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ORIGINAL ARTICLES

The long-term effect of fitting back-mounted radio tags to juvenile tawny owls *Strix aluco*

Steve J. Petty, Bridget M. Appleby, Christopher F. Coles & Romain Julliard

We investigated the long-term effect of fitting back-mounted radio tags to nestling tawny owls *Strix aluco* in northern England by comparing apparent survival rates of radio-tagged and non radio-tagged nestlings from two cohorts using capture-mark-recapture methodology. If radio tags had no effect, apparent survival rates should not have differed between the two groups of birds. Overall, juvenile survival was much lower than adult survival and yearling breeding probability much lower than adult breeding probability. Radios had no significant effect on yearling breeding probability, but they did have a significant negative effect on juvenile survival. Overall, just one bird (1.8%) was recruited from the radio-tagged group of 55 birds, whereas 14 (16%) were recruited from the control group of 89 birds. There was no significant difference in the distribution of sexes between groups that could account for these differences in apparent survival rates. Moreover, food supply and breeding performance of broods in the two groups did not differ significantly, indicating that differences in rearing conditions were not responsible for the disparity in survival rates. Based on our results, and those from other studies of tawny and spotted owls *Strix occidentalis*, we recommend that back-mounted radio tags should not be used on nestling or recently fledged *Strix* species.

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Radio telemetry provides unique spatial data on how animals use their environment (Kenward 1987). However, radio tags add an extra burden to individuals in a highly competitive system (Caccamise & Hedin 1985, Gessaman & Nagy 1988, Pennycuick, Fuller & McAllister 1989). The aim of successful telemetry is to minimise these additional costs so they do not adversely affect behaviour and demographic performance, such as reproduction and survival (Kenward 1987, Kenward, Pfeffer, Al-Bowardi, Fox, Riddle, Bragin, Levin, Walls & Hodder 2001). Thus, it is essential for wildlife ecologists to evaluate any adverse effects of radio tags on their study species, and if detected, to consider ways of alleviating the problem, including modifying radio design or attachment methods (Kenward et al. 2001).

Radio telemetry is a particularly valuable technique for quantifying habitat use and dispersal patterns of nocturnal species such as owls. These data can rarely be obtained in any other way and, not surprisingly, radio telemetry is widely used by owl biologists. However, we are only aware of two studies that have investigated how back-mounted radio tags affect the survival and breeding performance of owls, and both were on adult spotted owls *Strix occidentalis*. Paton, Zabel, Neal, Steger, Tilghman & Noon (1991) indicated that fewer radio-tagged pairs bred and that those who did fledged fewer young than non radio-tagged birds, whereas Foster, Foresman, Meslow, Miller, Reid, Wagner, Carey & Lint (1992) detected no effect of radio tags on survival or body mass, but again radio-tagged owls produced significantly fewer offspring. Theirs was an extensive study that used data on spotted owls from 4-8 study sites in Oregon and Washington, and at each site compared radio-tagged and non radio-tagged individuals. Recommendations from both studies were that tail-mounted radios should be used instead of back-mounted radios on adult spotted owls. This assumes that tail-mounted radios have less effect on behaviour and survival than back-mounted radios (Foster et al. 1992), although to our knowledge this has not been tested. Nevertheless, many studies on other species of owl, as well as on spotted owls, continue to use back-mounted radios. The main drawbacks with tail-mounted radios are (i) they have to be smaller than back-mounted radios, and thus have a shorter battery-life, and (ii) tail feathers that support the radio are prone to moult pre-

maturely (Arsenault, Hodgson & Stacey 1997, Ganey, Block, Dwyer, Strohmeyer & Jenness 1998). Thus, tail-mounted radios create extra problems in the determination of survival rates.

The radio-tagging of young owls, just before or just after they leave the nest, is being used increasingly to investigate post-fledging dispersal, habitat selection and survival (Petty & Thirgood 1989, Rohner & Hunter 1996, Arsenault et al. 1997, Coles & Petty 1997, Ellsworth & Belthoff 1997, Miller, Small & Meslow 1997, Ganey et al. 1998, Overskaug, Bolstad, Sunde & Øien 1999, Sunde 1999, Willey & van Riper III 2000). These include studies on endangered species, such as the spotted owl, but to our knowledge the safety of this technique has not been tested. Some recent studies on juvenile diurnal raptors fitted with back-mounted radio tags have indicated that there are no adverse effects on survival, providing care is taken when fitting the tags (Kenward, Walls, Hodder, Pahkala, Freeman & Simpson 2000, Kenward et al. 2001).

