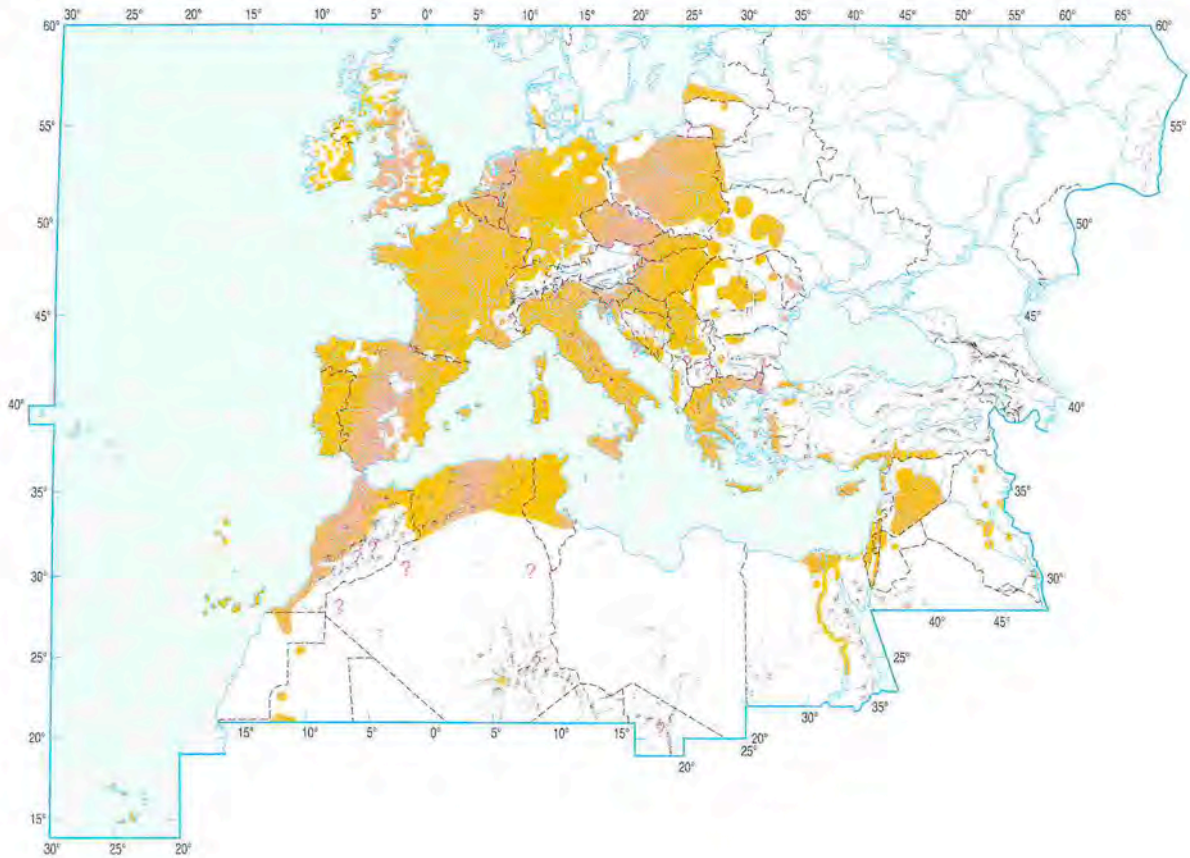


Fig. 1. *Tyto alba* Barn Owl distribution within the west Palearctic: brown = resident breeding; ? = status uncertain. Reprinted unamended from the Concise Edition of *BWP*.

November in 1983–9 (Fajardo 1990) and in April in 1990–9 (Fajardo 2001).

Apart from human-related mortality (see Shawyer 1987), crash in vole population causes more casualties than winter harshness (Schönfeld *et al.* 1977, de Bruijn 1994, Taylor 1994). In Scotland, Shaw (1994) estimated that adult survival in low vole years was better (53–55%) than after high vole year (32–44%). In another Scottish population, Taylor (1994) reports similar result with annual adult survival varying from 20 to 56%. Survival was highest at peak of vole cycle, lower in year of decline, and lower still the following year. Demographic implications of mortality have been studied in Scotland where population found to be stable when 35% of breeding adults survive from one year to next (Taylor 1994). First-year survival decreases with latitude (Roulin *et al.* 2001a) and altitude (Taylor 1994), and probability of recovering ringed juvenile dead lower just after fledging than 2–4 months later (Taylor 1994).

In France, Germany, Netherlands, and Scotland, age-related survival follows similar pattern, with 15–35% surviving first year of life, 40–50% second year, 60–70%

third year, 70–80% fourth year, and 45–65% fifth year (Taylor 1994). Put another way, life expectancy of first-year birds estimated to be 1.23 years, of second-year birds 1.65 years, and of third-year birds 1.87 years (Schifferli 1957, Schönfeld 1974, Glutz von Blotzheim and Bauer 1980, de Bruijn 1994). Oldest recorded Barn Owl 23 years old (Dannhauer 1958). Several studies indicate that juveniles and adults often die from different causes. In France (Baudvin 1986) and Scotland (Taylor 1994), fewer adults than juveniles reported dead along roads (for France 49.3% vs. 66.3% of all known causes of mortality), whereas among starved individuals larger proportion were adults (38.3% vs. 13.1%). In France, females found dead along roads more regularly than males (Massemin *et al.* 1998).

Conservation. (New section)

LOSS OF BREEDING SITES. Through 20th century, suitable breeding sites declined dramatically (Taylor 1994). As populations can recover with provision of nest-boxes (Brandt and Seebass 1994, de Bruijn 1994, Kéry 1995), nest-boxes should be systematically constructed and placed on buildings.

TRAFFIC CASUALTIES. Deaths due to traffic increased dramatically through 20th century and nowadays *c.* half of ringed birds recovered along roads; traffic can cause 10–20% of annual mortality (Glue 1971*b*, Braaksma and de Bruijn 1976, Shawyer 1987). In Spain, deliberate killing (mainly shooting and nest-robbing) decreased between 1980 and 1999, whereas casualties from car collisions increased (Fajardo 2001). Joveniaux and Durand (1984) also showed that 1.23 owls/km died every year along stretch of French highway and, along 2.5 km of German roads, Uhlenhaut (1976) found 51 dead owls in 3 weeks. In France, but not in Scotland, birds killed by traffic not necessarily in poorer condition than those not killed by traffic (Taylor 1994, Massemin *et al.* 1998). Two measures might reduce impact of traffic on population size. First, because most dead owls found along vole-rich road verges (van den Tempel in de Bruijn 1994), trees may be planted along dangerous stretches of roads to force owls to fly above cars. Secondly, because fewer owls die when roads are below level of fields (Lecompte 1995, Massemin and Zorn 1998), highways should be, when possible, constructed at lower level than surrounding open fields, again so that owls fly above traffic.

POISON. For historical use of poisons and effects on Barn Owls and other raptors, see Shawyer (1987) and Taylor (1994). Although level of diverse poisons [dieldrin, DDE, hydrochlorinated biphenyl (HCB), polychlorinated biphenyl (PCB)] in dead Barn Owls decreased from 1968 to 1971 (Braaksma and de Bruijn 1976), prevalence of rodenticides increased from 1983 to 1997 (Newton *et al.* 1999). In British Isles, rodenticides (difenacoum, flocoumafen, and particularly brodifacoum), organochlorine pesticides (aldrin/dieldrin), and second-generation poisons (i.e. poison contracted after having consumed poisoned prey) have all been suggested as causing casualties (Newton *et al.* 1990, 1991). DDE reduces thickness of egg shells, thereby increasing breakage and embryo mortality (Mendenhall *et al.* 1983). For levels of poisons in eggs, see Braaksma and de Bruijn (1976) and for geographic and annual variation in egg and bird contamination by PCB and organochlorine pesticides in Belgium see Joiris *et al.* (1977, 1979).

Movements. (Additional material to *BWP* Vol. IV, pp. 435–6 and 440)

POST-FLEDGING DISPERSAL. On the continent, long-distance movements are made in years when large proportion of breeding pairs produces two broods (Schönfeld *et al.* 1977, Baudvin 1986), abundance of voles is high (Bairlein 1985) or decreasing (Schönfeld *et al.* 1977), and juvenile mortality is pronounced (Schönfeld *et al.* 1977). In contrast, in British Isles where dispersal distances

shorter (Bunn *et al.* 1982), vole abundance did not alter propensity for long movements (Percival 1990, Taylor 1994). Using radio-telemetry, Seel *et al.* (cited in Taylor 1994) showed that eight individuals moved away from nest area 2–8 weeks after fledging, and Bairlein (1985) showed that dispersal distances stabilize 4–5 months after fledging. In Switzerland, but not France (Baudvin 1986), juveniles from first broods disperse for longer and further than those from second broods (Glutz von Blotzheim and Schwarzenbach 1979). To date speed with which juveniles disperse can be analysed only from ringing recoveries. Assuming that owls killed on roads are not transported by vehicles before being dislodged, Glutz von Blotzheim and Schwarzenbach (1979) report movement of 660 km in 70 days (on average 9.4 km/day), Schönfeld (1974) movement of 475 km in 105 days (4.5 km/day), and Baudvin (1986) 494 km in 130 days (3.8 km/day). Longest recorded displacement was 2272 km (Jahnel 1989).

