Dispersal Behavior and Survival of Juvenile Tawny Owls (*Strix aluco*) During the Low Point in a Vole Cycle

C.F. Coles and S.J. Petty[1]

Abstract.—In 1996 we investigated dispersal and survival of juvenile Tawny Owls (*Strix aluco*) by radio-tracking in Kielder Forest, Northumberland, a man-made conifer forest in northern England. Here, Tawny Owls fed largely on field voles (*Microtus agrestis*) which exhibited a 3-4 year cycle of abundance, with some spatial asynchrony. Generally, vole numbers were at the low point of the cycle in 1996. Twenty-two nestlings from 11 two-chick broods were radio-tagged when 22-31 (mean 26.3) days old. Birds fledged when 29-36 (mean 32.1) days old. Eight (36.4 percent) owls died 10-106 days after fledging and before dispersing from their natal territories. Five (22.7 percent) owls died outside their natal territories 40-147 days after fledging. Five (22.7 percent) owls disappeared suddenly at 8-51 days after fledging and before the end of the dependence period, and evidence suggested that they were predated. Contact was lost with four (18.2 percent) birds 58-178 days after fledging and after they had begun to disperse. Radio-tracking data are discussed in relation to movement patterns, food resources, and habitat preferences of juvenile owls in the post fledging period.

The dispersal behavior and survival of juvenile Tawny Owls (*Strix aluco* L.) has previously been studied in a lowland broadleaved woodland at Wytham, near Oxford, England (Southern *et al.* 1954, Southern 1970, Hirons 1976). They found that Tawny Owls remained in their natal territory, and were dependent on their parents for food for 2.5-3.0 months after fledging, and before dispersing (defined as the post-fledging period; Newton 1979). Southern (1970) gave the fledging age as 32-37 days but stated that the birds usually leave the nest at 25-30 days and hide on nearby branches. Survival and dispersal have also been investigated in an upland coniferous forest. Petty and Thirgood (1989) found that in a year of poor food supply, mortality was 91.7 percent and occurred in two peaks; (i) in the period immediately following fledging, (ii) later on, but before the end of the dependence period. The initial heavy mortality was due mainly to mammalian predators, whereas later on starvation was the chief cause of death. It was also found that broods reared in a predominantly coniferous habitat showed a strong preference for roosting in broadleaved trees.

A study of first-year survival of Great Horned Owls (*Bubo virginianus*) in different phases of the snowshoe hare (*Lepus americanus*) cycle found that juvenile survival collapsed parallel to the decline in hare densities, and that mortality rates peaked before, not during, dispersal (Rohner and Hunter 1996). Nestling survival remained high in all 3 years of the study.

Our study used radio telemetry to investigate dispersal behavior and survival of juvenile Tawny Owls in Kielder Forest, northern England. Here, the Tawny Owl's chief prey, the field vole (*Microtus agrestis*), exhibits population cycles with a periodicity of 3-4 years. Breeding parameters of Tawny Owls in Kielder are highly correlated with vole abundance, where field voles constitute 78 percent of the diet by weight (Petty 1992).

[1] Department of Biological Sciences, University of Durham, Science Laboratories, South Road, Durham DH1 3LE, U.K.; and Foresty Commission Research Division, Woodland Ecology Branch, Northern Research Station, Roslin, Midlothian EH25 9SY, U.K.

Petty (1992) showed that birds reared in the study area could take up to 4 years before being recruited into the breeding population. It was hoped that some birds would survive to become non-territorial "floaters" so that the behavior of this sector of the population could be studied in terms of our wider investigation into this hierarchical predator-prey system.

METHODS

Study Area

The study area in Kielder Forest (55°N, 2°W) was part of an extensive man-made conifer forest. It measured 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 also some larger areas of deciduous trees, including alder (*Alnus glutinosa*) and birch (*Betula spp.*). In 1996 the forest was a mosaic of stands of different species and ages of trees. There were extensive clear-cut patches which, once colonized by grasses and rushes, provided ephemeral islands of vole habitat within the forest.

