Home range and habitat selection in the Pygmy Owl *Glaucidium passerinum*

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Home range and habitat selection of eight adult Pygmy Owls *Glaucidium passerinum* (six males and two females) were assessed by radio-tracking in a fragmented forest-farmland landscape in southeastern Norway during January–September 1993, when small mammal populations were in their low phase. Minimum convex polygon home range size based on one location per day ranged 0.4–6.0 km², with a median of 2.3 km². The habitat composition in the Pygmy Owls' home ranges differed from that in the study area. In this landscape scale habitat selection, mature forest ranked highest, followed by young thinning stands, edge between forest and open areas, clear-cut areas, advanced thinning stands, and finally agricultural crop land where the Pygmy Owls were never observed. The Pygmy Owls' habitat use differed from random use of available habitats within the home range. In this home range scale habitat selection, edge between forest and open areas ranked highest, followed by mature forest, advanced thinning stands, young thinning stands, clear-cut areas and agricultural crop land. Forestry may be harmful to Pygmy Owl populations by harvesting the old forest, but also beneficial by creating more edges between the old forest and stands of younger successional stages.

1. Introduction

Old forest fragmentation and other habitat changes resulting from modern forestry influence the avian and mammalian communities of predators and prey in the boreal forest in Fennoscandia, as well as their predator-prey relationships (Sonerud 1991a). This includes changes in prey numbers and availability, and availability of preferred hunting and nesting habitats (e.g. Sonerud 1991a, 1997, Niemi & Hanowski 1997, Selås 1997, Widén 1997). Many avian predators, including all hole-nesting owls of the boreal forest, show affinity for the old forest currently declining (Sonerud 1991a). Among these is the Pygmy Owl *Glaucidium passerinum* (Sonerud 1991a).

The Pygmy Owl inhabits both pure coniferous forests and forests with a mixture of conifers and deciduous trees across the Palearctic region from Norway to the Sakhalin Peninsula (Mikkola 1983, Cramp 1985). It is the smallest of the European owls (body mass of males c. 60 g), and its diet consists of a variety of small mammals and small birds, in Fennoscandia mainly voles (Cri-

cetidae), warblers (Sylviidae), tits (Paridae) and finches (Fringillidae) (Mikkola 1983, Cramp 1985). The proportion of voles in the diet varies with the abundance of voles in the environment, and that of birds varies inversely (Kellomäki 1977, Solheim 1984, Ekman 1986, Suhonen 1993). The Pygmy Owl nests in cavities, in Fennoscandia mainly in those made by the medium sized wood-peckers (e.g. Haftorn 1971, Mikkola 1983, Sol-heim 1994) in Aspen *Populus tremula* or Norway Spruce *Picea abies*. It also uses cavities for roost-ing and for caching surplus prey in autumn and winter (e.g. Mikkola 1983, Solheim 1984, Cramp 1985, Kullberg 1995).

Although the Pygmy Owl is diurnal (Mikkola 1983, Cramp 1985), its hunting habitat is poorly known. In contrast, its nesting habitats are well documented, the favourite one being mature Nor-way spruce forest, often interspersed with Aspen (Mikkola 1983, Cramp 1985, Sonerud 1991a, b). Because the proportion of the mainly forest-liv-ing Bank Vole *Clethrionomys glareolus* is higher in the Pygmy Owl's diet than in the diet of other forest living owls in Fennoscandia, the Pygmy Owl's hunting habitat has been predicted to be largely mature forest (Sonerud 1991b).

The Pygmy Owl may be negatively affected by modern forestry, due to its predicted depend-ence on mature forest for hunting, and its docu-mented dependence on cavities both for nesting, roosting and caching. However, in order to assess the impacts of forestry on Pygmy Owl population density, information on its habitat preferences and home range size in relation to the size of the frag-mented forest stands is needed (cf. Rolstad 1991, Sonerud 1991a). Therefore, we studied home range and habitat selection of the Pygmy Owl in a mixed agricultural and modern forestry landscape by using radio telemetry. The following questions were addressed: 1) What is the home range size of the Pygmy Owl? 2) Does the Pygmy Owl fa-vour any forest succession stages over another, and does any such selection differ between the landscape and the home range scale? 3) Is the Pygmy Owl attracted to or repelled from the edges created by forestry?

2. Methods

2.1. Study area

The field work was conducted in Hamar and Ringsaker municipalities in Hedmark county, southeastern Norway (approx. 60°50´N, 11°10´E), from 27 January to 12 September 1993. The study area covers c. 45 km² at altitudes between 180 and 620 m, and forms a steep south-north gradi-ent from the boreonemoral zone to the northern boreal zone (*sensu* Abrahamsen *et al.* 1977), and from an agricultural landscape with patches of de-ciduous and coniferous forest to a coniferous for-est landscape without agricultural land. The main tree species are Norway Spruce and Scots Pine

Table 1. Characteristics of eight Pygmy Owls radio-tracked in a fragmented forest-farmland landscape in southeastern Norway in 1993. M denotes male and F denotes female. M2 was mated with F1, and M4 was mated with F2. M3, M5 and M6 were mated, but their mates were not radio-tagged. For breeding status, 1 denotes unmated, 2 denotes mated but non-breeding, and 3 denotes breeding. For cause of end of tracking, 1 denotes loss of radio-signals, and 2 denotes death of owl.