Siblings sometimes, but not always (Baeye 1955, Sauter 1956, de Bruijn 1994), move similar long distances in same direction (Muller 1984, Brandt and Seebass 1994). Commonly, movements of >50 km are undertaken in south/south-west for German (Bairlein 1985), French (Baudvin 1986, Chanson *et al.* 1988), and Dutch owls (Braaksma and de Bruijn 1976, de Bruijn 1994). In contrast, British owls move in apparently random directions (Bunn *et al.* 1982, Taylor 1994). Mountains and large water bodies act as barriers to short-distance movements (Sauter 1956, Glutz von Blotzheim and Schwarzenbach 1979, Juillard and Beuret 1983).

ADULT DISPERSAL. Although adults sometimes disperse far from breeding site (460 km: Brandt and Seebass 1994; 140 km: de Bruijn 1994), usually move shorter distances than young in first autumn (Martinez and Lopez 1995). In England, 85% of ringed adults recovered dead within 10 km of place of ringing, compared with 45% in Netherlands (Bunn *et al.* 1982). In Germany, median distance between breeding and recovery site was 49 km (Bairlein 1985).

Food. (Additional material to *BWP* Vol. IV, pp. 436–40)

VALIDATION OF PELLET ANALYSES. Prey remains determined from pellet analysis corresponded closely with actual food provided (Raczynski and Ruprecht 1974). Therefore, studies of diet based on pellet analyses are reliable but only to certain extent, since some bones better digested than others (Raczynski and Ruprecht 1974), especially of younger prey compared with older individuals (Schneider 1977). Furthermore, parents sometimes deliver decapitated prey items to young and if prey determination is based on skulls some items may be missed. May vary individually or regionally, since

decapitated prey items regularly observed in Switzerland (Juillard in Taylor 1994), but not in Scotland where none of 614 prey delivered by adults had been previously decapitated (Taylor 1994).

SEASONAL TRENDS. In north-eastern France and Netherlands, insectivorous mammals less often captured in autumn, when *Microtus arvalis* taken in greater proportion (Baudvin 1983, de Bruijn 1979). Baudvin (1983) did not find any obvious seasonal variation in capture of Muridae. In British Isles, *Sorex araneus* taken in greater proportion in summer and *M. agrestis* from late autumn to early spring (Brown 1980, Taylor 1994). Seasonal variation can differ from one year to another (Love *et al.* 2000).

GEOGRAPHIC TRENDS. In northern Europe, Barn Owls prey mainly on small mammals, whereas in southern regions diet more diverse, including insects, amphibians, reptiles, and birds in greater quantity (Herrera 1974, Taylor 1994). Similar increase in diversity from north to south was found in Spain (Barbosa and Benzal 1996) where it also decreased with altitude and rainfall (Barbosa *et al.* 1992, Torre *et al.* 1996).

HABITAT AND DIET. Several analyses demonstrated that diet varies according to habitat in which owls forage. In France, white-toothed shrews *Crocidura russula* and birds usually captured in suburban habitats, and common voles *M. arvalis* and shrews *S. araneus* in rural habitats (Lieurquin 1975). In another region, common shrews and wood/yellow-necked mouse *Apodemus* spp. more often preyed in regions rich in woods than meadows and agricultural fields (Baudvin 1983). Evidence for habitat-related prey assemblage comes from observation that prey species not randomly associated in pellet, which may contain 1–13 items (mean 3.4). Species that live in similar environments tend to be associated in pellet more often than would be expected by chance, although ubiquitous species like *Apodemus* do not show these associations (Baudvin 1983). In Spain, diet more similar among owls when in close proximity (Alegre *et al.* 1989); see also factorial analyses of Libois (1984), Taberlet (1986), and Torre *et al.* (1996). Change in habitat may explain significant change in diet of British owls between 1956 and 1997. Proportion of *S. araneus*, *Apodemus* spp., and water shrews *Neomys fodiens* significantly decreased, whereas pygmy shrews *S. minutus*, bank voles *Clethrionomys glareolus*, and harvest mouse *Micromys minutus* increased.

COMPARISON OF DIET WITH THAT OF OTHER RAPTORS. Pair-wise comparison of diet of different raptor species studied by same author was compared with coefficient of overlap D_2 . D_2 is given by formula $1 - \frac{1}{2} \sum |p_{ij} - p_{jk}|$, with p_{ij} and p_{jk} being proportion of prey species i in diet of species j (Barn Owl) and k (another raptor).

Table 1. Comparison of *Tyto alba* Barn Owl diet with that of *Athene noctua* Little Owl, *Falco tinnunculus* Kestrel, *Bubo luteo* Buzzard, *Strix aluco* Tawny Owl, *Bubo bubo* Eagle Owl, *Asio flammeus* Short-eared Owl, *A. otus* Long-eared Owl, and *Circus cyaneus* Hen Harrier

	Mean	CV	n
<i>Athene noctua</i>	0.40	0.54	10
<i>Falco tinnunculus</i>	0.51	0.60	7
<i>Bubo luteo</i>	0.54	0.18	2
<i>Strix aluco</i>	0.56	0.27	18
<i>Bubo bubo</i>	0.57	0.10	2
<i>Asio flammeus</i>	0.57	0.32	5
<i>Asio otus</i>	0.60	0.22	21
<i>Circus cyaneus</i>	0.67	0.48	2
Mean	0.55	0.34	8

Mean values and coefficient of variation (CV) are calculated from all available studies (*in*). After Heim 1958, Steiner 1961, Kulczycki 1964, Glue 1966, Thiollay 1966, 1968, Haensel and Walther 1970, Glue 1971a, Chalme *et al.* 1974, Lovam 1974, Saint-Girons *et al.* 1974, Selman 1975, Lopez-Gordo *et al.* 1977, Delméc *et al.* 1979, Hegger 1979, Veiga 1980, Amat and Sorriguer 1981, Goszcynski 1981, Massa 1981, Anker *et al.* 1983, Buise 1984, Sari and Massa 1985, Yalden 1985, Biber and Schmid 1987, Dionisi 1987, Mráz 1987, Saucy and Fasel 1994, Capizzi and Luiselli 1995, Montanari 1995, Roulin 1996c, Capizzi and Luiselli 1998, Alivizatos and Goutner 1999.

D_2 can be any value between 0 (different diet) and 1 (same diet). Mean D_2 values range between 0.40 and 0.67 (Table 1). Large coefficients of variation (CV) of D_2 values (Table 1) indicate that similarity in diet of Barn Owl and other raptors can vary markedly from one study to another. For instance, in Poland dietary overlap between *Tyto alba*, *Strix aluco*, and *Asio otus* larger when voles more abundant (Goszcynski 1981).

NUMBER OF PELLETS PRODUCED PER DAY. Guérin (1928) observed that owl needed 2.25 h to digest wood mouse and minimum time required to produce pellet determined to be 6.5 h (Smith and Richmond 1972). Both sight of vole and predictability of imminent meal induce pellet ejection (Bunn *et al.* 1982). In captivity, owls expel 1.89 ± 0.22 pellets per 24 h (Handrich *et al.* 1993b) and exceptionally 4 pellets can be produced per 24 h (Bunn *et al.* 1982).

FORAGING STRATEGY. In England, Bunn *et al.* (1982) observed owls hunting on average 79 min before sunset (maximum 268 min) and up to 139 min after sunrise. In summer, Scottish owls start to hunt between 19.00 and 20.00 hours, giving 3–4 h of daylight foraging (Taylor 1994). Proportion of prey captured using sit-and-wait hunting technique (i.e. sit on perch and wait from 15 s to 8 min until prey passes) increases from 54% in summer to 87% in winter (Taylor 1994). Brandt and Seebass (1994) reported similar seasonal change in hunting technique in Germany. This change may be due to summer birds foraging mainly in pastures and hayfields, and in winter along edges rich in perches (Taylor 1994). Under threat of Barn Owl predation, gerbils limited

activity to safer bush microhabitat (Brown *et al.* 1988, Abramsky *et al.* 1996, 1997). Owls exert higher predation rate when illumination good (i.e. full moon) (Kotler *et al.* 1988). In captivity, adult birds appeared to be more efficient than juveniles at capturing live mice (Csermely and Sponza 1995).

In Germany, after parents have delivered prey item to brood, do not return to same foraging place (Brandt and Seebass 1994). In France, radio-tagged male hunted more often in hedgerow habitats (55% of the time) than open fields (19%), although prey density was only one half. Note, however, that diversity of prey species greater in the former. Villages were visited for 24% of time and forest 2% (Michelat and Giraudoux 1993). In Scotland, owls catch most prey in woodland edges comprising irregular strips of rough grassland; tend to avoid hedgerows, although vole density is similar (Taylor 1994).