Sex Determination

Blood samples were taken from nestlings, which were sexed from female-specific mini-satellite fragments (Appleby *et al.*, in press).

Age Determination

Hatch dates were estimated using a wing length/age growth curve[2]. Owls were radio-tagged before fledging, at 22-31 (mean 26.3, S.E. 0.4) days of age, and then monitored daily using telemetry. This allowed fledging ages to be calculated to within half a day. Nestlings were weighed 1-10 (mean 4.1) days before fledging and we refer to this as pre-fledging mass.

Radio Telemetry

Within the study area, most Tawny Owls bred in nest boxes which had been provided for them. Nestling owls from 11 two-chick broods were radio-tagged. These were distributed throughout the areas in which owls bred. A soft nylon harness was used to fix the transmitter to the back of the owls, leaving adequate slack to compensate for further growth (fig. 5.1B in Kenward 1987). Radio tags (Biotrack Ltd) transmitted on 173.201-173.940 MHz. The combined mass of the radio and harness was 7.3 g. This represents 1.7-2.5 percent (mean 2.1 percent) of a juvenile's mass at fledging. The radios were expected to transmit for 1 year.

A TRX 1000S receiver (Wildlife Materials Inc.) was used with a hand-held three element Yagi antenna to find the position of radio-tagged birds. Daytime roost positions were determined every 1 to 3 (mean 2) days, the frequency increasing as the bird's movements grew in magnitude. It was usual to return to the position of the previous fix to determine roughly how far the bird had moved. They were then approached until seen or until the roosting tree was located. On a few occasions triangulation was necessary in order to avoid disturbance, for example, when the birds were roosting in early-thicket spruce crops. Initially it was possible to approach birds closely, but later on they became more wary and were liable to be flushed from their perches. As a consequence, some fixes were of poorer quality than location to a specific tree, but it was always possible to identify the type and age class of forest that owls were using. Positions were plotted on a 1:10 000 scale forest stock map.

Prey Availability

Relative densities of field voles were assessed using vole sign indices (VSIs). A 25 cm² quadrat was thrown 25 times within a 0.5 ha patch of vole habitat nearest to the roosting position of the owls. Within these quadrats the presence or absence of fresh grass clippings in vole runs was noted. Each patch was then assigned a score on a scale of 1 to 25. The validity of this method had previously been confirmed by trapping at VSI sites and a significant relationship was found between the two indices (Petty 1992). Bank voles (*Cleithrionomys glareolus*), which occurred widely in the study area, do not produce grass clippings and therefore VSIs reflect field vole abundance.

[2] S.J. Petty, unpublished data.

Movements and Behavior

Movements in Relation to Relative Abundance of Field Voles

Field vole abundance assessments were limited to patches near owl roosts and not performed in areas unused by owls. It was therefore not possible to analyze the data in terms of "selection" *per se*. Instead, the relative vole densities were compared for areas between which owls were moving. Analysis was conducted by using all patch to patch movements made by all owls. Each was grouped into one of three categories; (i) movement to an area of higher vole density (higher), (ii) movement to an area of similar vole density (similar), (iii) movement to an area of lower vole density (lower). Frequencies in the three categories were then compared using Chi-squared tests.

Habitat Selection

Locations of owls (*n* = 319) were compared with a random sample of tree species and age classes (*n* = 351) generated from a GIS forest stock database for the Tawny Owl study area.

RESULTS

Nestling Survival

Nestling survival was high for the 11 broods studied. Twenty-two (88 percent) of 25 young which hatched survived to fledging.

Post-fledging Survival

Juveniles fledged at 29-36 (mean 32.1, S.E. 0.6) days of age. A multiple regression was used to investigate the relationships between fledging age, pre-fledging mass, and gender. Sex and mass were significantly correlated (p = 0.004), but age at fledging was not related to mass (p = 0.87) nor sex (p = 0.67).

