

Relationships between Foraging Range, Prey Density and Habitat Structure in the Tawny Owl *Strix aluco*

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ABSTRACT

1. We examined the ranging behaviour of Tawny Owls *Strix aluco* in relation to the structure of their foraging habitat, and spatio-temporal variations in the abundance and dispersion of field voles *Microtus agrestis*, their main prey. We plotted 15 home ranges of radio-tagged owls on a GIS coverage of Kielder Forest, northern England.
2. Males ($n = 7$) generally had larger ranges than females ($n = 4$). There was no significant difference between the range sizes of male owls in two valley systems.
3. Owl home ranges comprised a similar proportion of vole habitat. There was no relationship between home range size and vole density, although birds studied in consecutive years showed some range contraction as vole densities increased.
4. Home range size was not correlated with habitat structure. Larger home ranges contained more patches of clear-cut than smaller ones.
5. We discuss potential influences on home range size. Resource-sharing and heterogeneity of the habitat mosaic may explain why home range size was not strongly affected by prey density and habitat structure, respectively.

INTRODUCTION

Unlike nomadic raptors that specialise on microtine prey, such as European Kestrels *Falco tinnunculus* (Village 1982) and Short-eared Owls *Asio flammeus* (Village 1987), Tawny Owls *Strix aluco* are highly sedentary predators (e.g. Cramp 1985). In Kielder Forest, northern England, Tawny Owls feed largely on field voles *Microtus agrestis*, which exist in discrete populations, in isolated islands of grassy habitat created by clear-cutting (the felling of mature trees) (Petty 1987, 1992). Most authors assume that resident Tawny Owls carry out most of their activities within their territorial boundaries (e.g. Southern & Lowe 1968, Southern 1970, Galeotti 1994) and range exclusivity has been demonstrated by radio tracking for a population in fragmented farmland (Hardy 1992). However, in Kielder several territories may adjoin a clear-cut, so that these patches could represent shared resources, with implications for the pattern of range dispersion. Recent work showed that ranges of

territorial Tawny Owls, determined by radio-telemetry, in a broadleaved woodland overlapped, and differed from the area defended (Appleby 1995). Redpath (1995) also suggested this possibility.

Home range and territory sizes have been shown to vary with landscape characteristics (Southern 1970, Hardy 1992, Galeotti 1994; Carey & Peeler 1995, Redpath 1995) social characteristics (Galeotti, 1994) and food density and dispersion (Lockie 1955, Village 1982, 1987, Carey & Peeler 1995, Zabel *et al.* 1995), leading to the construction of optimal feeding-territory size models (e.g. Dill 1978, Schoener 1983).

Here we ask whether habitat characteristics of Tawny Owl home ranges, and population fluctuations of field voles in time and space, are related to home range size in the landscape mosaic of our study area.

STUDY AREA

The study area was in Kielder Forest, Northumberland, northern England (55°N, 2°W) an extensive man-made upland conifer forest (Figures 1 and 2). Kielder Forest measures 480 km² and was planted mainly with Sitka spruce (*Picea sitchensis*) and Norway spruce (*Picea abies*) grown on 40-60 year rotations. Broadleaved trees grew along many of the watercourses and there were some larger areas of deciduous trees, including alder (*Alnus glutinosa*) and birch (*Betula pubescens*).

In 1996 and 1997 the forest was comprised of a mosaic of tree stands of different species and ages. Extensive clear-cut patches which, once colonised by grasses (*Deschampsia* spp., *Molinia caerulea*) and rushes (*Juncus* spp.), provided ephemeral islands of habitat suitable for voles. Some other grassy areas, such as powerline wayleaves, deer glades and unplanted areas along watercourses, also provided suitable habitat for voles.

Figure 1. Location of the Kielder study area in Great Britain.



