

Appendix AQ

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GOSHAWK HUNTING BEHAVIOUR, AND RANGE SIZE AS A FUNCTION OF FOOD AND HABITAT AVAILABILITY

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SUMMARY

(1) Four released goshawks were radio-tracked for up to 29 days at a time in Oxfordshire. Their hunting flights were mostly at 3–4 min intervals, for an average of 200 m in open country. They remained in woodland for 50% of the time although only 12% of their ranges was wooded. This preference resulted not from hawks flying less frequently in woodland, but because they flew half the distance between perches and doubled back twice as often in woodland as in open country.

(2) Most attacks were initiated from perches, and only 3% were at prey already in flight. Six percent of observed attacks were successful, but hawks were most successful when hunting out of sight. They killed, on average, once in every 262 minutes of hunting. Seventy percent of prey was taken in or from woodland, a higher proportion than expected from the time spent there.

(3) There were no sex or age differences in the preference for woodland of twenty-two wild goshawks radio-tracked in Sweden. Woodland within 200 m of open country was the most preferred habitat, and the majority of kills were made there. Range size was related to the proportion of a range that was woodland edge, and to prey availability. It is suggested that hawks covered the amount of woodland edge which gave adequate kills at the prevailing prey density, range size then being the area which happened to include that amount of woodland edge.

INTRODUCTION

Several studies of raptors which live mainly in open country have described relationships between habitat, flight behaviour and hunting success (Wakeley 1974, 1979; Warner & Rudd 1975; Tarboton 1978; Shrubb 1980; Village 1980), or have linked range size to food abundance (Craighead & Craighead 1956; Village 1981). The elusive accipiters, which hunt largely in woodland, are less easy to study. Observations of accipiter hunting have been mostly in open country (Rüdebeck 1950; Hantge 1980), where only 5–11% of attacks were successful. Little is known about woodland hunting or about habitat choice and range sizes, except that male sparrowhawks (*Accipiter nisus* L.) have a greater tendency than females to hunt in woodland (Opdam 1975; Marquiss & Newton 1981) and that sparrowhawk ranges are smaller in productive farmland than around hill forest (Marquiss & Newton 1981).

This paper is based on data obtained during radio-tracking studies of goshawk (*Accipiter gentilis* L.) predation on woodpigeon (*Columba palumbus* L.) and pheasant (*Phasianus colchicus* L.) populations (Kenward 1977, 1979; Kenward, Marcström &

Karlbom 1981). In a British study area, released hawks could be watched for long periods because there were many hills providing good view points and most trees lost their leaves in winter. This enabled detailed study of hunting techniques and habitat use outside the breeding season. Radio-tracking wild goshawks in Sweden indicated relationships between range size, food and habitat availability.

STUDY AREAS

The British study area was in north Oxfordshire near Chipping Norton, where the topography undulates gently between 80 m and 250 m above sea-level, with ponds of up to 1.5 ha and streams in the valleys. Scattered woodland, mostly less than 5 ha, but occasionally up to 100 ha, covered 8% of the area, with mature deciduous species predominating. Trees were also common along hedges in the farmland, which was mainly arable but also included some sheep and cattle pasture.

The three study areas in central Sweden were relatively flat, with occasional hills or ridges up to 50 m above surrounding lowland. Woodland, mainly mature conifers and birch (*Betula* spp.) but with some other deciduous species in copses, covered 41–61% of the different areas. Each area contained or bordered a lake of more than 200 ha, edged by reed beds connected to reedy ditches. The farmland was predominantly arable, with larger fields than in north Oxfordshire and few hedges or isolated trees. The three study areas were based on similar sized estates which differed markedly in pheasant abundance. At Frötuna, 4300 pheasants were released just before the study started. At Gäddeholm pheasants had last been released a year before the study, and the population was estimated at 100–500 birds during radio-tracking. At Segersjö an autumn census gave a wild pheasant population of 85 birds. Pheasants provided more than 95% of hawk food (biomass) at Frötuna, and contributed more biomass than any other prey elsewhere although a minority of hawks ate more hare.