Eight (36.4 percent) owls died 10-106 days after fledging but before dispersing. That is, before they had made substantial movements outside their natal territories. Of these, five were males. A further five (22.7 percent) owls (2 males) died 40 to 147 days after fledging, having begun to disperse. Five (22.7 percent) owls disappeared suddenly at 8 to 51 days after fledging and before the end of the dependence period. Contact was lost with a further four

(18.2 percent) birds at 58 to 178 days after fledging, having left their natal territories. The latter two groups were excluded from the survival and mortality analyses. The raw data is presented in table 1. On average, females lived longer than males, but this difference was not statistically significant (t = 0.96, d.f. = 11, p = 0.17).

Timing and Causes of Mortality

Peak mortality occurred at 21 to 60 days after fledging with a lower, fairly even distribution from 61 to 120 days (fig. 1). Three owls were predated by Northern Goshawks (*Accipiter gentilis*) early on (before 41 days) whereas starvation, which accounted for six deaths, occurred more evenly throughout the study period at between 10 and 93 days after fledging (table 1). No more deaths from starvation occurred after the end of the dependence period (75-90 days). An owl was found dead with a field vole lodged in its throat 73 days after fledging, but with no other signs of injury or disease. One bird was found buried, decapitated and wingless after 106 days, and another, found 147 days after fledging, had half its skull missing and a broken wing. In both cases the bird's pectoral muscle mass was relatively high and starvation was unlikely, and there were no other obvious signs of the cause of death. The injuries were likely to have been sustained *post mortem*, possibly as a result of scavenging by a red fox (*Vulpes vulpes*) and a weasel (*Mustela nivalis*) respectively. Finally, a juvenile female, found dying in a ditch 106 days after fledging, had suffered an eye injury but otherwise seemed to have been in fair condition.

Relationship Between Days Lived After Fledging and Fledging Date

For the 13 birds whose fate was known there was a highly significant negative correlation between their fledging date in June and the number of days lived prior to fledging (F = 23.25, p < 0.01). That is, birds which fledged earlier tended to live longer (fig. 2). A multiple regression was performed to investigate the effects of the possible confounding influences of sex and weight (close to fledging date). Only fledging date had a significant relationship with survival and accounted for 68 percent of the variation (F = 23.25, r^2 = 67.88, p < 0.01). Survival was not significantly correlated with pre-fledging mass (p = 0.17) nor sex (p = 0.13), but mass was significantly correlated with sex

Table 1.—*Survival, mortality and movements of 22 radio-tagged juvenile Tawny Owls in Kielder Forest, northern England. The forth column shows the number of days after fledging until death or loss of contact for each bird. Displacement represents distance moved in a straight line drawn from nest boxes to the position of the last fix.*