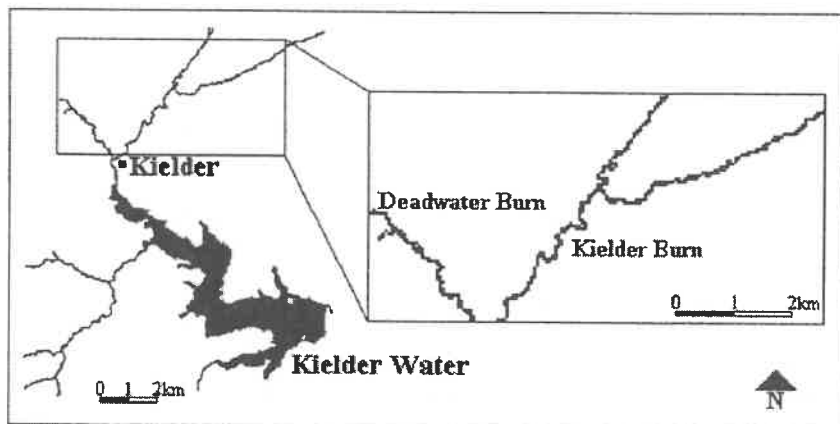
METHODS

In 1996 and 1997, we radio-tagged eight (four pairs), and seven (two pairs, two breeding males, one non-breeding male) adult Tawny Owls, respectively. All Tawny Owls in the study area bred in nest boxes. We caught males using nest-box traps (Petty 1992), except the non-breeding bird, which was caught in a small modified Chardonneret trap (Newton 1986). Brooding females were caught with a net.

Tawny Owl pairs, of which two were studied in both years, had territories in the Deadwater Burn valley system (Figure 2). Three male birds studied in 1997 had territories in the Kielder Burn valley system (Figure 2). Birds were radio-tracked from July (1996) and June (1997) until November (both years). Locations of females during the incubation and nestling periods were not included, but were during the fledging period.

A soft nylon harness was used to fix the transmitter to the back of the owls (Petty & Thirgood 1989). Radio tags (Biotrack Ltd) transmitted on 173.233-173.973 MHz and had a lifespan of approximately one year. The combined mass of the radio and harness was 7.3g. This represents 1.3%-1.9% of the mean mass of males and females, respectively. A TRX 1000S receiver (Wildlife Materials Inc.) with a hand-held three element Yagi antenna were used to find the position of radio-tagged birds.

Figure 2. The study area, represented by the rectangular box, included two valleys, the Deadwater and Kielder Burns.



Triangulation of signal bearings taken from at least two fixed points within a ten-minute period gave owl "fixes".

Analyses used harmonic mean home ranges, so that ranges were biased toward the centres of activity (Dixon & Chapman, 1980), calculated with Ranges V software (Kenward 1995). Home ranges were calculated from 18 to 35 (mean 24.4) fixes per bird. Utilisation plots on 15 individuals revealed that home range areas became asymptotic at about 20 fixes, on average. An isoline incorporating 95% of fixes was used to exclude occasional excursions outside the normal foraging range from area calculations. No more than one fix per night per bird was included, thus ensuring statistical independence. Minimum convex polygon (MCP) home range sizes were also calculated for comparison with other studies. MCP and harmonic mean home range sizes were compared using a paired samples T test.

Harmonic mean contours were overlaid on a Geographical Information System (GIS), based on a Forestry Commission database. We grouped the resulting habitat outputs into three categories: areas suitable for field voles, agricultural land and other land largely unsuitable for field voles, and

tree crops over 11 years old that were also unsuitable for field voles. "Patches" were defined as grassy clear-cuts up to 11 years after planting. These were often connected by corridors of the other types of habitat suitable for field voles.

Linear regression was used to examine the relationships between home range size and eleven variables (Table 1). Home ranges were averaged for each bird studied in both years. Data were normalised by log or arcsine (for percentages) transformation.

Variables that related to habitat structure were measured from GIS coverages. We assessed field vole abundance near Tawny Owl radiolocations using a vole sign index (VSI). This was based upon the presence or absence of fresh grass clippings in 25 quadrats thrown within a 0.25 ha area of suitable habitat (Petty 1992). Vole abundance indices were converted to densities using a formula derived from the regression of VSI scores on abundance data collected by live trapping (J.L. MacKinnon, unpublished data). There were 0-9 (mean 3.1) clear-cut patches per owl home range. In addition to these clear-cuts, VSI scores were also obtained for other habitats suitable for voles, such as streamsid es and powerline wayleaves.

