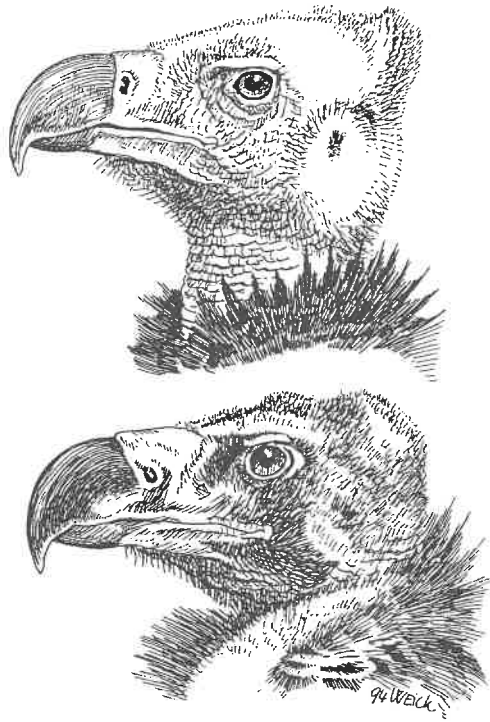


Part 4

Trapping, Marking and Radio-tagging Techniques



White-headed Vulture *Trigonoceps occipitalis* and
European Black Vulture *Aegypius monachus*

Conveners:

R. Bögel & Dr. R. Kenward

The Systematic Study of Radio-Tagged Raptors: I. Survival, Home-range and Habitat-use.

R.E. Kenward and S.S. Walls

SUMMARY

Studies which use radio-tagging frequently fail to provide worthwhile quantitative data, often because there is inadequate planning of data collection and analysis. We review techniques for obtaining and handling data on survival and movements of radio-tagged raptors, using examples from recent studies of Northern Goshawks (*Accipiter gentilis*) and Common Buzzards (*Buteo buteo*).

Survival monitoring requires (i) unbiased tagging of many individuals, (ii) long detection range, with aircraft always necessary (and able to compensate to some extent for low tag output), and (iii) reliable tags. Data from studies of 350 radio-tagged Goshawks and 60 Buzzards are used to show recent improvements in tag reliability and tagging techniques. Harness-mounted backpacks appear safe for long-life radio tagging of broadwinged species (buzzards, eagles), if fitted (i) very carefully and (ii) at times when birds can habituate without risk, ideally just before fledging. Survival of these raptors was higher than expected in the first year, indicating that healthy populations have a large non-breeding component.

Analysis of location data is best based on large samples of birds. Tracking effort can be reduced by analysing at an early stage to minimise the numbers of fixes/bird. RANGES IV software is used to demonstrate this process and to test for evidence of territoriality of Goshawks in an area with released pheasants. Goshawk data are used to illustrate new tests of habitat use, and there are suggestions for how radio-tagging can determine parameters of individual performance (PIPs) for use in future conservation programmes.

INTRODUCTION

Raptors have now been studied by radio-tagging for three decades, starting with work on eagles in North America (Southern 1964). Much of the early work was essentially qualitative, describing behaviour in small numbers of birds. Such descriptions can still be useful, for example if radio-tagging helps to record breeding and foraging habits of species which live so sparsely or in such

impenetrable habitats (eg rainforests) that they remain unstudied. Such work is enjoyable, combining the use of sophisticated technology with the ability to find and observe birds that are not accessible to other ornithologists. However, if the studies remain essentially descriptive, they are in danger of becoming a bird-watching indulgence, without contributing the quantitative data which should be used, for example, in conservation programmes. In an early review of publications on radio-tagging, Lance & Watson (1980) concluded that the technique "seldom exploited its full potential . . . due less to drawbacks in the equipment than to how the technique has tended to be used". A decade later, many studies still fail to achieve their full potential because of problems with the collection and analysis of data, especially location data (Harris *et al.* 1990).

In the early years, radio tags and attachment techniques were often unreliable and each person was obliged to develop new field techniques. Analyses typically involved polygons drawn on transparent plastic, and the weighing of paper cut-outs unless a planimeter was available. By 1992, however, the availability of reliable tags, and of information on field-techniques suitable for computerised display and analysis (Macdonald & Amlaner 1980; Kenward 1987; Garrott & White 1990), provide little further excuse for not gathering worthwhile quantitative data. In this and our subsequent paper (Walls & Kenward, this volume), we briefly review recent advances in the collection and analysis of data from radio-tagging, and end with some suggestions to help future projects bring results in line with expectations.

SURVIVAL AND PRODUCTIVITY

Data on survival and productivity of raptors have been especially important for monitoring effects of environmental contamination (Newton 1979), or for making predictions about other population changes (Mueller, Berger & Allez 1977). Understanding how survival and breeding are affected by environmental parameters is also important for population models to predict the effects of habitat modification or climate change. Data on productivity can be gathered by visiting nests, at which time the young can also be ringed for subsequent estimation of survival and dispersal rates. However, the rarity of many raptors means that relatively few are ringed, and it can therefore take many years to accumulate enough ring recoveries for survival analyses, even if all the records for a country are added together.

