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Productivity and density of tawny owls *Strix aluco* in relation to the structure of a spruce forest in Britain

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A population of tawny owls *Strix aluco* was monitored from 1981 until 1987 in approximately 90 km² of short-rotation spruce forest in northern England, where the owls fed largely on field voles *Microtus agrestis*. Vole populations showed a cyclic trend, with a peak every third year. This led to great annual variations in the number of young owls reared. The productivity of individual owl territories varied greatly over the 7 year period, but was not density-dependent. A multiple regression model incorporating 3 habitat categories explained 70% of this variability and emphasised the importance of habitat heterogeneity. The density of owl territories increased with the spatial diversity of the habitat.

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1. Introduction

In the last 60 years, large areas of the British uplands have been planted with exotic conifers; spruces *Picea* spp. have been increasingly used (Anon. 1984). Most crops are grown on short rotations and many of the earlier plantings are now being felled and replanted (restocked). A number of studies have looked at the effects of the afforestation of open ground on raptors (for reviews see Newton 1983, Ratcliffe & Petty 1986, Petty 1988) but little is known about how birds of prey react to restocking.

The tawny owl *Strix aluco* is a territorial, nocturnal predator of small mammals (Southern 1970, Cramp 1985), and it often colonises spruce forests by the end of the first rotation. Hirons (1985) studied the size of tawny owl territories in a spruce forest in south Scotland, and showed that they were larger than in mixed farmland and broadleaved woodland in southern England. He also noted a lack of data about the areas used by the owls for hunting, and about the distribution of their prey in conifer forests. Petty (1987a) showed that tawny owls in a spruce forest in northern England fed mainly on the field vole *Microtus agrestis,* and that newly restocked sites with their grassy vegetation provided a major vole habitat. The number of chicks produced annually from 47–50 pairs of owls ranged from 7 in a low vole year to 142 in a high vole year.

In addition to this annual variation in productivity, there is great variation between territories in the number of chicks produced. In this paper I investigate whether differences in the structure of a spruce forest can account for variations in the density and productivity of tawny owl territories over a 7 year period. Throughout this period the structure of the forest altered dramatically. An area of 1000 ha was felled and flooded for a reservoir, and each year large blocks of forest were felled and replanted.

2. Material and methods

2.1. Study area

The study area in Kielder Forest, northern England (55°N, 2°W), was part of a more extensive tract of forest which has been planted on the border between England and Scotland (Fig. 1). The study area measures about 90 km² and comprises largely plantations of Sitka spruce *Picea sitchensis* and Norway spruce *Picea abies* grown on rotations of 45–55 years. The forest was entirely man-made, afforestation having commenced in 1933, while clear felling and restocking with mainly Sitka spruce started in 1968. By 1987 there was an extensive patchwork of first and second generation tree crops, particularly at lower elevations. In 1981–1982, 1000 ha below 185 m elevation was flooded to form Kielder Water reservoir.

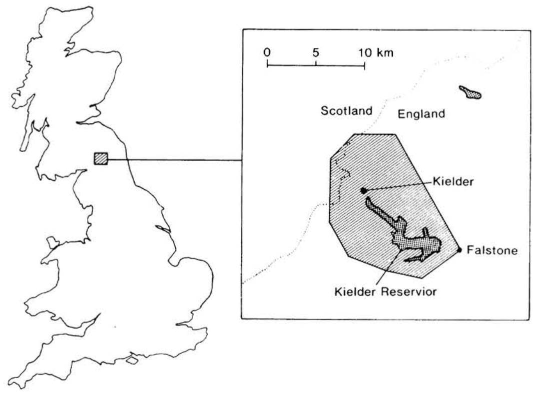

Fig. 1. The location of the study area in northern England.