Ind.	Body mass (g)	Wing length (mm)	Breeding status	Tracking			Weight of tag (% of body mass)
				Start	End	Cause	
M1	62.0	97.0	1	27 Jan.	9 April	1	3.5
M2	55.0	98.0	2	2 March	16 April	1	3.6
M3	57.5	99.0	2	20 March	13 April	1	4.7
M4	60.0	97.0	3	7 April	21 June	1	3.7
M5	62.0	95.0	3	29 April	23 July	1	4.0
M6	59.5	98.0	3	29 April	11 May	2	3.7
F1	76.0	106.5	2	10 March	26 March	2	4.6
F2	69.0	105.0	3	27 June	12 Sept.	1	3.2

Pinus sylvestris. The forest is strongly influenced by forestry, with a mosaic of clear-cut areas and forest stands of different ages as a result. The climate is continental and the ground is usually snow-covered from November to April or May. According to data from long-term snap-trapping (for method *see* Sonerud 1988), our study was performed in a year with low population densities of voles and shrews (G. A. Sonerud unpubl. data), and when *Microtus* voles were in a long-term population low with reduced cyclicity (G. A. Sonerud unpubl. data, cf. Hanski & Henttonen 1996, Steen *et al.* 1996).

2.2. Capture and radio tagging

Six males and two females of the Pygmy Owl were caught in mist-nets by imitating the territorial call of the male. The owls were weighed, measured for wing length, sexed (on the basis of wing length and weight) and ringed (Table 1). They were equipped with radio transmitters, either one that weighed 1.7 g (Holohil, Canada) or one that weighed 2.2 g (Biotrack, UK), mounted as a backpack and attached with dental floss or tubular teflon tape (Bally Ribbon Mills, PA, USA) locked with plier-flattened small cylinders of Sterling silver. The whole backpack weighed from 2.0–3.5 g, and made up on average 3.9% (SD = 0.4) of the body mass of the males and 3.8% (SD = 0.7) of the body mass of the females (Table 1). Each owl was allowed to habituate to the backpack for at least 24 hours before the collecting of data started. The owls were captured and equipped with radio transmitters with permission from the Directorate for Nature Management.

2.3. Radio-tracking

The owls were tracked on foot using a handheld 4-element Yagi antenna and receiver (Televilt, Sweden). Locations were confirmed visually, except a few where we were unable to spot the owl and therefore determined its position with a horizontal error of <10 m. Our presence was probably not a significant disturbance, because the owls often moved towards us and sometimes killed prey close by (*see also* Kullberg 1995). For the pur-

pose of habitat analysis each owl was located only once during each day, and at different hours on different days, to avoid temporary clumping of locations and thus autocorrelation of an owl's consecutive locations. On a number of days, however, the owls were tracked for up to eight hours to record data on foraging behaviour. Only the first location made on these days were included in the present habitat analysis, but all locations are used in one version of the home range estimate ("Total 100%" home range, *see* below). Due to logistical constraints, each owl was not localised every day. Locations were plotted on copies of aerial photos (scale 1:22 000) in the field and later transferred to maps (1:10 000) and digitalised. Observation periods for each owl are given in Table 1.

2.4. Home range analysis

Home range sizes were calculated according to the minimum convex polygon (MCP) method by using the Wildtrak software for Macintosh computers (Todd 1992). For habitat analysis the 95% MCP was used, calculated from the 100% MCP based on one location per day, after the 5% most distant locations from a calculated centre of activity have been removed (Todd 1992). To show the maximum home range size of the owls, and to make our results comparable with those of Kullberg (1995), we also calculated what we in the following term "Total 100%" MCP, which is based on all locations collected while radio tracking the owls (*see* above). The size of these calculated home ranges increased as the number of radio locations increased. For one half of the owls the increase levelled off, and for most of the others it became smaller, towards the end of the tracking period (Fig. 1). This indicates that there was little real change in the home ranges during the tracking period, and that sample size was sufficient to reliably describe the home range area.

2.5. Habitat analysis

Habitat selection was examined by use of compositional analysis (Aebischer *et al.* 1993), which avoids several problems inherent in earlier meth-
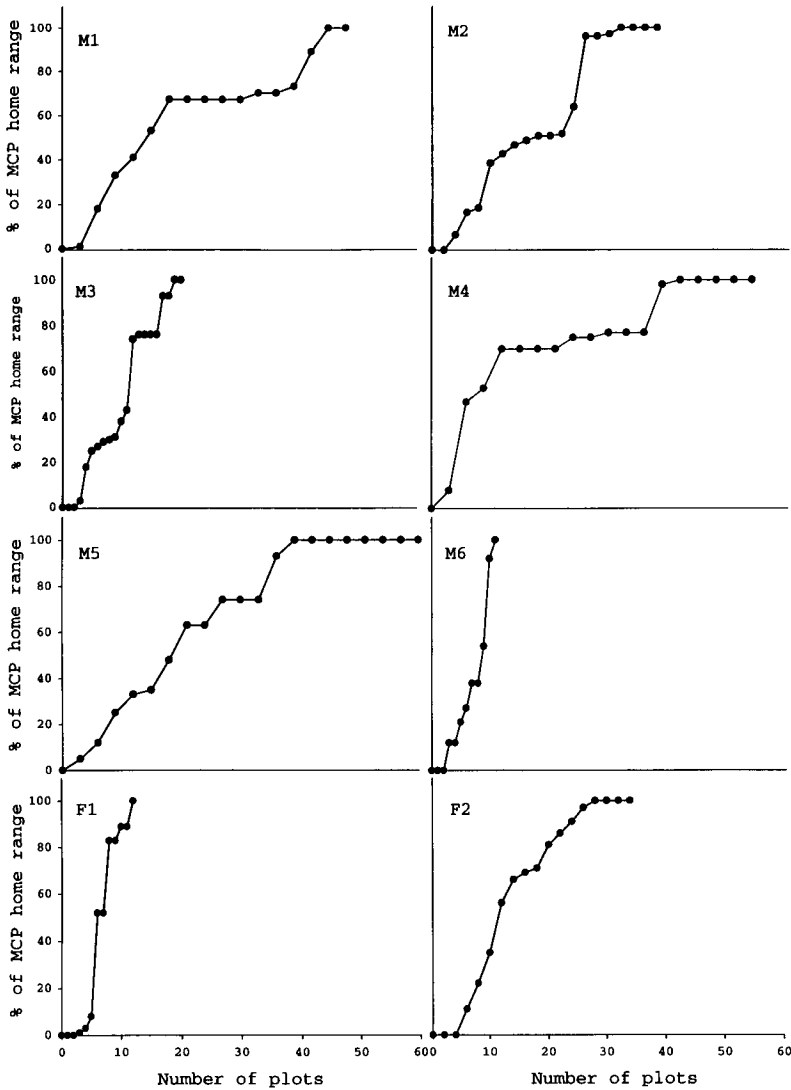
Fig. 1. The home range size (%) as a cumulative function of number of plots for each of the eight Pygmy owls radio-tracked from January to September 1993 in a fragmented forest-farmland landscape in southeastern Norway.