| Identity	Sex	Fate	Dead/missing @ (days)	Cause of death	Displacement (km)	Started to disperse?
GF36858	f	dead	80	starvation	0.39	n
GF36857	m	dead	39	starvation	0.04	n
GF36861	m	dead	147	?	3.04	y
GF36890	f	dead	106	eye injury	0.79	n
GF36883	f	dead	106	?	3.98	y
GF36884	m	missing	33			n
GF36900	f	dead	47	goshawk	2.17	y
GF36875	m	missing	61		2.85	y
GF36898	f	dead	27	starvation	0.11	n
GF36899	m	dead	54	starvation	1.6	y
GF36894	m	missing	51		0.9	n
GF36893	f	missing	50		0.95	n
GF36892	m	dead	22	goshawk	0.25	n
GF62107	m	dead	10	starvation	0.91	n
GF36859	m	missing	178		0.76	y
GF36860	m	missing	88		0.12	y
GF36881	f	dead	93	starvation	0.87	y
GF36882	m	dead	73	not starvation but ?	0.36	n
GF36867	m	dead	47	goshawk	0.65	n
GF36868	f	missing	40		0.65	n
GF36869	m	missing	8			n
GF36870	f	missing	58		1.03	y
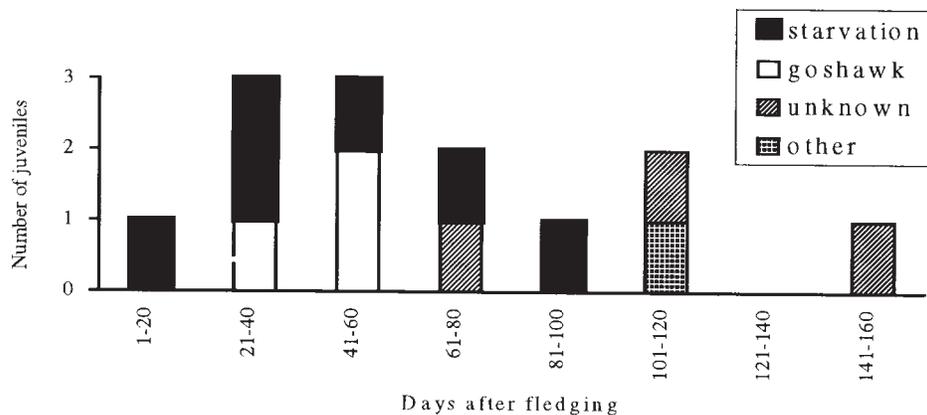
Figure 1.—*Timing and causes of mortality for 13 juvenile Tawny Owls in Kielder Forest, northern England. The dependence period ends at approximately 75-90 days.*
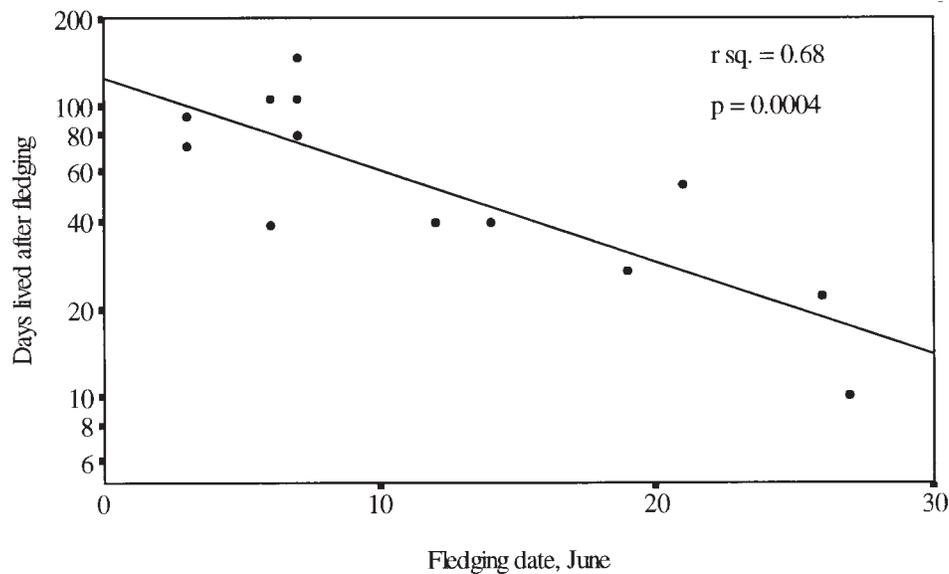
Figure 2.—*Relationship between the fledging date of juvenile Tawny Owls and the number of days lived after fledging in Kielder Forest, northern England. The points represent the 13 owls which were known to have died.*

($p = 0.02$), as one might expect given that female Tawny Owls are larger than males (Petty 1992, p. 8).

Prey Availability

In 1996, vole numbers were generally low, although there were "hotspots" of higher vole densities to which owls largely confined their breeding attempts. Thus, dispersing owls were presented with an extremely patchy food supply. The highest vole density at any one site in 1996 was 150/ha and the lowest was 0/ha. Recapture analysis indicated a 95 percent chance of catching whatever animals were present. Average densities for Kielder in 1996 were: (i) spring 46/ha, (ii) summer 54/ha, and (iii) autumn 35/ha (J.L. Mackinnon, unpubl. data).

