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The tolerance of lynxes *Lynx lynx* to human presence and disturbance in a hunted population in Norway was studied using telemetry. Forest land within 200 metres from the nearest road or house was avoided by lynxes when resting (P < 0.01). The tolerance distance of resting lynxes towards intruding people was short (median 50 m), though strongly correlated with the horizontal vegetation cover (partial correlation, P < 0.02) and forest maturation stage (partial correlation, P < 0.02), but not with terrain inclination (partial correlation, P > 0.3). The lynxes did not enter steeper country (P > 0.4) or alter their daily walking distance (P > 0.7) after being disturbed. The data indicate that lynxes, even when suffering extensive, man-induced mortality, may tolerate high human activity within their range as long as sufficient stands of undisturbed, mature forest with dense horizontal cover are present.

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A number of large carnivorous mammals have been reported to avoid suitable areas adjacent to human occurrence or human facilities (van Dyke, Brocke, Shaw, Ackerman, Hemker & Lindzey 1986, Brody & Pelton 1989, Thurber, Peterson, Drummer & Thomasma 1994, Lovallo & Anderson 1996, Mace, Waller, Manley, Lyon & Zuuring 1996). Behaviourally initiated avoidance of otherwise potential habitats because of human presence may have selective value for the individual, but may reduce the overall ecological carrying capacity and population size, especially if these habitats are of high quality (e.g. Mace et al. 1996).

In the present study, the lynx *Lynx lynx* tolerance to human presence was investigated in an area in central Norway where hunting caused the majority of lynx mortality. The tolerance distance of radio-collared lynxes to regular human presence (occupied houses and daily-used roads) within a rural area with mixed farmland and forest was investigated, and the behavioural response to experimental disturbance by intruding people was quantified.

## Study area

During 1994-1997, lynxes were studied in the northern part of Nord-Trøndelag County (Namdalen), cen-

tral Norway. The landscape was highly heterogeneous, ranging from rural areas in the lowland to alpine tundra in the mountains. For a further description of the study area see Sunde, Overskaug & Kvam (1998).

The rural areas in the lowland supported relatively higher densities of ungulate prey, primarily roe deer *Capreolus capreolus*, and were highly preferred by lynxes to habitats of higher elevations (P. Sunde, T. Kvam, P. Moa, A. Negård & K. Overskaug, unpubl. data) though more hazardous because of hunting. Hunting was concentrated near roads and accounted for all known deaths of radio-collared lynxes (Sunde et al. 1998). The rural areas are typical landscape mosaics with concentrations of fields surrounded by spruce forest with birch and alder in the transition zones. Almost all lowland forest is logged commercially and consists of a mosaic of young, successional stages.

## Material and methods

From January 1994 through March 1997, lynxes were tracked after being equipped with radio-collars (Sunde et al. 1998). Standard telemetric methods were used in summer. Usually, the lynxes were located using triangulation, but in winter, telemetry was widely supplemented with tracking of the radio-tagged lynxes in the snow.

### Habitat use in rural habitats

Three areas of concentrated woodland-farmland mosaics below 300 m a.s.l. in the centre of the study area were selected for an analysis of whether the lynx locations were altered near habitation and roads. The three areas covered approximately 500 km$^2$ and comprised 14% of fields, the rest being forest.

The investigated habitat parameters, measured on 1:50,000 scale maps (M711 series: Statens Kartverk) were: 1) the distance from nearest cultivated field (DF), 2) the distance from the nearest, predictable human occurrence (DPHO), i.e. occupied houses or daily-used roads (DR), 3) the elevation (EL) and 4) the slope of the terrain (SL). The traffic load on the roads varied from the daily use of a few families to the E6 primary road. EL was measured to the nearest 20 m equidistant line. SL was measured as the inclination of the terrain within 100 m from the chosen spot, i.e. as the highest possible number of 20 m equidistant lines crossing a 200 m cross section.

Habitat selection was examined for 10 radio-collared lynxes at rest during the daytime. A total of 197 lynx positions, located with an estimated error of less than ±50 m using telemetry and/or snow tracking, were selected for the analysis. Because of no significant individual or sexual differences in habitat preference (see Table 2), the observations were pooled letting each lynx fix be the observational unit in the further analyses. Accordingly, 11 resting sites from unidentified snow-tracked lynxes were added to the data set, yielding a total of 208 day locations.

Preference of varying DF within forest habitats was tested against a paired sample of semi-random positions (R1-fixes) placed 1,000 m from each of the original fixes within the forest. Because the habitat use was significantly constrained by DF that in turn was strongly correlated with DPHO and EL, preferences in relation to DPHO, SL and EL were tested against a second sample of semi-randomised fixes (R2-fixes) which in addition to a fixed distance (1,000 m) in a random direction had exactly the same distance to the nearest cultivated field as had the original fix.