HAWKS

The hawks released in Oxfordshire had been imported, because, although goshawks breed sporadically in Britain (Sharrock 1976), they were not established in the study area. One hawk had been obtained from a nest in Finland (an 'eyass'), while a Finnish 'passager' had been trapped in its first autumn, as had a German passager. The fourth hawk had been trapped as a 'haggard' (in mature plumage) in Finland. The Finnish eyass had been trained and had made eleven kills in falconry before release. The others had been tamed for handling but not trained for hunting. All four were male.

RADIO TRACKING

The hawks were equipped with tail-mounted radio transmitters as described in Kenward (1978a). A 3-channel RB4 'Falconer' receiver from Custom Electronics, Urbana, Illinois, was used for the four hawks in Britain. Swedish hawks were monitored with a 12-channel LA 12 receiver from AVM Instrument Co., Champaign, Illinois. A 3-element hand-held yagi antenna was used for both receivers.

The hawks in Britain were released for a total of 8 single days and 5 periods of 11–21 days between October and March in the 1973–4 and 1974–5 winters, and were recovered after each release except for the German passager, which was lost when its radio

malfunctioned. The birds were followed continuously, to record as many of their flights and kills as possible. The hawks spent much of their time in valleys, where they could be kept in view from the hills by using binoculars and a telescope. They were temporarily lost from sight when they crossed ridges into other valleys, or sometimes when they were in dense woodland. At these times, the hawks were relocated by using the radio and through mobbing by other species, especially corvids (*Corvus* spp.). When they were out of sight, their flights could often be timed from characteristic amplitude fluctuations of the radio signal. Soaring was distinguished from other flights by the regularity of signal amplitude variations as the hawk circled: the whip antenna alternately pointed at the observer (weak signal) or became parallel to him (strong signal). Observed flights were plotted on perspex sheeting overlying 1:10 000 (6") maps, to aid measurement of distances and directions.

In Sweden the emphasis was on obtaining predation data from a large number of hawks, and up to six were monitored at a time for 11–29-day periods between August and March in 1976–77 and 1977–78. Flights could rarely be observed, because the coniferous trees hindered vision in woodland and there were few vantage points. For comparison with the British data, signal amplitude changes were used to indicate the frequency of flights in four hawks, sampling each for five flights at a time. To standardize habitat preference recording, birds were always located four times a day: mid-morning, mid-day, mid-afternoon and at roost. These locations were recorded on a 100 m grid (1:50 000 map), although the few triangulations made for 2 km or more distant may have been in error by more than 100 m. Further details of the radio-tracking are in Kenward (1980).

RESULTS

Hawks released in Britain

The hawks tended to follow water courses and other line features, such as hedges and disused railway lines, most probably because trees and other vegetation along line features provided secluded hawk perches for surprise attacks and good prey habitat. Since these features were often near valley bottoms, the hawks tended to hunt along valleys and to move rapidly across the relatively exposed ridges. The distance flown per day ranged from 0.6 km to 19 km, averaging 6 km ($n = 67$). The shortest distances were flown on days when hawks returned to feed at kills left from the previous day. The German passenger was lost after four days, but the others moved 3–13 km from release points before establishing ranges (areas whose parts were revisited after intervals of at least a day).

Table 1 shows the proportion of perching, and the time spent, in parkland (OS classification) and woodland, compared with the frequency of these habitats (a) within convex polygon hawk ranges (Voight & Tinline 1980) and (b) within the whole of north Oxfordshire. The habitat used by the hawks was known for 68% of the observation

TABLE 1. Availability and use by goshawks of woodland and parkland in north Oxfordshire

	Hawk observations		Presence of habitat	
	Occasions perched (obs.)	Time spent (min)	In hawk ranges (grid points)	Throughout N. Oxfordshire (grid points)
Totals	1023	8254	576	1600
% in woodland	47.6	50.2	12.3	7.6
% in parkland	15.4	not recorded	14.8	3.4

periods, which totalled 12 070 min. Observations were discontinued when the hawks were eating, resting after eating or at roost, and therefore refer mainly to when they were hunting. There was enhanced use of woodland and parkland, both in where the hawks perched and in the ranges they developed.