In the whole of Britain and Ireland, for example, only 5 of 19 diurnal raptor and owl species have provided more than 30 ring recoveries in each of the last three years, with only Sparrowhawk, Kestrel, Barn Owl and Tawny Owl providing enough data to consider a study of variation in first-year survival rates (Table 1).

Table 1 The mean numbers of raptors ringed, and recovered, in Britain and Ireland each year, 1988-1990 (data from Mead and Clark 1989, 1990, 1991).

Species	N ringed	N recovered
Hen Harrier <i>Circus cyaneus</i>	338	17
Sparrowhawk <i>Accipiter nisus</i>	1892	188
Common Buzzard <i>Buteo buteo</i>	298	17
European Kestrel <i>Falco tinnunculus</i>	1956	134
Merlin <i>Falco columbarius</i>	741	42
Peregrine Falcon <i>Falco peregrinus</i>	337	26
Barn Owl <i>Tyto alba</i>	1093	156
Tawny Owl <i>Strix aluco</i>	1147	71
Total*	8678	(8%) 692

*Also includes: Red Kite *Milvus milvus* (46,3), White-tailed Eagle *Haliaeetus albicilla* (5,1), Marsh Harrier *Circus aeruginosus* (50,0), Montagu's Harrier *Circus pygargus* (21,0), Northern Goshawk *Accipiter gentilis* (171,6), Golden Eagle *Aquila chrysaetos* (45,1), Osprey *Pandion haliaetus* (59,4), Hobby *Falco subbuteo* (36,2), Little Owl *Athene noctua* (195,9), Long-eared Owl *Asio otus* (134,8), Short-eared Owl *Asio flammeus* (114,7).

Despite the exceptional ringing effort in Britain, where the British Trust for Ornithology now supervises the ringing of more than 800,000 birds each year, there are inadequate data to study annual variations in the survival rates of large raptors. Another problem is the possibility of recovery bias in favour of ringed raptors which hit human constructions or are killed deliberately. Since young and inexperienced raptors are not only more frequently trapped or shot at game farms than adults (Marcström & Kenward 1981), but may also be more prone to accidents, ring recovery may be more likely from juveniles than from adults, which die in the wilder areas. Such bias could lead to over-estimation of first-year mortality rates, which were at or above 60% in 17 of 26 analyses for 13 species of diurnal raptor (Newton 1979). A similar bias would result from ring loss by older birds, which has occurred among German and Swedish Goshawks (Ziesemer 1981; unpublished data).

Radio-tagging provides an alternative to ringing for gathering data on survival. Its potential was realised during the 1970s for release schemes, for example of Peregrines in North America and Goshawks in Britain (Sherrod *et al.* 1981; Kenward, Marquiss & Newton 1981), and more recently for the study of wild raptors. Between 1980 and 1987 in Sweden, 352 Goshawks were radio-tagged in a 650 km² area on the Baltic island of Gotland, an average of 50/year of which about 30/year were young hawks at nests (Marcström, Kenward & Karlbom 1990). Similarly, in 1990-91 we have radio-tagged 58 young Buzzards at nests in 150 km² of Dorset in southern Britain. In the Goshawk study, tags weighing 14g transmitted for 9-10 months, and could be detected up to 20 km away (although detection was at 2-6 km during most tracking). The Buzzard tags made in 1991 weigh 25g, have an expected life of about four years, and can be detected at 40 km, a more than fourfold improvement in performance. This means that when contact is lost with dispersing birds, an area of about 10 000 km² can now be searched with a light aircraft in two hours (Figure 1), which is about half the time it took to search the 3 000 km² island of Gotland. Tracking techniques and tag reliability have improved to the extent that only 4 of 51 Buzzards tagged in 1990 and 1991 remained lost in the following April (Table 2).

Figure 1 Movements of juvenile Buzzards radio-tagged in Dorset, southern England, showing aircraft flight paths in searches for lost birds on 21.09.90 (1½ hours), 13.12.90 (2½ hours covering all of SW Britain) and 15.01.91 (2 hours).