PREY SELECTION. Under captive conditions, *T. a. guttata* preferentially capture prey weighing 10–40 g. Among small mice owls prefer to capture active individuals, whereas among large mice mostly attracted by inactive individuals. Owls adopt defensive posture when capturing large prey items that can weigh up to 80 g (Ille 1991). In another laboratory study, *T. a. erlangeri* predated *Perognathus baileyi* (33 g) more than *P. amplus* (12 g) (Kotler *et al.* 1988).

Most rats captured by Barn Owls were young individuals weighing <160 g, suggesting that owls may select prey with respect to body size in nature (Barta 1983). In France, common voles and wood mice taken in summer were adults, whereas young animals were more abundant in the wild (Saint-Girons 1965). Similar observation with water voles *Arvicola sapidus* in Poland (Kulczycki 1964) contrasts with Garde and Escala (1993) showing that owls catch smallest water voles. Buser's data (1981) suggested that prey size increases when offspring become older, unlike Langford and Taylor (1992) who found that prey weighed on average 26.0 g during egg laying and incubation and 25.1 g at nestling stage. Among five pairs, prey consumed by male parent did not differ in size from items he brought to his mate and offspring (Taylor 1994). In Scotland, owls captured larger field voles *Microtus agrestis* than those trapped by researchers, and caught more males than females (Taylor 1994).

When voles abundant, Barn Owls mainly feed on them (Bohnsack 1966, de Bruijn 1979, Goszczynski 1981, Taylor 1994). Comparison of small mammals in diet and among trapped individuals showed that Barn Owls under-predated *Sorex araneus* and *M. agrestis*, took *M. avalis* in same proportion, and over-predated *Cricetulus rissula* (von Knorre 1973). During periods of

intense rainfall, owls switched from voles to birds and house mice *Mus musculus* (Hegger 1978). Non-random predation by Barn Owls also shown by Vargas *et al.* (1988), who found that predated Algerian mice *M. spretus* more often had bone deformities than trapped animals.

DAILY FOOD REQUIREMENT. When provided with fresh mice *ad libitum*, daily food intake of captive nestlings increased from 63 g at 20 days of age to 80 g at 31 days, followed by decrease to 60 g at c. 60 days. From 20 to 60 days mean daily food intake therefore 67 g (Durant and Handrich 1998). Taylor (1994) estimated that, at 30–40 days, daily food intake per nestling is 98–108 g. De Jong (1991) estimated that energetic demand of Dutch young peaks at 450–500 kJ/day at 40 days. In Scotland, this peak is little higher (540 kJ/day), probably because nestlings on average 12% heavier than in Netherlands. Taylor (1994) estimated daily food intake of two Scottish adult males to be 75 g in November (estimated metabolized energy 428 kJ/day), and Ceska (1980) 67 g for captive birds. Digestion efficiency 78.4% when fed with nestling *Gallus gallus* (Barton and Houston 1993) and 75% when fed with mice (Ceska 1980).

ENERGETICS. Zone of thermal neutrality, which describes temperature at which resting metabolic rate is minimal, ranges between 23 and 32°C (Thouzeau *et al.* 1999). At 4°C, resting metabolic rate is 70% higher than that at thermoneutrality, and above 32°C Barn Owls exhibit hyperthermia (Thouzeau *et al.* 1999). During forced fasting hypothermia takes place only shortly before dying, with body temperature being reduced by only 1.4°C and resting metabolic rate by 16% (Thouzeau *et al.* 1999). This means that, in most of European range, individuals have to alter behaviour and increase metabolic rate to maintain body temperature at c. 40°C, and may lose heat rapidly in cold, windy, and wet regions (McCafferty *et al.* 1997).

During forced fasting at ambient temperature of 5°C, most body loss occurs in first part of night (Handrich *et al.* 1993a). In first day of starvation (so-called phase I) birds lose on average 20.5 g/day, between first and eighth days (phase II) 8.6 g/day, and between eighth and ninth days (phase III) 13.1 g/day. Protein catabolism increases sharply from end of phase II to phase III, as owls switch from expenditure based on lipids to that based on proteins. Fat localized in bone marrow mobilized only at phase III, indicating that it is one of the very last sources of energy used during starvation (Thouzeau *et al.* 1997). Bone marrow fat in breeding females (2.5% of dry bone mass) is one-tenth that of non-breeding females (23.9%) (Durant *et al.* 2000). Ample inter-individual variation in duration of three phases, with birds completing third phase 6–12 days after start of

starvation. Although females heavier than males both before starvation and at end of phase III, no sex difference in duration of three phases. When birds re-fed at end of phase III (i.e. just before death), required 8 days to return to body mass before start of forced starvation, with little inter-individual variation (Handrich *et al.* 1993b). During re-feeding increase in body mass more rapid in females (13.9 g/day) than males (9.2 g/day), and owls remove viscera of offered laboratory mice and consume the rest. Energy assimilation higher during re-feeding than both before starvation and after body mass was fully re-gained (Handrich *et al.* 1993b). Hunger resistance, expressed as (normal body weight – body weight after starvation)/normal body weight, is relatively low (0.20–0.21) compared with Long-eared (0.32–0.33) and Tawny Owls (0.32–0.37) (Piechoki 1960). Among captive Barn Owls, hunger resistance was 0.26 in males and 0.30 in females (Handrich *et al.* 1993a).

From analysis of road kills, seasonal variation in body mass mainly due to lipid rather than protein (Massemin *et al.* 1997). Compared with non-breeding females, laying birds have 1.3 times more water, 1.1 times more body proteins, and 1.2 times more body minerals, but only c. 60% lipid. Muscles weigh 1.2 times more, liver 1.5 times, and skin 1.4 times (Durant *et al.* 2000). Thus, differences in body mass between breeding and non-breeding females come from water content.

Parasites. (New section)

ENDOPARASITES. Numerous endoparasites identified, including trematodes (*Strigea strigis*), cestodes (*Panthernia candelabraria*), nematodes (*Porrocaecum depressum*, *P. spirale*, *P. depressum*, *Spiroptera perihamata*, *Synhimantus affinis*, *S. lanceps*, *Capillaria tenuissima*), acanthocephala (*Centrorhynchus aluconis*, *C. globocandatus*, *C. tumidulus*) (Bunn *et al.* 1982), *Isoospora buteonis*, *Sarcocystis dispersa* (van Ijzendoorn 1948, Cerna 1984, Svobodová 1997), tuberculosis, trichomoniasis (Hardy *et al.* 1981), Newcastle disease (Keymer and Dawson 1971, Diehl in Schneider 1977), and small intestine endoparasite *Caryospora strigis* (Gottschalk in Schneider 1977).

ECTOPARASITES. Ectoparasites found on Barn Owls include feather-lice (*Kurodaia subpachygaster*, *Strigiphilus rostratus*, *S. cursitans*, *Kramerella humulata*) (Bunn *et al.* 1982, Kutzer *et al.* 1982), ticks (*Ixodes arboricola*), and louse fly (*Ornithomyia avicularia*) (Bunn *et al.* 1982). Fleas (*Ceratophyllus gallinae*, *C. rossitensis*, *Monopsyllus sciurum*) rarely found. In Germany, subcutaneous mites *Tyrodectes strigis* discovered in nest material of 5 of 33 nests and in 12 of 19 birds (Wurst and Havelka 1997).

In Switzerland, 98% of nests infested by ectoparasitic fly *Carnus hemapterus*. Parasite intensity increases from birth to 25 days after hatching (40 flies per individual),

then declines, and at fledging nestlings virtually parasite free. Within nests, flies not randomly distributed, since late-hatched nestlings more parasitized than early-hatched nest-mates (Roulin 1998b). This non-random distribution not due to late-hatched nestlings being in poorer condition, since nestling body condition not correlated with parasite loads (Roulin 1998b) or parasite fecundity (Roulin 1999c). No sex difference in parasite susceptibility detected (Roulin 1998b, 1999c, Roulin *et al.* 2000a). Ability to mount specific immune response against an antigen (sheep red blood cells) is origin-related, but did not differ between sexes (Roulin *et al.* 2000a).

Social pattern and behaviour. (Additional material to BWP Vol. IV, pp. 440–3)

NATAL DISPERSAL. In Germany, distance moved from birth to breeding was 13 km (range 7–23 km; Schönfeld *et al.* 1977) and in France 21 km (range 2–62 km; Baudvin 1986). In Scotland, two studies showed that yearling males settled at 6.1 km (maximum 11 km) from natal site and yearling females at 9.7 km (maximum 22 km) (Shaw 1994, Taylor 1994). In Switzerland, mean distance between birth and breeding was 5.8 and 9.6 km for yearling males and females, respectively (Roulin 1996d).

INCIDENCE OF NON-BREEDING. Based on observation of roosting birds at sites in Netherlands where no nest was found, de Bruijn (1994) estimated that 15% of mature birds did not breed. Both here and in Scotland, non-breeding was more prevalent in poor vole years (de Bruijn 1994, Shaw 1994). In another Scottish area, non-breeding was more frequent when vole abundance was declining or had already reached lowest values. Non-breeders have lower body mass than breeders (Taylor 1994).