The start and end points were known for 946 flights, of which 39 involved soaring and 79 were attacks. Five attacks (6%) were successful. The remaining 828 flights were more or less directly from perch to perch. The length of these 'direct inter-perch flights' differed between hawks in both woodland and open country (Fig. 1, χ^2 test, $P < 0.001$). In general, observed direct inter-perch flights averaged 100 m in woodland, and 200 m in open country, the difference being significant for each hawk (median test, $P < 0.001$). In making these statistical comparisons, the assumption of independence of observations would be violated if consecutive flights were similarly influenced by other factors, such as weather or short-term variation in hawk condition.

Using a straight line between perches to give the approximate track of each direct inter-perch flight, the angle between consecutive flights could be measured. With a straight-on movement indicated by 0° and a complete reversal of direction by 180° , the hawks doubled-back two to three times as often in woodland as in open country (Fig. 2, χ^2 test, $P < 0.001$) with no significant difference between birds. Flights which crossed a habitat boundary were excluded from the analysis.

There was neither an inter-hawk nor an inter-habitat difference in the time interval between flights (Fig. 3), the median interval being 4 min. The 3–4 min interval between flights was much the most common. This interval mainly represented time spent perched, since 200 m flights seldom took more than 20 s.

All the hawks made soaring flights. Thirty-nine of these flights were observed, in which the birds travelled a horizontal distance of up to 2090 m (average 780 m) in up to 17 min, at an estimated maximum height above ground of 100 m. Dividing the hours of daylight

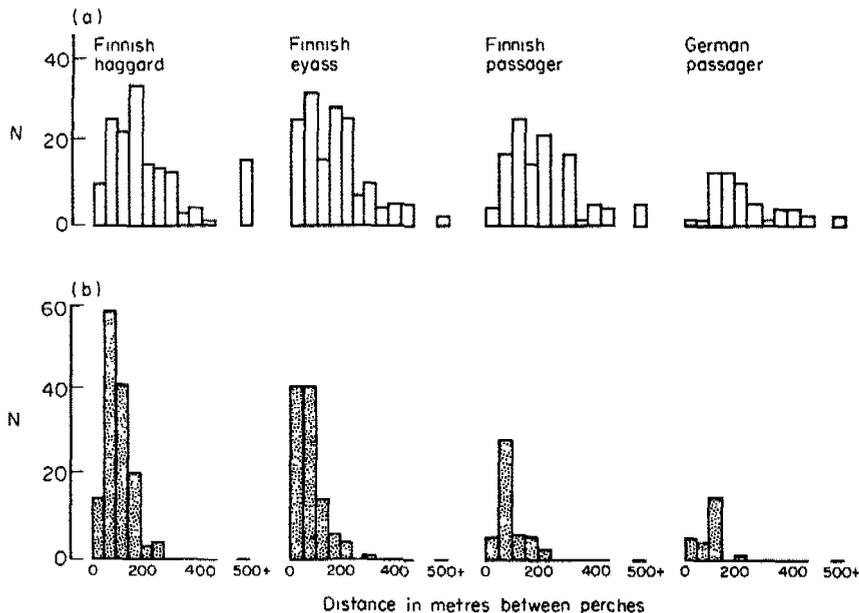


FIG. 1. The length of inter-perch flights for four goshawks released in Oxfordshire (a) in open country, (b) in woodland. Lengths differ between birds and between habitats.