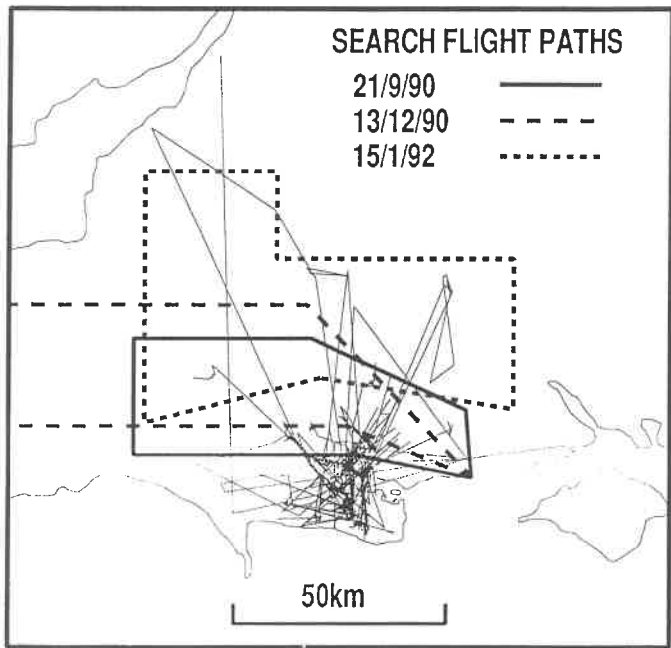


Table 2 The fate of long-life radio tags during the first and last two years of the Goshawk study on Gotland, and of the first two years of the Buzzard study in Dorset.

Years	N Tagged	Known to fail	Shed	Lost	Tracking completed†
1980-1	69	6	4	38	22 (32%)
1983-4	78	0	16	18	44 (56%)
1990-1	51	0‡	1	4*	46 (90%)

† Tracking was completed for birds that died or whose tags lasted at least to the next spring.

‡ Two faulty tags give intermittent signals, but can still be monitored.

* Three of the four lost birds are known emigrants, the other probably emigrated

There are, however, complications when using radio-tagging to monitor survival. An essential consideration, for reasons of animal welfare as well as scientific rigour, is that the tagging should not itself influence survival. The only satisfactory technique for long-term tagging of raptors is the use of back-packs on body harnesses, but this technique itself has been shown to bias behaviour and fitness in a number of bird studies (review by White and Garrott 1990). No such effects have been reported for tail-mounted tags, but these are shed at the next moult, and the antennas on leg tags seldom survive more than a few months. During 1990 and 1991, we have monitored the survival of 35 Buzzards with harnesses and 22 which were equipped initially with 12g leg-tags and later with 15g tail-mounts. We used a harness design of Dunstan (1972), with Teflon ribbon (recommended by M. Fuller), in which a 1/4" strap round the body behind the wings was joined to a 10% larger neck loop by a short strap of 3/8" Teflon along the keel. The tail-mounts were similar to those which had no detectable adverse effect on Goshawks (Kenward 1985).

The mortality of birds with tail-mounts has been 38% (SE=16%) to the end of their first March (after which the tags moulted or exhausted their cells), compared with 27% (SE=8%) for birds with harnesses. Mortality of Buzzards with harnesses was still 27% after a year, which is half the 51-57% first-year mortality estimated for Buzzards by ringing (Mebs 1964; Olsson 1958). Moreover, mortality of only about 10% in the first year has been recorded by Chandler *et al.* (this volume) for Bald Eagles (*Haliaeetus leucocephalus*) with similar harnesses, and by Nygård, Envik and Kenward (unpubl.) for Sea Eagles (*Haliaeetus albicilla*). It therefore seems safe to mount back-packs on nestling broadwinged raptors, which have plenty of time to adjust to the harness before they become independent, and can then have their survival and behaviour monitored for several years.

This is an encouraging finding, but does not necessarily mean that it is safe to put harnesses on all raptors, without at least a pilot study to compare with a safer technique, such as tail-mounting.

Moreover, it is essential that harnesses are very carefully fitted. In Buzzards, variation of only five percent above or below the ideal size of harness loops was found to cause loss of feathers or even chafing of skin on the back. Those who are not familiar with mounting harnesses on raptors must have someone with experience to help them get started.

With equal ability to tag all nestlings, or birds in release projects, it is possible to avoid the marking bias which may occur if birds are trapped. There may, for example, be selection of the better adults if trapping is at nests, or of the hungrier individuals elsewhere. In the Goshawk study, it was possible to catch almost all the birds. Of 187 individuals targeted for capture in the post-fledging period, to attach tail-mounts when their feathers were full grown, only 18 (10%) were not caught (in most cases because trapping was not attempted at some nests where birds were already equipped with leg-mount tags). In contrast, of 31 Buzzards targeted for tail-mounts at the same stage, 15 (48%) could not be caught ($\chi^2=28.2$, $P<0.001$), despite trapping for up to two weeks near some nests. Since trapping was easiest with the hungriest broods of Buzzards (with feather fret marks) and youngest birds in a brood, we were probably selecting the weaker ones for tail-mounts. This would explain why these had higher mortality and more tendency to disperse than Buzzards with back-packs.

A complication in estimating survival with radio tags, shown in Table 2, is that contact may be lost with a high proportion of tags. If such birds were omitted from the analysis, survival estimates would be biased downwards, because some individuals might have lived for many

months before being lost. The solution to this problem is to estimate overall survival as the product of survival in many consecutive small intervals, using only the birds that died or survived through an interval to estimate survival in that interval. The survival of lost birds is then included for all intervals before the one in which they are lost, at which point they are omitted (censored) from further estimates. This approach, which also makes provision for tagged animals to enter the population at different times, is described thoroughly by Pollock *et al.* (1989), with another useful recent review in White & Garrott (1990).