Movements and Behavior

Movements of owls between roosting sites were measured as linear distances between fixes. It became apparent that movements of owls between roosting sites over a period of time were seldom unidirectional. Individual birds made "to and fro" movements between favored stands of trees, sometimes leaving the natal territory, only to return later. There were also large scale circular movements, often with over 1 km between stages.

Birds with which contact had been lost had moved between 0.12 and 2.85 km (mean 0.88 km) before they "disappeared".

For the birds which were found dead, movement distances, defined as linear distance between the natal nest box and the position of the last fix, ranged from 0.02 to 3.98 km (mean 1.10 km). This underestimated total distance covered by dispersing owls, because to and fro and circular movements, and forays were not taken into account. Two owls moved suddenly from their natal territories well before the end of the dependence period and subsequently died. Of these, one starved 1.60 km from its nest box, and the other was predated by a goshawk 2.17 km from its nest site (table 1). Eight owls remained within their natal territories, moving 0.02 to 0.79 km (mean 0.33 km) from their nest boxes before dying. Five owls moved outside their natal territories, moving 0.87 to 3.98 km from their nest boxes in gradual, stepped movements of up to 1.2 km. The behavior of two of these, plus another where contact was subsequently lost, is described in detail below.

Movements in Relation to Relative Abundance of Field Voles

For this preliminary analysis, expected values were calculated assuming that birds had a free choice of the three patch types each time they
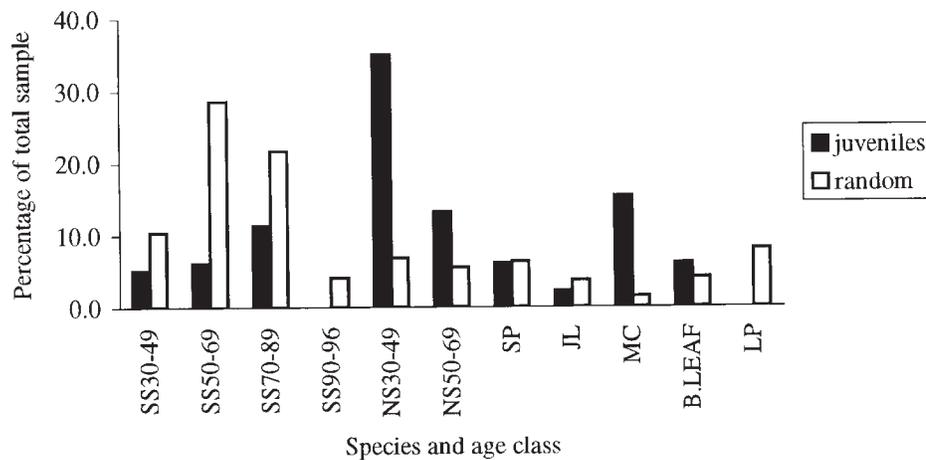
115

Figure 3.—*Comparison of habitats used by juvenile Tawny Owls for roosting with a random sample of similar size from a GIS database of the Kielder Forest, northern England Tawny Owl study area. Numbers on the X axis represent planting years, and the species are coded as follows: SS = Sitka spruce, NS = Norway spruce, JL = Japanese larch, MC = mixed conifers, B.LEAF = broadleaved trees, LP = Lodgepole pine.*

moved. In reality this may not have been the case. Overall, the frequencies in these groups were significantly different (χ^2 = 7.92, d.f. = 2, p < 0.05, *n* = 32). Chi squared tests were calculated for each group of values. There were significantly fewer movements to similar areas (χ^2 = 4.2, d.f. = 1, p < 0.05) and roughly equal numbers of movements to lower areas than would be expected by chance (χ^2 = 0.008, d.f. = 1, p > 0.05). There were more movements to higher areas than expected by chance but this result was not statistically significant (χ^2 = 3.7, d.f. = 1, p > 0.05).