In our study, we tested the long-term effect of using back-mounted radio tags on nestling tawny owls *Strix aluco*, a highly philopatric woodland owl that, in temperate Europe, is largely dependent on small rodents for food (Cramp 1985). In our study area in northern England, the most important prey for the owls were field voles *Microtus agrestis*, which had 3-4 year cycles of abundance (Petty 1992, Petty 1999, Lambin, Petty & MacKinnon 2000). We radio-tagged a proportion of nestling owls from the 1996 and 1997 cohorts to investigate dispersal and survival during their first autumn/winter in relation to vole abundance; the results of which have been or will be published elsewhere (Coles & Petty 1997, Coles 2000, Coles, Petty, MacKinnon & Thomas 2003). All owls from both cohorts were ringed and most were sexed by molecular techniques.

We investigate the long-term effect of radio tags on the probability that fledgling owls survive and breed in the study area. Since tawny owls have a flexible age at first reproduction, radio tags could either reduce survival to the age at first potential breeding (from fledging to one year old) or delay age at first breeding (from one year old to two years old). Both effects will result in a reduced observed proportion of radio-tagged fledglings found breeding in the studied population. Because potential effects lasted well beyond the lifespan of radio trans-

mitters, the fate of each individual could not be assessed with certainty, and estimates are based on recapturing breeding individuals. We controlled for annual variations in capturing breeding owls by using capture-recapture methodology (Lebreton, Burnham, Clobert, & Anderson 1992, Clobert, Lebreton, Allainé & Gaillard 1994). In addition, we were able to estimate separately survival probability to age at first potential reproduction and age-specific probability of first breeding (Clobert, Julliard & McCleery 1993). If radio tags had no effect, both components of local recruitment should be similar between radio-tagged and non radio-tagged birds.

Material and methods

Study area
Our study area measured 180 km^2 and was situated in the centre of Kielder Forest (55°13'N, 2°33'W), northern England (Petty 1992). It was part of a much larger area of conifer forest planted with non-native species over the last 70 years in the border area between England and Scotland. Kielder Forest comprised largely Sitka spruce *Picea sitchensis* and Norway spruce *Picea abies* managed on a clear-cutting system (40-60 year rotation length), which over the last 30 years has created a mosaic of different-aged stands of trees (McIntosh 1995).

The owl population
The population was the subject of a long-term study (1980-2002) into the ecology of tawny owls in man-made conifer forests (Petty 1992, Petty & Thomas 2003). Since 1983, all breeding attempts by tawny owls in the study area were in nest boxes, which had been erected mainly during the 1979/80 and 1980/81 winters (Petty, Shaw & Anderson 1994). Each year, visits to potential nest sites (nest boxes and natural sites) commenced in March to determine territory occupancy, with subsequent visits timed to obtain data on breeding performance with a minimum of disturbance. The start of incubation, used as a measure of the timing of breeding, was expressed as a numerical value in days with 1 March = day 1. Clutch size was determined in the first half of the incubation period (see methods in Petty & Fawkes 1997). The number of chicks hatching was defined as clutch size minus any unhatched eggs. All chicks were ringed after they reached 150 g (9-10 days old), and nests were revisited in the last week of the nestling period to count and remeasure chicks. The number of chicks leaving the nest (brood size) was the number recorded on the last visit before fledging minus the remains of

any dead chicks in the nest after fledging (Petty 1992). Fledging was defined as when a chick left the nest site. None of these reproductive parameters were normally distributed. Therefore, non-parametric statistical tests were used when testing for differences in breeding performance between the radio-tagged and non radio-tagged groups.