DEMOGRAPHY. Sexual maturity achieved within first year of life. In captivity, female bred at 26 weeks of age and male at 34 weeks (Shawyer 1994). In recently established British population, 81% of breeding females were yearlings (Petty *et al.* 1994). In two German populations, this percentage was 47% (Schönfeld and Girbig 1975) and 23% (Kniprath *et al.* 1999), whereas in Switzerland varied annually from 2 to 23% (Roulin 1996a). Based on age at last capture, female breeders had mean age of 2.3 years and males 2.9, and one 15-year-old male produced two broods in same year (Roulin *et al.* 1999). In Scotland, majority of recruits are yearlings (63.4%) (Taylor 1994) and mating with respect to age is assortative, i.e. first-year females breed more frequently with first-year than older males (Taylor 1994).

BOND. Polygamy is rare in Barn Owl with only 1.7% of male breeders feeding two broods simultaneously,

both in Spain (Martinez and Lopez 1999) and Scotland (Taylor 1994). Two broods of bigamous males found in same building three times (Shawyer 1994, Taylor 1994), at distance of 40 m (Martinez and Lopez 1999), six times at few–1000 m (Taylor 1994), at 1000 m (Roulin 1996e), and at 4500 m (Schönfeld and Girbig 1975). Shawyer (1994) also reports case of three females rearing offspring within same roof and fed by two males. Following Taylor (1994), primary female of bigamous males produce on average 2.6 fledglings and secondary female 1.1 fledglings. In Switzerland, males captured in nest-box with female, while primary female was incubating clutch at mean distance of 1.2 km (range 0.5–1.5 km; five different cases). Apparently, none of these males became bigamous (Roulin 1996e). Two Swiss males successfully produced two annual broods in succession in single nest-box, but with two different females (Roulin 1996e).

Polyandry seems to be more common than polygyny in Switzerland (Roulin 2002a). There are 21 mentions of females deserting offspring half-way through nestling period to start second breeding attempt with new mate (Altmüller 1976, Taylor 1994, Roulin 1996e, 2002a). Baudvin's observation (1986) of female having moved 17.5 km to lay second annual clutch indicates that offspring desertion occurs in France too. In Germany, Schönfeld and Girbig (1975) mention five pairs that produced two clutches in same year, indicating that not all females change mate to start second annual clutch. In Switzerland, 18 of 39 (46%) of females producing second brood deserted offspring before completion of parental duties to remate with another partner at distance of 1–10 km. Nestlings at first nest were 21–65 days of age when mother laid first egg of second clutch. Late-breeding females deserted offspring at younger age compared with early breeders. Offspring desertion did not reduce breeding success at first nest. In most cases, new mate of deserting females was yearling and had probably not previously bred. Deserting females produced second clutch 2 weeks earlier than non-deserting double-brooded females. Although former laid more eggs than latter at second nest, nesting success did not differ (Roulin 2002a).

Among 157 Scottish and 111 Swiss pairs, 1 and 3 pairs, respectively, were composed of closely related individuals (Taylor 1994, Roulin 1996d). Four reports of full siblings breeding together (Shawyer 1994, Taylor 1994, Roulin 1996d): one pair bred at site where they were born (Shawyer 1994), and two other pairs at 3 and 7.5 km from natal site (Roulin 1996d). Pair composed of father and daughter observed only once (AR personal observation), of mother and son four times (Petty *et al.* 1986, Shaw and Dowell 1989; AR personal observation),

and one pair composed of uncle and niece (Roulin 1996d). No mention that offspring of inbred pairs in any way malformed (Petty *et al.* 1986, Shaw and Dowell 1989, Shawyer 1994, Taylor 1994, Roulin 1996d, Literak *et al.* 1999; AR personal observation).

BREEDING DISPERSAL. In Scotland, although most breeding females trapped in two successive years at same nest-site (71%), males appear to be more site faithful (Shaw 1994). In another Scottish population, 99% of males and 95% of females bred in same nest-site in successive years. Change of nest-site followed loss of mate, or perhaps because female previously mated with bigamous male that became monogamous. Successive nest-sites were within 8 km (Taylor 1994). In France, Baudvin (1986) re-trapped all of 8 males but only 1 of 26 females in same nest in successive years, further exemplifying greater male fidelity. Although Swiss female had dispersed 387 km in first year of life, was recaptured in winter 2 years later 18 km from natal site (Roulin 1997).

HOME-RANGE. Using telemetry Brandt and Seebass (1994) found that home-range of four German owls covered on average 188 ha (range 90–369 ha) and that parents hunted at average distance of 637 m from nest (maximum 3.5 km). After offspring independent, area increased to 363–465 ha, with parents hunting on average at 2.2 km from nest (maximum 4.2 km). During breeding season, adults foraged mainly in fields, and, after offspring became independent, visited houses and gardens more frequently. For single French male, mean home-range was 763 ha and average area foraged in any one night was 250 ha (Michelat and Giraudoux 1991). This male hunted on average at 1.5 km from nest (maximum 3.2 km). In Scotland, 23 adults sighted up to 2.0 km from nest (although 90% of observations within 1 km of nest) and in years of high vole abundance birds captured prey closer to nest. Mean range of six males was 319 ha (245–392 ha) and of mates 308 ha (253–376 ha). In winter, birds seen up to 4.5 km from nest with only 40% of observations within 1 km (Taylor 1994). Ranges of neighbouring birds frequently overlap, but no sign of aggression observed unless intruder came very close to nest (Taylor 1994). In winter, foraging range can increase from 1–2 km around nest to 4–5 km (Cayford in Shawyer 1994). In Spain, Barn Owls display territorial behaviour in response to playback during breeding season (from March to July) but less frequently in winter or bad weather (Zuberogoitia and Campos 1998).

ANTAGONISTIC BEHAVIOUR. Although Kestrels and Barn Owls can breed close to each other without any apparent negative effect on breeding success (Fellowes

1967, Baudvin 1975, Michelat and Ganzer 1987, Beaud *et al.* 1991; but see Hasenclever and Tiemeyer 1991), often compete over nest-sites. Barn Owls usually out-compete Kestrels (Bunn *et al.* 1982, Minder 1990) by destroying clutch or young (Roulin 1996b; AR personal observation) or by forcing Kestrels to abandon clutch. In 19 cases, Barn Owl observed to mix clutch with one of Kestrel after latter abandoned nest-box (Hasenclever and Tiemeyer 1991, Ravussin 1994). In two nests, eggs of both species hatched, and in one case Barn Owls raised 'alien' nestling successfully (Ravussin 1994). Converse observation of nest containing brood of Kestrels alongside abandoned eggs of Barn Owls (Hasenclever and Tiemeyer 1991) and of Kestrel incubating 3-egg clutch mixed with 6 Barn Owl eggs (Roulin 1996b) suggests that Kestrels may sometimes evict Barn Owls from nest. In one case, pair of Barn Owls, whose nest was destroyed, took over nest-box and adopted two 7-day-old Kestrels. Raised them successfully before starting to lay their own replacement clutch (Schmidt 1993).

Eagle Owl *Bubo bubo* has been recorded eating Barn Owls on 10 occasions (Knobloch 1963, Mikkola 1976, Brandt and Seebass 1994), Goshawk *Accipiter gentilis* eight times (Gendebien 1973, Mikkola 1976), Buzzard *Buteo buteo* four times (Rosnoblet 1974, Mikkola 1976), Eleonora's Falcon *Falco eleonora* once (Schneider 1977), and one Tawny Owl *Strix aluco* predated a nest (Guérin 1932). In French churches, stone martens *Martes fiona* predated only 5 of 1031 nests at egg stage and 2 at rearing stage (Baudvin 1986).

ROOSTING. In Germany, 70% (Schönfeld *et al.* 1977) and 99% (Brandt and Seebass 1994) of daytime roosts in houses, the other roosts being in trees. Trees seem to be more regularly used as roosts in England (Bunn *et al.* 1982). Three to five different roosts may be used and individual may use same roost for 2–19 days (Brandt and Seebass 1994). Distance between daylight roosts and nest varies from few meters to 3.5 km with most being located at <500 m (41% of cases; Brandt and Seebass 1994). In Scotland, mean distance between daylight roost and nest was 2.25 km. Males roosted farther from nest than females (Taylor 1994).

In winter in Scotland, 40% of females and 15% of males roost at nest-site (Taylor 1994). Winter food caching in nest-boxes observed in England (Shawyer 1994) but not in Switzerland (Roulin 1998a). *c.* 40–60 days before laying, 80% of females roost at nests, and 10 days before laying all of them do so. Males move to nest-site later and, by *c.* 10 days before laying, almost all roost beside mate. After clutch complete, males progressively roost away from nest. At night, spend only 26% of time away from nest in contrast to 72% in 10 days following clutch

completion (Taylor 1994). Baudvin (1986) reported that, just before first egg laid, two partners often occupy nest (72% of cases), whereas during egg laying and incubation usually only female is in nest (69%). When nestlings half-to full-grown, both parents roost outside nest (Baudvin 1986) at distance of up to 1.5 km for males and 0.5–1.0 km for females (Brandt and Seebass 1994). During night-time foraging, owls frequently rest for short periods in farm buildings (Brandt and Seebass 1994). By roosting in building rather than in tree, Barn Owls estimated to reduce metabolic heat production by 19 vs. 10% compared with outside roost. Comparing estimates of heat production for owl in roost with one in the open revealed that metabolic savings were 26% in wet and windy conditions and only 12% on dry-calm days (McCafferty *et al.* 2001).