ods, including inappropriate level of sampling, non-independence of proportions, differential habitat use by groups of individuals, and arbitrary definition of habitat availability (Aebischer *et al.* 1993). The analysis was run in two steps: first by including all six habitat categories, then by including the forest categories only (*see* below). The hypothesis whether habitat use was random or not was tested at two levels: habitat composition in the MCP home ranges compared with habitat composition in the study area, and habitat use determined from radio locations compared with habitat composition in the MCP home ranges. To make the habitat analysis conservative, we defined the

study area as the 100% common MCP generated by pooling all locations of the eight Pygmy Owls (Fig. 2), and each home range as the 95% MCP. Defining a larger and arbitrarily delineated study area, and defining home range as the "Total 100%" MCP or 100% MCP, would have biased the estimates of proportions of available habitat even more by including unavailable areas, and areas traversed only during occasional long distance sallies, respectively.

The habitats used by the owls were classified into six categories, based on the system of the Norwegian National Forest Inventory, which has five development classes (DC) and regards forest
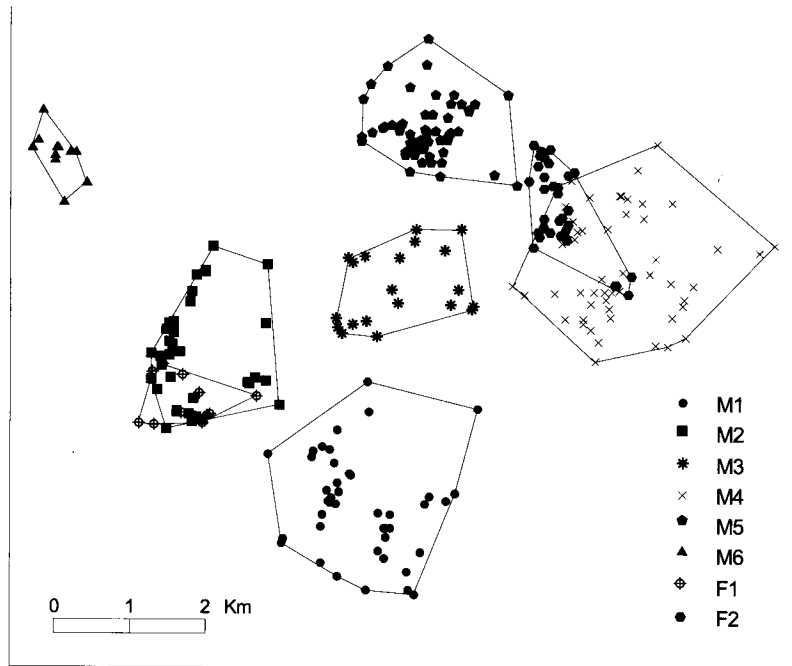
Fig.2. The 100% MCP home ranges of eight Pygmy Owls (six males and two females) radio-tracked from January to September 1993 in a fragmented forest-farmland landscape in southeastern Norway.

age in relation to site quality (Tomter 1994). In the habitat analyses, however, we pooled development classes I and II into one category, and included two more categories; forest edge and crop land. The habitat abbreviations used in the text are explained and described in Table 2.

We estimated the habitat availability for each owl from aerial photos taken in July 1991 (scale 1:22 000), onto which each owl's 95% MCP was overlaid. After correcting for relevant habitat changes (e.g. harvesting of old forest) that had occurred between July 1991 and the start of our study in 1993, the photos were covered by a suitable-sized grid with numbered intersections (cf. Sullivan & Dinsmore 1992). The habitat was

classified at each intersection by use of a stereoscope. This yielded from 80 to 135 habitat classifications per home range, depending on home range size. Intersections difficult to classify from the aerial photos were classified in the field.