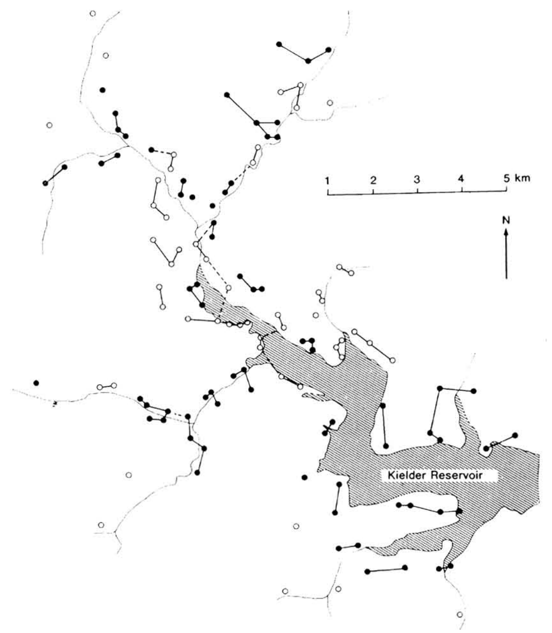

Fig. 2. The location of 58 tawny owl nesting territories in Kielder Forest. Circles joined by a solid line show alternative nest sites in the same territory, circles joined by a broken line indicate where adjacent pairs sometimes use the same nest site. The filled circles show the 30 nesting territories used in the present analysis.

2.2. The tawny owl population

Most of the tawny owls bred in nestboxes, many of which had been erected prior to 1981, although some boxes were added in subsequent years (Petty 1987b). Between 80% and 100% of the females were caught each time they bred by netting them at the nest-site after the chicks became 5 days old. Many of the captured owls were of known identity, having been ringed in the past as breeding females or chicks. Over the years it was possible to determine groups of nestboxes and natural sites that had been used by individual females. There were 58 such "nesting territories", which were regularly spaced along all the major valleys in the study area (Fig. 2). In the present analysis, 30 of these nesting territories were selected, where the results of each breeding attempt during 1981–1987 were known (Fig. 2). Only once in these 210 territory-years was a territory unoccupied. The remaining 28 territories were excluded from this analysis as breeding data for some of the earlier years were not collected. There were no predators in the study area which could remove tawny owl chicks or eggs from nestboxes.

In the studies of Southern (1970) and Hirons (1985), the extent of the tawny owl territories was determined from the position of calling birds. I used a different method, based on the nearest neighbour distance between owl pairs (2.4), which was not an accurate measure of the areas used by owls but more an estimate of what was available.

2.3. The field vole population

In 1984–1987 a trapping method was used three times each year to determine fluctuations in the field vole poulation on one restocked site (Petty 1987a). A quicker method of estimating vole abundance was also developed which used vole signs (faeces and grass clippings). This method was then used in an additional 13 sites in the study area during 1984–1987 (Petty unpublished data). For the years 1981 to 1983, vole abundance was subjectively scored using vole signs on a scale of 1 (low) to 10 (high). These methods were adequate to classify each of the 7 years into years with high, declining or low vole populations.

2.4. Habitat classification and measurements

In each of the 30 owl territories, 13 habitat variates were measured (Table 1). The centre of each owl's nesting territory was fixed at the nest site when only one was used, or at the mid point between nests when more than one had been used. The nearest neighbour distance (NND) was the linear measurement to the centre of the nearest neighbouring owl's territory (Newton et al. 1977). The size of each nesting territory (ARA), was calculated from the area of a circle with a radius of half the NND. The different habitat categories within this circle were then measured to the nearest 0.5 ha from Forestry Commission Stock Maps (scale 1:10000); for some of the analysis these values were converted to proportions of the nesting territory area (ARA). Habitat edge (used in variates EDG and DIV) was the linear

Table 1. Habitat variate acronyms for measurements taken in 30 tawny owl territories. The areas (ha) of the last 8 variates are measured within ARA. (See Ratcliffe & Petty 1986 for definitions of the forest growth stages.)

Variate name	Description of habitat measurement
NND	Nearest neighbour distance (m) — see text.
ALT	Altitude (m.a.s.l.) at the centre of the nesting territory.
ARA	Area (ha) enclosed by a circle with a radius of NND/2 drawn from the centre of a nesting territory.
EDG	Total length (m) of habitat edges within ARA.
DIV	The length of habitat edges per ha (EDG/ ARA).
MAT	Area planted prior to 1935. Extended rotation broadleaf and conifer forest with well developed ground vegetation.
PFL	Area planted 1935–1949. Pre-felling conifer forest with little ground vegetation.
THK	Area planted 1950–1969. Thicket conifer forest with no ground vegetation.
PTK	Area planted 1970–1980. Pre-thicket conifers with dense ground vegetation.
EST	Area planted 1981–1985. Recently established conifers with developing ground vegetation.
GRZ	Area of grassland grazed by domestic stock.
UNG	Area of grassland ungrazed by domestic stock.
WAT	Area of water.