COURTSHIP. In winter, pairs often occupy nest-sites during daylight hours (Bunn *et al.* 1982, Taylor 1994). Study in Switzerland showed that males captured in nest-box in this season were more likely to breed there than females. Birds older than 1 year and paired individuals also more likely to breed following season than yearlings and solitary individuals. Solitary females occupied nest-boxes during daytime more frequently than solitary males suggesting that females prospect nest-sites and mates in winter (Roulin 1998a). Would not be surprising, for three reasons. First, in Germany, copulation recorded from January to November (Epple 1985). Second, allo-preening occurs in winter (Bunn *et al.* 1982), with male preening partner more regularly than vice versa (Epple 1985). Third, sexual displays already take place in December in Germany (Schönfeld and Girbig 1975, Epple 1985). Males start to vocalize 6–7 weeks before egg laying, usually near nest-site (maximum 250 calls in one sequence; Epple 1985) and maximal display intensity occurs 4–6 weeks before egg laying (Schönfeld and Girbig 1975, Epple 1985). Based on captive pairs, male calling rate during courtship decreases in intensity from first to third annual breeding attempt. Male also starts to offer prey items to partner on average 9 days (range 4–21 days) before egg laying both at first and second breeding attempt (Epple 1985). Assuming that mummified prey items in abandoned empty nest-boxes evidence of courtship that failed to attract female, 10% of courtship did not result in clutch in Switzerland. Mean number of mummified prey was 7.1 (range 1–27) (Roulin 1996c).

COPULATION. For calls produced during copulation and when male delivers prey item to partner, see Bühler and Epple (1980). Female produces specific call during copulation that may still be made 24 days after end of laying. Copulation usually (but not invariably) occurs in

nest-site (Bunn *et al.* 1982, Epplé 1985). In captivity, copulation commences on average 25 days before laying (first clutch on average 32 days; second clutch 17 days; range 10–48 days; Epplé 1985). Couple of days before egg laying, copulation frequency is $>1/h$, and during egg laying *c.* $1/h$. Maximum number of copulations recorded in 24 h is 70. Single copulation lasts 10–20 s (Bunn *et al.* 1982) or 16–60 s (mean 29 s) (Epplé 1985). Mate-feeding does not necessarily precede copulation (Epplé 1985), but, when cock offers prey item, hen consumes it after copulation (Bunn *et al.* 1982, Epplé 1985). Both in captivity and in the wild, copulation frequency correlated with clutch size (Epplé 1985). Offspring of first annual breeding attempt sometimes interrupt copulation of parents by begging (Epplé 1985).

HOMOSEXUAL BEHAVIOUR. In captivity, females attempted to mount each other and displayed diverse sexual behaviour (Epplé 1985). Similar finding holds for wild birds (Schönfeld *et al.* 1977).

RELATIONSHIPS BETWEEN SIBLINGS. Older nestlings sometimes feed younger siblings with prey items deposited in nest by parents (Bunn and Warburton 1977, Epplé 1979, Bühler 1981). Allopreening frequent (Bühler 1981) and siblings commonly not aggressive to each other (Masurat 1980). Although these observations suggest widespread pacific behaviour, sibling competition over parental food distribution can nevertheless be intense. Bühler (1981) reports that, although satiated, nestlings continue to fight among each other to monopolize prey items and sit on them. Siblicide can occur when nestling is so starved that it does not react towards violent aggression from healthy sibling (Bühler 1981).

CANNIBALISM. Of 2369 hatched nestlings, Baudvin (1986) showed that 30 were cannibalized (1.3%), and suspected cannibalism in further 376 cases (15.9%) although 89 (3.8%) nestlings that died had not been cannibalized. Apparently, cannibalized nestlings died from starvation or illness and not from siblicide. Nestlings older than 15 days usually not eaten by siblings or parents. Cannibalism not more frequent in larger broods (Baudvin 1978). In Switzerland, of 60 nestlings that died, 10 were cannibalized, 9 were found uneaten in nest, while disappearance of 41 other nestlings was unclear (Roulin *et al.* 1999).

ADOPTION. De Bruijn (1994) reports recently fledged individual captured in foreign family 23 km from natal nest. Seven other cases of nest-switching have been reported in Switzerland including three females, three males, and one individual of unknown gender. They were 64–91 days of age and mean distance separating natal site from foreign nest was 5.4 km (range 0.5–12 km). In two cases, could be shown that foreign fledgling

stayed more than 1 day, suggesting successful fostering. An experiment, in which one 58-day-old nestling experimentally swapped between nests, showed that foster families tolerated or were unable to expel foreign fledgling from nest (Roulin 1999a). Brandt and Seebass (1994) also report double-brooded female that changed mate after first male died. Laid second clutch with new mate alongside 5-week-old offspring, suggesting that new mate had to adopt female's brood to copulate with her.

PARENTAL FEEDING RATE. Table 2 shows measurements of feeding rate per night per nestling. Across nine studies, parents delivered on average 3.0 prey items per nestling per 24 h. Exceptionally, pair brought 33 prey items to six offspring in 95 min (Shawyer 1994). In Switzerland, when nestlings were 18–49 days (mean 36; 27 broods), males provided 6.5 prey items per night to brood (mean size 3.8 nestlings) and female 3.0. Sex differences in feeding rate may be slightly larger, since in 1.7% of cases male transferred prey item to mate on perch, implying that females sometimes deliver items captured by male. Only male feeding rate correlated with brood size, and hence male and female feeding rates not correlated with each other (Roulin 1998c). In Langford and Taylor's study (1992), feeding rate at 19 broods (mean size 3.6) increased from 8.11 items delivered per 24 h during incubation to 14–16 items at 30 days after hatching followed by decrease. Feeding rate can be estimated from formula: brood mass gain index (g) = $-118 + 14.3$ number of prey items delivered to the nest per night. Brood mass gain index is the difference in the sum of the masses of all nestlings + $0.78 \times$ mass of surplus prey items between two successive days (Roulin *et al.* 1999), where 0.78 is digestive efficiency to convert vole to owl flesh (Barton and Houston 1993).

Two studies showed that male parent fed brood without himself consuming any prey item in first half of night (Handrich *et al.* 1990, Taylor 1994). May explain why feeding rate decreases from sunset to sunrise (Ritter and Görner 1975, Michelat and Giraudoux 1992) in both parents (Roulin 2001c). Based on observations made during 7 nights at two nests, Festetics (1967) detected two peaks of feeding activity, one at 21.00–23.00 hours and another at 02.00–04.00 hours. Feeding rate is impaired on rainy nights (Ritter and Görner 1977, Michelat and Giraudoux 1992).

WITHIN-BROOD FOOD DISTRIBUTION. According to Bunn and Warburton (1977), mother consumes offspring faeces until 2 weeks after hatching, behaviour that Bühler and Epplé (1980) did not, however, observe. When nestlings less than 25 days old, mother often calls while delivering prey item (Bühler and Epplé 1980), mainly

Table 2. Feeding rate (number of prey items delivered per nestling per 24 h) measured in nine studies

Reference	Country	No. of broods	No. of nights recorded per brood	Brood size	Feeding rate per nestling
Pikula <i>et al.</i> (1984)	Czech Republic	1	2	7	2.1
Michelat and Giraudoux (1992)	France	2	13	4	3.3
Baudvin (1986)	France	—	—	—	3–4
Ratzer and Gömer (1975)	Germany	1	10	3	1.8
Festetics (1967)	Germany	2	3	3	3.22
Langford and Taylor (1992)	Scotland	19	?	3.6	4
Bussman (1937)	Switzerland	1	30	4	2.1
Juillard in Baudvin (1986)	Switzerland	?	?	?	4.5
Roulin (1998c)	Switzerland	27	2	3.8	2.7
Mean		—	10		3.0

when nestlings satiated and beg at low rate (Bühler and Epple 1980). Female parents cease caring for offspring before male, and double-brooded females observed to cease feeding offspring *c.* 21 days before laying second clutch (Epple 1985). Independence from parents achieved at 70–90 days of age (Langford and Taylor 1992), although Bunn *et al.* (1982) report fledgling being fed until 112 days. Parents deliver prey items that weigh on average 31–35 g (range 11–73 g; Pikula *et al.* 1984) and offspring able to swallow item whole from 15 days onwards (Baudvin 1986). Prior to this, if parents do not dismember large prey items, offspring can sometimes not eat them and wait for subsequent feeding (Bunn and Warburton 1977). In absence of prey, mother observed to kill recently hatched offspring and to eat it (Epple 1985) or to offer it to offspring (Bühler 1981). In one case, Baudvin (1980) found live prey item *Apodemus* sp. in nest and AR (personal observation) captured male Barn Owl bringing live skylark *Alauda arvensis* with no sign of injury to nest. Thirty-four-day-old nestlings did not react to field vole *Microtus arvalis* that mother brought alive to nest (AR personal observation).