2.6. Statistical tests

Statistical tests were computed by using the StatView 4.02 (Abacus Concepts Inc.) software for Macintosh computers, and the Excel 5.0 (Microsoft Corporation) software for PC. All statistical tests are two-tailed. Non-parametric tests

Table 2. Description of the six habitat categories used in the habitat analysis of the Pygmy Owl radio locations, based on the system of the Norwegian National Forest Inventory (Tomter 1994).

Category	Habitat description
DC I/II	Forest under regeneration, regenerated areas and young forest (including clear-cut areas with or without scattered Scots Pines left as seed trees, and gardens, pastures and bogs).
DC III	Young thinning stands.
DC IV	Advanced thinning stands.
DC V	Mature forest stands.
EDGE	A 10 m wide belt of DC III, DC IV or DC V bordering DC I/II or CROP.
CROP	Agricultural crop land (including roads, industrial areas, gravel pits, rivers and landfills).

are corrected for ties. The habitat analysis was computed using the MacComp software for Macintosh computers (Carroll 1996).

3. Results

3.1. Home range size

For the eight Pygmy owls, median "Total 100%" MCP home range was 2.4 km^2 (range 0.5–6.2), while median 100% and 95% MCP home ranges were 2.3 km^2 (range 0.4–6.0) and 1.8 km^2 (range 0.3–4.6), respectively (Table 3). When excluding the areas made up by the habitat category CROP, which the owls never used, median 95% MCP home range was reduced to 1.5 km^2 (range 0.2–4.0).

Home range size varied considerably between individual owls, even when areas made up by the unused habitat category CROP was excluded (Table 3). There was a significant correlation between home range size and number of locations both for "Total 100%" MCP and for 100% and 95% MCP (Spearman's rank correlation; $r_s = 0.83$, $n = 8$, $P = 0.03$ in all cases). In a linear regression model with the 95% MCP home range size as the dependent variable, and the sample size as the independent variable, the sample size explained 55% of the variation in home range size ($F = 7.17_{1,6}$, $R^2 = 0.55$, $n = 8$, $P = 0.036$).

Each sex considered separately, median "Total 100%" MCP home range covered 3.0 km^2

(range 0.5–6.2) for males and 1.2 km^2 (range 1.0–1.4 km^2) for females (Table 3), while median 100% MCP and 95% MCP home ranges were 2.9 km^2 (range 0.4–6.0) and 2.1 km^2 (range 0.3–4.6), respectively, for males and 1.0 km^2 (range 0.7–1.3) and 0.8 km^2 (range 0.5–1.1), respectively, for females (Table 3). Due to the dependence of the calculated home range size on sampling effort, the home range size of the sexes could not be directly compared. However, a comparison of the residuals calculated from the regression of 95% MCP home range size on number of locations showed no significant intersexual difference (Mann-Whitney U-test; $n_1 = 6$, $n_2 = 2$, $U = 3$, $P = 0.32$). There was no range overlap between males or between females (Fig. 2), but there was extensive range overlap between the male and the female of each of the two mated pairs studied (Fig. 2). For the two females (F1 and F2), 79% and 68%, respectively, of the 95% home range was within the 95% home range used by their mates (M2 and M4). The corresponding figures for the two males were only 17% and 16%.

When correcting for sample size (*see* Table 3), there was no significant correlation between the 95% MCP home range size and the proportions of either DC I/II, DC III, DC IV, DC V, EDGE and CROP within the 95% MCP home ranges (Kendall's partial rank-order correlation; $t = -0.45$, $t = -0.26$, $t = 0.14$, $t = 0.02$, $t = -0.34$ and $t = 0.35$, respectively; $n = 8$ and $P > 0.10$ for all categories).

Table 3. Home range sizes (km^2) for six male (M) and two female (F) Pygmy Owls radio-tracked from January to September 1993 in a fragmented forest-farmland landscape in southeastern Norway, estimated by the minimum convex polygon method. The term 100% MCP means that all radio locations were included, while 95% MCP means that the 5% most distant locations were excluded. "Total 100%" MCP is based on the same locations as 100% MCP, as well as on locations made outside the 100% MCP when the owls were roosting or hunting (*see* text). N denotes the total number of radio locations on which the different home range calculations are based.

Ind.	Total 100% MCP	N	100% MCP	N	95% MCP	N	% Crop land	95% MCP without crop land
M1	6.2	52	5.3	46	4.0	44	14.4	3.4
M2	3.2	39	2.9	38	2.4	36	41.5	1.4
M3	1.9	20	1.9	20	1.7	19	15.3	1.5
M4	6.2	55	6.0	53	4.6	50	14.1	4.0
M5	2.8	61	2.8	60	1.9	57	7.3	1.7
M6	0.5	13	0.4	11	0.3	10	7.5	0.2
F1	1.0	15	0.7	12	0.5	11	16.5	0.4
F2	1.4	36	1.3	34	1.1	32	2.4	1.1

3.2. Habitat selection

None of the Pygmy Owls were ever observed outside forest habitats. However, the edge between forest and crop land were used by four of the owls (M1, M2, M5 and F1). All owls were observed in all forest habitats, except DC I/II (no observations of M4, M6, F1 and F2) and DC IV (no observations of M6). For all owls included in the analysis all habitat classes were available within the 95% MCP home range.