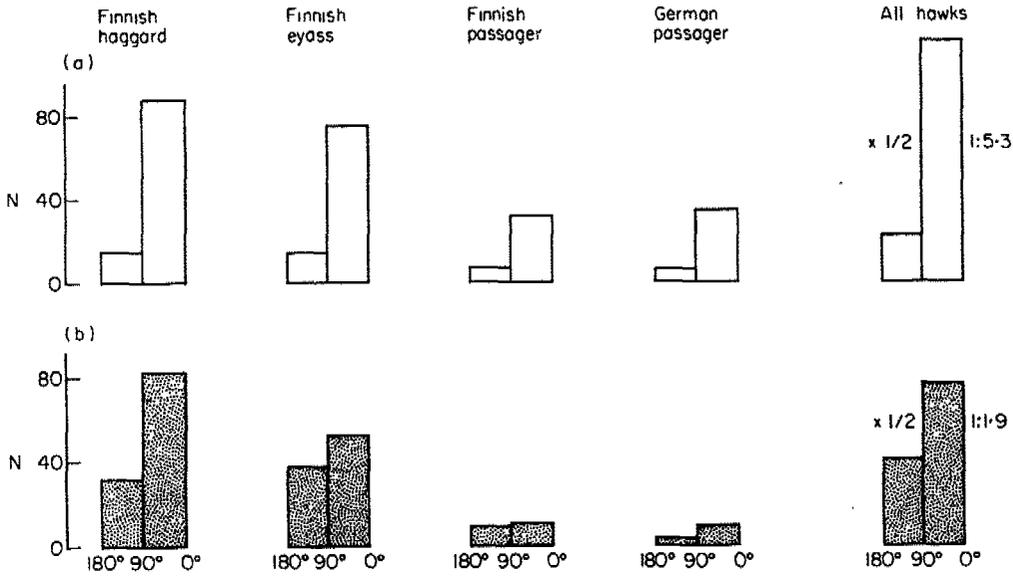


FIG. 2. The angle between tracks of consecutive inter-perch flights of goshawks in Oxfordshire (a) in open country, (b) in woodland. The distribution differs between habitats but not between hawks.

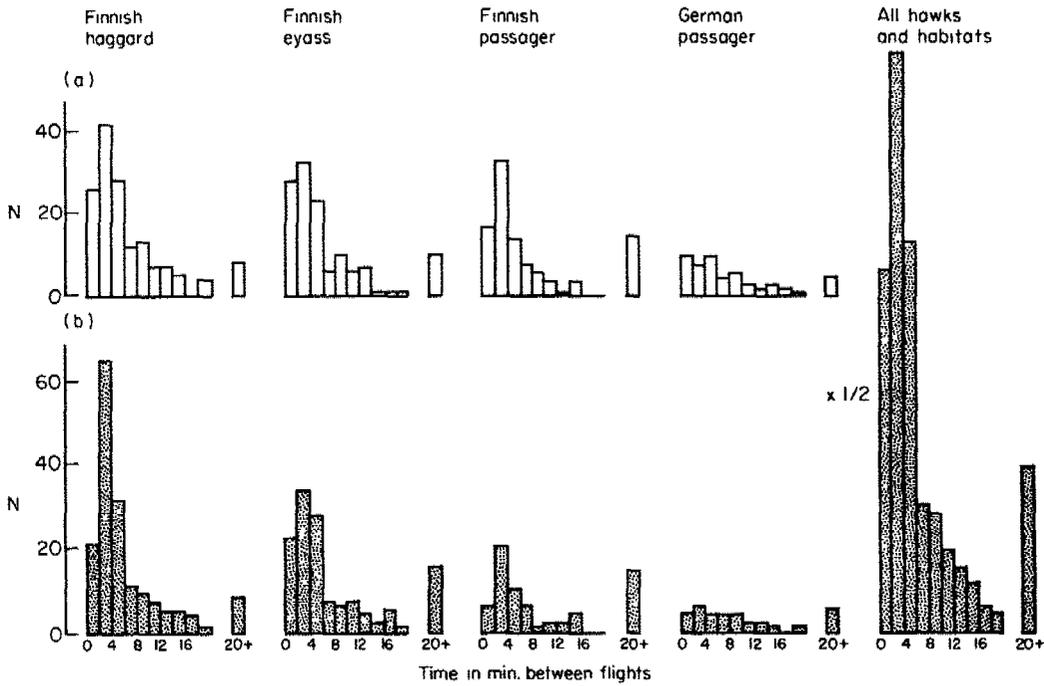


FIG. 3. Time intervals between consecutive inter-perch flights of goshawks released in Oxfordshire (a) in open country, (b) in woodland. The distribution does not differ between habitats or hawks.

into five equal periods, 67% of soaring flights occurred in the third and fourth periods (mid-day and early afternoon).