Distances between occupied nestboxes in territories were used as an indication of breeding dispersal.

Differences between male and female owls, valley systems, and birds tagged in both years were analysed using the Mann-Whitney U test. A Spearman's Rank correlation matrix was constructed to examine relationships between variables. Spearman's Rank correlation coefficient was used to examine the relationship between the magnitude of temporal changes in range size and average vole densities. Data were analysed using Systat, Inc., Illinois (1993).

RESULTS

Radio telemetry

Recaptured individuals had no apparent injuries caused by tags and bred successfully in both years. One female was killed by a Goshawk *Accipiter gentilis*, the main natural predator of Tawny Owls in Kielder Forest, and one male, found dead next to a road, had probably been killed by a vehicle. In both cases, there were sufficient numbers of fixes to calculate their home ranges.

Increment plots on 15 individuals showed that, on average, ranges reached size asymptotes at about 20 fixes. Home ranges were constructed from 18-32 (mean 24) fixes. Harmonic mean ranges were generally smaller than MCP ranges (mean = 122.22 and 165.59, respectively; Tables 2 and 3), but this difference was not statistically significant (d.f. = 10, $t = 1.62$, $P = 0.136$).

Owls were rarely recorded crossing large open spaces, such as clear-cuts, and moved up and down stands of mature trees or along streamsid es. On several occasions, owls were seen flying across roads when moving between tree stands.

Table 1. Variables measured in home ranges. Vole habitat includes grassy clear-cuts as well as features such as deer glades, unplanted streamsid es and wayleaves. Hard edge refers to the boundary between vole habitat and tree crops, suitable for perching on by foraging owls.

Variable	Description
SEX	Sex of bird
PCVH	Percentage composed of field vole habitat
VPH	Number of field voles per hectare, calculated from sign indices using formulae derived from live trapping.
HEPH	Length of hard edges (suitable for perch-foraging) per hectare
APTPD	Average inter-patch (clear-cut) distance
ABTPD	Average box to patch (clear-cut) distance
NP	Number of patches (clear-cuts and adjoining grassy habitat)
APA	Average patch area (ha)
ANND	Average distance (m) to nearest occupied territories

Table 2. Harmonic mean home range sizes, in hectares, for males, females, two pairs studied in consecutive years, and two valley systems in 1997. All Kielder Burn birds were males. Home range sizes of birds studied in both years were averaged, except for year to year comparisons.

<i>Group</i>	<i>n</i>	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>	<i>Median</i>	<i>S.E.</i>
Male	7	17.75	396.56	166.72	113.76	52.98
Female	4	14.86	89.99	44.38	36.35	18.18
2 pairs, DW 1996	4	16.36	189.21	93.51	84.24	39.76
2 pairs, DW 1997	4	13.33	73.58	46.56	49.66	13.23
Deadwater (males)	4	17.75	134.59	90.02	103.87	25.48
Kielder Burn (males)	3	8	81.10	14.86	396.56	134.59
Deadwater (all birds)	269.06	67.20	329.53	73.68	95.93	16.86

Table 3. Minimum convex polygon home range sizes, in hectares, for 11 owls. Again, range sizes of birds tagged in consecutive years were averaged.

<i>Group</i>	<i>n</i>	<i>Minimum</i>	<i>Maximum</i>	<i>Mean</i>	<i>Median</i>	<i>S.E.</i>
Male	7	42.02	545.05	192.53	113.19	67.95
Female	4	16.34	272.53	128.45	112.46	57.00
All	11	16.34	545.05	169.23	113.19	47.04

Table 4. Changes in home range area and field vole density from 1996 to 1997 for two pairs of owls studied in consecutive years. Vole densities were extrapolated from indices based upon signs of vole feeding activity.

<i>Bird</i>	<i>Pair</i>	<i>Change in area, ha</i>	<i>Change in voles/ha</i>
Female 919/817	1	+32.3	+6.2
Male 279/562	1	-150.7	+3.3
Male 296/573	2	-66.4	+27.7
Female 909/829	2	-3.0	+21.6

Table 5. Densities of field voles per hectare in 11 Tawny Owl home ranges.