Food supply
The demography of tawny owls was significantly influenced by the abundance of their main prey, field voles, which had 3-4 year cycles of abundance (Petty 1992, Petty 1999). The most important vole habitat was on clear-cuts. Vole abundance was measured in March and June with a vole sign index (VSI) on 20 clear-cuts scattered throughout the study area, which had been replanted 2-12 years previously (Petty 1992, Petty 1999). The VSI scores were converted to vole density (voles ha^{-1}) from seasonal regressions derived from live trapping (Lambin et al. 2000). This allowed us to investigate if food supply differed between treatment and control groups. Vole density for each pair of owls in the treatment and control groups was estimated from the nearest VSI area to the nest. The mean distance ($\pm$ SE) between occupied nest boxes and VSI sites in the two years was 0.828 ± 0.062 km (N = 63). Previous work has shown that vole density on clear-cuts changed in a wave-like manner, with densities being synchronised up to about 4 km in the direction of the wave (Lambin, Elston, Petty & MacKinnon 1998).

Radio tags and harnesses
Complete broods were either radio-tagged or left as controls. Radio-tagged broods were scattered throughout the study area, not clumped in particular areas. In 1996, when the modal brood size was two, 22 chicks were radio-tagged (11 broods of two chicks) from a total of 25 broods in the study area (48 chicks in total; Table 1). In 1997, when the modal brood size was three, 33 chicks were radio-tagged from 13 broods (nine broods of three chicks, two broods of two and two broods of one) from a total of 38 broods in the study area (96 chicks in total; see Table 1).

Nestlings were radio-tagged when 22-31 days old, by which time they had reached their maximum weight. Tawny owl chicks leave the nest site 29-36 days after hatching (Coles & Petty 1997). Thus, nestlings had a few days in the nest to get used to the tags before fledging. Observations after fledging showed that they ignored the radios. Radio tags were fitted to the back of the owl with a harness made from soft nylon cord, leaving sufficient slack to compensate for further growth (similar to Fig.

Table 1. Recruitment into the breeding population of radio-tagged and non-radio-tagged (control) tawny owl nestlings from two cohorts in Kielder Forest during 1996-1997.

Recruitment year	1996 cohort		1997 cohort		Total	
	Radio-tagged (N = 22)	Control (N = 26)	Radio-tagged (N = 33)	Control (N = 63)	Radio-tagged (N = 55)	Control (N = 89)
1997	0	0	0	0	0	0
1998	0	3	0	5	0	8
1999	0	0	0	1	0	1
2000	0	1	1	3	1	4
2001	0	0	0	1	0	1
Total (%)	0 (0.0)	4 (15.4)	1 (3.0)	10 (15.9)	1 (1.8)	14 (15.7)

5.1b in Kenward 1987; also see Petty & Thirgood 1989, Coles & Petty 1997). Subsequent examination of dead juveniles showed that harnesses fitted well, had been groomed under the feathers and had caused no skin abrasions. The radio and harness weighed 7.3 g and was designed to either stay on a bird for life or be removed when recaptured (none were). The radio tags were made by Biotrack (UK), transmitted on 173.233-173.973 MHz and had a lifespan of approximately one year. During the breeding season, the mean weight of adult male owls was 364 ± 2.2 g (N = 89) and adult females 536 ± 3.6 g (N = 237; Petty 1992). Thus, radios were approximately 2.0% of the mass of males and 1.4% of the mass of females.

Sex determination of nestlings

The sex of nestlings was determined from blood samples taken from the brachial vein (Appleby, Petty, Blakey, Rainey & Macdonald 1997). In 1996, nestlings were sexed using Polymerase Chain Reaction (PCR) with a sex specific primer (Griffiths, Daan & Dijkstra 1996). In 1997, a different primer was used (Griffiths, Double, Orr & Dawson 1998).

Assessing the effect of radio tags

To test the hypothesis that radios had no deleterious effect, we compared recruitment rates of radio-tagged (treatment group) and non radio-tagged (control group) nestlings from the 1996 and 1997 cohorts. All nestlings from both cohorts were ringed. Owls of both sexes can breed for the first time as yearlings, but not all individuals

do (Petty 1992). Consequently, many scenarios may lead to a locally born individual not being recaptured as a breeder; (i) it may die before its first birthday, (ii) it may survive, but not breed as a yearling and then die in the following year, or (iii) it may eventually breed one or more times at any age, but by chance avoid being captured until it dies. In tawny owls, the age at first reproduction is flexible and appears to be partially dependent on body condition (Hirons 1985, Petty 1992). Thus, it is reasonable to hypothesise that radios may affect the probability of breeding as a yearling, in addition to any effect on first-year survival. Clearly, the mere analysis of the effect of radios on the proportion of fledglings eventually recruited into the population will be difficult to interpret. Fortunately, the separation of these different probabilities and the testing of the effect of radios on any parameter is possible using modern capture-recapture methodology.