Hawks were usually lost to sight when they flew over ridges or round hills, in open country. Knowing the time spent and the approximate distances travelled out of sight, it

TABLE 2. Capture location of goshawk kills in north Oxfordshire. (Four kills with unknown capture location are omitted)

	In the open		
	In woodland	Within 100 m of woodland	More than 100 m from woodland
<i>n</i>	35	15	10
%	58	25	17

can be estimated that the birds would have made 781 unseen flights, averaging 226 m, if they flew as frequently as when they were under observation. The distance is slightly greater than the average observed in open country, and much greater than flights observed in woodland. There was either a bias against observing the longest flights, or a tendency for unobserved flights to occur at shorter intervals than observed ones, or both. Without this bias, flight distances would have been longer, or inter-flight times shorter, by 37% at most.

Seventy-five of the seventy-nine observed attacks were straight from a perch, with the hawks diving, gliding, or flapping close to the ground towards the prey. Three attacks not launched from a perch were consecutive stoops at rabbit (*Oryctolagus cuniculus* L.) by a hawk soaring along a ridge, and the fourth was at pigeons which flushed as a hawk flew past. Only two observed attacks were initiated at flying prey. Attack flights average 54 m from perch to prey in woodland, and 103 m in open country, half the distance of direct inter-perch flights in each habitat.

During the 12 070 min of radio-tracking there were 46 kills: one in 262 min of hawk hunting. There were another 18 kills during short interludes in the tracking. Only 5 kills occurred during the 6638 min in which hawks could be seen, a rate of 1 in 1328 min which is very significantly different from the kill rate of 1 in 132 min when hawks were temporarily out of sight (χ^2 test, $P < 0.001$).

When the location of hawk kills was known, 58% were made in woodland (Table 2). Moreover, on ten occasions when prey was captured within 100 m of cover the hawks were either seen to attack out of the woodland, or could be assumed to have done so because they had been in woodland immediately beforehand. Thus, the proportion of prey taken from woodland (70%) was significantly higher than expected on the basis of time spent there (χ^2 test, $P < 0.001$).

Wild hawks in Sweden

Owing to lack of time for these observations, only 92 inter-flight times were recorded in Sweden (Fig. 4). The median interval, 3 min, was significantly shorter than in Britain (median test, $P < 0.001$). However, the 3–4 min interval was again the most frequent, and the main difference from Fig. 3 was a relative lack of long inter-flight times.

Sixth-nine percent of thirty-nine flights in Sweden occurred in the second and third fifths of the day, slightly (but not significantly) earlier than soaring in Britain. Soaring was used for hunting by at least one hawk: in August a juvenile male frequently soared up in thermals and was seen on three occasions to stoop on pigeon flocks. No successful stoops were observed, although he killed one pigeon in the open where he had been soaring. A juvenile female once soared to a height of 830 m (estimated from the relative size of her wingspan to that in a photograph at a known magnification). Soaring was often associated with movement from one part of a range to another, or completely away from an area,

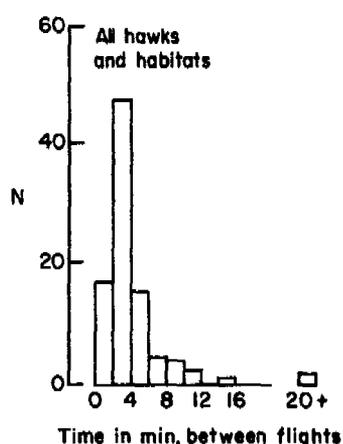


FIG. 4. Time intervals between consecutive inter-perch flights of wild goshawks in Sweden.

rather than with obvious hunting activity, and a soaring signal preceded permanent loss of contact with a hawk on several occasions. Thirteen of sixteen radio-tracked hawks soared during August to October, whereas no soaring was recorded for seventeen hawks tracked later in the winter, probably partly because weather was then unsuitable.