	<i>n</i>	<i>Maximum</i>	<i>Minimum</i>	<i>Mean</i>	<i>S.E.</i>	<i>Variance</i>
2 years	15	178.08	49.58	98.25	12.74	2434.93
1996	8	60.36	49.58	56.03	1.45	16.82
1997	7	178.08	118.07	146.57	9.01	567.71

Table 6. Correlations between variables of 11 home ranges. Few of the variables were inter-related.

	<i>PCVH</i>	<i>VPH</i>	<i>HEPH</i>	<i>ABTPD</i>	<i>APTPD</i>	<i>NP</i>	<i>APA</i>
VPH	—						
HEPH	—	—					
ABTPD	—	0.067*	—				
APTPD	—	0.005**	—	0.016*			
NP	—	—	—	0.026*	—		
APA	—	—	—	—	—	—	
ANND	—	—	—	—	—	—	—

(Spearman's rank test, significance of coefficients: * = $P < 0.05$, ** = $P < 0.01$, — = not significant.)

Figure 3. Harmonic mean 95% isoline home ranges for 8 owls in the Deadwater valley system in 1996. Numbers indicate radio frequencies.

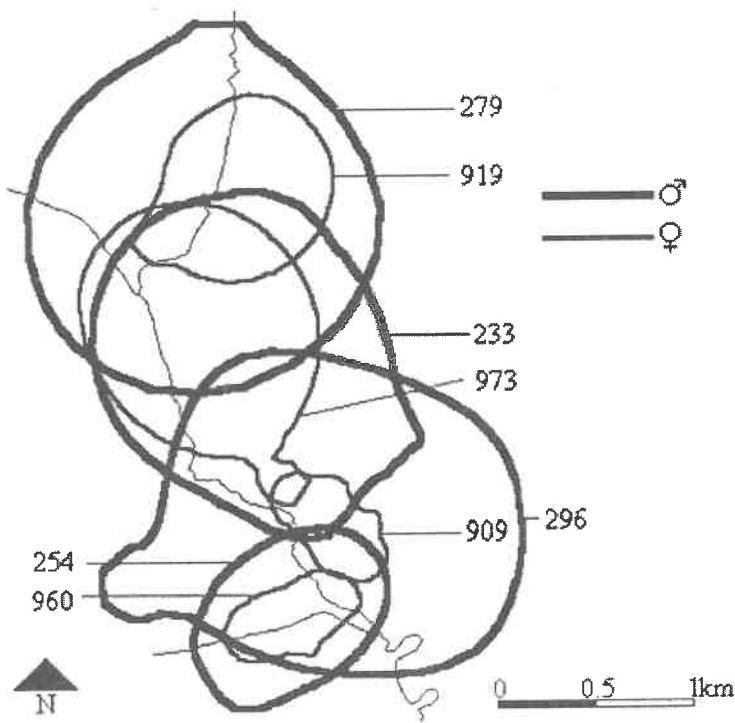


Figure 4. Harmonic mean 95% isoline home ranges for 7 owls in the Deadwater and Kielder Burn valleys in 1997. Again, isolines are represented by thicker lines. The two pairs in Deadwater (left) were also tagged in the previous year (table 4).

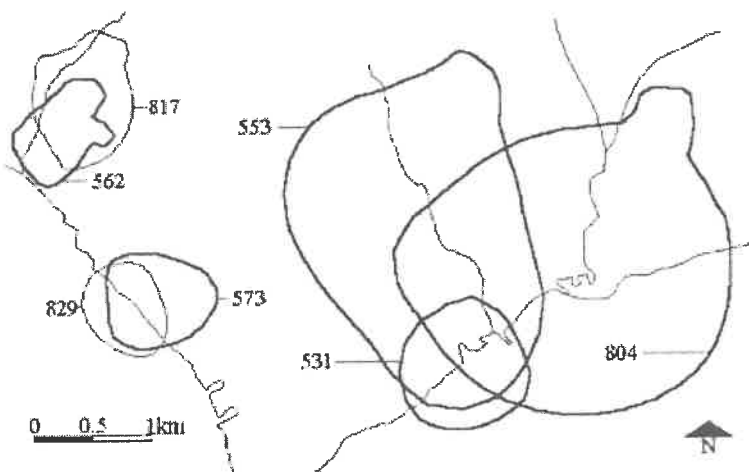


Figure 5 There was no relationship between home range area and the proportion of vole habitat within them ($n = 11$, $r = 0.021$, $P = 0.95$)

