Meyburg, B.-U. & R. D. Chancellor eds. 1989 Raptors in the Modern World WWGBP: Berlin, London & Paris

Do Goshawks Accipiter gentilis need Forests? Some Conservation Lessons from Radio Tracking

Robert Kenward & Per Widén

ABSTRACT

Habitat conservation, including both habitat protection and habitat management, has an important role to play in preserving raptors. Whether protecting or managing habitats, it is important to discover what factors make them preferred. For instance, the habitats preferred by nesting raptors may happen to be those where human disturbance is least, but have been chosen because of high prey availability.

Goshawks have been described as birds of the northern forests. Indeed, Goshawks in boreal areas of Sweden showed a preference for hunting in stands of mature coniferous forest. They showed none for woodland edge zones, probably because their main winter prey was squirrels, which were distributed regularly throughout the habitat. In the more agricultural parts of Sweden the hawks preferred edge zones, probably because their main prey were most available there. Hawk range sizes were smallest where prey density was greatest, and were largest when they contained least woodland edge.

These and other observations indicate that the availability of prey, not that of woodland habitat, is the main factor which determines an area's suitability. Some land-use changes can be beneficial to Goshawks. Those who would conserve raptors should seek not merely to preserve the habitat that exists, but to understand what the raptors really need, so that unavoidable land-use changes can be managed in the best way possible.

INTRODUCTION

In this paper we will examine the use of habitat analysis as a tool for conserving raptors. We take as an example the Goshawk, a bird which supposedly "thrives best in extensive coniferous forest" (Brown 1976). It is an abundant species and has therefore been convenient to study, for political as well as practical reasons. However, the points we will make are probably most important, in terms of conservation, for rare raptors.

Habitat protection and habitat management

Growth and development of human populations cause land-use changes throughout the world. These changes affect raptors and other wildlife. Wildlife enthusiasts are accustomed to look at the negative aspects of these changes, and therefore try to prevent them. If there is a rare raptor found in a particular habitat, they may seek to have a large area of that habitat left untouched as a nature reserve. However, this protection of habitats, like that of species, is only one aspect of conservation.

Another approach is to learn what makes the particular habitat important for the species, and then to use this knowledge to ensure that the changed habitat is still useful for the species - or even better than the previous one! This second approach is one of habitat management. Habitat management has parallels in species management, when compared with the protection approach. Just as campaigns to prevent persecution of raptors can divert attention and funds from combating more important adverse effects such as pollution, so can campaigns to protect habitats. For example, it would be a mistake to spend large sums establishing reserves round raptor nesting sites if the prey-base was vanishing in the surrounding countryside. Like species management, habitat management requires research to determine what a species really needs for survival.

Why is a habitat?

The fact that a species tends to live in a particular habitat tells us that the habitat contains something important, but what is it? There are four main possibilities:

- (i) It may provide protection for the raptors' nests.
- (ii) It may provide cover for individual raptors against their predators.
- (iii) It may provide resources for the raptor's prey (food abundance).
- (iv) It may provide perch sites or cover without which the raptor cannot catch its prey (food availability).
 - If biologists can discover what is important about a particular habitat, careful management may enable utilisation of its resources by man without adverse effects on its raptors.

Nesting habitats

Many analyses of raptor habitat-use have been based on nest sites. The simplest are qualitative descriptions of the areas where nests are found, in terms of preferred terrain for nests in open country, or preferred tree species, density and height for forest species. Although this basic information is available for most temperate raptors, and those of open country, the nest and eggs have not been described at all for 57 of 111 rainforest species (52%), and only 1-2 nests are reported for 17 more (Thiollay 1985).

Multivariate statistical techniques, including Principle Component Analysis and Discriminant Function Analysis, are now being used to compare the nest area characteristics of different species (Titus & Mosher 1981; Andrew & Mosher 1982; Kostrzewa, this volume). However, care must be taken in the interpretation of such data for conservation purposes, because observed relationships may not be causal and, even if they are, they may not represent major restraints. For example, a tendency for birds to shun areas near man may not mean that they suffer from disturbance there but that man's activities adversely affect their prey base. Even if the effect is caused by disturbance, the sites near dwellings may merely be less preferred when many other sites are available, and be used successfully if birds are constrained to them.