Fig. 3. Annual variation in the number of tawny owl chicks fledged from 30 territories in each of 7 years. High, declining and low refer to the state of the field vole population.

Table 2. Variation in tawny owl productivity in relation to field vole abundance. The difference between the mean number of chicks fledged in high compared to declining vole years is very highly significant ($t = 4.40$, $df = 148$, $P<0.001$).

Years	Field vole population	Number of chicks fledged per territory Mean±*SE* (*n*)
1981, 1984, 1987	High	2.58±0.16 (90)
1982, 1985	Declining	1.65±0.14 (60)
1983, 1986	Low	0.20±0.07 (60)

length of distinct ecotones between any of the last 8 habitat types in Table 1.

3. Results

3.1. Annual variation in the productivity of tawny owls

During the 7 year period, vole populations were "high" in 3 years (1981, 1984 and 1987), "declining" in 2 years (1982 and 1985), and "low" in 2 years (1983 and 1986) (Fig. 3). This cyclic trend in the owls' food supply peaked every third year and corresponded to significant differences in the number of chicks fledged (Table 2). In poor food years, a high proportion of the female owls failed to lay eggs, while in good food years as many as five chicks were occasionally produced by individual pairs (Petty 1987a).

3.2. Long-term variations in the productivity of individual tawny owl territories

One way of measuring the quality of individual tawny owl territories, is to look at the total number of chicks produced over a number of years. This overcomes short-term variations in chick production due to fluctuating food supplies (3.1). Over the 7 year period, the productivity of the 30 territories varied greatly, with the poorest fledging only 2 chicks and the best producing 16 (Fig. 4).

3.3. Relationship between habitat composition and tawny owl productivity

A summary of the habitat statistics is given in Table 3. Territories calculated from nearest neighbour distances were on average 70 ha, which were

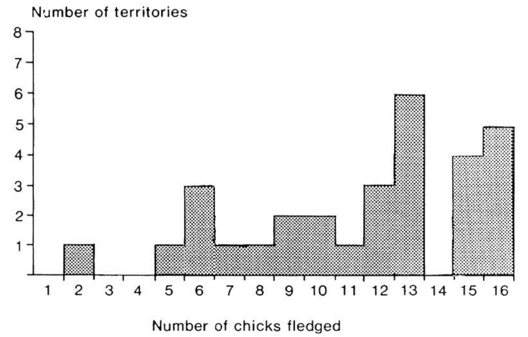

Fig. 4. Long-term variation in the total number of tawny owl chicks fledged from each of 30 territories over a 7 year period, the median was 12 chicks.

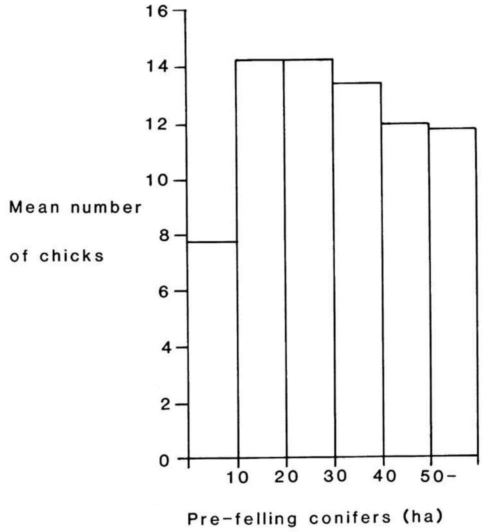

Fig. 5. Relationship between the mean number of chicks fledged from 30 territories over a 7 year period, and the area of pre-felling conifers (PFL) in an owls territory.

Table 3. Summary statistics for the habitat variates.

Variate	Mean		*SE*	Range
NND	0.89	m	0.06	0.32 - 1.58
ALT	220.67	m	5.07	190 - 320
ARA	69.87	ha	9.04	8 - 196
EDG	3054.67	m	256.47	780 - 6020
DIV	58.37	m	5.68	19 - 146
MAT	0.63	ha	0.26	0 - 5.5
PFL	23.43	ha	4.76	0 - 101
THK	19.95	ha	7.40	0 - 159
PTK	5.65	ha	1.75	0 - 43
EST	2.37	ha	0.93	0 - 25
GRZ	3.90	ha	1.23	0 - 32
UNG	4.37	ha	1.01	0 - 22
WAT	9.57	ha	3.00	0 - 64

larger than Hirons (1985) found in another spruce forest in south Scotland. The average territory comprised 63% closed canopy forest (MAT, PFL and THK), 11% early (open) forest growth stages (PTK and EST), 11% grassland (GRZ and UNG) and 14% water (WAT). Absolute and proportional habitat measures were initially used in the analysis, but as there was little difference between the two, all the reported analyses use absolute measures.