There remains, however, the problem of what happens to censored individuals. If some are lost because of a traumatic death which also destroys the tag (*eg* impact from a vehicle or lead shot), then censoring overestimates the true survival. There is a way round this problem if there are (i) resightings and recoveries of animals from which signals were lost, and (ii) if tags that were known to fail without prejudice to survival can be separated from tags lost inexplicably. This is done in Table 2: birds whose tags were heard to be failing (*eg* the signal became slow or erratic before contact was lost), or which shed tail-mounts, are separated, in columns two and three respectively, from tags whose signal was lost without explanation. Among all the juvenile Goshawks, the former category included 70 birds which moulted their tags, or for which signal changes indicated that tags were failing; 17 (24%) of these were later recaptured or found dead. There were also 68 tags that were lost without explanation; 16 (24%) of these were recorded again well after the loss. There was thus no evidence of a reduced recovery rate for hawks that were lost inexplicably. They must therefore have been lost mainly because of undetected failures, and not because hawks and their tags were destroyed at the same time. The observed survival rates (with unexplained tag losses censored) could therefore be considered representative of the tagged cohort.

In the case of the Buzzards, only four were lost. Since three were known emigrants, and the fourth disappeared (during a conference) in the peak period for emigration, it can reasonably be assumed that these were alive at the time of signal loss. The survival rate, with these four birds censored, can again be considered representative.

In comparing radio-tagging with ringing for estimating survival, a final concern is the cost. For a fair comparison, the precision of the two techniques should be similar. The precision of a survival estimate with 50 radio-tagged birds is about the same as from 100 ring recoveries: the standard error is 4%. To have 50 radio-tagged raptors at the end of the year, with a 30% annual mortality, requires the marking of 70. For 100 recoveries, with an 8% recovery rate (Table 1), 1250 must be ringed. Except for raptors with very dispersed breeding sites, such as eagles, a skilled operator can track 35 birds annually for sedentary species, and this is comfortably above the 20 individuals/cohort considered by Pollock *et al.* (1989) to be the minimum for inter-cohort comparisons. Movements and survival can be recorded with a minimum of about two days of tracking per month for most of the year, increasing to two days per week for a month during autumn and spring when there are many dispersal movements. That totals 80 man-days over two years. With optimism, a team of two people might hope to find and ring or radio-tag six large raptors a day; they would need 393 workdays for ringing 1180 (= 1250 - 70) birds, or at least 313 more than for radio-tagging and tracking 70. Although more miles would be driven during radio tracking than during the ringing, with extra funds required for radio equipment (*ca.* £6 000 for tags) and hire of aircraft (in the order of 2-10 hours per year), labour costs would make radio-tagging the less expensive technique for projects in which ringing could not be done by volunteers.

Since the ringing of 1250 birds would require many years of work in one area, or spreading the work over a wide area if the species were common, radio-tagging may often be the more practical technique for gaining data rapidly on rare species, or for building models based on annual variation in weather and food supplies, which can be defined locally but not so precisely over a whole country. In Goshawks, too, ringing data from the same area were biased in favour of hawks killed at farms, and against recording natural deaths at the right time of year (Kenward, Marcström & Karlbom *in press*). Radio-tagging also provided data not available from ringing, for example by allowing dead hawks to be recovered quickly enough for a thorough *post mortem* examination, and by helping to find nests. The latter saved time which would otherwise have been needed for visual searches, and helped to detect nests in unusual sites. On Gotland, at least two nests were found in pinewoods which would normally have been considered too young. Radio tags can thus aid rational habitat management, in this case by removing the misconception that the Goshawks nest only in old-growth stands. Moreover, in population modelling it is important to record birds whose

breeding fails so early that their attempt might not otherwise have been detected.

Perhaps as a result of the bias in ringing, or increased tolerance of raptors and reductions in pollution, the population models obtained by radio-tagging may look rather different from those based on ringing records from earlier this century. Just as the first year mortality of Buzzards was half that estimated previously by ringing, so too the mortality of Goshawks, at 50% for males and 35% for females, was much lower on Gotland than in Fennoscandian ringing studies. Without human intervention, the juvenile mortality of medium-sized raptors may well lie between 20 and 30%. If so, then healthy populations of these species must have many more non-breeding adults than was previously realised. One implication for future conservation is that monitoring nests may give relatively late detection of environmental threats that do not affect reproductive success, because a large proportion of the population may have been lost before numbers of breeding pairs are reduced.