Further evidence of the causality and importance of a factor can be provided by analyses of nest success, but again the data must be treated with caution. Bald Eagle (*Haliaeetus leucocephalus*) nests are least successful near human dwellings, but not necessarily because of disturbance (McEwan & Hirth 1979; Andrew & Mosher 1982). The individuals using these sites may simply be less experienced breeders. Other analyses have produced conflicting results. For instance, the occupancy of Merlin (*Falco columbarius*) nests could be predicted with 90% certainty from vegetation characteristics within 4km of the nests, but the success of each attempt was not significantly related to these characteristics (Bibby 1986). Analyses of nest success in different habitats may be the most useful for showing that particular factors are not important for a species. Thus, Newton *et al.* 1981 showed that limited re-afforestation had no serious adverse effect on Red Kites (*Milvus milvus*).

Perhaps the best positive evidence of causality, and for the importance of a particular factor, is obtained by comparing nest densities from areas which differ in the extent of a factor. For example, Sparrowhawks (*Accipiter nisus*) in Britain nest most densely at low altitude, where land is most productive and, perhaps most importantly, where song-bird densities are highest (Newton *et al.* 1977; Newton *et al.* 1986). Only field experiments could prove that song-bird densities determine Sparrowhawk densities, but the correlative evidence does provide strong support for the hypothesis.

Hunting habitats

To find the important elements of hunting habitats, one needs to know exactly where raptors hunt, and their hunting success in each place. Early studies described relationships between habitat and hunting success for species which could be seen easily because they forage in open country (Wakeley 1974, 1979; Warner & Rudd 1975; Tarboton 1978; Shrubb 1980; Mendelsohn, this volume). Visual techniques are still suitable for such species, but it is important to be sure that the results are not biased in favour of observations in the most conspicuous sites.

An important advantage of radio tagging over purely visual techniques is the opportunity to avoid visibility bias. Known individuals can have their positions sampled systematically and not merely when they happen to be seen. The home ranges of Kestrels (*Falco tinnunculus*), for example, were larger when determined by radio tracking than when the same birds are located by wing-tags alone (Village 1982), and the winter diet of Goshawks (*Accipiter gentilis*) was very different when recorded by radio tracking than when kills were found by eye alone (Ziesemer 1981). Radio tagging has now been used to study habitat use in a wide variety of raptors (e.g. Platt 1973; Dunstan 1979; Petersen 1979; Marquiss & Newton 1982; Bechard 1982; Holtzhuijzen *et al.* 1985), and automatic recording has been used for a few species with relatively small ranges (Fuller *et al.* 1974; Fuller 1979). For secretive species, like the Goshawk, radio tagging is the only way to study hunting habitats systematically.

METHODS FOR RECORDING GOSHAWK HABITAT USE

Study areas

The four study areas were in central Sweden. Three were woodland-farmland areas, at the estates of Frötuna, Gúddeholm and Segersjö in the boreo-nemoral region of Sweden (Sjörs 1985), in relatively flat country at 10-85m above sea level. These areas contained 41-61% of woodland, dominated by mature conifers but with some birch and other deciduous trees, well broken by arable farmland. Lakes edged by reed-beds formed 5-10% of these areas. At Frötuna there was an artificial abundance of Pheasants (*Phasianus colchicus*), which were released in late summer for shooting. The fourth study area was in continuous coniferous forest, in the boreal forest region of Sweden (Sjörs 1965), at Grimsö Wildlife Research Station. Of this area, at 75-100m above sea level, 74% was forest, strongly dominated by conifers but with a greater variety of age classes than in the woodland-farmland areas as a result of more intensive forest management. Bogs and fens comprised 18% of this area, and only 3% was arable farmland.

Radio tagging and tracking

Goshawks were caught in box-traps baited with live pigeons (Kenward *et al.* 1983), and marked with 12-20g radio tags, sewn dorsally to two rectrices with the main antenna attached along the shaft of one feather (Kenward 1978). Habitat-use data were obtained between August and February (i.e. outside the breeding season) from 5-9 hawks at the three woodland-farmland study areas, and from 43 hawks in the boreal forest area.

Radio fixes were obtained by triangulation. Bearings were taken with a three-element hand-held Yagi, usually from within 2km, at the woodland-farmland sites. The hawks were located systematically at mid-morning, mid-day, mid-afternoon and at roost. In the boreal forest area, bearings were usually taken from within 3km, using a 6-element Yagi mast-mounted on a mini-bus (Cederlund *et al.* 1979). Hawks were usually located 1-4 times a day, but at hourly intervals in some months (further details in Widén 1985a). Fixes were recorded on a 100m grid for habitat assessment, although a few of the most distant ones may have been in error by more than 100m.