The behavior of three longer-lived juveniles differed in two areas with widely different average vole abundance scores. In area 1, with an average VSI score of 1.7, GF36861 made circular and reciprocal movements between six patches of vole habitat, rarely stopping at each one for more than 2-3 days. This bird continued to move widely until it was found dead. By contrast, in area 2, where the average VSI score was 7.7, GF36859[3] and GF36881 roosted in a stand of trees between two large clear-felled patches for 80 and 21 days respectively, after previously having made extensive movements between patches of lower vole densities.

Habitat Selection

Overall, there were highly significant differences between the habitat where owls chose to

roost and that which was available to them (χ^2 = 882, d.f. = 10, p < 0.01).

Owls used older stands of Sitka spruce (χ^2 = 65, d.f. = 1, p < 0.01) less than expected by chance. Older stands of Norway spruce (χ^2 = 323, d.f. = 1, p < 0.01), and stands of mixed coniferous crops (χ^2 = 387, d.f. = 1, p < 0.01) were used more than would have been expected by chance. Proportions of Scots pine (*Pinus sylvestris*), Japanese larch (*Larix kaempferi*), and broadleaved species used by owls were similar to their availability (fig. 3). Lodgepole pine was represented in the forest but grows at higher elevations on blanket peat bogs and was therefore unused by the owls. This preliminary analysis does not take altitudinal and planting patterns into account, and does not necessarily represent the habitat available to owls in specific territories.

DISCUSSION

Like Rohner and Hunter (1996), we found high nestling survival even though owls were under food stress.

We were able to confirm previous estimates of the age at which chicks fledged (Southern 1970) and show that one calendar month is a fair approximation.

It was expected that heavier nestlings would fledge earlier than lighter nestlings, but we found no relationship between age and pre-fledging mass, nor between fledging age and

---

[3] This bird subsequently disappeared from the area and contact was lost.

gender. Tawny Owls are sexually dimorphic (mass = 1.3:1 female:male, Petty 1992) which accounted for the significant relationship between sex and mass. A possible problem with this analysis was variation in the period of time which elapsed between the last weighing and fledging, although there were relatively few birds which were last weighed more than 5 days before fledging.

Survival rates of Tawny Owls in spruce forests were much lower in decreasing vole years (Petty 1992). In Kielder Forest in 1996, juvenile mortality was extremely high, with a large proportion of birds starving. A trend toward greater longevity in females may simply be a function of the analysis, in that missing birds were excluded and these included some relatively old males (table 1).

Unlike Petty and Thirgood (1989), our study found that owls starved throughout the post-fledging period, rather than just before the on-set of independence. This could be a function of low vole densities in Kielder in 1996, as opposed to densities which were declining from a higher level in Glenbranter, Argyll in 1986 (Petty and Thirgood 1989). However, there was agreement between the two studies in that predation was an important factor early in the dependence period, although predators responsible differed between the two studies. Younger owls may be less able to evade predators before their flight feathers are fully developed, and this may have been exacerbated by an interaction between food shortage and predation, where owls in poor condition seem to be more vulnerable (Rohner and Hunter 1996). For example, one bird could be approached to within a few meters before it flew to a safer perch. It was subsequently killed by a goshawk. Hungry juveniles also call more and their parents are less aggressive towards potential predators.

The period for which our juveniles survived after fledging was strongly correlated with their fledging date. Petty (1992) showed that hatch-date (a surrogate for fledging date) had a strong influence on future recruitment in declining vole years, but not in low or increasing vole years. Thus, in declining vole years, a greater proportion of early-hatched chicks survived to breed. In most previous low vole years, vole numbers increased towards the autumn so that owls entered the winter with a good food supply. However, 1996 was different because

vole numbers did not recover later on in the year. This may account for the particularly heavy mortality that we observed.