Preferences concerning SL and EL were tested with Wilcoxon's signed rank test for matched pairs using the paired differences between the observed locations and their corresponding R2-fixes.

The 'distance' variables, DF and DPHO, were tested on the largest difference between the cumulated distributions of observed and randomised fixes, $D_{max}$. The null-hypothesis of no difference was simulated by randomly mixing the two values within each pair of observed and semi-random fixes a huge number of times and by comparing the 'true' $D_{max}$ with the randomised $D_{max}$ values.

The test of preference of DF was made two-tailed with the significance of the alternative hypothesis being equal to half the proportion of the randomised values of $Diff_{max}$ that had a higher numeric value than originally observed (Manly 1997).

DPHO was tested one-tailed, with P being the proportion for $D_{max}$ being more negative than originally observed, since only the negative preference for areas near habitation and roads was of interest. Preference for a given distance interval from human installations was measured on an index of selectivity (SI) given by the natural logarithm to the ratio of the number of observed versus expected fixes. SI deviated significantly from unity if the upper or lower 2.5-percentile of the randomised estimates, when added to the observed SI, overlapped with 0 (Manly 1997).

In the randomisation tests, 2,000 (DPHO) or 8,000 (DF) permutations were generated.

## Experimental disturbance of radio-collared lynxes

To measure the reactions of the lynxes to human disturbance, resting radio-collared lynxes were approached. The lynx should have stayed at the same place for several hours, and its location be known with a precision of ±25 m before the trial. One or two people walked slowly towards the lynx, while simulating a normal behaviour of people unaware of its presence. Usually the lynx was aware of the intruders at a long distance as recorded by motion signals from the radio-transmitter. It was, in the same way, possible to detect when the lynx rested again.

The immediate behavioural response was measured by the tolerance distance (TD): the distance from the intruders when the lynx fled; the movement distance (MD): the linear distance to the place were it settled again; and the period of provoked activity (PPA): the time it was in activity from it was chased until it rested again. To examine whether or not the chased lynxes preferred steeper surroundings for the second rest, SL for the original place was compared with SL of the new loafing place. The effect of the following habitat parameters on lynx response was investigated: horizontal visibility index {HVI; 1: very dense vegetation (< 5 m sight), 2: dense (6-10 m), 3: moderate (10-25 m), 4: open forest (25-50 m), 5: open land (>50 m)}, forest maturation stage {FMS; 1: clear-cuttings (0 - ½ m tall), 2: small trees (½ - 5 m), 3: young forest (6 - 10 m), 4: middle-aged forest (10 - 15 m), 5: mature forest (forest ready for timber harvest) and 6: pristine forest (no logging had occurred)} and terrain inclination within a radius of 15 m from the day bed {INC; 1: 0 - 5% inclination, 2: 6 - 10%, 3: 11 - 20%, 4: 21 - 50% and 5: > 50%}. TD, MD and PPA were correlated with the habitat parameters with Pearson's r that allowed for partial correlation.

A longer term effect on behaviour was measured by 1) the linear walking distance the previous night against the linear walking distance the night after the disturbance and 2) SL at the disturbed resting place compared with SL at the resting site the day after. It was also examined whether females with mobile cubs (4-10 months old) responded differently to disturbance than did single lynxes.

## Results

### Habitat use of resting lynxes

About 45% of the activity of radio-collared lynxes (estimate (not biased by habitat) based on 281 fixes from fixed-winged aircraft obtained from 11 independent lynxes) were located within the three studied areas of woodland-field mosaics.

Tests of homogeneity revealed that use of DF, EL and SL were different for different lynxes (Table 1). However, there was no difference in preference

Table 1. Mean values (SE) of the use (OBS) and preference (OBS - R) of various habitat variables of the lynxes that contributed with fixes to the analysis. The preference measures are given as the difference between each true lynx location and its corresponding semi-random fix. R1 and R2 refer to different definitions of the semi-random fixes (see text for explanation). F are females, M, males, whereas UI stands for unidentified lynx registered during snow-tracking. DF: distance to nearest cultivated field. DPHO: distance to nearest predictable human occurrence, i.e., permanently used roads or occupied houses. EL: elevation in m a. s. l.. SL: slope, the maximum number of 20 m equidistant lines intersecting a 200 m cross-section through the fix. Homogeneity among the different individuals was tested with Kruskall-Wallis one-way ANOVA. Significance levels: ns: $P > 0.05$, **: $P < 0.01$, ***: $P < 0.001$. Only the preference measures were used in the further analyses.