3.2.1. Habitat selection on the landscape scale

The habitat composition in the 95% MCP home ranges differed significantly from that in the study area as a whole (Wilk's lambda = 0.02, χ_5^2 = 29.3, P < 0.001). In the comparisons between the 95% MCP home ranges and the study area, DC V ranked highest, followed by DC III, EDGE, DC I/II, DC IV and CROP (Table 4a; Fig. 3a). When compared to what would be expected from the habitat composition in the study area, the proportion of DC V in the home ranges was significantly higher than that of both DC I/II, DC IV and CROP, and the proportion of DC III in the home ranges was significantly higher than that of DC IV (Table 4a).

When the habitat categories EDGE and CROP were excluded from the analysis, the habitat composition in the 95% MCP home ranges still differed significantly from that in the study area (Wilk's lambda = 0.05, χ_3^2 = 23.9, P < 0.001).

Table 4. Matrix of mean (±SE) log-ratio differences with corresponding probabilities for the eight Pygmy Owls radio-tracked, based on comparing proportional habitat availability within the 95% MCP home ranges with the proportional habitat availability within the study area. Habitats are ranked according to the sum of the number of positive log-ratio differences in the rows and the number of negative log-ratio differences in the columns. Significant p-values are shown in bold. For explanation of habitat types, *see* Table 2.

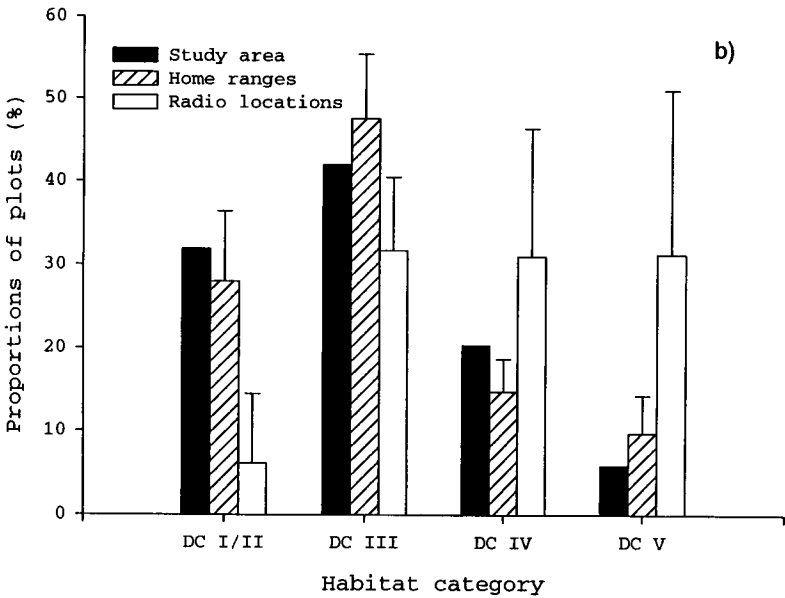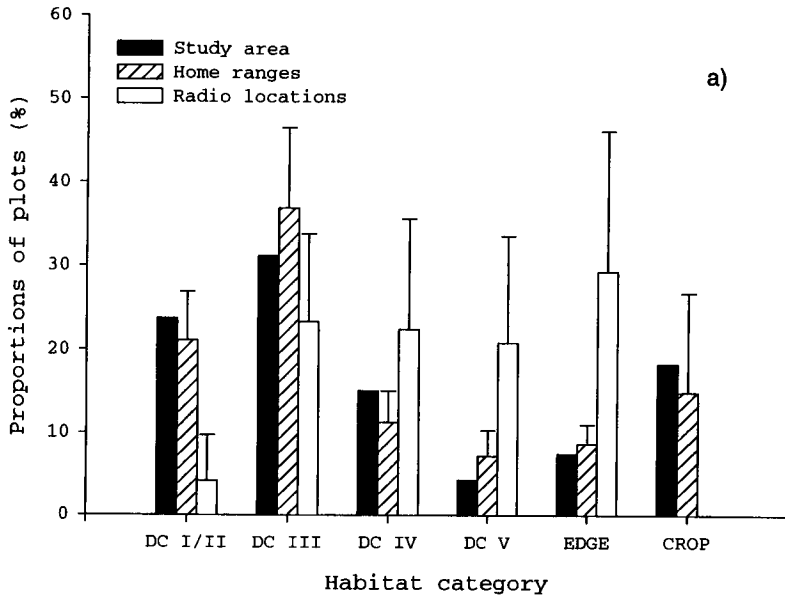| Hab. cat.	DC III	DC IV	DC V	EDGE	CROP	Rank
a) All habitat categories						
DC I/II	−0.29	0.16	−0.65	−0.19	0.32	2
	(±0.15)	(±0.20)	(±0.21)	(±0.10)	(±0.33)	
	0.097	0.441	**0.020**	0.101	0.359	
DC III		0.46	−0.35	0.09	0.62	4
		(±0.08)	(±0.26)	(±0.11)	(±0.39)	
		<0.001	0.219	0.420	0.158	
DC IV			−0.81	−0.36	0.15	1
			(±0.24)	(±0.18)	(±0.39)	
			0.012	0.090	0.696	
DC V				0.45	0.97	5
				(±0.26)	(±0.33)	
				0.126	**0.021**	
EDGE					0.52	3
					(±0.37)	
					0.207	
CROP						0
b) EDGE and CROP excluded						
DC I/II	−0.28	0.16	−0.52			1
	(±0.16)	(±0.20)	(±0.23)			
	0.109	0.441	0.061			
DC III		0.45	−0.23			2
		(±0.09)	(±0.28)			
		0.001	0.430			
DCIV			−68			0
			(±0.26)			
			0.032			
DC V						3

Fig. 3. Habitat composition in the study area in a fragmented forest-farmland landscape in southeastern Norway, of the home ranges of the eight Pygmy Owls radio-tracked from January to September 1993, and of all radio locations of the eight Pygmy Owls. The bars of the two latter denote means with one standard deviation. a) EDGE and CROP included; b) EDGE and CROP excluded. For explanation of habitat types, see Table 2.