Data analysis

We compared habitat use with habitat availability at two levels. Planimetry and random positions were used to estimate the availability of woodland and woodland edge on maps of land-use. The percentage of land with these habitats was then compared:

- (i) with the percentage of these habitats within hawk range outlines, to see whether hawks chose to live in atypical areas, and
- (ii) with the percentage of these at range fixes, to see whether hawks tended to perch preferentially in particular habitats.

Assuming that the time interval between fixes is sufficiently long for animals to have traversed

several habitat patches, fixes may be taken as statistically independent for testing the preferences of individual animals. Our observations conformed with this criterion, since hawks typically flew at 2-4 minute intervals while hunting, and typically covered at least 100m per flight (Kenward 1982; Widén 1984), thus covering a minimum distance of 1500m in the minimum interval between fixes (1 h). Our analysis excludes consecutive fixes at the same site, where hawks had killed or were resting, and roost positions: it is an analysis of hunting locations.

RESULTS

In the three woodland-farmland areas, the hawks showed a strong preference for perching in woodland (Chi-square tests, P < 0.001). Although woodland was 41-46% of the three areas, and a very similar proportion (40-62%) of their home ranges, no less than 80% of fixes were recorded in woodland (Table 1). In the boreal-forest area the preference for woodland was relatively weak but there was a strong preference for the mature forest: only 24% of the land area was mature conifers, but 44% of hawk fixes were there (P < 0.001).

Table 1: Perch and kill locations of radio-tagged Goshawks

Study area	No. of hawks	No. of fixes	% of on map	woodland in ranges	% of fixes in woodland	No. of kills	% of kills in woodland
Boreal							
forest	43	1108	76	not done	77	59	81
Farmland							
- woodland:	9	813	41	40	85	62	90
	5	165	52	48	80	30	77
" with							
released							
pheasants	9	381	61	62	84	81	99

In the woodland-farmland areas the hawks also had a strong preference for hunting within 200m of edge zones (P < 0.001). They were found there about twice as often as expected from the availability of the edge zones (Table 2).

	% on map		% of fixes		% of kills			
Study area	0-200m from edge	>200m from edge	0-200m from edge	>200m from edge	0-200m from edge	>200m from edge		
Boreal							_	
forest	34	32	37	34	38	38		
Farmland								
- woodland:	31	9	75	10	80	10		
	34	14	76	7	61	16		
" with								
released								
pheasants	35	27	73	8	99	0		

Table 2: Perch and kill locations of radio-tagged Goshawks in woodland

In the boreal forest area there was no preference for edge zones. Hawks also tended to hunt most in the largest patches of mature forest, which had relatively less edge than the smaller plantations. The habitat use was similar for both hawk sexes in all cases (see also Widén 1985a; Kenward 1982).

Kills were made in woodland more often than expected from the habitat use for three of the four areas (Table 1). The difference was significant (P < 0.001) for the area with released pheasants. Kills were also made at woodland edge more frequently than expected in the area with released pheasants, and this was the area where hawks most strongly avoided hunting in woodland which was beyond the edge zones (P < 0.001). In the boreal forest area there was no tendency for kills to be made disproportionately at edge zones.

As well as the differences between study areas in habitat preferences, there were also differences in the hawks' prey (Table 3). Squirrels (*Sciurus vulgaris*) were killed far more frequently than any other species in the boreal forest and provided 56% of the prey biomass there. Pheasants were almost the only prey in the area where these were released. The hawk diet did not differ significantly between the other two woodland-farmland areas; squirrels provided only 15% of the biomass for male hawks, whose food intake was dominated by pheasants, and only 10% of the food for females, which obtained nearly four times as much from Brown Hares (*Lepus europaeus*).

The size of hawk ranges was smallest, averaging 20km^2 , where pheasants were released. They averaged 45km^2 for the other two farmland-woodland areas and 57km^2 in the boreal forest. Ranges in each woodland-farmland area tended to have a constant area of woodland edge, such that this was a smaller percentage of the larger ranges. Where pheasants were released, ranges contained an average 5km^2 of woodland edge, much less than the $10-17 \text{km}^2$ in the other areas.