Analysis of the difference in tawny owl productivity could not be satisfactorily explained by any single habitat variable. The best of the individual habitat models, the linear regression of numbers of fledged owls upon area of water, was significant ($P<0.01$) but only explained 28% of the variation. A more complex model was required. The relationship between number of fledged chicks and the area of pre-felling conifer is curvilinear (Fig. 5), and suggests a possible optimal amount of pre-felling conifer (PFL) to be contained within each owls territory. Other habitat categories showed a similar curvilinear relationship with the number of chicks reared. If habitat heterogeneity it is an important factor in successful tawny owl reproduction, then one would have expected the fit of a bivariate linear regression model to be poor, as was the case, and a multiple regression model to be more appropriate. Square transformations of the habitat variables were added to the explanatory set of variables and a stepwise multiple regression analysis produced the following equation using three variables:

$$\text{Total chicks} = 8.44 - 0.00159\ \text{WAT} + 0.238\ \text{PFL} - 0.00253\ \text{PFL}^2 + 0.665\ \text{UNG} - 0.0386\ \text{UNG}^2$$

In this equation all three variables are statistically significant ($P<0.05$) and 70% of the variation is accounted for. The model can be interpreted as follows:

a) The numbers of fledged owls decrease with the amount of water in the territory.

Table 4. Spearman rank correlation coefficients showing the relationship between the number of young tawny owls fledged in high, declining and low vole years within each of 30 territories. (* = $P<0.05$).

	High	Declining	Low
High	1.00		
Declining	0.46*	1.00	
Low	–0.27	–0.15	1.00

Table 5. Sorted Spearman rank correlation coefficients showing the relationship between 12 habitat variates and the total number of young tawny owls fledged from 30 pairs during high, declining and low vole years (* = $P<0.05$).

All years		High		Declining		Low	
PFL	0.45*	PFL	0.39*	PFL	0.46*	MAT	0.43*
UNG	0.29	UNG	0.37*	EST	0.45*	DIV	0.36
PTK	0.27	PTK	0.37*	UNG	0.20	THK	0.18
EST	0.28	ALT	0.30	DIV	0.08	GRZ	–0.01
DIV	0.26	DIV	0.20	WAT	0.08	EST	–0.10
ALT	0.13	EDG	0.15	PTK	0.05	PTK	–0.13
EDG	0.03	EST	0.07	ALT	0.05	WAT	–0.13
NND	–0.15	GRZ	–0.04	EDG	0.01	UNG	–0.14
GRZ	–0.22	NND	–0.05	NND	–0.03	ALT	–0.17
WAT	–0.22	MAT	–0.09	THK	–0.27	PFL	–0.38*
MAT	–0.27	THK	–0.34	GRZ	–0.31	EDG	–0.41*
THK	–0.39	WAT	–0.35	MAT	–0.46*	NND	–0.46*

b) The number of fledged owls reared had a quadratic relationship with the amount of pre-felling conifer (Fig. 5).

c) The number of fledged owls had a quadratic relationship with the amount of ungrazed grasslånd, between 8–9 ha produced the most chicks.

The effect of food supply on owl productivity was also investigated by looking at the relationship between the number of chicks fledged within each territory for the high, declining and low vole years (Table 4). If certain territories contained an optimum habitat composition, or if certain owls were more prolific than others; then the better territories should have constantly produced more chicks compared to the poorer territories, independant of vole abundance. This was not the case (Table 4). The best territories for rearing chicks in high vole years were also among the most successful in declining vole years. But, in low vole years the most successful territories were uncorrelated with those of the high and declining vole years.

