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VALUE OF NEST BOXES FOR POPULATION STUDIES AND CONSERVATION OF OWLS IN CONIFEROUS FORESTS IN BRITAIN

STEVE J. PETTY
Forestry Authority, Wildlife Ecology Branch, Ardentinny, Dunoon, Argyll PA23 8TS, Scotland

GEOFF SHAW
Forest Enterprise, South Scotland Region, 55-57 Moffat Road, Dumfries DG1 1NP, Scotland

DAVID I.K. ANDERSON
Forestry Authority, Wildlife Ecology Branch, Ardentinny, Dunoon, Argyll PA23 8TS, Scotland

ABSTRACT.—The response of cavity-nesting owls to nest boxes was studied in man-made coniferous forests in northeast England and southwest Scotland. In both study areas field voles (*Microtus agrestis*) were the owls' main food. Voles were abundant on afforested and replanted areas up to 15 yr after planting. Forty territories of tawny owl (*Strix aluco*) were located in one study area prior to 1979. All of these pairs bred in natural sites. In the first year (1980) that nest boxes were available 83% of the population switched to breed in them, and 100% by the fourth year. The number of occupied territories subsequently increased to 66 by 1990, and was attributed to an improvement in food supply resulting from clear-cutting. In another forest, barn owls (*Tyto alba*) declined as abandoned buildings became unavailable due to decay and renovation. The provision of nesting barrels led to a rapid increase in the breeding population, initially by yearlings reared on adjacent farmland. Therefore, nest boxes (barrels) were an essential element in conservation of barn owls in coniferous forests. In contrast to tawny owls, resident barn owls did not switch to nesting barrels. Therefore, in the early years of the study, breeding results may have been biased by a lack of breeding experience in most of the population. The development of an age-structured population took several years.

KEY WORDS: *Barn owl*; *nest boxes*; Strix aluco; *tawny owl*; Tyto alba.

Valor de cajas anideras para estudios poblacionales y la conservación de búhos en bosque de coníferas en Bretaña

RESUMEN.—Se estudió la respuesta de búhos, que nidifican en cavidades "naturales," en relación a cajas anideras ubicadas en plantaciones de coníferas al nor-este de Inglaterra y al suroeste de Escocia. En ambas áreas de estudio *Microtus agrestis* fue la principal categoría alimentaria de los búhos. *Microtus agrestis* fue abundante en áreas desforestadas y reforestadas hasta 15 años despues de su plantación. Cuarenta territorios de *Strix aluco* se localizaron en un sitio de estudio hasta 1979. Todas las parejas se reprodujeron en sitios naturales. En el primer año (1980) en el que se dispuso de cajas anideras, el 83% de la población se reprodujo en ellas y el 100% al cuarto año. Subsecuentemente, el número de territorios ocupados se incrementó a 66 en el año 1990, lo que fue atribuido a un mejoramiento en el suplemento alimentario el que a su vez fue resultado del talaje del área. En otro bosque, la población de *Tyto alba* declinó a medida que los edificios abandonados no estuvieron disponibles debido a su destrucción y renovación. La provisión de barriles de nidificación, inicialmente ubicados en terrenos de cultivo adyacente, llevaron a un rápido incremento en las poblaciones reproductivas. Así, las cajas (barriles) fueron un elemento esencial en la conservación de *T. alba* en bosques de coníferas. En contraste a *S. aluco,* individuos de *T. alba* residentes no nidificaron en los barriles. De esta manera, en los inicios del estudio los resultados de reproducción pueden haber estado errados por una falta de experiencia reproductiva en la mayoría de la población. El desarrollo de una población con estructura de edad toma varios años.

[Traducción de Ivan Lazo]

Humans have had a dramatic effect on British forests. Initially this was through deforestation resulting in less than 5% of Britain being forested by 1900. Over the last 75 yr the amount of forest has increased to about 10%, mainly by planting large coniferous forests in upland regions (Petty and Avery 1990). Such major habitat changes combined with a reduction in persecution have greatly influenced raptor populations (Newton 1972, 1979, Petty 1988, Petty and Avery 1990).

In this paper we report on studies of tawny owl (*Strix aluco*) and barn owl (*Tyto alba*) in coniferous forests where we have investigated the owls' use of nest boxes. These are the only species of owl to regularly breed in cavities in upland Britain (Petty 1988). The barn owl breeds in large cavities in trees, cliffs, and buildings. The tawny owl is more adaptable, being able to use the abandoned stick nests of ubiquitous species such as carrion/hooded crow (*Corvus corone*) and red and gray squirrels (*Sciurus vulgaris* and *S. carolinensis*) (Cramp 1985). When stick or cavity sites are lacking it can also breed on the ground, typically against the buttress of a tree (Petty 1992a).