For the five owls which disappeared suddenly, there was no evidence of transmitter failure prior to loss of contact—similar tags on adult owls remained functional throughout this study. The birds may have been predated but it is also possible that the tags had been damaged or buried by predators, such as foxes, or lay in "dead ground" such as a ditch, stream or hollow, where the signal range would have been reduced. Goshawks pluck avian prey and may remove the carcass, so piles of feathers without a radio transmitter could have been overlooked. Indeed, on one occasion a goshawk was disturbed and a decline in signal strength was heard as the predator removed the carcass. Of the four owls where contact was lost after 58 days, all except one had made wide-ranging movements prior to their disappearance. Although predation or tag failure could not be ruled out, it is possible that these birds had suddenly dispersed.

It was evident from this study that telemetry can provide valuable information on movement and behavioral patterns during dispersal that cannot be gathered in any other way. In particular, the relationship between owl movements and their food supply was tentatively illustrated. The contrasting behavior of owls in two areas of widely different food availability was a particularly noteworthy result, although the sample size was small.

Paton *et al.* (1991) showed that backpack-mounted radio tags had adverse effects on the survival of Spotted Owls (*Strix occidentalis*), although few deaths could be directly attributed to the radio tag or harness. Also, radios represented 2.8-4.1 percent of their owl's mass which was on average rather more than the burden that our birds carried. Future work will use tags and harnesses of the same design as those used in 1996, so that any effects can be quantified and standardized between years.

Unlike Glenbranter in 1986 (Petty and Thirgood 1989), in Kielder there was no evidence that juveniles showed a strong preference for roosting in broadleaved as opposed to coniferous trees. However, there are fewer broadleaves in Kielder than Glenbranter. In general, the forest structure in Kielder seemed important with birds preferring to roost in

taller, more widely spaced stands, and avoiding more dense stands (personal observation). Our use/availability analysis took the study area as a whole, and was not necessarily an accurate representation of the habitat available to owls in individual territories. Further analysis is required.

Due to the very high rates of mortality observed in this study it may be concluded that none or few of the 1996 cohort will have survived to become recruits or "floaters". If there are non-territorial owls in Kielder, then it is likely they were hatched in years when vole densities were higher. We will repeat this work in 1997 when vole numbers should be increasing.

ACKNOWLEDGEMENTS

LITERATURE CITED

Appleby, B.M.; Petty, S.J.; Blakey, J.K.; Rainey, P.; Macdonald, D.W. 1997. Does variation of sex ratio enhance reproductive success of offspring in tawny owls *Strix aluco*. Proceedings: Biological Sciences. [In press.]

Hirons, G.J.M. 1976. A population study of the Tawny Owl *Strix aluco* L. and its main prey species in woodland. University of Oxford. Ph.D. dissertation.

Kenward, R. 1987. Wildlife radio tagging. London: Academic Press. 222 p.

Newton, I. 1979. Population ecology of raptors. Berkhamsted: T & A.D. Poyser. 399 p.

Paton, P.W.C.; Zabel, C.J.; Neal, J.L.; Steger, G.N.; Tilghman, N.G.; Noon, B.R. 1991. Effects of radio tags on spotted owls. Journal of Wildlife Management. 55: 617-622.

Petty, S.J. 1992. Ecology of the Tawny Owl (*Strix aluco*) in the spruce forests of Northumberland and Argyll. Open University. 295 p. Ph.D. dissertation.

Petty, S.J.; Thirgood, S.J. 1989. A radio tracking study of post-fledging mortality and movements of Tawny Owls in Argyll. Ringing and Migration. 10: 75-82.

Rohner, C.; Hunter, D.B. 1996. First-year survival of Great Horned Owls during a peak and decline of the snowshoe hare cycle. Canadian Journal of Zoology. 74: 1092-1097.

Southern, H.N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). Journal of Zoology. 162: 197-285.

Southern, H.N.; Vaughan, R.; Muir, R.C. 1954. The behaviour of young Tawny Owls after fledging. Bird Study. 1: 101-110.