HOME RANGE AND HABITAT USE

Although radio-tagging has not yet been used widely for monitoring survival of wild raptors, many projects have used radio tags for short term studies of ranging behaviour and habitat use. Just as radio-tagging can minimise bias in carefully planned studies of survival and productivity, so too it enables locations and behaviour to be sampled systematically and not just when individuals happen to be most easily detected. The avoidance of bias is not merely of academic interest if, for example, visual sightings focus attention on the immediate surroundings of nests whereas the birds also need preservation of separate hunting areas where they are less easily seen. In creating reserves, there is a need for measurement both of range size and shape, because the latter shows which habitats are most abundant in the area covered by each bird and how much overlap occurs between individuals. Measures of range structure may be required too, for instance to see whether an apparently large range is composed of a small core area in which the bird does most of its foraging and a much greater area used only occasionally, and whether there is a single core or many separate patches, and what the spacing of range centres indicates about the social status of individuals.

One difficulty with estimating the size, shape and structure of home ranges is that there are at least six different analysis techniques, with further variations on each main theme. To be brief, these are summarised in Table 3, with more thorough reviews by Harris *et al.* (1990) and Kenward (1992).

Table 3 Some features of six different home range analysis techniques.

	Grid cells	Normal ellipsoids	Concave polygons	Convex polygons	Contour methods	Cluster analysis
Home range outlines conform well to all recorded fixes	Yes	No	Yes	Yes	No	Yes
Home range outlines conform well to multi-nuclear cores	Yes	No	No	No	Yes	Yes
A single home range centre is estimated	No	Yes	No	Yes	Yes	No
Home range structure statistics (patchiness or fix dispersion)	Yes	Yes	No	No	Yes	Yes
Home range size stabilises with fewer than 100 fixes	No	Yes	?	Yes	Yes	Yes

The grid cell approach (Siniff & Tester 1965) is used relatively infrequently, mainly because it usually requires more than 150 fixes, and sometimes 200-300, to obtain a record of home range

size which increases little if more fixes are added. Although ranges are still sometimes plotted as circles or ellipses (Jennrich & Turner 1969; Koepl, Slade & Hoffman 1975), the estimation assumes that animals distribute their movements about a single range centre, with activity reducing smoothly away from the centre. However, animals often lack a single range centre, at least outside the breeding season, and seldom conform to a statistically normal distribution of locations, so that circular or elliptical outlines usually conform poorly to the fixes (Macdonald, Ball & Hough 1980). Few studies have used concave (minimum area) polygons (Voight & Tinline 1980; Clutton-Brock; Guinness & Albon 1982), at least partly because it is hard to agree on rules for constructing them; their lack of core outlines or structure statistics is a further disadvantage.

Convex polygons are simple to plot and have therefore been used very widely, and thus have the advantage of compatibility with previous studies. They define a convenient limit to the area which may be visited by an animal, and thus to the habitat types and neighbours it can encounter, but their size is strongly influenced by outlying locations. These may be peeled away, by excluding fixes furthest from a range centre, but this is not appropriate for multinuclear or curved ranges. The techniques used for plotting contours of location density can handle multinuclear ranges, are ideal for defining range centres, and provide a very good visual representation of range cores. Harmonic mean contouring (Dixon & Chapman 1980) is used most frequently, but can produce very variable results without the location-centering procedure from Spencer & Barrett (1984). Contouring based on kernel estimators (Worton 1989) is more rigorous. Even so, the density estimation is a smoothing process, so that even the core isolines do not always conform well to the fixes, tending to "balloon" into areas not visited by the animal. This can be avoided by using cluster analysis to define range cores and putting a tight outline round the resulting group of locations (Kenward 1987).