Newton (1979) stated that "in any landscape, an upper limit to the number of established raptor pairs is set by food or nest sites, whichever is in shortest supply." These two factors are likely to be the most important for the owls considered in this paper, although we accept that additional factors may also be involved in limiting raptor populations elsewhere.

STUDY AREAS AND METHODS

Study Areas. Tawny owls were studied in 180 km^2 in the center of Kielder Forest District in northeast England (55°15'N, 2°35'W; Petty 1992a). Prior to afforestation the area was used extensively for sheep grazing. Planting started in 1933 and was largely completed by 1980. Clear-cutting and replanting commenced in 1968 and has been designed to alter spatial patterns within the forest. This is being achieved by shortening and advancing optimum rotation lengths for timber production of 45–55 yr, and felling areas much smaller than the original plantings to create a fine-grained patchwork of different aged trees. Sitka spruce (*Picea sitchensis*) comprised 75% of the forest area, Norway spruce (*P. abies*) 14% and the rest mainly pines and larches.

Barn owls were studied in 490 km^2 of Newton Stewart Forest District in southwest Scotland (55°00'N, 4°30'W). Before afforestation most of the area was rough grassland, used for sheep grazing. The forest now covers 350 km^2 with farmland and ungrazed montane habitat comprising the rest. The bulk of the planting, which began in 1934, was carried out in the 1950s and 1960s and was largely complete by the 1980s. The main tree species planted was Sitka spruce (>80%). Clear-cutting and replanting began in 1980, and follows a forest design plan with the same aims as Kielder Forest.

Location of Territories. Occupied tawny owl territories were first located during 1975–78 from pellet/roost stations, nest sites, fledged broods and molted feathers. Erection of nest boxes started in the winter of 1979/80 and subsequently most of the breeding females were caught each time they bred, and, since 1988, most of the males. Over the years it was possible to determine groups of nest boxes and natural nest sites used by individually known adults. For present purposes each group was considered to form one nesting territory.

Barn owl pairs were located by searching all potential nest sites. Since there were no large cavity-bearing trees in the forest, methods consisted of searching buildings, whether occupied or abandoned. Sightings of birds in the vicinity of a few suitable cliffs were followed up by searching for nests. Searches were carried out in 1970–72 and from 1977 onward, but it was possible to identify nest sites used in earlier years from the accumulation of decayed pellet debris in nest spaces within buildings. Beginning in 1987 most breeding females were trapped each time they bred; a smaller number of males were trapped each year. Many trapped birds were of known age, having been banded as chicks at adjacent farmland nest sites.

Unbanded barn owls were aged by the pattern of feather molt (Cramp 1985, Taylor 1993) as one-year-old (born in the previous year), two-year-old, or older. Tawny owls that were not banded as nestlings were aged by the molt pattern of juvenile regimes and placed into the same age categories as barn owls but with three-year-old as an additional class (Petty 1992a, 1992b).

Occupancy of Territories. Prior to egg laying, each pair of tawny owls would visit several nest sites in their territory. Signs from these visits included traces of down or small body feathers adhering to the entrance hole. These signs occurred up to 1 mo before the eggs were laid. Closer to laying, a deep scrape was formed in the debris at the bottom of the chosen site, usually with down and small body feathers around the edge. In years when pairs did not produce eggs they still went through this process (Petty 1989, 1992a). Nesting territories were classified as occupied when a fresh scrape, with down and/or small body feathers were found in at least one nest site in March–April. Territories were regarded as unoccupied when no signs of owls were found at any nest sites during this period. Tawny owls did not roost in nest sites during the winter (Petty 1992a), so any signs present related to breeding behavior.

Barn owl nest sites showing no fresh signs of owls after 1 April were counted as unoccupied. We had no instances of winter breeding in our study, but in good vole years pairs would sometimes breed into the late summer and early autumn. Buildings were sparsely distributed within the forest at 2–4 km intervals, and most pairs had only one potential nest site. Birds roosted in buildings throughout the year. In spring, occupation was confirmed by flushing the birds, or by the presence of fresh feces, pellets and downy feathers within buildings. Barn owls using tree-mounted nest boxes rarely roosted in them, but visited boxes frequently from mid-winter onward. Occupied boxes had fresh feces and pellets below one or more perches adjacent to the nest box. Prior to egg laying, the female began to roost inside the box and occupancy was confirmed by an accumulation of pellets and small feathers within. Non-laying pairs also conformed to this pattern, particularly during courtship.