In 1997 and 1998, 93% of breeding females and 81% of breeding males were caught when nestlings were 5-15 days old (Table 2). Females were caught at the nest box with a net, whereas males were caught with a nestbox trap (Petty 1992). Our long-term study ceased after the breeding season of 1998, but members of the local ringing group caught 40-74% of breeding females annually during 1999-2002, but no males (see Table 2). Some owls reared in the study area would have settled to breed outside the study area. We assumed that the probability of this occurring was equal between treatment and control groups providing the distribution of sexes between groups was not significantly different (see lat-

Table 2. Number of adult tawny owls caught annually in Kielder Forest during breeding attempts in relation to the number of occupied territories and breeding pairs.

Year	Occupied territories	Breeding pairs[a]	Successful pairs[b]	♀♀ caught (% breeding pairs)	♂♂ caught (% breeding pairs)
1997	54	45	38	42 (93)	37 (82)
1998	56	45	36	42 (93)	36 (80)
1999	-	40	32	16 (40)	0
2000	-	45	38	33 (73)	0
2001	-	45	42	26 (58)	0
2002	-	31	-	23 (74)	0

[a] Pairs laying at least one egg.
[b] Pairs fledging at least one chick.

er). Previous work has shown that there was no significant difference in natal dispersal distance between sexes of birds recruited into the study area (geometric mean = 2.85 km; see Petty 1992).

Statistical analyses

The recapture of a breeding owl that was ringed as a nestling in the study area is the product of several conditional probabilistic events, such as an individual surviving to breed, staying and successfully breeding in the study area, and being captured. Local studies cannot separate survival from permanent dispersal out of the study area. Estimated survival is therefore called apparent survival and denoted ϕ. Apparent survival and breeding probability may vary with age; survival during the first year (apparent juvenile survival; ϕ_{juv}) is typically lower than survival later in life (apparent adult survival; ϕ_{ad}), and the breeding probability of yearlings (α_1) is typically lower than the breeding probability of older birds, but was assumed to be independent of age in this study. ϕ_{juv} and α_1 may vary with sex and year and may be affected by radio tags, the effect of which is the focus of this study. Capture probability (p) is only applicable for breeding individuals and was therefore considered independent of age. Trapping success (see Table 2) shows that capture probability varied among years and between sexes. All these parameters were estimated with the software MARK (White & Burnham 1999) using the parameterisation of Clobert et al. (1994) for estimating age specific breeding probabilities.

When breeders only are captured, as in the case of tawny owls captured when feeding nestlings, absence of breeding will result in probability of capture equal to zero. Thus, the estimated capture probability is the combination of the trapping success (proportion of breeders that are captured) and the breeding probability. Hence, delayed breeding by yearlings will result in a lower estimated capture probability for this age group.

Delayed breeding may thus be evaluated by comparing capture probabilities of young and adults. Two data sets were built, one containing the capture-recapture histories of breeding adults from 1996 to 2002 (318 captures of 141 individuals) split by sex, and another containing capture-recapture histories of juveniles (N = 135) split by sex and radio-tagged versus control group. Goodness-of-fit of these data were first assessed with program RELEASE implemented in MARK software (White & Burnham 1999). Survival and capture probability were first modelled for the adult data set, and then all parameters were modelled in a joint analysis of the two data sets (for details on data manipulation see Clobert et al. 1993, Clobert et al. 1994). The model best describing variation in the data was selected with the Akaike Information Criterion (AIC; see Anderson & Burnham 1999), while the significance of specific effects was assessed with the Likelihood Ratio Test (LRT; see Lebreton et al. 1992).

Results

Rearing conditions of treatment and control groups

In birds, the timing of breeding often influences the chance of future recruitment, with more recruits coming from earlier breeding attempts (Newton 1989). However, no significant differences were detected in the start of incubation, clutch size or brood size between the treatment and control groups in either 1996 or 1997 (Table 3). Nor was there a significant difference in vole abundance estimates between the two groups in either year (see Table 3). Thus, the apparent survival of birds in the treatment and control groups was unlikely to be biased by differences in rearing conditions.