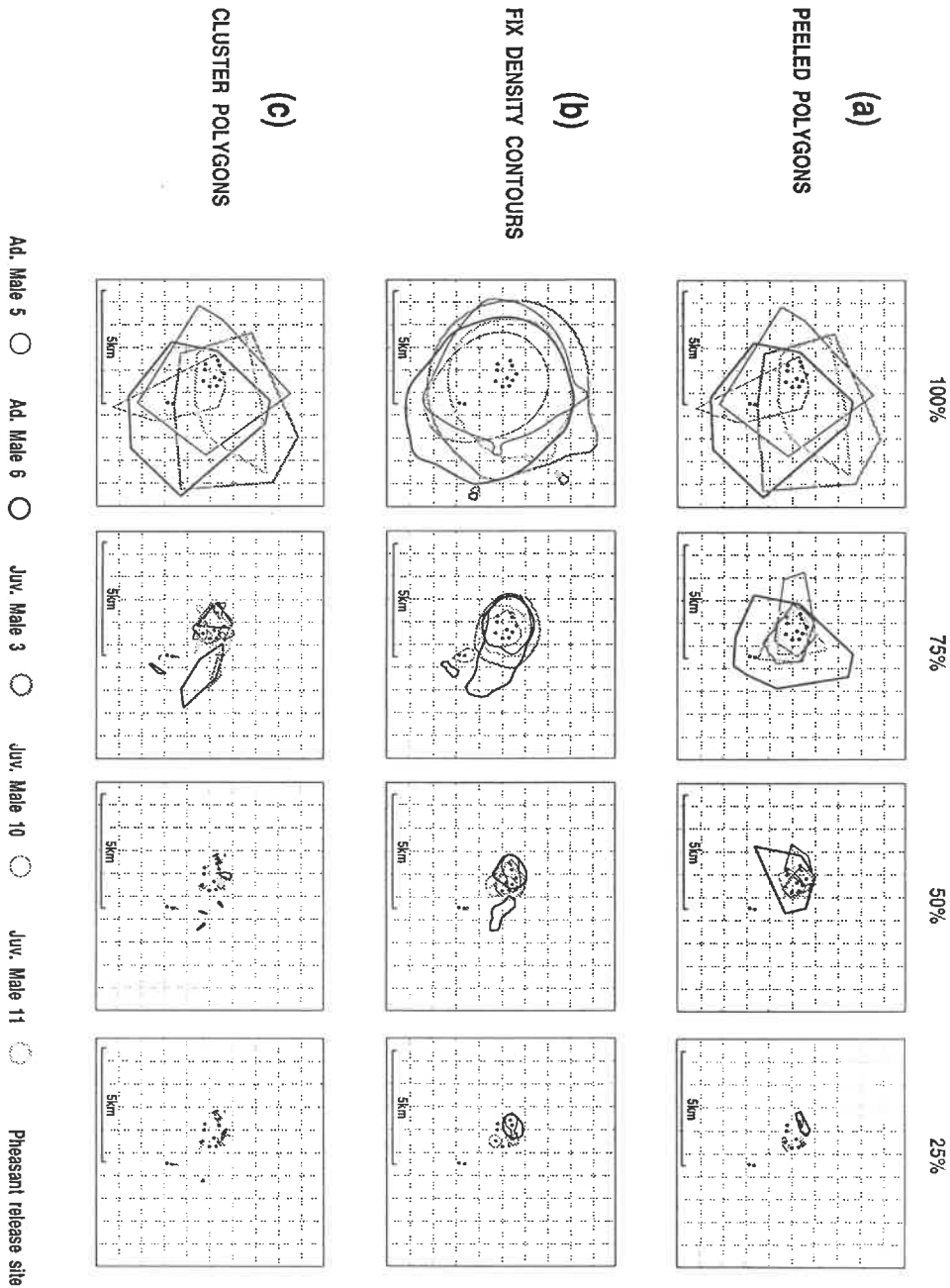
Now that the different estimation techniques are starting to be tested on different data sets, it is becoming apparent that each of the last three methods can be useful, for providing different information. Convex polygons, including cores obtained by peeling, are useful for comparing range areas with previous studies (tests should be based on geometric means, by taking logarithms of the areas), and for defining available habitats, or neighbours with which the animal may interact. The contouring approach is good for visual display and for defining a range centre, whereas cluster analysis appears to be best for defining range cores and resulting structure statistics.

Range cores estimated with the last three approaches can be seen in Figure 2. The data came from five male Goshawks which were radio-tracked in October 1976, at an estate in Sweden where 5 000 pheasants were released each summer and fed at 12 sites with thick cover. The convex polygons containing 100% of the fixes all overlap in the area containing 10 of the 12 feeding sites, and extensive overlap in this northern area remains for (a) the peeled polygons (excluding locations furthest from the location where density was highest) and (b) the harmonic mean contours for the densest 50% of locations. In both cases the two adult male ranges (solid black lines) overlapped extensively at all core sizes, although in cluster analysis (c) the overlaps were much less marked even for the 75% outlines. It is clear that the Goshawks were not being territorial in the sense of excluding each other from hunting areas, so that predation could not be reduced by leaving resident adults to keep others away, although cluster analysis suggested that their foraging was more independent than indicated by the other techniques. Our second paper (Walls & Kenward, this volume) provides further analysis of their sociality.

If location analyses are to provide useful quantitative results, studies need careful planning. Just as conclusions about predation should not be based on observing a single raptor, which may be specialising in a particular prey, nor should assessments of range size and habitat-use come from tracking one animal. Since the movements of each individual are likely to be influenced by its past experience, leading to favoured hunting sites, roosts and routes between them, its location records are not really statistically independent even if they are taken at long enough intervals to avoid serial correlation (*eg* as tested by Swihart & Slade 1985). Comparisons between different categories of animal (*eg* age and sex classes), in different areas, seasons and experimental treatments (*eg* release techniques), should therefore be based on numbers of range records, not numbers of individual locations.