Nest Boxes. Tawny owl nest boxes were made from 25-mm-thick, rough-sawn softwood timber, except for the tops which were made from 9-mm-thick exterior grade

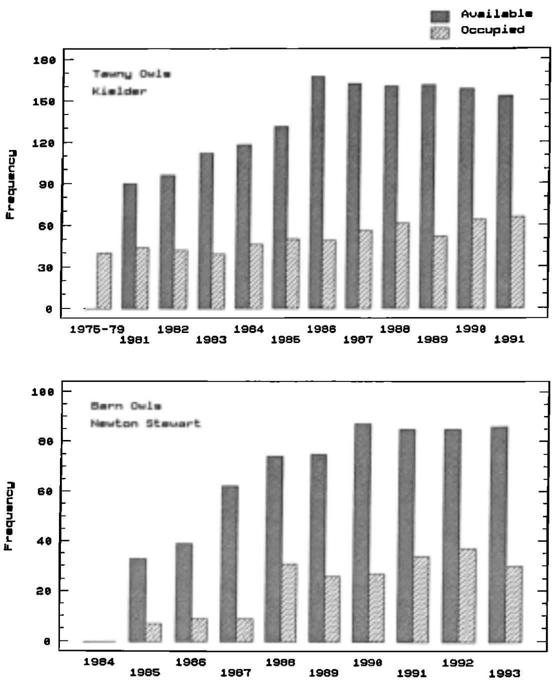

Figure 1. Number of nest boxes available and occupied by tawny owls in Kielder and barn owls in Newton Stewart. Nest boxes were available from 1980 in Kielder and 1985 in Newton Stewart. During 1975–79, tawny owls used natural nest sites; 1980 is excluded because nest boxes were available in only part of the study area. In Kielder, the years 1983, 1986 and 1989 were low vole years.

plywood (Petty 1987a, 1992a). Box exteriors were treated with brown wood preservative. The exterior measurements (mm) were 280 (width of front and back) × 250 (width of sides) × 560 (height), with a square entrance (140 × 150) at the top of the box front. The internal basal area was 340 cm^2. Inside each box a 100–150 mm layer of dry conifer needles was provided to allow the bird to form a scrape for its eggs. This layer was replaced with new litter after the chicks had fledged. Boxes were fixed to trees at heights of 1.6–5.2 m (but mainly at 3.0–3.5 m) measured from the ground to the base of the box. Boxes were situated to allow the owls a clear flight path into the box and spaced so that one box was available near the center of each of the 40 territories identified during 1975–78, with an additional box between territories and in areas that lacked owls but appeared suitable. This initial placement of boxes resulted in approximately 400 m between boxes along valley systems where the original territories were located. The number of boxes available each year varied because some were moved as areas were clear-felled.

We used three designs of nest boxes for barn owl (Shaw and Dowell 1990). (1) Triangular wooden boxes with

Table 1. Natural and man-made nest sites used by tawny owls in or near to the Kielder study area during 1975–90 and barn owls in the Newton Stewart area during 1975–93.

NEST SITE	TAWNY OWL FREQUENCY (%)	BARN OWL FREQUENCY (%)
Tree hole, enclosed	13 (22.8)	0 (0.0)
Tree hole, open	6 (10.5)	0 (0.0)
Tree crotch, open	3 (5.3)	0 (0.0)
Crow nest	5 (8.8)	0 (0.0)
Goshawk nest	2 (3.5)	0 (0.0)
Cliff ledge	5 (8.8)	0 (0.0)
Ground[a]	10 (17.5)	0 (0.0)
Building (inside)	8 (14.0)	102 (100.0)
Haystack	4 (7.0)	0 (0.0)
Deer high seat[b]	1 (1.8)	0 (0.0)
Total	57 (100.0)	102 (100.0)

[a] All sites were at the base of a tree.
[b] Elevated platform from which deer are shot.

equal sides of 900 mm and a depth of 320 mm were made of rough-sawn boards 25 mm thick and coated with a wood preservative. An entrance hole (100 × 100 mm) was situated below the frontal apex. (2) Eighty-liter heavy-duty plastic drums, 620 mm high and with an internal diameter of 420 mm, with wooden landing-boards bolted on. The drums were mounted vertically, with a square entrance hole (100 × 100 mm) near the top. (3) The same as design (2) but mounted horizontally with the entrance hole at one end.

To avoid possible competition for nest sites between barn owls and earlier breeding tawny owls, two nest boxes were erected at most sites, 30–80 m apart. A layer of conifer needles or chain saw chips 50–120 mm deep, was provided to facilitate nest scrapes. This layer was renewed annually after successful breeding. The boxes were fixed to trees, 4–6 m high (from ground to box base), situated to allow a clear flight line to the entrance, and were placed adjacent to areas providing good habitat for field voles such as young plantations, rough grasslands and firebreaks. Thirty-three nest box sites were established for barn owls in the winter 1984–85; these were increased to 87 by the end of 1989, after which the number remained constant (Fig. 1).

An important point is that there were far more boxes available each year in both study areas than there were pairs of owls (Fig. 1), ensuring that any increase in the breeding population was quickly detected. All known natural nest sites in both study areas were also checked annually.