DISCUSSION

Goshawk predation can be a problem for poultry farmers and game conservers. Habitat management therefore tends to be aimed at reducing their presence rather than benefiting them, one approach being to remove trees which provide hunting perches at game food sites (e.g. Mekkelsen 1984). It is the rarer raptors for which habitats have been protected, or managed by creating new nests and hunting perches (Nelson & Nelson 1977; Olendorff & Kochert 1977; reviews in Saurola 1978; Newton 1979), and whose behaviour has been modified to encourage the use of different habitats (Cade & Temple 1977; Temple 1978, Saar & Gerriets in press). Nevertheless, if the aim were to preserve Goshawks, would one seek to prevent human exploitation of the extensive northern forests? The differences in use of woodland edge between the boreal and woodland-farmland areas most probably reflected prey availability. For boreal forest hawks, squirrels would have been most common in mature woodland and relatively evenly distributed through it (Lemnell, pers. comm.), so that the hawks would have obtained relatively little advantage by favouring the edges. Moreover, the larger the patch, the more squirrels which might be found without the need to fly some distance to another patch. Deciduous woodland, as found in many of the smaller woods and copses (i.e. seldom more than 200m from edges) is one of the preferred habitats for Brown Hares in England (Tapper & Barnes 1986), and pheasants are usually found there too. Although hares forage in the open fields at times, they are probably most vulnerable to surprise attacks when in or near woodland edges, and that is where they were usually killed.

These results suggest that food was the main factor determining habitat use by Goshawks (given adequate hunting perches). Further support for this hypothesis was provided by the area where food abundance was "experimentally" enhanced at woodland edges by pheasant releases. This was the area where hawks were least often deep in the woods. Moreover, range sizes were much the smallest there, and contained least of the preferred habitat. It may be that hawks cover sufficient of the most prey-rich habitat to meet their food requirements, with range size then being the area which happens to contain that quantity of preferred habitat (Kenward 1982). On that basis, each Goshawk probably requires 10-20km² of optimal habitat for its range in areas with a prey-base like that of central Sweden.

There is further evidence that Goshawks thrive best in areas with more food and less woodland than in the boreal forest. The Goshawk breeding density in the boreal forests round Grimsö was about 3 pairs/100km² (Widen 1985b), rather higher than the 1-2 pairs/100km² found in the boreal forests of northern Sweden (Nilsson 1981), but less than the 4-5 pairs/100km² found in woodland-farmland areas of Sweden and Finland (Douhan 1979; Wikman 1977). An even higher density, 6.5 pairs/100km², occurs on the large Baltic island of Gotland (Kenward, Marcström & Karlbom, unpublished), where Rabbits (*Oxyctolagus cunniculus*) form an important addition to the winter diet. In Germany, where Rabbits are supplemented by abundant feral Pigeons (*Columba livia*) as winter food, densities can reach 10 pairs/100km² in areas where well-fragmented woodland is a mere 12-15% of the land area (Bednarek 1975).

We conclude:

(i) that habitat conservation for raptors should be based not merely on observed habitat preferences, but also on the reasons for the preferences. If habitat use depends on food supply, then conservation of the food is at least as important as conservation of the habitat alone.

- (ii) that habitats and prey favoured in one area may not be the most important ones elsewhere. Studies in a variety of areas are necessary to define general conservation priorities.
- (iii) that landscape alterations by man may not always disfavour raptors. They can also improve raptor food supplies and hunting opportunities.

	Boreal forest	Woodland-farmland	Woodland-farmland with released pheasants
Squirrels	7 9%	33%	1%
Hares	3%*	14%**	0%
Other mammals	s 0%	3%	0%
Game birds	10%+	28% ++	96%+++
Other birds	8%	22%	3%
Total number	61	127	93
* 2 <u>Ler</u> ** 18 <u>Ler</u>	pus timidus pus europaeus		,
+ 3 Ha: 1 Caj ++ 29 Pho	zel Grouse (Bonasa percaillie (Tetrac easant (Phasianus	a bonasia), 2 Black Grou o urogallus) colchicus), 6 Grey Part	se (<u>Tetrao tetrix</u>), ridge (<u>Perdix perdix</u>)
(See also Ker	nward et al. 1981	<u>colcnicus</u>) L; Widén 1987)	

Table 3:	Prev taken	by radio-tagged	Goshawks in	central	Sweden	during winte
----------	------------	-----------------	-------------	---------	--------	--------------

REFERENCES

ANDREW, J. M. & J. A. MOSHER 1982. Bald Eagle nest site selection and nesting habitat in Maryland. J. Wildl. Manage. 46, 383-90.