There were significant differences in breeding performance between years, with breeding commencing ear-

Table 3. Field vole density (vole ha⁻¹) in March and June and reproductive performance of radio-tagged and control tawny owl broods in Kielder Forest during 1996-1997 (means ± SE). Only nests that reared at least one chick are included in this comparison. Mann-Whitney U-tests were used to test for differences between groups.

Year Category	No of broods	Vole density March	Vole density June	Start of incubation[a]	Clutch size	Brood size
1996						
Radio-tagged	11	68.3 ± 14.8	41.5 ± 8.6	41.4 ± 2.2	2.3 ± 0.1	2.0 ± 0.0
Control	14	77.3 ± 10.4	51.9 ± 7.8	41.2 ± 1.6	2.5 ± 0.2	1.9 ± 0.1
U		70.0	57.5	77.0	63.5	66.0
P		0.70	0.28	1.00	0.38	0.35
1997						
Radio-tagged	13	92.6 ± 15.0	127.9 ± 20.6	26.3 ± 2.9	3.1 ± 0.2	2.5 ± 0.2
Control	26	87.5 ± 8.6	142.7 ± 13.3	24.4 ± 1.2	3.1 ± 0.1	2.5 ± 0.1
U		152.5	143.5	155.5	152.5	150.0
P		0.76	0.56	0.83	0.76	0.72

[a] Start of incubation when 1 March = day 1.

lier (Mann-Whitney U = 67.0, P < 0.001) and larger clutch (Mann-Whitney U = 202.5, P < 0.001) and brood sizes (Mann-Whitney U = 220.0, P < 0.001) being produced in 1997 than in 1996. This corresponded to vole abundance reaching its lowest point in the current cycle in 1996, then increasing in 1997, to peak in 1998 (Petty 1999; see Table 3).

Sex ratios of treatment and control groups

Overall, 144 chicks fledged from the two cohorts, of which 136 were sexed using molecular methods and eight were not sexed; of these seven came from the control group and one from the treatment group. The unsexed nestlings were excluded from the capture-recapture analysis, which had to rely on individuals sexed in the nest. Two of the seven unsexed individuals from the control group were recaptured as breeding females, a proportion higher than the 12 recruits out of the 82 sexed nestlings from that group. The exclusion of unsexed nestlings was thus conservative with respect to our hypothesis.

More males (54%) than females (46%) were produced when broods were pooled, but the sex ratio did not differ significantly from unity ($\chi^2_1 = 0.7$, P = 0.39). Moreover, there was no significant difference in distribution of sexes between treatment (32 males, 22 females) and control groups (41 males, 41 females; $\chi^2_1 = 0.8$, P = 0.38 with Yates correction). Consequently, differences in dispersal distances between sexes could be discounted as a factor influencing the recruitment of treatment and control birds.

Capture-recapture estimation
Adults
RELEASE goodness-of-fit tests indicated no important heterogeneity in the data set (P = 0.52). As no males were captured between 1999 and 2002, male capture probabilities for these years were fixed to 0 throughout the analysis. The best model describing survival and capture probability variations (the model with the lowest AIC) indicated constant survival through time (LRT for time variation on survival, $\chi^2_5 = 6.0$, P = 0.31) and no effect of sex (LRT for sex variation on survival, $\chi^2_1 = 0.3$, P = 0.58); but since no males were captured between 1999 and 2002, detection of any sex effect was unlikely. Capture probability variation was adequately modelled by sex-specific trapping success estimated from the ratio of the number of captured individuals to the number of breeding attempts (see Table 2; LRT for residual time variation of capture probability beyond the model, $\chi^2_6 = 8.4$, P = 0.21; LRT for no time variation of capture probability, $\chi^2_1 = 35.1$, P < 0.001).