PREY REMAINS AT THE NEST. During laying and incubation, Baudvin (1986) found prey in 23.5% of occupied nests, with average of 2.4 items in each nest with at least one prey item. When nestlings less than 20 days old, found prey in 57.8% of nests (average of 4.7), and when older than 20 days 3.2 in 18.8% of occupied nests. Prey remains more numerous in years of high breeding success (Baudvin 1980). Largest recorded prey store totalled 136 items, some of which were decomposed (Taylor 1994). In France, each prey item weighed on average 28 g (Baudvin 1986) and large species were over-represented in food stores compared with frequencies in pellets (Baudvin 1983) and trapped individuals (Taylor 1994). Small items probably eaten more rapidly than large ones since, in France, shrews represented 2.3% of species found in food caches but 33.8% of prey in pellets (Baudvin 1983). In Scotland, Taylor (1994) did not find

any difference in prey species found in pellets and prey stores. Food stores are consumed at night but also during daytime (Roulin *et al.* 2000b).

TRADE-OFF BETWEEN CURRENT AND FUTURE REPRODUCTIVE SUCCESS. To investigate whether parents can be induced to change feeding rate above initial level, two experiments were conducted in Switzerland. First, two hatchlings were added to or removed from brood. Nestling survival and body mass significantly reduced in enlarged broods. In contrast, no significant effect on parental body mass or feeding rate in year when experiment was performed, or on parental survival prospects and reproductive success in following year. Size and quantity of prey items stored at nest did not differ significantly between enlarged and reduced broods (Roulin *et al.* 1999). Suggests that, when broods require extra parental effort, parents do not jeopardize future reproductive success and brood reduction occurs. In second experiment, prey remains were artificially added to nests or removed from those with food stores. The following night, parents did not provide significantly less prey items in food-added than food-removed broods (Roulin *et al.* 2000b), again suggesting that parents allocate fixed budget to rearing brood.

Voice. (Additional material to *BWP* Vol. IV, pp. 443–5)

CALLS OF YOUNG. Nestlings produce so-called 'chittering' calls (Bunn 1974) when attacked or disturbed by nest-mates (Bühler and Epple 1980). Chitter when cold until warmed by siblings or mother prior to 20 days of age (Bühler and Epple 1980). Both at night and by day, nestlings produce harsh 'frightening' calls when scared by potential predator like human (Roulin 2001d) or sometimes by parent that arrives at nest (from 12 days of age onwards with peak at 21 days). Single 'frightening' call lasts 1.8–7.7 s (increasing with age) with intensity of 10–14 kHz. In front of potential predators, nestlings also perform so-called Bill-snapping (Bühler and Epple 1980).

In contrast to many birds, Barn Owl nestlings vocalize

in both presence and absence of parents. In first day of life, nestlings produce begging calls lasting on average 0.38 s and at 60 days 0.63 s (Bühler and Epple 1980). In presence of parents, each nestling produces on average 30.4 calls/min (range 16–88) and in absence 3.7 calls (2–10) with intensity of 6–10 kHz. In absence of parents, only few nestlings vocalize but on arrival all of them start to do so and more intensively. Most vocal nestling has priority access to prey items delivered by parents (Roulin *et al.* 2000b, Roulin 2001b, c, 2002a). When nestlings dismember item, continue to vocalize. After fledging, nestlings less vocal (Bühler and Epple 1980).

Recent studies suggest that, in absence of parents, siblings communicate vocally amongst each other to negotiate priority of access to impending food resources. In brood of two nestlings, for instance, hungrier nestling vocalizes intensely to signal willingness to contest next prey item. Momentarily outcompeted sibling refrains from vocalizing, and thereby signals withdrawal from contest. After hungry nestling has eaten prey item, sibling resumes intense vocalization to indicate that it now contests priority of access to next item. Hypothesis that siblings vocally negotiate resources can explain why they vocalize less intensely in larger broods. Indeed, for each nestling, chance of monopolizing prey item is lower in larger broods, and hence nestlings may be less willing to compete among each other leading them to vocalize less intensely (Roulin *et al.* 2000b, Roulin 2002a). Food supply affects begging rate more in absence of parents. In presence of parents, manipulated nestlings vocalize at similar level, whereas in absence food-removed nestlings are 1.8 times more vocal than food-added (Roulin 2001c).

Breeding. (Additional material to *BWP* Vol. IV, pp. 445–6)

SEASON. In Germany, clutches laid from 26 February to 21 September (Schönfeld and Girbig 1975), in England from February to November (mean 9 May; Hardy *et al.* 1981) and in Switzerland from 5 March to 30 July (mean 31 April; Roulin 2002c). In Europe, earliest record is on 18 December in Sardinia (*T. a. ernesti*) (Demartis 1985). Food supply is major determinant of laying date, since years of good food supply characterized by early initiation of breeding activity (Taylor 1994). Food supplementation in captivity (Bühler 1965, Bunn *et al.* 1982, Epple 1985) and the wild (Shawyer 1994) confirmed importance of food supply for early initiation of breeding. Winter and spring rainfall did not appear to influence laying date (Baudvin 1986, Taylor 1994), whereas warm winter (Baudvin 1986; but see Chanson *et al.* 1988) and spring (Taylor 1994) favour early breeding. Within Scottish population, no relationship between laying date and female size, as measured by wing length, and first-year

females laid later than older birds (Taylor 1994). Young fledged before median fledging date of population were more likely to be recruited to breeding population in subsequent years than those fledged after median date (Taylor 1994, Roulin 2002c).

SITE. Highest breeding record is at 1500 m in France (Lehnheer 1991) and in poor vole years these high altitude sites are deserted first (Taylor 1994). Dense populations found at low altitude and in regions rich in nest-sites and hedgerows, wooded banks, lines of trees, and woodland edges (Baudvin 1986, de Bruijn 1994). Nests usually located in man-made structures and use of hollow trees almost restricted to British Isles, with 32–45% of pairs breeding in trees (Blaker 1933, Bunn *et al.* 1982) vs. only 3% in Netherlands (Braaksma and de Bruijn 1976). Proportion of nests found in trees was 7.6% in Wales, 8.9% in Scotland, 16.2% in Ireland, 34.8% in England, and 80% in Isle of Wight (Shawyer 1987). In UK, only 3% of birds breed in cliffs (Blaker 1933, Bunn *et al.* 1982).

NEST. Schaden (1992) showed in experiment using hand-reared owls that early experience influences nest-site selection. Birds reared in given type of nest (wooden or stone nest-box, bales of straw) later showed more courtship and breeding activities in same type of nest. In Scotland, Taylor (1994) observed six cases of young reared in tree holes that subsequently nested in buildings, or vice versa. During courtship both partners build nest cup (Epple 1985).

EGG LAYING. Epple (1983) recorded egg-laying intervals of 30 clutches: eggs in clutches of 4–9 eggs were laid at usual 2– to 3-day intervals, whereas two clutches of 3 eggs were laid at unusual 5- to 7-day intervals. In three cases, Taylor (1994) noticed that during period of 6–9 cold days females may temporarily give up laying eggs.

EGG SIZE. Nominate *T. a. guttata* ($n = 719$ eggs): 39.4 (range 45.0–36.1) \times 30.9 mm (range 34.9–27.4) (Schönfeld and Girbig 1975, Schneider 1977, Hayo 1978, Pikula *et al.* 1984). Nominate *T. a. alba* ($n = 62$ eggs): 42.1 \times 31.8 mm (Taylor 1994). Hybrid populations of *T. a. guttata* \times *T. a. alba* ($n = 74$ eggs): 38.9 (range 42.9–33.5) \times 30.8 mm (32.4–28.8) (Baudvin 1975, Baudvin and Fodimbi 1978). Nominate *T. a. schmitzi* ($n = 2$ eggs): 41 \times 33 and 42 \times 32 mm (Schönwetter 1960). In Germany, egg size does not co-vary with clutch size or female age (Schönfeld and Girbig 1975), whereas in Czech Republic egg length increases with clutch size (Pikula *et al.* 1984). Compared with other European owls, eggs relatively small in relation to female body mass (Taylor 1994). For seven females, Schönfeld and Girbig (1975) calculated that mass of first clutch represents

32.5% of female body mass and mass of second clutch 40.4%.

CLUTCH SIZE. High potential for egg production of Barn Owl is exemplified by 16-egg clutch observed in nature (Hummitzsch 1953) and by captive female having laid 26 eggs (21 were fertile) in 62 days (Shawyer 1994). Variation in clutch size related to several factors. First, both clutch and brood sizes may have progressively increased from 1964 to 1995 in UK (Toms 1996). Second, on mainland of Europe, clutches increase in size from south Spain to Hungary (Roulin *et al.* 2001a). Such clinal variation may differ in British Isles, since clutches seem to be smaller in Scotland than in England and Wales (Shawyer 1987). Third, clutch size positively correlated with field vole abundance (Schönfeld and Girbig 1975, Taylor 1994) potentially explaining why owls produce smaller clutches in years when breeding activities initiated relatively late in season (Taylor 1994). Fourth, within most populations pronounced seasonal variation in clutch size. In Germany, France, and Switzerland, clutch size increases through season up to July and then decreases (Schönfeld and Girbig 1975, Baudvin 1986, Roulin 2002a), whereas in Scotland clutch size decreases as season progresses. Finally, clutch size may be related to individual and site quality. Indeed, pairs in nest-boxes produced larger clutches than those in tree cavities or buildings (Johnson 1994). Although, in wild and captive birds, Epple (1985) did not find any significant correlation between intensity of courtship-feeding and clutch size, Taylor (1994) found that females that were heavier just before egg laying also laid larger clutches (Taylor 1994). In same population, first-year breeders did not produce significantly fewer eggs than older females (Taylor 1994).