Food Supply. Pellet analysis and the identification of prey cached in the nest were used to quantify the main foods of tawny and barn owls (Petty 1987b, 1992a, Shaw unpublished data). In both study areas the main prey of

Table 2. Use of various nest structures (%) by tawny owls in Kielder (1979–84), showing the response of owls to the provision of nest boxes first available for the 1980 breeding season.

NEST SITE	YEAR					
	1979	1980	1981	1982	1983	1984
Nest box	0 (0.0)	15 (83.3)	36 (87.8)	31 (91.2)	10 (100.0)	43 (100.0)
Tree hole, covered	1 (12.5)	2 (11.1)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Tree hole, open	2 (25.0)	0 (0.0)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Tree crotch, open	1 (12.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Crow nest	0 (0.0)	0 (0.0)	1 (2.4)	0 (0.0)	0 (0.0)	0 (0.0)
Crag ledge	1 (12.5)	0 (0.0)	1 (2.4)	0 (0.0)	0 (0.0)	0 (0.0)
Ground	2 (25.0)	1 (5.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Deer high seat	1 (12.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Barn	0 (0.0)	0 (0.0)	1 (2.4)	1 (2.9)	0 (0.0)	0 (0.0)
Total	8 (100.0)	18 (100.0)	41 (99.8)	34 (99.9)	10 (100.0)	43 (100.0)

both owl species was the field vole (*Microtus agrestis*). This rodent feeds largely on grasses, and is most abundant in ungrazed (by domestic animals) grassy habitats such as young conifer plantations (Hansson 1971, Charles 1981, Corbet and Harris 1991). The main grassy habitat within both of our study areas was newly afforested/replanted sites which remained suitable for voles for 12–15 yr after planting.

In Kielder, snap-trapping and vole-sign indices were used to investigate both spatial and temporal changes in vole abundance during 1981–91 (Petty 1992a, Petty and Peace 1993). Populations exhibited a pronounced 3-yr cycle of abundance. Springs with increasing vole abundance occurred in 1981, 1984, 1987, and 1990. Similar trends in vole abundance were observed but not quantified in the barn owl study area until 1989 when vole sign indices were used.

RESULTS

Nest Sites Other Than Nest Boxes. Information on the type of natural and other nest sites (excluding nest boxes) used by tawny owls came from 57 nests located in or near to the Kielder study area during 1975–90 (Table 1). Tree cavities of various types comprised 38.6%, crag and ground nests 26.3%, unused stick nests of other species 12.3%, and man-made structures other than nest boxes 22.8%. These data were probably biased toward the most easily found nests. Crow nests and ground sites used by tawny owls were particularly difficult to locate.

Prior to the erection of nest boxes, barn owls bred exclusively in buildings (Table 1) except for two cliff sites which were used on one and two occasions, respectively, prior to 1975. Twenty-one buildings were confirmed as breeding sites from 1970, but most (62%) of these had been lost, either through dereliction (38%) or renovation (24%), and by 1985 only eight remained suitable for barn owls (Shaw and Dowell 1990, Taylor et al. 1992).

Use of Nest Boxes. Boxes for tawny owls were erected for the first time during the winter of 1979–80. In the first year (1980) with boxes available, 83% of the nesting attempts were in boxes, and by 1983 all natural sites in the study area had been abandoned (Table 2). Subsequently (1984–91), only one clutch out of 317 was not laid in a nest box.

Barn owl use of boxes increased from 0–37 pairs during 1985–93 (Fig. 1). A major increase occurred in the 1988 breeding season, following a year when vole populations were increasing. Over the same period the number of nest sites in buildings remained stable at five to six. No suitable buildings were abandoned as breeding sites.

Sector of the Owl Populations Using Nest Boxes. *Tawny owls.* Some females were trapped at natural nest sites to investigate individual responses to nest boxes. Two were caught at ground nests in 1979 and banded. Nest boxes were erected in both territories in November to December 1979. One female switched to breeding in a box in 1980 and for each breeding attempt up to 1991, while the other bred on the ground in 1980 but changed to a box in 1981 and for each breeding attempt up to 1985, after which she died.

Another female was caught at a cliff-ledge site in 1981, probably the one that bred there in 1980, even though a box was available from January 1980. She bred in the box for the first time in 1982 and subsequently up to 1985, after which she died. Other

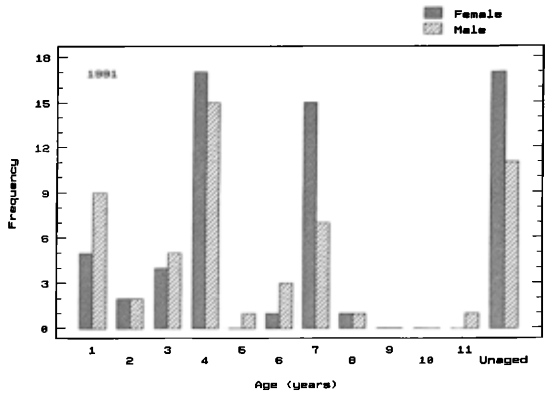

Figure 2. Age structure of breeding male and female tawny owls in Kielder in 1991. One-, four- and seven-yr-old owls were reared in years when vole populations were increasing (see text). The unaged category includes owls caught prior to 1985 before an age determination technique was available, and a few birds caught after 1985 that were too old to be accurately aged (Petty 1992a, Petty 1992b).

females (1986–91) never used the cliff sites, even though at least three ledges on two separate cliffs had been used in the past.