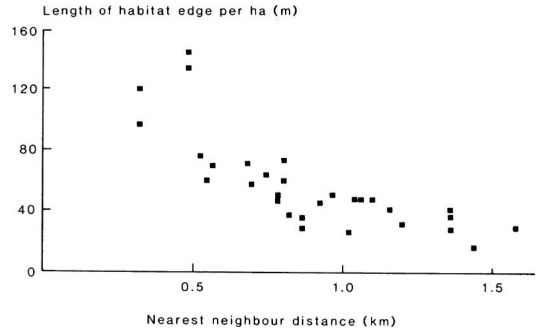

Fig. 6. Relationship between nearest neighbour distance and length of habitat edge per ha ($s = -0.840$, $df = 28$, $P<0.001$) in 30 tawny owl nesting territories.

The most successful territories in each of the three vole abundance classes exhibited significant differences in habitat composition (Table 5). In high and declining vole years the most successful territories contained relatively larger amounts of pre-felling conifer (PFL), ungrazed grassland (UNG) and prethicket conifers (PTK). In other words most chicks were produced from territories with some good vole habitat (UNG and PTK) opposed to poor vole habitat (THK). However, in low vole years these habitats were less important, as the most successful territories were closer together (NND), and with a spatially more diverse habitat (DIV).

3.4. Relationship between habitat composition and tawny owl density

A Spearman rank correlation matrix of the untransformed habitat data was used to try and explain variations in tawny owl density (NND). Variates which showed significant positive correlations with NND were; UNG, EDG and WAT; while MAT and DIV showed a significant negative correlation. DIV can be considered a measure of the spatial diversity of a territory, and had the highest correlation coefficient with NND (Fig. 6). Therefore, it was considered the most useful explanation of tawny owl density because all territories contained some DIV, unlike other significant variates such as MAT, UNG and WAT which had some zero values. It should be noted, however, that DIV is not totally independent of NND. Altitude, which is often related to the density of other raptors, for instance sparrowhawk *Accipiter nisus* (Newton

1979, Newton 1986a), appeared to have little effect on the spacing of tawny owls in this study. However, the lower altitude range had been truncated by the flooding of Kielder Water.

4. Discussion

There have been few studies which have quantified the effect of habitat composition on the density and productivity of any species of owl, although Newton et al. (1979) were the first to use a similar type of analysis for sparrowhawks. Southern (1970) showed in lowland broadleaved woodland, that the density of tawny owls and the number of young produced, were greater in closed canopy woodland. Here the owls fed largely on bank voles *Clethrionomys glareolus* and wood mice *Apodemus sylvaticus* which were both more abundant in woodland than in other habitats. Hirons (1985) showed a similar density effect in farmland, with the smallest tawny owl territories containing the most closed-canopy woodland.

The present study investigates what habitat characteristics are important for tawny owls in a conifer forest, where the main food throughout the year is field voles (Petty 1987a, Petty unpublished data). These rodents fed largely on grasses, and were most abundant in ungrazed (by domestic animals) grassy habitats such as young plantations and grassland. They are least common in heavily grazed areas or in closed canopy conifer forests with little ground vegetation (Hansson 1971, Corbet & Southern 1977, Charles 1981). Tawny owls also require trees for roosting and breeding. Martin (1986) showed that tawny owls' vision was similar to that of humans, and so the structure of the forest must be open enough to allow the birds good access below the tree canopy at night. It was important to consider these opposing habitat requirements of owls, on one hand for foraging while on the other hand for roosting/nesting.

Therefore, it was not surprising that no single habitat measurement explained a large proportion of the variation in the productivity of tawny owl territories. Many habitat categories showed a non-linear relationship with productivity. For instance, the effects of pre-felling plantations (PFL) increased to an optimum and then declined (Fig. 5). PFL crops provide tawny owls with roosting and nesting habitat but with little food, whereas UNG, EST and PTK provide the opposite. Therefore, it was reasonable to expect productivity to decline when too little or too much of either of these habitats were present, and it was not surprising that much of the variability in the productivity of territories was better explained by a curvilinear model incorporating a number of habitat variables.

The importance of different habitats for tawny owls changed in relation to the vole population levels. In years with high vole numbers, the best vole habitats showed the highest correlation with productivity, whereas in low vole years, habitat diversity appears to be more important, presumably because tawny owls were better able to find alternative food here. Songbirds, for instance, are more numerous in complex as opposed to structurally simple habitats (Newton 1986b, French et al. 1986), and frogs *Rana temporaria* would be available along wetland edges. Both birds and frogs are taken by tawny owls in spring and summer (Petty 1987a).