There were no sex or age differences in the preference for woodland, or for deep woodland more than 200 m from open country (Table 3). The analysis was confined to the period August–February to eliminate breeding season effects. The hawks showed a clear preference for woodland edge (Woodland 0–200 m from open country) compared with open country or deep woodland, not only in where they were located within their ranges but also in that their ranges tended to have more woodland edge than the region as a whole (Table 4). This indicated that the birds were selecting for their ranges the areas with small woods rather than extensive forest. Hawk presence in woodland remained remarkably constant, at 80–85% of their positions, despite the availability of woodland in their ranges varying from 40 to 60%. There was a uniformly two-fold preference for woodland edge, with an avoidance of both open country and deep woodland which increased as these habitats increased in hawk ranges. Only in poorly forested Oxfordshire was hawk presence in woodland reduced, although the preference for woodland (time spent there/availability) was stronger than in Sweden. The proportion of kills made in or within 100 m of woodland was as high as, or higher than, the hawk's presence in woodland, with a much higher proportion of kills in or near woodland edge than expected on the basis of the habitat's availability.

The size of hawk ranges differed between the three areas in Sweden. Ranges were

TABLE 3. Use of woodland by male and female goshawks, in three areas of central Sweden

Area	Hawk sex	Number of:		% of positions in woodland		
		hawks	positions	Total	0–200 m from edge	>200 m from edge
Frötuna	Male	6	281	86	76	10
	Female	3	100	82	74	8
Gäddeholm	Male	1	13	85	85	0
	Female	4	152	80	73	7
Segersjö	Male	6	613	84	73	11
	Female	3	200	85	79	6

TABLE 4. Locations of goshawks and their kills with reference to availability of woodland in three Swedish and one British study area. (Kills with unknown capture locations are omitted)

Area	Hawks	Number of			% of hawk positions in woodland			% of woodland in hawk ranges			% of woodland in 10 km squares around hawk trap sites			% of kills in woodland or within 100 m outside it		
		Positions	Kills	Total	0-200 m from edge	>200 m from edge	Total	0-200 m from edge	>200 m from edge	Total	0-200 m from edge	>200 m from edge	Total	0-200 m from edge	>200 m from edge	
Frötuna	9	381	81	84	76	8	62	35	27	61	31	30	99	99*	0	
Gäddeholm	5	165	30	80	73	7	48	34	14	52	31	21	77	61	16	
Segersjö	9	813	62	85	75	10	40	31	9	41	27	14	90	80	10	
N. Oxon	4	1023	60	48	48	<1	12	12	<1	8	8	<1	83	83†	0	

* All but three kills were made near pheasant release sites, which were located at woodland edges.

† Woodland more than 200 m from an edge was virtually absent in north Oxfordshire.

smallest at Frötuna, where pheasants were superabundant as a result of releases, largest at Segersjö with its sparse wild pheasant population, and intermediate at Gäddeholm with its moderate pheasant stock. Range size was significantly related to the proportion that was woodland edge in each area (Spearman rank correlation, $P \leq 0.05$), with some tendency for the total woodland edge content (=range area \times woodland edge proportion) to remain constant, at a different level, in each area (Fig. 5). Three Segersjö hawks with ranges markedly smaller than others in that area also differed from the other Segersjö hawks in obtaining at least 75% of their food (biomass) from hares during range recording; these relatively small 'hare-eater' ranges may indicate that hawks hunting hares did not need to travel far to encounter prey, or may reflect the long time (up to 7 days) spent eating each hare kill and roosting nearby. Excluding these hawks, the woodland edge content of ranges averaged 5 (range 2–9) km² in the pheasant release area, 10 (6–15) km² in the area with the slightly enhanced wild pheasant population and 17 (10–22) km² in the wild pheasant area. However, individual range observations diverge markedly from the curves of average woodland edge content for Segersjö at least (Fig. 5), probably because the largest ranges tended to contain large tracts of forest with relatively little edge.