In another territory with two tree holes and a box erected in November 1979, the female bred in the tree hole in 1979 and 1980. In 1981 she used one tree hole followed by the box and then the other tree hole in three nesting attempts, the first two having failed during egg laying. In 1982 she first bred in the box but deserted during incubation and subsequently reared chicks from one of the tree holes. Subsequently, all breeding attempts by this female and her territorial replacement were in nest boxes even though one of the tree holes was still available in 1991. Thus, the switch to breeding in boxes by tawny owls was achieved by established pairs changing from natural sites.

The age structure of the breeding population exhibited pronounced annual variation, dependent on a pulse of recruitment associated with high productivity and survival of chicks reared in years when vole abundance was increasing (Fig. 2; Petty 1992a). For instance, of the adults that were of a known age in 1991, 82% (N = 45) of females and 70% (N = 44) of males were from cohorts reared in years when vole abundance was increasing.

Barn owls. Initially, few were trapped at nest boxes (<5), but from 1988 the sample was sufficient to estimate the age structure of the breeding population of females (Table 3). The large increase in occupied nest boxes in 1988 was entirely due to the recruitment of yearling females (81% of breeders). Fewer male owls were trapped, but at 10 newly occupied nest boxes all males were yearlings. The natal origin was known for 18 out of 22 females and seven out of 10 males banded in the previous year as chicks in the local forest and surrounding farmland (Shaw and Dowell 1989). The older females in 1988 had bred in boxes in previous years. Therefore, there was no indication that adult owls already established in buildings switched to breed in nest boxes. This pattern was maintained during 1989–93, when recruitment into the nest box population came from first-time breeders (Table 3).

Because the expansion of the barn owl population breeding in boxes in 1988 was based primarily on a single pulse of recruitment, breeding experience

Table 3. Population age structure (%) of female barn owls breeding in nest boxes in Newton Stewart Forest District, south Scotland, 1988–93.

	YEAR											
AGE (YEARS)	1988		1989		1990		1991		1992		1993	
1	22	(81.5)	8	(40.0)	4	(21.1)	16	(51.6)	10	(47.6)	0	(0.0)
2	1	(3.7)	9	(45.0)	5	(26.3)	2	(6.5)	3	(14.3)	8	(42.1)
3	3	(11.1)	1	(5.0)	7	(36.8)	4	(12.9)	0	(0.0)	3	(15.8)
4	1	(3.7)	2	(10.0)	1	(5.3)	6	(19.4)	2	(9.5)	2	(10.5)
5	0	(0.0)	0	(0.0)	2	(10.5)	1	(3.2)	4	(19.0)	1	(5.3)
6	0	(0.0)	0	(0.0)	0	(0.0)	2	(6.5)	0	(0.0)	4	(21.1)
7	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)	2	(9.5)	1	(5.3)
Mean age (SE)	1.37 (0.16)		1.85 (0.21)		2.58 (0.28)		2.35 (0.30)		2.76 (0.47)		3.63 (0.41)	
Total	27	(100.0)	20	(100.0)	19	(100.0)	31	(100.0)	21	(99.9)	19	(100.0)

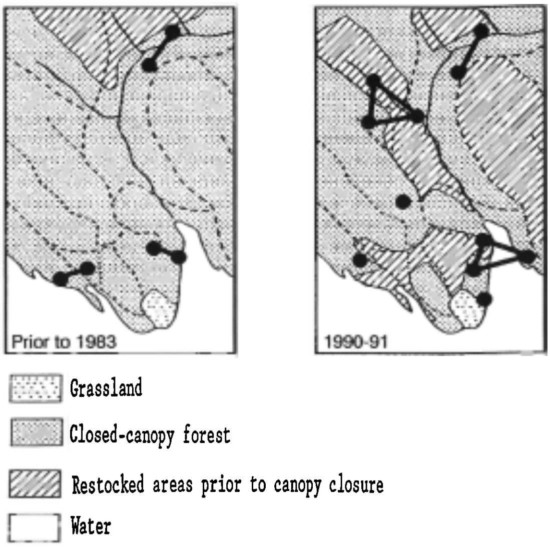

Figure 3. The Plashetts Burn area in Kielder prior to 1983 (left-hand) and in 1990–91 (right-hand). The black circles joined by solid lines show nest sites used by individual pairs of tawny owls. The area measures 2.5 × 1.5 km.

within the population was initially low. During 1988–93 the mean age and breeding experience of the female owls progressively increased (Table 3).