Also, in the comparisons between the 95% MCP home ranges and the study area, the DC V still ranked highest, followed by DC III, DC I/II and DC IV (Table 4b, Fig. 3b). When compared to what would be expected from the habitat composition in the study area without EDGE and CROP, both the proportion of DC V and that of DC III in the home ranges was significantly higher than that of DC IV (Table 4b).

3.2.2. Habitat selection on the home range scale

The Pygmy Owls' habitat selection within their 95% MCP home ranges differed significantly from random (Wilk's lambda = 0.01, $\chi_5^2 =$ 33.3, P < 0.001). In the comparisons of relative use of habitat types within the 95% MCP home ranges, EDGE ranked highest, followed by DC V, DC IV, DC III, DC I/II and CROP (Table 5a;

Fig. 3a). When compared to what would be expected from the habitat composition in the 95% home ranges, both EDGE and DC V were used significantly more than both DC I/II, DC III and CROP, while both DC III and DC IV were used significantly more than both DC I/II and CROP (Table 5a).

When EDGE and CROP were excluded from the analysis, habitat use within the 95% MCP home ranges still differed significantly from random (Wilk's lambda = 0.06, $\chi^2_3 = 22.4, P < 0.001$). In the comparisons of relative use of habitat types within the 95% MCP home ranges, DC V ranked highest, followed by DC IV, DC III and DC I/II (Table 5b, Fig. 3b). When compared to what

would be expected from the habitat composition in the 95% home ranges without EDGE and CROP, DC V was used significantly more than both DC I/II and DC III, while both DC III and DC IV were used significantly more than DC I/II (Table 5b).

4. Discussion

4.1. Home range size

Our estimates of home range size are very similar to those Kullberg (1995) found for six Pygmy Owls (four males and two females) radio-tracked

Table 5. Matrix of mean (±SE) log-ratio differences with corresponding probabilities for the eight Pygmy Owls radio-tracked, based on comparing the proportions of radio-locations for each individual in each habitat type with habitat availability within the individual's 95% MCP home range. Habitats are ranked according to the sum of the number of positive log-ratio differences in the rows and the number of negative log-ratio differences in the columns. Significant p-values are shown in bold. For explanation of habitat types, *see* Table 2.

Hab. cat.	DC III	DC IV	DC V	EDGE	CROP	Rank
a) All habitat categories						
DC I/II	−2.26	−2.96	−3.83	−3.92	1.21	1
	(±0.67)	(±0.73)	(±0.74)	(±0.67)	(±0.88)	
	0.012	**0.005**	**0.001**	**<0.001**	0.211	
DC III		−0.69	−1.56	−1.65	3.48	2
		(±0.61)	(±0.15)	(±0.35)	(±0.34)	
		0.297	**<0.001**	**0.002**	**<0.001**	
DC IV			−0.86	−0.96	4.18	3
			(±0.68)	(±0.68)	(±0.74)	
			0.244	0.205	**<0.001**	
DC V				−0.09	5.05	4
				(±0.37)	(±0.31)	
				0.805	**<0.001**	
EDGE					5.14	5
					(±0.48)	
					<0.001	
CROP						0
b) EDGE and CROP excluded						
DC I/II	−2.51	−3.17	−4.10			0
	(±0.76)	(±0.81)	(±0.84)			
	0.013	**0.005**	**0.001**			
DC III		−0.66	−1.58			1
		(±0.66)	(±0.17)			
		0.351	**<0.001**			
DCIV			−0.92			2
			(±0.72)			
			0.243			
DC V						3

the year around in southeastern Sweden. The latter, which ranged from 0.4–2.5 km^2 with a median of 2.2 km^2, were based on all locations and are comparable with our "Total 100%" MCP home range estimates, which ranged from 0.5–6.2 km^2 with a median of 2.4 km^2. To our knowledge no other studies have reported home range sizes of the Pygmy Owl based on radio telemetry.

Estimates of MCP home range size are sensitive to tracking effort (e.g. White & Garrott 1990), which varied considerably between the owls in our study. The recorded home range size increased with the number of locations, and the variation of the latter explained 55% of the variation in the former. An owl's home range size may also change during the course of a year (e.g. Forsman *et al.* 1984, Bull *et al.* 1988). In our study, not all owls were tracked in the same part of the year. Inter-individual differences in the estimated home range sizes may thus simply be an effect of different area use in different parts of the year. However, because our sampling effort accounted for more than half of the variation in home range size, and because the number of tracked owls was restricted, we are unable to reveal which factors other than sample size may have affected home range size. This may also explain why we found no correlation between the home range size and the proportion of any habitat category within the home range.

4.2. Habitat selection

The Pygmy Owls in our study had home ranges larger than most forest stands found in modern managed forests, i.e. they exhibited a fine-grained habitat utilisation pattern (cf. Rolstad 1991). This implies that a Pygmy Owl may utilise forest stands of different successional stages within its home range, and thus may exhibit habitat selection, and that forest fragmentation may be less dramatic for the Pygmy Owl than previously thought (cf. Rolstad 1991, Sonerud 1991a). Pygmy Owls are probably distinctly forest-dependent, because we never observed any of the radio-tagged owls outside forest habitats. However, they utilised the edge between forest and open landscapes (e.g. agricultural land) to a large extent, and areas with low densities of trees (e.g. clear-cut areas with

seed trees, and pastures and gardens) to a small extent.