Over the 7 years, the spacing of owls (NND) was unrelated to the number of chicks produced (Table 4). This was true also in the 3 high and 2 declining vole years; but in the 2 low vole years, when a density-dependent effect might have been expected, the opposite occurred. The pairs closest together produced the most chicks. The spacing of owls (NND) was strongly associated with habitat diversity (DIV), which also suggested that it might be the presence of alternative food in these smaller but structurally richer territories, which were better able to maintain tawny owls when field voles were scarce.

The object of this analysis was twofold; to determine how the flooding of 1000 ha for Kielder Water and the felling and establishment of second generation forest, affected both the production and density of tawny owls. The creation of Kielder Water can be viewed as having a negative effect of productivity and also density (Table 5). It may also have resulted in the complete loss of some territories at the southeastern end of the reservoir. In contrast, restocking appeared to be beneficial particularly in good vole years, by providing foraging habitats which are surrounded by forest from which the owls can hunt. The density of tawny owls was related to the spatial diversity of the habitat. So management practices which provide more edges per unit of habitat, such as small opposed to large felled sites, are in the long-term likely to sustain a greater density of tawny owls.

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References

Anon. 1984: Census of woodlands and trees 1979–1982, Great Britain. — Forestry Commission, Edinburgh.

Charles, W. N. 1981: Abundance of the field vole Microtus agrestis in conifer plantations. — In: Last, F. T. (ed.), Forest and woodland ecology: 135–137. Institute of Terrestrial Ecology, Cambridge.

Corbet, G. B. & Southern, H. N. 1977: The handbook of British mammals. — Blackwell Scientific Publications, Oxford.

Cramp, S. (ed.) 1985: The birds of the Western Palearctic. Vol. IV. — Oxford University Press, Oxford.

French, D. D., Jenkins, D. & Conroy, J. W. H. 1986: Guidelines for managing woods in Aberdeenshire for songbirds. — In: Jenkins, D. (ed.), Trees and wildlife in the Scottish uplands: 129–143. Institute of Terrestrial Ecology, Huntingdon.

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

Hirons, G. J. M. 1985: The effects of territorial behaviour on the stability and dispersion of tawny owl (Strix aluco) populations. — J. Zool., London (B) 1:21–48.

Martin, G. R. 1986: Sensory capacity and the nocturnal habits of owls (Strigiformes). — Ibis 128:266–277.

Newton, I. 1979: Population ecology of raptors. — Poyser, Berkhamsted.

—"— 1983: Birds and forestry. — In: Harris, E. H. M. (ed.), Forestry and conservation: 21–30. Royal Forestry Society, Tring.

—"— 1986a: The sparrowhawk. — Poyser, Berkhamsted.

—"— 1986b: Principals underlying bird numbers in Scottish woodlands. — In: Jenkins, D. (ed.), Trees and wildlife in the Scottish uplands: 121–128. Institute of Terrestrial Ecology, Huntingdon.

Newton, I., Marquiss, M. & Moss, D. 1979: Habitat, female age, organochlorine compounds and breeding of European sparrowhawks. — J. Appl. Ecol. 16:777–793.

Newton, I., Marquiss, M., Weir, D. N. & Moss, D. 1977: Spacing of sparrowhawk nesting territories. — J. Anim. Ecol. 46:425–441.

Petty, S. J. 1987a: Breeding of tawny owls (Strix aluco) in relation to their food supply in an upland forest. — In: Hill, D. J. (ed.), Breeding and management in birds of prey: 167–179. University of Bristol, Bristol.

—"— 1987b: The design and use of a nestbox for tawny owls Strix aluco in upland forests. — Quart. J. Forestry 81: 103–109.

—"— 1988: The management of raptors in upland forests. — In: Jardine, D. C. (ed.), Wildlife management in forests: 7–23. Institute of Chartered Foresters, Edinburgh.

Ratcliffe, P. R. & Petty, S. J. 1986: The management of commercial forests for wildlife. — In: Jenkins, D. (ed.), Trees and wildlife in the Scottish uplands: 177–187. Institute of Terrestrial Ecology, Huntingdon.

Southern, H. N. 1970: The natural control of a population of tawny owls (Strix aluco). — J. Zool., London 162:197–285.

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