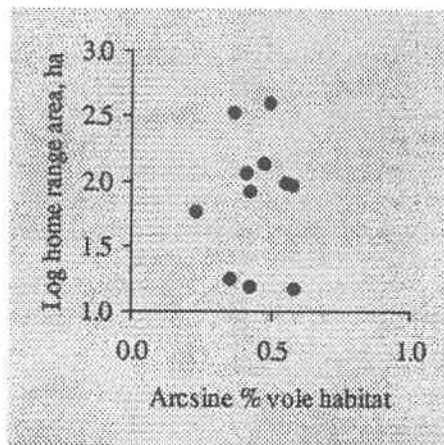
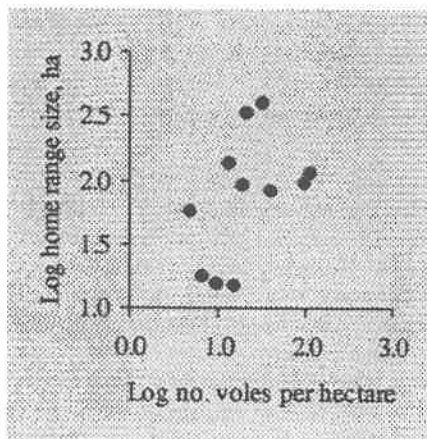


Figure 6. There was no statistically significant relationship between home range area and field vole density ($n=11$, $r = 0.468$, $P = 0.147$).



Sex and temporal differences

Generally, male owls had larger home ranges than females (d.f. = 7, 4, Mann-Whitney $U = 3$, $P = 0.05$, Table 2, Figures 3 and 4). Female home ranges overlapped less than those of males and male ranges included those of several females (Figure 3).

Comparing the home ranges of two pairs tagged in both years, all but one bird reduced its range size in 1997 (Table 4, Figures 3 and 4). However, this difference was not statistically significant (d.f. = 4, 4, Mann-Whitney $U = 5$, $P = 0.486$). There was no correlation between the change in range size and change in average vole densities (Spearman's rank coefficient $S = 0.200$, $P = 0.800$, $n = 4$), which increased in every home range studied in consecutive years (Tables 4 and 5).

In 1996, in all cases but one, female ranges were totally enclosed by those of their mates (Figure 3). The two largest and two smallest female ranges were grouped together at the northern and southern

ends of the Deadwater Burn, respectively. This was not the case in 1997, when male/female differences in range size and shape became less marked and inter-pair overlap decreased (Figures 3 and 4).

Spatial differences

The home ranges of male Tawny Owls were compared between the Deadwater Burn and the Kielder Burn. On average, male range sizes were larger in the Kielder Burn than in the Deadwater Burn but this relationship was not statistically significant (d.f. = 4,3, Mann-Whitney $U = 3$, $P = 0.400$, Figure 4).

Adding the generally smaller ranges of Deadwater Burn females to the comparison still failed to produce a statistically significant difference between range sizes in the two valley systems (d.f. = 8,3, Mann-Whitney $U = 4$, $P = 0.043$). There was no difference between the areas of clear-cut patches in the two valleys (d.f. = 11,18, Mann-Whitney $U = 37$, $P = 0.930$). Home ranges in the Deadwater and Kielder Burns showed a high degree of overlap (Figures 3 and 4). On one occasion all three males from the Kielder Burn were located foraging at the edge of the same clear-cut.