The habitat composition in the Pygmy Owls' home ranges differed from that in the study area as a whole, suggesting that the home ranges were not randomly located in the overall landscape. Mature forest ranked highest, and clear-cut areas, advanced thinning stands and agricultural land ranked lowest, in the comparison of home ranges with the study area. This indicates a large-scale affinity for mature forest. Exclusion of edge and agricultural land from the analysis did not change the ranking of the forest categories.

4.2.1 Mature forest

Old forest ranked highest in the comparison between Pygmy Owl home ranges and the landscape, and second highest with respect to use relative to availability within the Pygmy Owls' home ranges. This indicates both a large-scale and a small-scale affinity for mature forest, and is in accordance with previous predictions (e.g. Sonerud 1991a, b). The high proportion of mature forest in the home ranges compared to the landscape may not only be due to the affinity to mature forest as hunting habitat, but also to the Pygmy Owl's preference for mature forest as nesting habitat (*see* Mikkola 1983, Cramp 1985). The nests of the two pairs in our study were situated in mature spruce forest, and at least for the female the breeding season constitutes a period of reduced hunting range (Mikkola 1983, Cramp 1985). However, the two females were tracked either prior to the egg-laying period (F1) or after the young had left the nest (F2), which should make them less associated with the nest site. Nor did any other owl in our study concentrate its activity to the vicinity of the nest. Moreover, the relatively large home ranges, the high mobility of the owls, and the fine-grained mosaic of the study area relative to the owls' home ranges, makes it less likely that the use of mature forest as nesting habitat have biased our result.

The habitat selection of birds of prey may be an indirect effect of the habitat selection of their prey (Janes 1985). The Pygmy Owl's affinity for mature forest may thus be explained by a higher prey availability in mature forest than in younger successional stages. Because the proportion of

voles in the Pygmy Owl's diet varies with the abundance of voles in the environment, whereas the that of birds varies inversely (Kellomäki 1977, Solheim 1984, Ekman 1986, Suhonen 1993), and because our study took place in a year with low population densities of voles (G. A. Sonerud unpubl. data), the habitat use of the radio-tagged Pygmy Owls was probably more influenced by the habitat distribution of small birds than of the habitat distribution of voles.

In the boreal forest in Fennoscandia, breeding bird density increases during the early stages of succession, and reaches a peak in medium-aged or old forest (Haapanen 1965, Ødegaard 1982, Helle 1986, Helle & Mönkkönen 1990, Jokimäki & Huhta 1996, Solonen 1996, *see also* Helle 1985, Virkkala 1987). Whereas overall proportion of tropical migrants is highest in the early stages of forest succession, and overall density of migrants peak in the intermediate stages (Mönkkönen 1991), the old forest is especially important for sedentary birds (e.g. Järvinen *et al.* 1977, Helle 1985). Thus, for the Pygmy Owl, abundance of avian prey is highest in old forest in winter, and in medium-aged or old forest during rest of the year.

The mammalian part of the Pygmy Owl's diet consists mainly of Bank Vole and Field Vole *Microtus agrestis* (e.g. Haftorn 1971, Kellomäki 1977, Mikkola 1983, Solheim 1984, Cramp 1985, Ekman 1986, Suhonen 1993). Field voles are found almost exclusively in clear-cut areas, whereas Bank Voles occur in a wide range of habitats, but more commonly in forested than in clear-cut areas, especially during spring (e.g. Henttonen *et al.* 1977, Sonerud 1986). Because the field vole population was in a long-term population low with reduced cyclicity during our study (G. A. Sonerud unpubl. data, cf. Hanski & Henttonen 1996, Steen *et al.* 1996), and because the availability of voles for an avian predator which rely on sight to locate prey in general is lower in clear-cut than in forested areas during most of the year (*see* Sonerud 1997), the Pygmy Owl's relative gain of hunting voles was probably lower in clear-cut than in forested areas.

4.2.2. Forest edge

Within the Pygmy Owls' home ranges the 10 m wide belt of forest bordering open areas ranked higher than all other habitat categories with respect to use relative to availability. However, in statistical terms, the ranking of this edge zone did not differ from that of mature forest. This indicates a small-scale affinity for both the mature forest and for the edge between mature forest, advanced thinning stands, or young thinning stands on one side, and agricultural land or clear-cut areas on the other. Affinity for edge zones when hunting has also been reported for the other diurnal owl in the boreal forest, the Hawk Owl *Surnia ulula* (Bækken 1988, cf. Sonerud 1997).

The Pygmy Owl's affinity for edge zones may be explained by several factors, not mutually exclusive. From the boreal forest in Fennoscandia, there is some evidence of an enhanced density in forest edges for passerines (e.g. Helle & Helle 1982, Hansson 1983, Helle 1983, Jokimäki & Huhta 1996, Solonen 1996) and for small mammals (Hansson 1982). Hence, because passerines and small mammals constitute the main prey of the Pygmy Owl (*see* above), its affinity for forest edge may thus be explained by a higher prey abundance there.