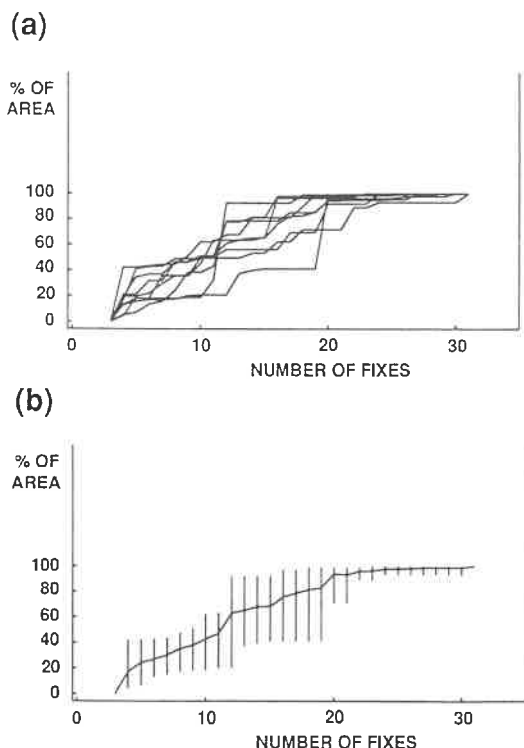
The number of range records can be maximised if data can be obtained from many individuals at a time, by sampling each animal at intervals rather than monitoring single animals continuously. Continuous monitoring of single animals can provide useful insights at the very start of a study,

Figure 2 Ranges of 5 wintering male Goshawks overlapped extensively where pheasants were released, even when single peeled polygon outlines (a) or harmonic mean density contours (b) contained only 25-50% of the radio fixes, but not when cluster analysis (c) was used to separate foraging areas.



and is sometimes necessary for recording movements or other behaviour in detail, or because very large species are too far apart for an observer to move quickly between them. For systematic sampling, however, a much better approach is to locate a number of individuals in rapid succession, and repeat this at regular intervals. By sampling at regular intervals along a time base, the area containing, say, the densest 80% of the locations is also the area in which the animal spent 80% of its time. By checking all the individuals at a similar time, there is minimum variation in weather and time of day, and data are also most suitable for analysis of sociality. It does require more travel, but we have both used interval sampling to track reasonable samples of large raptors at the same time: REK tracked six Goshawks in October 1976 to record kills as well as locations, and SSW tracked 16 Buzzards in October 1991. Much effort is needed to obtain such records, which makes it desirable to collect no more locations than are needed to define each range. Recording each range rapidly may also be useful for comparing records from consecutive periods, for instance at different points during the breeding season. Even when ranges must be recorded by continuous monitoring, the number of separate records can be maximised by minimising the number of locations in each range. The number required will be least if the locations are not serially correlated, which in principle means that an animal has had time to move across its range between locations (Swihart & Slade 1985). In practice, it seems adequate to record locations at 2-4 hour intervals three times a day. Using this approach, Figure 3 shows that minimum polygon ranges of Common Buzzards (*Buteo buteo*) increased little in size after the first 20 fixes were added. In fact, 30-35 fixes taken over 10-15 days have provided similar sampling saturation for convex polygon ranges of several bird and mammal species (Kenward 1987), although around 60 fixes may be needed for range areas to reach an asymptote with harmonic mean contouring (Harris *et al.* 1990).

Figure 3. Convex polygons round all the fixes increased little in size after the first 20 fixes were collected for 11 Buzzards in October 1990. Plots from RANGES IV are (a) for the individual birds, and (b) for the means, with bars showing maximum to minimum values.



Software which automates incremental analyses and provides multi-range plots is a great help for deciding how many fixes are needed for a standard range record: there is little point in collecting 150 fixes for each home range if 30 will suffice. Such software should if possible be obtained before starting fieldwork because, as noted by Harris *et al.* (1990) "it is important to test the radio-tracking regime before launching into the detailed study". The analysis in Figure 3, and the others in our papers, all used the RANGES IV suite (from ITE Furzebrook, Wareham BH20 5AS, Great Britain), which was designed to handle radio location data from pilot study through to comprehensive analyses of very large data sets.

The range-as-sample approach can be extended to habitat analyses. In fact, if this is not done, statistical testing may be invalid. For example, one should not pool locations from different individuals for χ^2 tests of habitat preference. The final example in this paper shows how such data should be tested.

In habitat analyses it is necessary not only to determine what is available (A) in an area, but also what is used (U) by each animal, where

U is defined as (observations in habitat i)/(observations in all habitats), and

A is defined as (area of habitat i)/(area of all habitats).

Expressing U as a single value for each animal avoids any assumption of independence between locations. However, there is still the problem that all the A_i values, and the U_i for each individual lack independence because they sum to 1. This means that strong avoidance of one habitat can lead to apparent preference for all others. The solution is to investigate habitat use by comparing pairs of habitats. This gives a single comparison if there are only two habitats (because one must be preferred if the other is avoided), and a matrix of $(n-1)!$ comparisons if there are n habitats.

Testing can be done with a parametric or a non-parametric approach. The parametric approach is based on compositional analysis (Aebischer, Robertson & Kenward, in press), using a logratio transformation, $\ln(U/A_i)$, for all the habitats used by each animal. The resulting values are positive if the habitat is used more than expected from its availability, negative if used less than expected, and 0 if use and availability are equal. To compare the use of habitats i and j , the difference $\ln(U/A_i) - \ln(U/A_j)$ is found for each animal: habitat i is preferred to habitat j if the mean of this difference is significantly greater than 0. If there are more than two habitats, a likelihood ratio test can be applied to the matrix of difference scores to discover whether overall habitat use differs from random.