| Lynx | N | DF (m) | | DPHO (m) | | EL (m a.s.l.) | | SL (20 m/200 m) | |
|---|---|---|---|---|---|---|---|---|---|
| | | OBS | OBS - R1 | OBS | OBS - R2 | OBS | OBS - R2 | OBS | OBS - R2 |
| F1 | 26 | 335 (51) | -217 (72) | 553 (64) | -60 (51) | 116 (10) | 16 (11) | 3.2 (0.2) | 1.3 (0.3) |
| F2 | 38 | 287 (47) | 16 (49) | 472 (45) | -10 (38) | 144 (12) | -14 (9) | 2.1 (0.2) | 0.6 (0.2) |
| F3 | 5 | 550 (0) | -260 (211) | 590 (60) | 90 (60) | 152 (8) | 20 (0) | 3.8 (0.2) | 0.2 (0.2) |
| F5 | 16 | 779 (132) | -5 (154) | 806 (137) | 9 (80) | 212 (25) | 38 (24) | 2.8 (0.4) | 1.0 (0.5) |
| F6 | 21 | 271 (70) | -228 (71) | 464 (73) | 52 (77) | 116 (23) | 2 (19) | 2.4 (0.3) | 0.9 (0.3) |
| M1 | 39 | 444 (49) | -100 (79) | 498 (44) | 44 (42) | 153 (11) | 14 (11) | 2.8 (0.3) | 0.6 (0.3) |
| M2 | 8 | 311 (95) | -111 (78) | 538 (139) | 113 (149) | 115 (27) | 21 (25) | 1.6 (0.4) | 0.5 (0.7) |
| M3 | 14 | 661 (137) | -43 (159) | 675 (121) | -64 (96) | 215 (37) | 69 (37) | 5.0 (0.9) | 3.1 (0.9) |
| M4 | 30 | 411 (61) | -266 (79) | 591 (66) | 25 (72) | 136 (14) | 14 (15) | 3.5 (0.3) | 0.8 (0.4) |
| UI | 11 | 464 (79) | -127 (173) | 555 (93) | -182 (110) | 124 (23) | -14 (23) | 5.2 (0.8) | 2.6 (1.1) |
| Homogeneity test (Kruskall-Wallis one-way ANOVA): | | | | | | | | | |
| $\chi^2$ (df = 9) | | 27.854 | 11.464 | 8.264 | 6.240 | 23.922 | 15.097 | 40.681 | 14.125 |
| Significance: | | *** | ns | ns | ns | ** | ns | *** | ns |
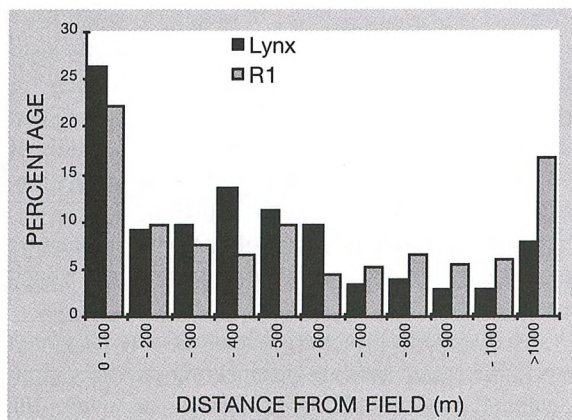
Figure 1. Percentage distribution of used and available woodland habitats in varying distances from the nearest cultivated field in 208 day locations of lynxes. The availability is measured by the distribution of the corresponding semi-random fixes (R1) which were randomly placed in woodland, 1,000 m from each of the original fixes.

(measured as the difference between the observed and the semi-randomised fix) for any of the variables (see Table 1). Hence, the data of the individuals were pooled for further analyses.

Even though 14% of the area selected for study was covered by fields, all 208 fixes were found in forests. However, forest within 600 metres from fields was used more than expected from R1-fixes ($D_{max} = 0.192$, two-tailed randomisation test: P< 0.001) (Fig. 1). Compared with available sites with

Table 2. Percentage frequency of 208 day locations of resting lynx (OBS) in varying distances from nearest predictable human occurrence (DPHO), i.e., the nearest, occupied house or daily used road, compared with the distribution of corresponding semi-random fixes (R2, see text for definition). D denotes the accumulated percentage difference between the two distributions (D = ΣOBS - ΣR2). The avoidance of areas near human installations was tested (one-tailed), using the numerically largest accumulated difference, $D_{max}$, as test statistics with P = the proportion of 2,000 randomised $D_{max}$ values that were more negative than the observed value. Because the accumulated distributions in the test were not rounded to nearest hundred metre, its $D_{max}$ is slightly more negative than the value obtained from the table. Relative preference for each of the intervals of distance was measured on a selectivity index (SI = ln (OBS : R2)). Significant (two-tailed) deviations of SI from unity in the intervals, revealed by the randomisations, are marked with an asterisk.