Influence of Nest Boxes on Owl Density. The annual number of occupied tawny owl territories increased from 40 prior to the erection of nest boxes to 66 in 1991 (Fig. 1). After the provision of nest boxes, this increasing density of tawny owls was related to greater spatial diversity of the habitat, and hence more edge habitat (Petty 1989). This can be demonstrated by comparing two areas of the same size (375 ha) in Kielder (Fig. 3, 4). Prior to 1983, both comprised mostly closed-canopy forest (20–50 yr of age), one area had three pairs of tawny owls and the other had two pairs. By 1990–91 much clear-cutting had broken up the first area and the number of pairs had increased to six (Fig. 3). In the second area, little change occurred during the same period and the number of pairs increased by only one, the additional pair having established near to the only new clear-cut in the area (Fig. 4).

Annual variation in the occupancy of tawny owl territories was also related to field vole abundance (Table 4). In low vole years occupancy averaged 81%, compared to 90–91% in increasing and decreasing vole years.

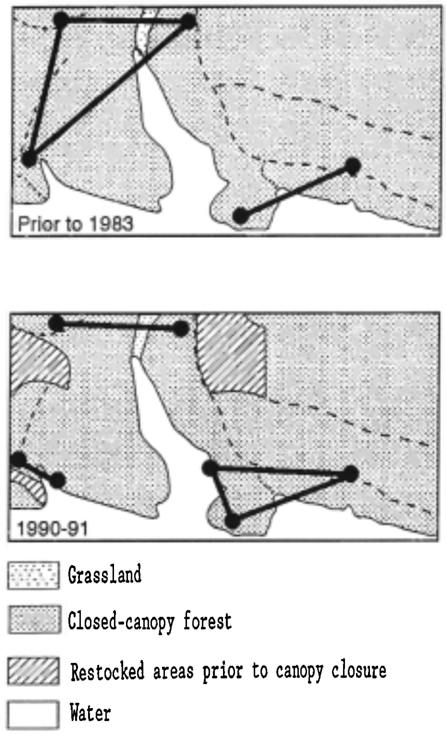

Figure 4. The Belling Burn area in Kielder prior to 1983 (upper) and in 1990–91 (lower). The black circles joined by solid lines show nest sites used by individual pairs of tawny owls. The area measures 1.5 × 2.5 km.

Barn owl numbers increased primarily due to the availability of nest boxes. Boxes were mainly situated on forest edges and planting breaks, where no major habitat changes were identified during the course of the study. The number of pairs breeding in buildings remained stable, while the pairs based in nest boxes increased from zero, allowing barn owls to exploit small mammal populations in areas where nest sites had previously been absent.

DISCUSSION

Tawny Owls. No work has been done with tawny owls to test experimentally whether nest boxes affect population density. In the present study we consider that boxes had little influence on the increasing owl density. The ultimate reason for the higher owl density was an improved food supply resulting from patchy clear-cutting, producing more vole-rich habitat. This was especially evident between parts of the study area where much clear-cutting occurred

Table 4. Occupancy of tawny owl territories in Kielder (1982–91) in relation to vole abundance.[a]

		TERRITORIES		
YEARS	VOLE ABUNDANCE	OCCUPIED (%)	UNOCCUPIED (%)	TOTAL
1983, 1986, 1989	Low	140 (80.5)	34 (19.5)	174
1984, 1987, 1990	Increasing	166 (90.2)	19 (9.8)	184
1982, 1985, 1988, 1991	Decreasing	219 (90.9)	22 (9.1)	241
All years		525 (87.6)	74 (12.4)	599

[a] A significantly higher proportion of territories were occupied in years when voles were increasing and decreasing than in low vole abundance years classes ($\chi^2 = 10.22$, df = 1, $P < 0.01$).

(Fig. 3) compared with other parts where there was much less (Fig. 4). It was unlikely that the tawny owl population was limited by the lack of nest sites prior to the study, because of the abundance of unused stick nests and potential ground sites. Southern (1970) was also confident that the provision of nest boxes in his study was not responsible for the number of territories increasing from 20–32 during the 10 yr when boxes were available. He attributed the increase to recovery from the severe winter of 1946–47.

In Kielder the whole population switched quickly from natural sites to nest boxes, which suggested that boxes were superior to sites previously used. If so, then tawny owls may be more productive when breeding in boxes. Unfortunately our data from natural sites are largely from earlier years before nest boxes were available; they are not directly comparable to the later data from nest boxes, but show surprisingly little difference in productivity (S.J. Petty unpublished data). However, if the population had still been breeding in natural sites and productivity was lower, the main effect would have been to slow the recorded population increase; the proximate factor most closely associated with increased density was recruitment, of which over 60% came from within the study area (Petty 1992a).