In *T. a. guttata* populations, second clutches larger than first (7.68 vs. 5.61 eggs; Frylestam 1971, Schönfeld and Girbig 1975, Kaus 1977, Brandt and Seebass 1994, Poprach 1996). Similar finding applies to populations in which *T. a. guttata* and *T. a. alba* interbreed, although difference less pronounced (6.65 vs. 5.54 eggs; Baudvin 1986, Chanson *et al.* 1988, Muller 1991, Roulin 2002b). In contrast, in *T. a. alba* populations, second clutches smaller than first (4.23 vs. 5.47 eggs; Taylor 1994, Martinez and Lopez 1999). These subspecific differences between two annual breeding attempts may not be due to differences in reproductive tactics, since in Switzerland clutch size is not correlated with male and female plumage coloration (*T. a. alba* individuals white, whereas *T. a. guttata* individuals reddish-brown; Roulin *et al.* 2001a). Likewise, food supply may not be sufficient explanation because captive birds fed *ad libitum* throughout year nevertheless lay larger second (6.5 eggs) than first clutches (5.6 eggs) (Epple 1985).

REPLACEMENT CLUTCHES. In France, 16% of pairs that failed to produce any offspring at first breeding attempt to lay replacement clutch in same nest, whereas only 6% of pairs that failed at second breeding attempt did so. More breeding failures replaced in years when second clutches frequent (33%) than scarce (2%). For eight pairs that failed at egg stage, time interval between first and replacement clutches was 43 days and for those failing at nestling stage 79 days. In one case, female incubated five eggs of replacement clutch mixed with five eggs of first clutch that had failed to hatch (Baudvin 1986).

SECOND ANNUAL CLUTCHES. In 8-year French study, second clutches regularly found only in the 4 years when first clutches had been laid early in season and prey remains frequently found at nest. Rainfall in May and June did not correlate with occurrence of second clutches (Baudvin 1986), whereas second broods were more frequent in good than in poor vole years (de Bruijn 1979, 1994, Taylor 1994). This relationship was experimentally demonstrated in England where food-supplemented pairs produced second brood more often than non-supplemented pairs (Shawyer 1994). Second broods frequent in Spain (Martinez and Lopez 1999), rare in British Isles (Taylor 1994), and increase in frequency from south France to south Sweden (Muller 1991).

Muller (1991) calculated that, in eastern France, second annual brood increases productivity by 32%, since each pair produced on average 4 offspring at first breeding attempt and 1.3 at second. Double-brooded pairs produced similar-sized clutch and brood at first breeding attempt to those of single-brooded pairs, but 16 days earlier (Muller 1991). In Germany, mean time between laying first and second brood was 100 days (range 81–122; Schönfeld and Girbig 1975), in France 100 days (73–127 days; Baudvin 1986) and 99 days (65–140; Muller 1990), in Switzerland 90 days (67–133; Roulin 2002a), and in Scotland 98 days (Taylor 1994). In captivity, where food was provided *ad libitum*, 12 successive clutches laid at mean interval of 89 days (range 56–119 days; Epple 1985). This interval was shorter for pairs breeding in nest-boxes (mean 112 days) than churches (98 days; Muller 1990) and for females that desert first brood before end of rearing period than for non-deserting females (83 vs. 98 days; Roulin 2002a). When female lays second clutch in same nest-site as that used for first breeding attempt, sometimes behaves aggressively towards fledglings (Epple 1985).

THIRD ANNUAL CLUTCHES. Proof that female can lay three clutches in same year has been given in captivity (Bunn *et al.* 1982, Epple 1985). In the wild, and using feather moult to recognize breeding females, Martinez and Lopez (1999) found that 12.8% of breeding pairs

produce three annual clutches in south-east Spain. In study population in Switzerland, where most females captured between 1990 and 2001, no third brood recorded (AR personal observation).

INCUBATION. Incubation usually starts when first egg is laid. Although Baudvin (1986) observed two males sitting on eggs, brood patch was found only in females (Bunn *et al.* 1982, Baudvin 1986). During incubation, female turns eggs on average every 10–15 min (range 3–39 min; Epple and Bühler 1981). Eggs need to be incubated for 33 days (Schönfeld and Girbig 1975) or 29–34 days (Taylor 1994). Females may incubate non-hatched clutch for 50–60 days (Schönfeld and Girbig 1975). In relation to body weight, Barn Owls have significantly longer incubation period than other European owls (Taylor 1994).

HATCHING. Just before hatching, nestlings vocalize and mother helps them out of the shell. Mothers may consume shells, leave them in nest, or drop them some distance outside (Bühler 1970). Hatching of single egg lasts 12–36 h (Bühler 1970) and interval between hatching of two successive eggs can be 3–14 days (Taylor 1994). Proportion of eggs that successfully hatched in France was 0.82 (Baudvin 1986), in Scotland 0.81 (Taylor 1994), in Germany 0.87 (Schönfeld and Girbig 1975, Kaus 1977, Hayo 1978), in Czech Republic 0.70 (Pikula *et al.* 1984, Poprach 1996), and in Spain 0.83 (Martinez and Lopez 1999). In France, hatching success was lower in August than in earlier months (Baudvin 1986), and in Scotland annual variation in hatching success was not correlated with vole abundance or weather conditions (Taylor 1994). Taylor also noted that 83% of unhatched eggs were last or penultimate eggs.

BROODING. Mothers brood offspring until youngest nestling is 12–16 days old (Taylor 1994).

NESTLING GROWTH. Pikula *et al.* (1984) characterized body mass growth of Czech owlets with formula: age in days = $-4.7957 + 6.8154x + 0.5708x^2 - 0.0178x^3 + 0.0001x^4$, where x is wing length. In curve of Durant and Handrich (1998) we can see that maximal growth rate takes place at 17 days. Nestlings achieve maximal body mass of 391 g at 40 days and then lose weight to achieve asymptotic body mass of 314 g (see also Schönfeld and Girbig 1975, Baudvin 1986, de Jong 1991). Body mass recession is spontaneous and nestlings fed *ad libitum* or under restricted food supply fledged with similar body mass (Durant and Handrich 1998). Also found in Swiss population in which nestlings raised in experimentally modified broods fledged with similar body mass, although growth rate from enlarged broods was impaired (Roulin 1998*d*). In Scotland, body mass at fledging was lower in larger broods and in poor vole years (Taylor 1994).

Durant and Handrich (1998) did not find any evidence of sexual dimorphism in body mass of captive owlets, whereas in wild population female nestlings were significantly heavier than brothers (Roulin *et al.* 1999). Nestlings placed at bottom of age hierarchy and raised in experimentally enlarged broods had impaired body mass growth. In contrast, nest-mate placed at top of same hierarchy showed growth rate comparable to that of nestlings raised in smaller broods. This means that last-hatched nestlings may be outcompeted in large broods but not in small ones. Both early- and late-hatched nestlings fledged with similar body mass (Roulin 1998*d*) and are equally likely to be recruited in breeding population the following year (Roulin 2002*c*).

For estimating nestling age, growth curves of wing length more reliable than growth curve of body mass because poor food supply does not alter wing growth but does alter body mass (Durant and Handrich 1998). In Scotland, wings grow at linear rate between 20 and 60 days [wing length (mm) = $-22.3 + 5.1 \times \text{age in days}$] (Taylor 1993). For growth curves of tarsus see Taylor (1994) and Durant and Handrich (1998), for tail and bill lengths see Schönfeld and Girbig (1975).

FLEDGING TO MATURITY. Nestlings take first flight at c. 56 days of age (Bunn *et al.* 1982) and return to nest until they reach 11–14 weeks of age before dispersing (Taylor 1994). Parents preferentially feed nestlings inside rather than outside nest (Bunn *et al.* 1982).

BREEDING SUCCESS. In Czech Republic, fledging success (proportion of hatchlings that fledged) was 75% (Pikula *et al.* 1984), in Germany 91% (Bethge and Hayo 1979) and 79.5% (Schönfeld and Girbig 1975), and in France 65% (annual variation 0.39–0.70; Baudvin 1986). In Switzerland, some males constantly more productive at every breeding attempt than other males, although one territory does not necessarily always produce more nestlings than another (Roulin *et al.* 2001*a*). Note that in Netherlands pairs breeding in nest-boxes are more successful than those breeding in other nest-sites (de Bruijn 1994). In France, larger clutches are more productive, as are pairs that breed before end of July. Mean brood size at fledging is larger in years when many pairs produce second brood (3.99 vs. 3.04 nestlings per pair) and in years when it rains less (Baudvin 1986). Impact of food access on reproductive success in Germany is further exemplified by observation that number of fledglings per pair is lower in poor than in peak vole years (2.4 vs. 4.3; Schönfeld and Girbig 1975). In Scotland, pairs with more voles in diet also produced more fledglings. Furthermore, in high vole years only 5–10% of nestlings die and 70% of mortality occurs before young are 10 days old, despite presence of prey remains at nest.