Local recruitment
Two specific parameters were introduced to describe recruitment of juveniles into the breeding population; apparent juvenile survival (ϕ_{juv}) and yearling breeding probability (α_1). ϕ_{juv} did not vary with sex, and α_1 did not vary with either sex or year ($\chi^2_3 = 1.3$, P = 0.73). However, there was a year effect on ϕ_{juv} ($\chi^2_1 = 4.5$, P = 0.03). Overall, juvenile survival was much lower than adult survival ($\chi^2_3 = 55.5$, P < 0.001), and yearling breeding probability was much lower than adult breeding probability ($\chi^2_1 = 27.4$, P < 0.001). Radios had no significant effect on yearling breeding probability ($\chi^2_1 = 1.1$, P = 0.29), but a significant negative effect on juvenile survival ($\chi^2_1 = 6.00$, P = 0.01). AIC of models including radio effect on juvenile survival or on yearling breeding probability differed by 2.77 AIC units in favour of the former. Thus, radio tags are far more likely to have affected juvenile survival than yearling breeding probability. Point estimates for the best models are given in Table 4. Overall, just one bird (1.8%) was recruited from the radio-tagged group of 55 birds, but 14 (16%) from the control group of 89 birds (see Table 1).

Discussion

Survival estimates
To our knowledge this is the first published study to use MARK software to estimate survival rates in tawny owls. Estimated adult survival rates of 0.80 were similar to earlier estimates using larger data sets, but less sophisticated methodology (0.854 for females and 0.843 for males, with no significant difference between the sexes in Petty 1992). As expected, first-year survival rates of the control group (0.11-0.41) were much lower than the adult survival rate.

As far as we are aware, the spotted owl is the only other *Strix* owl for which survival rates have been calculated using MARK software. This is a forest owl from western North America that has been the centre of controversy over the felling of old-growth forests (Gutiérrez,

Table 4. Parameter estimation from the capture-mark-recapture analysis of tawny owls in Kielder Forest. The treatment group and year effect on juvenile survival were constrained to be additive.

Parameter	Estimate	SE
Adult survival	0.80	0.03
Juvenile survival control 1996-97	0.11	0.08
Juvenile survival control 1997-98	0.41	0.12
Juvenile survival treatment 1996-97	0.01	0.02
Juvenile survival treatment 1997-98	0.07	0.07
Yearling breeding probability	0.25	0.05

Table 5. Survival rates obtained in studies of *Strix* owls that have used MARK software to estimate survival rates.

Species	First-year survival rates	Adult survival rates	Source
Tawny owl *Strix aluco sylvatica*			
Control group	0.11 ± 0.08 - 0.41 ± 0.12	0.80 ± 0.03	This study
Treatment group	0.01 ± 0.02 - 0.07 ± 0.07	-	
Californian spotted owl *Strix o. occidentalis*	0.333 ± 0.055	0.827 ± 0.015	Blakesley, Noon & Shaw 2001
Californian spotted owl *S. o. occidentalis*			
♀	-	0.795 ± 0.012	Seamans, Gutiérrez, Moen & Peery 2001
♂	-	0.843 ± 0.011	
Mexican spotted owl *S. o. lucida*			
Arizona	0.179 ± 0.081	0.814 ± 0.050	Seamans, Gutiérrez, May & Peery 1999
Mexico	0.109 ± 0.041	0.832 ± 0.029	
Northern spotted owl *S. o. caurina* (meta-analysis of 11 study areas)	0.258 ± 0.036	0.844 ± 0.003	Burnham, Anderson & White 1996

Franklin & LaHaye 1995). This has resulted in extensive studies of the three subspecies of spotted owl, for which survival estimates have been published (Table 5). The spotted owl is about 25% larger in wing length than the tawny owl in our study. Nevertheless, the survival rates we have reported for adult and yearling (control group) tawny owls correspond closely to those for spotted owls of the same age (see Table 5).

The effect of radio tags on juveniles

Radio telemetry is being used increasingly to understand what happens to individual owls between leaving their natal territories and being recruited into the breeding population (Petty & Thirgood 1989, Rohner 1996, Rohner & Hunter 1996, Coles & Petty 1997, Miller et al. 1997, Ganey et al. 1998, Overskaug et al. 1999). Natal dispersal, settlement patterns, pre-breeding survival and the role played by non-territorial 'floaters' in population regulation are some of the least known aspects of owl ecology. However, we are not aware of any study that has tested the safety of using radio tags on nestling or fledgling owls. The approach we used was to test if radio tags affected the chance of owls being recruited into the breeding population. We considered this a crucial test

of fitness, as survival to first breeding is the greatest challenge facing most individuals; with mortality rates being higher during this period than later in life. Our results indicate that radio-tagging had an adverse effect on juvenile survival rates, which were 6-11 times lower in treatment than in control groups (see Tables 4 & 5), and importantly, we were able to discount either rearing conditions or an imbalance of sexes in the treatment and control groups as factors biasing our results.