Southern (1970) gave details of the number of nest boxes and the number of pairs of tawny owls using them in his study. In 1950, 2.15 boxes/territory were available, and this had declined to 0.91 boxes/territory by 1959. Overall 55.6% of the nests were in boxes, with no increase in box use during the study. In the first 5 yr, 58.6% of nests were in boxes compared to 52% in the last 5 yr. The reluctance of just under half the population to use nest boxes may have been because the quality of tree holes was good compared to natural nest sites in Kielder.

In broad-leaved woodlands, nest boxes and tree holes are regularly used by both sexes of tawny owls in the winter for roosting. Tawny owls have been recorded roosting in boxes in Wytham Wood, the study area used by Southern (Hirons pers. comm.), in oak (*Quercus* spp.) forests in Belgium (Delmée et al. 1978) and in oak and beech (*Fagus sylvatica*) forests in France (Baudvin and Dessolin 1992). Delmée et al. (1978) also showed that in broad-leaved woodlands the male will often roost in a box near to the nest.

In contrast, tawny owls in coniferous forests do not roost in nest boxes outside the breeding season. If boxes had been used, traces of down and small body feathers would have been present around the entrance hole. P. Saurola (pers. comm.) also found that nest boxes were not used for roosting during the winter in Finland. In winter, coniferous forests may provide sheltered roosting places for tawny owls, whereas broad-leaved woodlands do not, apart from tree cavities or nest boxes. Boxes placed in pairs in a number of territories, in the hope of catching the male roosting in one during the breeding season, failed to attract males in Kielder. This technique had been used successfully by Delmée et al. (1978).

Barn Owls. Nest box provision for barn owls resulted in an increased breeding density. The breeding population expanded in one major pulse by recruiting large numbers of first-time breeders from one cohort (1987; Fig. 1 and Table 3). This initially resulted in a population with a skewed age distribution and a lack of breeding experience unlikely to be encountered in a long-established population. Taylor et al. (1992) reported that first-year females never exceed 40% of a natural barn owl population in the Esk Valley, south Scotland, during 1979–88. The nest box population in the present study resembled the "introduced population" of the model proposed by Taylor and Massheder (1992), where initial colonization was established by the release of a large number of yearling birds.

Many raptors produce fewer young in a first breeding attempt (Newton 1979). In situations where the provision of artificial nest sites has produced a sudden population increase, it should be recognized that the resultant population may initially show an unnatural age structure, and breeding performance may differ from that expected in an established population until a more balanced age structure is achieved through differential survival rates.

The responses of tawny and barn owl populations to nest box provision demonstrates that prior study combined with individual identification is necessary to determine what the effects are of adding nest boxes.

The Validity of Results from Nest Box Studies of Owls. Møller (1989, 1992) has suggested that nest boxes reduce the negative effects of nest predation and ectoparasitism, are often provided at unnaturally high densities, and differ in shape to natural tree cavities. He has argued that together these factors may alter the dynamics of a population compared to one using natural nest sites.

We consider that some of Møller's arguments can be misconstrued when considering cavity-nesting raptors (see also Koenig et al. 1992). Forestry activities, not only in Britain but throughout most of Europe, have had an enormous influence on the structure of woodlands, particularly by the removal of trees with large cavities. Even in seminatural woodlands, the size and frequency of potential nesting cavities are likely to be much reduced through human activities. This may limit breeding density, depending on a species response to alternative nest sites. In addition, when raptors are using natural cavities which vary greatly, it is often difficult to isolate the influence of nest site quality when investigating the effects of other environmental factors on reproduction. Nest boxes allow nest site quality and availability to be standardized therefore reducing the number of variables in such analyses.

Conservation Implications. Tawny owls are well suited to exploit small mammal populations in coniferous forests due to their ability to use a wide variety of nest types, so it is unlikely that nest boxes are essential to maintain breeding populations. In contrast, barn owls are likely to be limited by a lack of large nesting cavities.

Coniferous forests in upland Britain are relatively young, and although current forest policy stipulates that at least 5% of new plantings should be broadleaved trees, it will be many years before these produce cavities of a size suitable for barn owls. The broad-leaved trees are for conservation purposes and will not be clear-cut for timber production. So, in the long term they have the potential to provide cavities. Therefore, it is essential that tree species capable of producing large cavities are incorporated. Ash (*Fraxinus excelsior*) and common alder (*Alnus glutinosa*) are particularly valuable and well-suited to many upland sites (Low 1986). In the short term, nest boxes can be used to allow barn owls to exploit vole-rich habitats in the lower valleys of coniferous forests in Britain. As such they allow barn owls to extend their range and breeding density, providing there is a nearby source population to provide recruits.