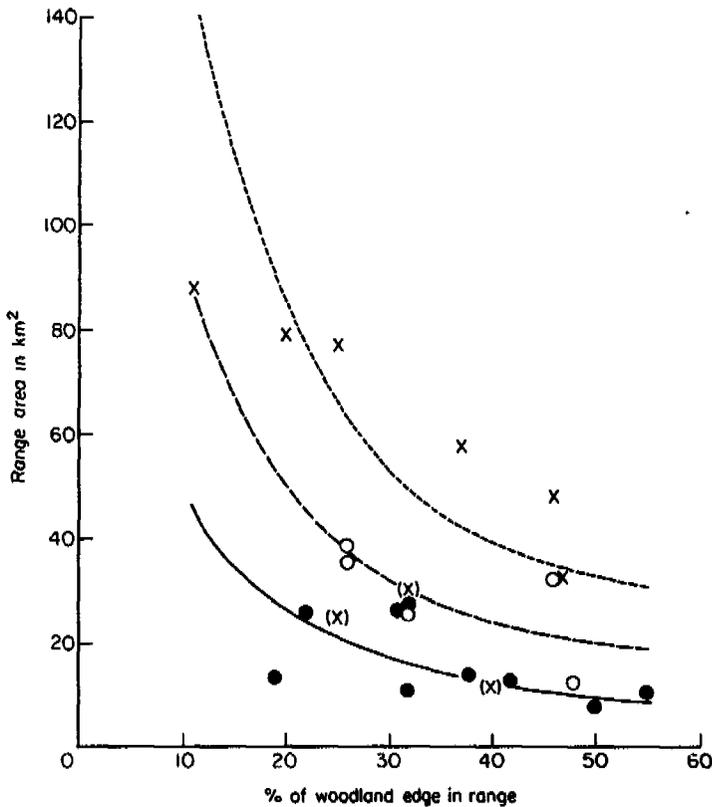


FIG. 5. Convex polygon range area as a function of woodland edge content for wild Swedish goshawks in three areas with differing prey densities: ●, area with pheasants released in study winter; ○, area with pheasants last released a year before the study winter; ×, area with wild pheasants; (×), hawks which obtained > 75% of their food biomass from hare kills during range observations. Curves represent ranges with 17 km² (.....), 10 km² (---) and 5 km² (—) of woodland within 200 m of an edge (equivalent to woodland edge lengths of 85, 50 and 25 km, respectively).

DISCUSSION

At the 6% success rate of observed attacks, the forty-five unobserved kills during radio tracking would be equivalent to 711 attacks. There were an estimated 781 unobserved flights, or 1591 with the maximum likely bias in observed inter-flight intervals. Since it is unimaginable that at least every other unobserved flight was an attack, the success rate of observed attacks must have been below average, probably because attacks which were conspicuous to the observer were also detected early enough for escape by the prey. There was probably also a bias against observing any attacks, not just successful ones. Chance observations of accipiter attacks (Rüdebeck 1950; Hantge 1980) are likely to miss an even higher proportion of inconspicuous attacks than during radio-tracking, and thus have an even greater downward bias in attack success estimates. A more practical measure of success is the rate of one kill per 262 min while hawks were known to be hunting.

Meinertzhagen (1959) considered that 'still-hunting' is usual for the goshawk. In that almost all observed attacks were initiated from perches, the released goshawks could be said to have still-hunted. However, the hawks were certainly not sitting and waiting for prey to come to them. They could be seen to scan their surroundings from each perch, and then to fly on to another, repeating the process at fairly short intervals, a technique best described as 'short-stay perched-hunting'. The distribution of inter-flight times was very similar between woodland and open country (Fig. 3). This may mean that the time needed for scanning, or the optimal foraging 'giving-up-times' (Krebs, Ryan & Charnov 1974), were similar in both habitats, or the hawks may simply have rested until flight muscles were again ready for peak performance. In Sweden the hawks flew more frequently, mainly because of fewer long rests than in Britain. The Swedish birds may have been hungrier, because they were killing at approximate 3-day intervals, compared with 1.5-day intervals in Britain.