The main disadvantage of this approach is that it requires the distribution of difference scores to be statistically normal. This would not be the case, for example, if there were divergent strategies between animals, with some favouring habitat i whereas others favour j . If there are enough animals, evidence of divergence can be sought with a test for extreme reactions (eg Moses 1952). Alternatively, a non-parametric approach can be used. For example, Kenward (1992) uses Ivlev's index $(U_i - A_i)/(U_i + A_i)$ for each animal, because this gives scores from -1 to +1 without the problem of estimating $\ln(U/A_i)$ when U_i is 0, and a signed-rank test is used to compare pairs of preference scores. This is done in Table 4 for data from seven Goshawks wintering in a Swedish study area.

In this case there was no sign of a divergence in habitat preferences, although this might have arisen if there had been tracking during breeding: some adults would probably have shown a strong preference for nest areas deep in the woods. As it was, woodland within 200m of an edge ranked most preferred by each bird, and open country ranked less preferred than deep woodland for only two of them (AM9, AF15). Comparing Ivlev indices between pairs of habitats, woodland edge was preferred significantly more than deep woodland or open country (Wilcoxon signed-rank matched-pair tests, two-tailed $P = 0.018$ in each case), but there was no significant tendency to avoid deep woodland more than open country in winter ($P = 0.107$). Fortunately, the results are the same as in a previous paper (Kenward & Widén (1989), which used X^2 tests.

The next decade will see data from radio-tagging used for combined analyses of how range structure and habitat use relates to survival, dispersal and productivity. We are already combining demographic data from Buzzards with habitat analyses based on a landcover map from satellite data. Software advances will make it possible to investigate many parameters of individual performance (PIPs), such as range structure, habitat use and sociality, and to use these in conservation studies. In theory at least, PIPs which predict dispersal, death or breeding failure (Predictors of Impending Peril!) could be used for rapid assessment of an area's suitability for re-

stocking, by releasing very few radio-tagged raptors. For example, if animals in a healthy population prove unsuccessful when they have large range cores, the recording of large range cores for all the individuals released at a new site would cast early doubts on its suitability.

Table 4 Habitat use, availability and Ivlev index scores for seven Goshawks in Sweden.

<u>Fixes in</u>	JM4	AM6	AM8	AM9	JF10	AF11	AF14	
Open country	58	32	38	14	22	4	5	
Woodland edge	203	92	162	139	70	70	81	
Deep woodland	4	2	3	13	1	1	12	
<u>Utilisation (U)</u>								<u>Availability (A)</u>
Open country	0.22	0.25	0.19	0.08	0.24	0.06	0.05	0.46
Woodland edge	0.76	0.73	0.80	0.84	0.75	0.93	0.83	0.26
Deep woodland	0.02	0.02	0.01	0.08	0.01	0.01	0.12	0.28
<u>(U-A)/(U+A)</u>								
Open country	-0.4	-0.3	-0.4	-0.7	-0.3	-0.8	-0.8	
Woodland edge	+0.5	+0.5	+0.5	+0.5	+0.5	+0.6	+0.5	
Deep woodland	-0.9	-0.9	-0.9	-0.6	-0.9	-0.9	-0.4	

CONCLUSIONS

Radio-tagging is a simple concept, looks easy and can give exciting results. However, it is a tool which is easy to abuse, particularly by underestimating the skill required. Results presented in this paper, especially in Table 2, represent nearly 20 years spent developing equipment and techniques. Starting projects with the expectation of immediate success can easily lead to frustration and wastage of scarce conservation resources. Would you give a scalpel to a paramedic and expect effective brain surgery?

Although field skills cannot be quickly transferred, it is possible to make recommendations for new projects, as follows:

- (i) Be sure that the study species can be caught for tagging and licences are available.
- (ii) In projects using harnesses, a pilot study must include training from someone experienced in the technique; it should test safety in species which lack a previous test.
- (iii) Location studies should start by obtaining software to develop sampling techniques.
- (iv) Sample sizes should be adequate for the investigation concerned, aiming for cohorts of at least 20 in survival studies and never less than five per category in location studies.
- (v) It is wise to arrange *post mortem* services in advance and to overestimate travel costs.

ACKNOWLEDGEMENTS

Data on Goshawks were collected in collaboration with V. Marström and M. Karlbom, with funding from the Swedish Sportsmens Association. Both projects were also funded by the Natural Environment Research Council, with further support for the Buzzard study from Biotrack, the Nature Conservancy Council and the Royal Society for the Protection of Birds. We are deeply grateful to these funding agencies, and to the many landowners and others who provided permissions and assistance in Britain and Sweden. An early manuscript was improved by comments from M.G. Morris.

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African Harrier Hawk *Polyboroides typus*