In poor vole years, mortality reaches 45% and deaths occur for first 20 days after hatching (Taylor 1994). In France, 80% of nestlings that die are last or penultimate (Baudvin 1986) and in Switzerland 97% (Roulin *et al.* 1999). In Scotland, in poor vole years 26% of early-hatched and 94% of late-hatched nestlings within brood die (Taylor 1994). In Switzerland, pairs producing larger broods more often had at least one offspring recruited into local breeding population. Reproductive success of yearling recruits was not correlated with birth date or within-brood hatching rank, or size of brood from which they fledged (Roulin 2002c).

Plumages. (Additional material to *BWP* Vol. IV, p. 446)

PLUMAGE COLORATION. Plumage of ventral body side varies from dark reddish-brown to white. Males commonly lighter in colour than females (Roulin 1999b, Roulin *et al.* 2001a) and both sexes become lighter only or mainly between first and second years of age (Taylor 1994, Roulin 1996a, 1999b). Inter-individual variation in plumage colour has genetic basis and neither quality of rearing environment nor body condition alter expression of colour (Roulin *et al.* 1998). Most genes coding for this trait, or those of major effect, probably located on autosomal chromosomes since mothers resemble sons to same extent that fathers resemble daughters (Roulin *et al.* 2001a). Among birds with plumage aberration, three were completely white (Hanak and Sitko 1997; AR unpublished data from museum collections) and two others had melanic plumage (Literak *et al.* 1999). Two captive siblings taken from nest in Czech Republic produced 7 (23%) melanic offspring of 30 offspring, ratio indicating that melanism is coded by autosomal recessive allele (Literak *et al.* 1999).

In Swiss population, proportions of breeding females and nestlings of different plumage colour morphs varied slightly between years, whereas proportion of white males decreased from 1992 to 1995 as frequency of yearling breeders increased (Roulin 1996a). Both in Switzerland and France, male and female breeders do not mate assortatively with respect to plumage coloration (Baudvin 1975, Roulin 1999d). In Switzerland, darker males produce on average more offspring per breeding attempt, feed their brood at greater rate, and (in France) have heavier heart. Lighter coloured females breed earlier in season (Roulin *et al.* 2001a).

PLUMAGE SPOTTINESS. Birds vary in extent to which feathers of ventral body size are marked with black spots that vary in size. Proportion of plumage covered with black spots is referred to as 'plumage spottiness'. Females are on average more spotted than males and inter-individual variation in plumage spottiness is genetic, and

not because they live in a different environment or are in different condition (Roulin *et al.* 1998). Since mothers resemble sons twice as much as fathers resemble daughters, principal genes probably located on sex chromosome Z (Roulin *et al.* 2001a). In birds, males are homogametic ZZ and females heterogametic ZW, so that single maternal Z-chromosome is always transmitted to sons and either of two male Z-chromosomes is passed on to each daughter.

Female nestlings display more and larger black spots than brothers (Roulin 1999b, *d*). Based on recapture of Swiss individuals from fledging to third year of age, males appeared to become less spotted between first and second year. Among females, yearlings exhibit fewer spots than at fledging probably because they are renewing feathers at time of recapture. From first to second year of age, breeding females become more spotted, and from second to third year no change in number of spots was detected (Roulin 1999b). In Scotland, males and females become less spotted from fledging to first year of age (Taylor 1993).

Studies in Swiss population have shown that plumage spottiness has signalling function in females. Successive mates of same male were similarly spotted, and mates of father and sons displayed plumage spottiness to similar extent. Mating with respect to this plumage trait was assortative, and paternal investment decreased after plumage spottiness of mate was experimentally reduced. In non-manipulated birds, offspring were also heavier when mother was more heavily spotted (observations from two years; Roulin 1999d). Roulin *et al.* (2000a) showed that females that were more spotted produced offspring that can mount greater specific antibody response against immune challenge of sheep red blood cells. Furthermore, blood-sucking flies *Canutus hemapterus* were less abundant on nestlings raised in nests of more heavily spotted females and these flies were also less fecund (Roulin *et al.* 2001b). More heavily spotted females had smaller Bursa of Fabricius, organ that produces B cells that in turn produce antibodies (Roulin *et al.* 2001b). Male plumage spottiness did not appear to signal offspring parasite resistance or to co-vary with size of Bursa of Fabricius. Because female plumage spottiness is heritable (Roulin *et al.* 1998), males may therefore be choosing females by assessing this trait as indicator of female genetic quality. Finally, plumage spottiness is not correlated with body size, except that more spotted females have longer tail (Roulin 1999d). In some years, older females are more spotted (Roulin 1999d, Roulin *et al.* 2001b) and different females breeding in nest-site in different years do not resemble each other with respect to this trait (Roulin 1999d).

Bare parts. See *BWP* Vol. IV, pp. 446–7.

Moult. (Additional material to *BWP* Vol. IV, p. 447)

MOULT PATTERN OF PRIMARY, SECONDARY, AND TAIL FEATHERS. Same moult pattern in German (Piechocki 1974, Schönfeld and Piechocki 1974) and Scottish birds (Taylor 1994). For primaries, usually only p6 shed in bird's second year, but sometimes p7 also replaced. At second moult p5, p7, p8, and p9 (and sometimes p4 and p10) replaced. Other primaries renewed during third moult in bird's fourth year. For secondaries, moult pattern appears to be much more variable. In second year, from one to four feathers may be shed (usually s12 and some other feathers between s11 and s14). Most other secondaries renewed in third year. Tail moult begins in second year, starting with central (t1) and outer feathers (t6). At subsequent moults, several tail feathers renewed without any clear pattern (Baker 1993, Taylor 1994).

In Scotland, females begin to moult 2 months earlier with peak in July and in August/September for males when most offspring are independent. Unmated males start to moult earlier than breeding birds, and females that resume breeding activity early in season also start to moult later in reproductive cycle than females breeding later. One quarter of females begin to moult during incubation and two-thirds in second half of nestling stage (Taylor 1994). In peak vole years, more breeding females are moulting than in poor vole years (Taylor 1994).

GROWTH RATE OF RENEWED FEATHERS IN BREEDING FEMALES. Wing: p10 (5.32 mm/day), p9 (5.18), p8 (5.04), p7 (4.91), p6 (4.77), p5 (4.63), p4 (4.49), p3 (4.35), p2 (4.22), p1 (4.08), s1 (3.94), s2 (3.80), s3 (3.66), s4 (3.53), s5 (3.39), s6 (3.25), s7 (3.11), s8 (2.97), s9 (2.84), s10 (2.70), s11 (2.56). Tail: t1 (2.94 mm/day), t2 (2.88), t3 (2.82), t4 (2.76), t5 (2.70), t6 (2.64) (AR, personal observation).

VENTRAL BODY SIDE. All of 2 fledgling and 7 breeding females, for which feathers of ventral body side had been marked, partially or completely renewed plumage before following breeding season (Roulin 1999b). In Scotland, contour feathers were replaced on 2- or 3-year cycle (Taylor 1994).

Measurements. (Additional material to *BWP* Vol. IV, p. 447)

BIOMETRICS. Among Scottish birds, Taylor (1994) did not find any significant correlation between body mass during breeding season and lengths of longest toe, tarsus, wing, or tail. Trait that reliably reflects size of skeleton is bill length (Roulin *et al.* 2001b). Among dead French Barn Owls, females were heavier than males because of larger structural size (i.e. skeleton) rather than because females accumulate more protein or lipid (Massemin *et al.* 1997).

ANATOMY. Average length of small intestine is 37.8 cm (Barton and Houston 1994). Weight of liver represents 2.83% of total body mass, heart 0.87%, kidney 0.78%, stomach 1.94%, and small intestine 0.42% (Barton and Houston 1996). Among dead birds, heart size was significantly correlated with body condition (Barton and Houston 1996).

Weights. (Additional material to *BWP* Vol. IV, p. 447)

During egg laying and incubation in France, females and males had mean body mass of 395 vs. 319 g, when nestlings were <20 days old 365 vs. 314 g, when 20–40 days 335 vs. 317 g, and when older than 40 days 331 vs. 313 g. Heaviest recorded female weighed 460 g (Baudvin 1986). In Scotland, female body mass increases by 75 g when first egg is laid and this extra body mass is lost in c. 50 days (Taylor 1994). In France, female body mass was not related to either presence of prey remains at nest or brood size (Baudvin 1986).

Structure. (Additional material to *BWP* Vol. IV, p. 448)

Several physical malformations observed, e.g. young born with only one wing (Schermer 1974), five digits (hyperdactylie; Kumerloewe 1968), bill malformation (Schönfeld 1974), 14 instead of 12 tail feathers (Duerr 1993), blindness at 60 days of age (Schwarz 1987), and strong behavioural troubles (Roulin and Etter 1996).

Geographical variation. See *BWP* Vol. IV, pp. 448–9.

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