The forest edge may also offer perches from which the predator can search for prey in nearby open habitats, e.g. clear-cut areas (Sonerud 1986, 1997, Bækken 1988). All birds of prey use eyes as well as ears for prey detection and localisation, but the relative importance of these senses varies among species, and determines the type of habitat that can be efficiently exploited, and the way prey can be efficiently searched for (e.g. Norberg 1977, 1987, Sonerud 1986). The Pygmy Owl, in common with other diurnal owls, differs from nocturnal owls in lacking the bilateral ear asymmetry that enables the latter to locate prey in total darkness or prey hidden subniveally (Norberg 1977, 1987, Sonerud 1986), so its hunting attacks are triggered by optical stimuli (Schertzinger 1970, Mikkola 1983). Diurnal birds of prey hunting small mammals usually select high vantage points from where they can search a large ground area for prey (e.g. Sonerud 1980, 1997, Rice 1983, Norberg 1987). The lack of such perches in clear-cut areas are suggested to prevent these predators from exploiting clear-cuttings efficiently (Sonerud 1980, 1997). By using the edge, however, at least prey in the margins of clear-cut areas may become available (Sonerud 1997). The Pygmy Owls

frequently used forest edges for locating voles which thereafter were captured in the clear-cut areas (H. Strøm and G. A. Sonerud, pers. obs.). Thus, the affinity for edge shown by the Pygmy Owls in our study may be explained both by a higher availability of small mammal and passerine prey in the edge zone, and by the fact that the edge zones provide an ample supply of elevated perches from which the Pygmy Owl can locate small mammals in the nearby clear-cut areas.

4.3. Affinity to mature forest: minimising competition and predation risk?

Birds of prey may not utilise the full range of available habitats due to interactions with both competitors and predators (Janes 1985). We suggest that this may have contributed to the Pygmy Owl's affinity to mature forest in our study. Due to its small size, diurnal habit, and dependence on avian prey in years when voles are few, the Pygmy Owl is probably most exposed to competition and predation from Sparrowhawk *Accipiter nisus* and Goshawk *Accipiter gentilis* (cf. Mikkola 1983). Because birds weighing 50–80 g are most at risk to be taken by Sparrowhawk (Selås 1993), the Pygmy Owl constitutes a highly suitable prey. Also, because the diet of the Pygmy Owl resembles that of the Sparrowhawk (*see* Kellomäki 1977, Selås 1993), these two predators may mutually depress their avian prey supply, not only through exploitation, but also through interference causing behavioural prey depression (cf. Charnov *et al.* 1976, Andersson & Norberg 1981). Because the Sparrowhawk prefers medium-aged forest when hunting (Selås & Rafoss 1999), the Pygmy Owl may minimise predation risk as well as prey disturbance and exploitation posed by the Sparrowhawk by utilising mature forest. However, the larger Goshawk prefers hunting in old forest (Widén 1989), and mostly prey on medium-sized and large bird species like thrushes, corvids, pigeons and grouse (Widén 1987, Selås 1989). Thus, although the Pygmy Owl risks falling prey to the Goshawk in mature forest, the Goshawk mostly takes larger prey and breeds at a considerably lower density than the Sparrowhawk (Selås 1997), and therefore probably constitutes less of a danger to the Pygmy owl.

5. Conclusion

We found that the Pygmy Owl's home range is larger than most forest stands found in modern managed forest landscapes. This may make the effect of old forest fragmentation on Pygmy Owl populations less dramatic than previously thought. Our results also indicate an affinity for mature forest on both a large scale (landscape) and a small scale (home range), and for the edge between forest and open areas on the small scale. We suggest that the former may be a strategy to minimise predation risk and competition from the Sparrowhawk, while the latter may be due to both a higher abundance of prey in the edge zone, and to an ample supply of elevated perches from which to hunt prey in bordering open areas. Fragmentation of the old forest by modern forestry may be harmful to Pygmy Owl populations by harvesting the old forest, but also beneficial by creating more edges between old forest and stands of younger successional stages. Future studies should focus on effects of the interannual vole density fluctuations on Pygmy Owl habitat selection, and on the effects of mature forest patch size, patch shape and interpatch distance on Pygmy Owl area use and population density.

Sammanfattning: Hemmaområde och habitatselektion hos sparvuggla

Hemmaområdet och habitatselektion för åtta vuxna sparvugglor (sex hannar och två honor) blev uppmätt med använding av radiotelemetri i ett

fragmenterat skogs- och jordbruksområde i sydöstra Norge från januari till september, 1993, då bestånden av små däggdjur var i bottenfasen. Hemmaområdet (minimum konvex polygon) baserat på en lokalisering per dag varierade från 0.4 till 6.0 km², med ett genomsnitt av 2.3 km². Habitatsammansättningen i sparvugglornas hemmaområden avvek från habitatsammansättningen i studieområdet. I denna habitatselektion i stor skala rangerade avverkningsmogen skog högst, etterföljd av yngre produktionsskog, kant mellan skog och öppna områden, avverkningsytor, äldre produktionsskog, och till slut odlad mark, var sparvugglorna aldrig blev observerade. Sparvugglornas använding av habitat avvek från utbudet av habitat i hemmaområdet. I denna habitatselektion i liten skala rangerade kant mellan skog och öppna områden högst, efterföljda av avverkningsmoden skog, äldre produktionsskog, yngre produktionsskog, avverkningsytor och odlad mark. Sparvugglan blir drabbad av skogsbruket genom avverkning av gammal skog, men den blir också gynnad genom att det skapas mer kant mellan gammal skog och skog i yngre successionsstadier.

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