BECHARD, M. J. 1982. Effect of vegetative cover on foraging site selection by Swainson's Hawks. *Condor* 84, 153-9. **BEDNAREK, W. 1975.** Vergleichende Untersuchungen zur Populationsökologie des Habichts (*Accipiter gentilis*): Habitatsbesetzung und Bestandsregulation. *Deutscher Falkenorden* (1975), 47-53.

BIBBY, C. J. 1986. Merlins in Wales: site occupancy and breeding in relation to vegetation. J. Appl. Ecol. 23, 1-12. BROWN, L. 1976. British Birds of Prey. Collins, London.

CADE, T. J. & S. A. TEMPLE 1977. The Cornell University falcon programme. In: Chancellor, R. D. (ed) Proceedings of the World Conference on Birds of Prey. ICBP.

CEDERLUND, G. & P. A. LEMNELL 1980. A simplified technique for mobile radio tracking. In: Amlaner, C. J. & Macdonald, D. W. (eds) A Handbook of Biotelemetry and Radio Tracking. Pergamon Press, Oxford.

DOUHAN, B. 1979. Duvhöken i Roslagen. Faglar i Uppland 6, 47-53.

DUNSTAN, T. C. 1979. Snake river birds of prey natural area. Nature Conservancy News 29, 19-21.

FULLER, M. R. 1979. Spatiotemporal ecology of four sympatric raptor species. Ph.D. thesis, Univ. Minnesota.

FULLER, M. R., T. H. NICHOLLS & T. R. TESTER 1974. Raptor conservation and management applications of biotelemetry studies from Cedar Creek Natural History Area. *In:* Hamerstrom, F. N., Harrell, B. E. & Olendorff, R. R. (eds) *Management of Raptors.* Raptor Research Foundation.

GERRIETS, D. & C. SAAR. 1987. Hacking back Peregrines in North Germany. pp. 121-132 in D. J. Hill (ed.). Breeding and Management in Birds of Prey. Univ. of Bristol.

HOLTZHUIJZEN, A. M. A., L. OOSTERHUIS & M. R. FULLER 1985. Habitat use by migrating Sharp-shinned Hawks at Cape May Point, New Jersey, U.S.A. *In:* Newton, I. & Chancellor, R. D. (eds) *Conservation Studies of Raptors.* ICBP Tech. Publ. No. 5.

KENWARD, R. E. 1978. Radio transmitter tail-mounted on hawks. Orn. Scand. 9, 220-3.

KENWARD, R. E., V. MARCSTRÖM & M. KARLBOM 1981. Goshawk winter ecology in Swedish pheasant habitats. Journal of Wildlife Management 45: 397-408.

KENWARD, R. E. 1982. Goshawk hunting behaviour and range size as a function of food and habitat availability. J. Anim. Ecol. 51, 69-80.

KENWARD, R. E., M. KARLBOM & V. MARCSTRÖM 1983. The price of success in Goshawk trapping. Raptor Res. 17, 84-91.

KOSTRZEWA, A. (this volume). Nest habitat separation of three European raptor species (*Buteo buteo, Accipiter gentilis* and *Pernis apivorus*) - a multivariate analysis.

MARQUISS, M. & I. NEWTON 1982. Habitat preferences in male and female Sparrowhawks Accipiter nisus. *Ibis* 124, 324-8.

McKEWAN, L. C. & D. H. HIRTH 1979. Southern Bald Eagle productivity and nest site selection. J. Wildl. Manage. 43, 585-94.

MIKKELSEN, J. D. 1984.Effect af duehøge og andre rovfugle ved fasanudsaetningssteder. Special report, Viltbiologisk Station Kalø.

NELSON, M. W. & P. NELSON 1977. Power lines and birds of prey. In: Chancellor, R. D. (ed) Proceedings of the World Conference on Birds of Prey. ICBP.

NEWTON, I. 1979. Population Ecology of Raptors. Poyser, Berkhamsted.