In the Swedish study areas, too, short-stay perched-hunting seemed to be the main technique. However, in an area of Swedish taiga with more than 90% tree cover, a preliminary study using radio signal fluctuations from unseen hawks indicated that they were flying at 12-min intervals. They then stayed airborne for a minute or so, enough to cover 600–900 m at 10–15 m/s (Widén 1981). Perhaps dense tree cover and reduced availability of open areas in the Taiga caused hawks to adopt different hunting tactics there, flying long distances between patches of favourable habitat which were mostly small enough to scan from one perch.

Female sparrowhawks are to be seen, trapped, and radio-located more frequently than males in open country, the proposed explanation being that there is more small prey for males in woodland and large prey for females in the open (Opdam 1975; Marquiss & Newton 1981). Female goshawks too take larger prey than do males in winter (Höglund 1964), but in the Swedish study areas the most frequent prey of both sexes, red squirrels (*Sciurus vulgaris* L.) and pheasants (Kenward, Marcström & Karlbom 1981), were woodland and woodland-edge species, respectively. Only females took full-grown hares, and these were usually taken in or within 100 m of woodland. There was little reason for the sexes to hunt different habitats.

The hawks were in woodland two to six times as much as expected from its availability (Tables 1 & 4). They did this in Oxfordshire not by waiting longer on each perch in woodland than in open country (Fig. 3), but by flying half the distance between perches, and tending to double back twice as frequently, in the woodland (Figs 1 & 2). The hawks probably also headed for woodland when in open country. The long flights in open country

may at least partly have reflected the greater tree spacing there than in woodland, but the hawks relatively seldom merely flew from one tree to the next.

The very high proportion of kills made in, or from woodland suggests that this was the reason for, rather than the result of, the preference for woodland. The preference for parkland is probably explained by good prey availability there: most parks contained rabbit warrens, lakes with moorhens (*Gallinula chloropus* L.) and trees where pigeons rested, these prey forming 78% of the hawks' diet in Oxfordshire (Kenward 1979).

In a recent review, Franzblau & Collins (1980) concluded that although territory size varies inversely with food supply in a number of bird species, this could be an ultimate effect of a response to varying habitat quality, or competition, because there was no good experimental evidence that food was a proximate regulator of territory size. However, when goshawk food was 'experimentally' manipulated by releasing pheasants, there was an effect on range size (Fig. 5). The goshawks appeared not to base their range size on an assessment of its woodland edge content, regardless of prey content, but to cover the amount of this habitat which resulted in adequate kills at the prevailing prey density, range size then being the area which happened to include that amount of woodland edge. Since the goshawk ranges were not defended, it remains possible that competition or habitat quality are proximal regulators of living space in more territorial species.

The value of woodland edge for hunting was probably linked partly to the abundance there of prey, such as pheasants and hares, which may forage in both open country and woodland but keep close to cover for refuge. Another factor must be the opportunities for surprise attacks from woodland on species such as woodpigeons, which may feed in the open near woodland and can outfly goshawks unless taken by surprise (Kenward 1978b). The importance of woodland edge explains how the highest goshawk densities known, of less than 100 ha per pair, can occur in areas of Westphalia with only 12–15% woodland (Bednarek (1975); the woods are well scattered and the land very fertile, which implies a high availability of both woodland edge and prey. Sparrowhawks, too, have low nesting densities in continuous forest and the highest on the most productive ground (Newton *et al.* 1977). The goshawk is not a bird that 'thrives best in extensive coniferous forest' (Brown 1976), but has probably benefited greatly where man has created a patchwork of fields and woods out of more continuous primal forest.

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