Value of Nest Boxes for Population Studies and Conservation of Owls in Coniferous Forests in Britain

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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 afrorested 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.

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...

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 km² 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 km² 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 km² 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 upper limit to the number of established raptor pairs.

**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.

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.
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.

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.

<table>
<thead>
<tr>
<th>NEST SITE</th>
<th>TAWNY OWL FREQUENCY (%)</th>
<th>BARN OWL FREQUENCY (%)</th>
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<tbody>
<tr>
<td>Tree hole, enclosed</td>
<td>13 (22.8)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Tree hole, open</td>
<td>6 (10.5)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Tree crotch, open</td>
<td>3 (5.3)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Crow nest</td>
<td>5 (8.8)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Goshawk nest</td>
<td>2 (3.5)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Cliff ledge</td>
<td>5 (8.8)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Grounda</td>
<td>10 (17.5)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Building (inside)</td>
<td>8 (14.0)</td>
<td>102 (100.0)</td>
</tr>
<tr>
<td>Haystack</td>
<td>4 (7.0)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Deer high seatb</td>
<td>1 (1.8)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>Total</td>
<td>57 (100.0)</td>
<td>102 (100.0)</td>
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a All sites were at the base of a tree.
b Elevated platform from which deer are shot.

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...
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...
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


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<tbody>
<tr>
<td>1</td>
<td>22 (81.5)</td>
<td>8 (40.0)</td>
<td>4 (21.1)</td>
<td>16 (51.6)</td>
<td>10 (47.6)</td>
<td>0 (0.0)</td>
</tr>
<tr>
<td>2</td>
<td>1 (3.7)</td>
<td>9 (45.0)</td>
<td>5 (26.3)</td>
<td>2 (6.5)</td>
<td>3 (14.3)</td>
<td>8 (42.1)</td>
</tr>
<tr>
<td>3</td>
<td>3 (11.1)</td>
<td>1 (5.0)</td>
<td>7 (36.8)</td>
<td>4 (12.9)</td>
<td>0 (0.0)</td>
<td>3 (15.8)</td>
</tr>
<tr>
<td>4</td>
<td>1 (3.7)</td>
<td>2 (10.0)</td>
<td>1 (5.3)</td>
<td>6 (19.4)</td>
<td>2 (9.5)</td>
<td>2 (10.5)</td>
</tr>
<tr>
<td>5</td>
<td>0 (0.0)</td>
<td>0 (0.0)</td>
<td>2 (10.5)</td>
<td>1 (3.2)</td>
<td>4 (19.0)</td>
<td>1 (5.3)</td>
</tr>
<tr>
<td>6</td>
<td>0 (0.0)</td>
<td>0 (0.0)</td>
<td>0 (0.0)</td>
<td>2 (6.5)</td>
<td>0 (0.0)</td>
<td>4 (21.1)</td>
</tr>
<tr>
<td>7</td>
<td>0 (0.0)</td>
<td>0 (0.0)</td>
<td>0 (0.0)</td>
<td>0 (0.0)</td>
<td>2 (9.5)</td>
<td>1 (5.3)</td>
</tr>
<tr>
<td>Mean age (SE)</td>
<td>1.37 (0.16)</td>
<td>1.85 (0.21)</td>
<td>2.58 (0.28)</td>
<td>2.35 (0.30)</td>
<td>2.76 (0.47)</td>
<td>3.63 (0.41)</td>
</tr>
<tr>
<td>Total</td>
<td>27 (100.0)</td>
<td>20 (100.0)</td>
<td>19 (100.0)</td>
<td>31 (100.0)</td>
<td>21 (99.9)</td>
<td>19 (100.0)</td>
</tr>
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</table>
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.

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.

<table>
<thead>
<tr>
<th>Years</th>
<th>Vole Abundance</th>
<th>Occupied (%)</th>
<th>Unoccupied (%)</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983, 1986, 1989</td>
<td>Low</td>
<td>140 (80.5)</td>
<td>34 (19.5)</td>
<td>174</td>
</tr>
<tr>
<td>1984, 1987, 1990</td>
<td>Increasing</td>
<td>166 (90.2)</td>
<td>19 (9.8)</td>
<td>184</td>
</tr>
<tr>
<td>1982, 1985, 1988, 1991</td>
<td>Decreasing</td>
<td>219 (90.9)</td>
<td>22 (9.1)</td>
<td>241</td>
</tr>
<tr>
<td>All years</td>
<td></td>
<td>525 (87.6)</td>
<td>74 (12.4)</td>
<td>599</td>
</tr>
</tbody>
</table>

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

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 pro-
posed 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. Moller (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 Moller'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 broad-leaved 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.

ACKNOWLEDGMENTS

We are grateful to Forest Enterprise staff in Kielder and Newton Stewart Forest Districts for their cooperation over the years. We also thank Andy Dowell and Iain Taylor for their contribution to the barn owl study, Fred Gehlbach and two anonymous referees for helpful comments on the manuscript, and Diane Chadwick for word processing.

LITERATURE CITED


Received 3 December 1993; accepted 18 May 1994