Another explanation for this difference between groups could be that radios deferred recruitment but did not affect survival. However, our results clearly indicated that this explanation was unlikely. Furthermore, none of the 1996 radio-tagged cohort were known to survive longer than 178 days post-fledging, and only one bird from the 1997 cohort survived to 299 days post-fledging, after which radio contact was lost (Coles 2000, Coles & Petty 1997). These data further supported the idea that different recruitment rates were due to greater mortality in the treatment group than in the control group, not just to recruitment being deferred in the treatment group.

We recorded no negative physical or behavioural effects of radio tags and envisage that the adverse effects

Table 6. Summary of radio-tagging studies of juvenile *Strix* owls; - indicates not recorded.

Species	Type of radio-tag[a]	Age when tagged[b]	No. tagged	No. found dead[c] (% tagged)	No. lost[d] (% tagged)	No. surviving to first spring (% tagged)	No. breeding (% tagged)	Source
Tawny owl	B	N	55	33 (60)	21 (38)	-	1 (2)	Current study
Tawny owl	B	N	12	11 (96)	0 (0)	-	-	Petty & Thirgood (1989)
Tawny owl	L	N	53	29 (55)	-	-	-	Overskaug et al. (1999)
Tawny owl	B	N	12	8 (67)	1 (8)	-	-	Sunde (1999)
Spotted owl	B	F	13	9 (69)	4 (31)	-	-	Gutiérrez et al. (1985)
Spotted owl	-	F	25	19 (76)	3 (12)	3 (12)	-	Miller & Meslow (1985)
Spotted owl	T	F	12	0 (0)	11 (92)	-	-	Arsenault et al.(1997)
Spotted owl	T	F	24	10 (42)	13 (54)	2 (8)	1 (4)	Ganey et al. (1998)
Spotted owl	T	F	31	20 (65)	11 (35)	3 (10)	-	Willey & van Riper (2000)

[a] B = back-mounted with harness; T = tail-mounted; L = leg-mounted.

[b] N = nestling, just before leaving the nest; F = fledging, caught after leaving the nest once feathers were fully grown.

[c] Main causes of mortality were predation and starvation.

[d] Contact was lost with owls due to radio failure, premature moulting of tail-mounted or bird dispersing outside the search area.

were linked to an increased weight burden that made birds less efficient at foraging and more vulnerable to predators, such as northern goshawks *Accipiter gentilis*, which were responsible for at least 10 deaths (C.F. Coles, unpubl. data).

Management implications

Our results demonstrated clearly a significant negative effect of fitting radio tags. This has implications for similar studies in the future, particularly on *Strix* owls. Previous research on dispersal in spotted owls also raised doubts about using radio tags on this age class, although tail-mounted tags were mostly used. Verner, McKelvey, Noon, Gutiérrez, Gould & Beck (1992) summarised results from a number of studies on juvenile dispersal in spotted owls that used radio-tagging. Only one juvenile out of 56 was subsequently found as a member of a mated pair, but it never nested. No control groups were used in these studies, but if accurate, populations would be unsustainable with such low recruitment rates. A review of other studies where juvenile tawny and spotted owls have been radio-tagged gave similar results, with high mortality rates and only one bird successfully breeding, although many studies did not monitor juveniles long enough to detect breeding (Table 6). Based on all these studies, we believe convincing evidence exists for not using back-mounted radio tags on this age class of *Strix* species. Similar conclusions may apply to the use of tail-mounted tags (see Table 6), but to our knowledge the impact of these tags has not been tested experimentally. Thus, we recommend that such research is undertaken. This is important, as the use of large numbers of radio tags on spotted owls, as advocated by Ganey et al. (1998), could have a serious effect on a species already under threat from forest fragmentation.

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