NEWTON, I., M. MARQUISS, D. N. WEIR & D. MOSS 1977. Spacing of Sparrowhawk nesting territories. J. Anim. Ecol. 46, 425-41.

NEWTON, I., P. E. DAVIS & D. MOSS 1981. Distribution and breeding of Red Kites in relation to land-use in Wales. J. Appl. Ecol. 18, 173-86.

NEWTON, I., I. WYLLIE & R. MEARNS 1986. Spacing of Sparrowhawks in relation to food supply. J. Anim. Ecol. 55, 361-70.

NILSSON, S. G. 1981.De svenska rovfagelbestandets storlek. Vår Fågelv. 40, 249-62.

OLENDORFF, R. R. & M. N. KOCHERT 1977.Land management for the conservation of birds of prey. In: Chancellor, R. D. (ed) Proceedings of the World Conference on Birds of Prey. ICBP.

PETERSEN, LeR. 1979. Ecology of Great Horned Owls and Red-tailed Hawks in southeastern Wisconsin. Wisc. Dept. Nat. Res. Tech. Bull. 111.

PLATT, J. B. 1973. Habitat and time utilisation of a pair of nesting Sharp-shinned Hawks (Accipiter striatus velox) - a telemetry study. M.Sc. thesis, Brigham Young Univ.

SAUROLA, P. 1978. Artificial nest construction in Europe. In: Geer, T. A. (ed) Bird of Prey Management Techniques. British Falconers' Club.

SHRUBB, M. 1980. Farming influences on the food and hunting of Kestrels. Bird Study 27, 109-15.

SJÖRS, H. 1965. Forest regions. In: The plant cover of Sweden. Acta Phytogeographica Svecica 50, 48-63.

TAPPER, S. C. & R. F. W. BARNES 1986. Influence of farming practice on the ecology of the Brown Hare (*Lepus europaeus*). J. Appl. Ecol. 23, 39-52.

TARBOTON, W. R. 1978. Hunting and energy budget of the Black-shouldered Kite. Condor 80, 88-111.

TEMPLE, S. A. 1978. Manipulating behavioural patterns of endangered birds. In: Temple, S. A. (ed) Endangered Birds: Management Techniques for Preserving Endangered Species. Univ. Wisconsin Press, Madison.

THIOLLAY, J. M. 1985. Falconiforms of tropical rainforests: a review. In: Newton, I. & Chancellor, R. D. (eds) Conservation Studies of Raptors. ICBP Tech. Publ. No. 5.

TITUS, K. & J. A. MOSHER 1981. Nest-site habitat selected by woodland hawks in the central Appalachians. Auk 98, 270-81.

VILLAGE, A. 1982. The home range and density of Kestrels in relation to vole abundance. J. Anim. Ecol. 51, 413-28. WAKELEY, J. S. 1974. Activity periods, hunting methods, and efficiency of the Ferruginous Hawk. Raptor Res. 8, 116-19. WARNER, J. S. & R. L. RUDD 1975. Hunting by the White-tailed Kite (Elanus leucurus). Condor 77, 226-30.

WIDÉN, P. 1984. Activity patterns and time budget in the Goshawk Accipiter gentilis in a boreal forest area in Sweden. Orn. Fenn. 61, 109-12.

WIDÉN, P. 1985a. Habitat utilization of the Goshawk in a boreal forest area of Central Sweden. In: Population ecology of the Goshawk (Accipiter gentilis) in the boreal forest. Ph.D. thesis, Univ. Uppsala.

WIDEN, P. 1985b. Breeding and movements of Goshawks in boreal forests in Sweden. Holarctic Ecology 8, 273-9.

WIDÉN, P, 1987. Goshawk predation during winter, spring and summer in a boreal forest area of Central Sweden. *Holarctic Ecology* 10 (in press).

WIKMAN, M. 1976. Duvhökspredation pa skogsfagel i sydvästra Finnland. Viltrapport 5, 59-72.

TIESEMER, F. 1981.Methods of assessing Goshawk predation. *In:* Kenward, R. E. & Lindsey, I. M. (eds) *Understanding the Goshawk*. Int. Assoc. Falconry & Cons. Birds of Prey.

Robert Kenward Institute of Terrestrial Ecology Furzebrook Research Station Wareham BH20 5AS, U.K.

Per Widén Grimsö Wildlife Research Station 770 31 Riddarhyttan Sweden