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LITERATURE CITED

BAUDVIN, H. AND J-L. DESSOLIN. 1992. Analyse de la morphométric de la Chouettes Hulottes (*Strix aluco*) en Bourogone. *Alauda* 60:93–104.

CHARLES, W.N. 1981. Abundance of the field vole *Microtus agrestis* in conifer plantations. Pages 135–137 *in* F.T. Last [ED.], Forest and woodland ecology. Inst. Terrestrial Ecol., Cambridge, U.K.

CORBET, G.B. AND S. HARRIS. 1991. The handbook of British mammals. Blackwell Sci. Publ., Oxford, U.K.

CRAMP, S. [ED]. 1985. The birds of the western Palearctic, Vol. IV. Oxford Univ. Press, Oxford, U.K.

DELMÉE, E., P. DACHY AND P. SIMON. 1978. Quinze annees d'observations sur la reproduction d'une population forestiere de Chouettes Hulottes (*Strix aluco*). *Le Gerfaut* 68:590–650.

HANSSON, L. 1971. Habitat, food and population dynamics of the field vole *Microtus agrestis* (L) in south Sweden. *Viltrevy* 8:267–378.

KOENIG, W.D., P.A. GOWATY AND J.L. DICKINSON. 1992. Boxes, barns and bridges: confounding factors or exceptional opportunities in ecological studies? *Oikos* 63. 305–308.

LOW, A.J. 1986. Use of broadleaved species in upland forests: selection and establishment for environmental improvement. Forestry Comm. Leaflet 88. Her Majesty's Stationery Office, London, U.K.

MØLLER, A.P. 1989. Parasites, predators and nest boxes: facts and artefacts in nest box studies of birds? *Oikos* 56:421–423.

———. 1992. Nest boxes and the scientific rigour of experimental studies. *Oikos* 63:309–311.

NEWTON, I. 1972. Birds of prey in Scotland: some conservation problems. *Scot. Birds* 7:5–23.

———. 1979. Population ecology of raptors. T. and A.D. Poyser, Berkhamsted, U.K.

PETTY, S.J. 1987a. The design and use of a nestbox for tawny owls *Strix aluco* in upland forests. *Q. J. For.* 81: 103–109.

———. 1987b. Breeding of tawny owls *Strix aluco* in relation to their food supply in an upland forest. Pages 167–179 *in* D.J. Hill [ED.], Breeding and management in birds of prey. Univ. Bristol, Bristol, U.K.

———. 1988. The management of raptors in upland forests. Pages 7–23 *in* D.C. Jardine [ED.], Wildlife management in forests. Inst. Chartered Foresters, Edinburgh, U.K.

———. 1989. Productivity and density of tawny owls *Strix aluco* in relation to the structure of a British spruce forest. *Ann. Zool. Fenn.* 26:227–233.

———. 1992a. Ecology of the tawny owl *Strix aluco* in the spruce forests of Northumberland and Argyll. Ph.D. dissertation, The Open Univ., Milton Keynes, U.K.

———. 1992b. A guide to age determination of tawny owl *Strix aluco.* Pages 89–91 *in* C.A. Galbraith, I.R. Taylor and S. Percival [EDS.], The ecology and conservation of European owls. Joint Nature Conservation Committee, Peterborough, U.K.

——— AND M.I. AVERY. 1990. Forest bird communities. Forestry Comm. Occas. Paper 26. Forestry Comm , Edinburgh, U.K.

——— AND A.J. PEACE. 1993. Temporal and spatial fluctuations in field vole abundance in predator/prey study. Rep. on Forest Research 1992, 40–42. Her Majesty's Stationery Office, London, U.K.

SHAW, G. AND A. DOWELL. 1989. Breeding by closely related barn owls. *Ringing & Migr.* 10:98.

——— AND ———. 1990. Barn owl conservation in forests. Forestry Comm. Bull. 90. Her Majesty's Stationery Office, London, U.K.

SOUTHERN, H.N. 1970. The natural control of a population of tawny owls (*Stric aluco*). *J. Zool. (Lond)* 162:197–285.

TAYLOR, I.R. 1993. Age and sex determination of barn owls *Tyto alba. Ringing & Migr.* 14:94–102.

———, A. DOWELL AND G. SHAW. 1992. The population ecology and conservation of barn owls *Tyto alba* in coniferous plantations. Pages 16–21 *in* C.A. Galbraith, I.R. Taylor and S. Percival [EDS.], The ecology and conservation of European owls. Joint Nature Conservation Committee, Peterborough, U.K.

——— AND J. MASSHEDER. 1992. The dynamics of depleted and introduced farmland barn owl *Tyto alba* populations: a modelling approach. Pages 105–110 *in* C.A. Galbraith, I.R. Taylor and S. Percival [EDS.], The ecology and conservation of European owls. Joint Nature Conservation Committee, Peterborough, U.K

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