Relationship between variables and home range size

Of the nine variables, only NP ($n = 11$, $r = 0.659$, $P < 0.05$) and ABTPD ($n = 11$, $r = 0.826$, $P < 0.01$) were significantly correlated with home range size. Both correlations were positive. The number of voles per hectare and proportion of ranges comprised of habitat suitable for field voles did not vary significantly with home range size (Figs. 5 and 6).

Vole densities varied relatively little between home ranges in the same year and in 1997 were higher in each home range than in any of the ranges studied in 1996 (Table 5).

Correlation between numerical variables

Few of the variables were highly inter-related (Table 6), but those which were, precluded the use of multivariate models in the analysis.

DISCUSSION

Sex differences in home range size

The most striking result was the large size difference in home range size between sexes in 1996. Males appeared to respond more to increased prey densities than females, based upon their greater degree of range contraction in the increasing phase of the vole cycle. They also generally ranged over much larger areas than their mates. This difference was not so marked in 1997 when voles were more abundant. This suggested that males foraged more widely than females and are more sensitive to variation in prey densities. Females may have been more tied to the area in which breeding had just occurred, when there were dependent chicks within the territory during some of the tracking period. Female Tawny Owls are more predisposed to protect nestlings than males (Wallin 1987) and this defensive role may extend until after fledging, while they still have dependent juveniles.

Spatio-temporal differences

The inverse relationship between range size and prey abundance, consistent with previous studies (e.g. Village 1982, 1987, Zabel *et al.* 1995), over time but not in space suggests that this interaction was affected here by other factors. That all home ranges contained a similar proportion of habitat suitable for field voles may reflect uniform distribution of such patches throughout the area we studied. A comparison between areas (elsewhere in the forest) with and without Tawny Owl territories may show if owls are selecting areas similar to those in the study area. It is possible that owls require prey availability to equal or exceed a threshold for breeding and survival, and that in larger home ranges the extra area was associated with other factors. Not all habitat suitable for voles within a home range boundary would necessarily have been used for foraging.

Tawny Owls need older forest for roosting and breeding, and clear-cuts for feeding. Therefore, fine-grained (rather than coarse-grained) habitat mosaics are likely to hold a higher density of breeding

owls (Petty 1989). This may go a long way in explaining the lack of relationships between home range size and habitat variables.

Topography may explain differences in range size between the two valleys where, at any one time, vole densities were similar. Territories in Kielder Burn were generally at higher altitude than those in Deadwater, and had their centres at a greater distance from the main patches of habitat suitable for field voles, which were located in the valley bottoms. Immediately after the fledging period, the male 553 foraged along stream-sides of a Kielder Burn tributary near to the nesting area. It was then seen to switch its efforts to a more distant clear-cut, possibly after depleting the vole population on the smaller patch. Unfortunately, our prey index did not operate on a small enough temporal scale to detect such short-term changes.

Given that clear-cuts in the Kielder Burn were generally no larger than those in the Deadwater Burn, and that there was not a general relationship between home range and patch sizes, differences in range sizes between the valleys did not relate to the graininess of the habitat mosaics.

Up to three tagged males were found around the same clear-cut simultaneously, and it is likely that untagged individuals were also using the same area (pers. obs.). This pattern of resource sharing could invalidate the assumptions of feeding territory size models based upon animals foraging within exclusively defended areas (Dill 1978, Schoener 1983). In habitats with great spatial variation, it may be advantageous to share resources. Thus, defence costs were not a limiting factor in foraging range size as they only applied to territories. Territorial owls could sub-divide clear-cuts, so although the high degree of range overlap that we observed suggested that this was not the case, more information is needed before this possibility can be fully rejected.

Topographical constriction at the southern end of the Deadwater valley may have caused owls to encounter others more regularly. This situation leads to increased vocal behaviour, in contrast to birds which only rarely encounter conspecifics (Redpath 1995). Here, birds may allocate more time to territorial defence and range less widely than birds in more open country, thus causing the observed range constriction, which was not explained by nearest neighbour distance *per se*.

Accurate territorial mapping may have given further insight into the social factors in operation, particularly given that territories are not necessarily centred on the nestbox (Appleby 1995).

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