| DPHO (m) | Frequency (in %) | | | |
|---|---|---|---|---|
| | OBS | R2 | D | SI |
| 0 - 100 | 8.2 | 9.1 | -0.9 | -0.11 |
| 101 - 200 | 10.1 | 17.8 | -8.6 | -0.57* |
| 201 - 300 | 11.5 | 4.3 | -1.4 | 0.98* |
| 301 - 400 | 9.1 | 12.0 | -4.3 | -0.28 |
| 401 - 500 | 13.9 | 13.0 | -3.4 | 0.07 |
| >500 | 47.1 | 43.8 | -0.1 | 0.07 |

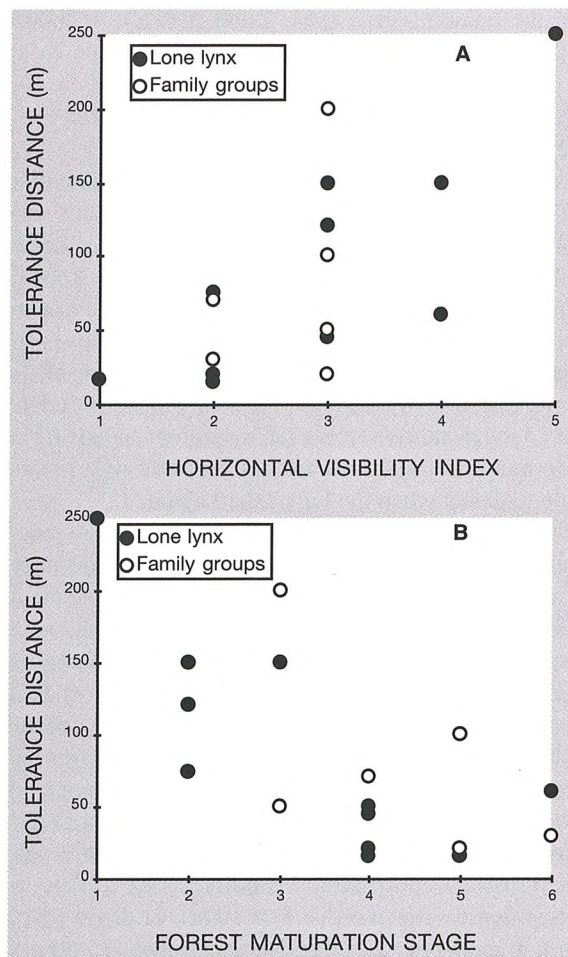Model test: $D_{max}$ = -8.7, P = 0.006



Figure 2. A) Tolerance distance of resting lynxes towards intruding people correlated with the horizontal visibility index. Lynxes accept people at closer proximities when the vegetation cover is dens (see Table 3). B) Tolerance distance of resting lynxes towards intruding people correlated with forest maturation stage. The tolerance distance decreases with increasing forest succession (see Table 3).

the same distance from fields, lynxes preferred steeper terrain (SL; Wilcoxon's test: P< 0.001, mean diff. = 1.0), but no particular elevations were preferred (EL; Wilcoxon's test: P = 0.65, mean diff. = 12 m). The closest distances ever found from resting lynxes to houses and roads were 60 and 40 m, respectively. Lynxes generally avoided areas within 200 m from houses or roads, but compensated with a positive preference for the 200-300 m distance zone (Table 2).

## Behavioural response to experimental disturbance

Twenty-four experimental disturbing sessions were

Table 3. Pearson's correlation coefficients between habitat factors and immediate behavioural response to intruding people of radio-collared lynxes at rest. By partial correlation, the implementing effects of the other two factors are eliminated. TD: tolerance distance; the distance to the intruding people at which the lynx left its bed site. MD: movement distance; the distance walked by the lynx before it rested again. PPA: provoked period of activity; the duration of activity after being chased. Habitat parameters: HVI - horizontal visibility index; ranging from 1 (very dense) to 5 (open land). FMS - forest maturation stage; index ranging from 1(clear cutting) to 6 (pristine forest); INC - inclination at the loafing place; index ranging from 1 (0-5%) to 5 (>50%).

| Response to disturbance | Habitat factor | Bivariate | | | Partial | | |
|---|---|---|---|---|---|---|---|
| | | r | P | df | r | P | df |
| TD | HVI | 0.710 | 0.001 | 17 | 0.589 | 0.016 | 14 |
| | FMS | -0.682 | 0.002 | 16 | -0.581 | 0.018 | 14 |
| | INC | -0.507 | 0.027 | 19 | -0.270 | 0.311 | 14 |
| MD | HVI | 0.253 | 0.244 | 21 | 0.240 | 0.309 | 18 |
| | FMS | 0.202 | 0.367 | 20 | 0.362 | 0.117 | 18 |
| | INC | -0.264 | 0.223 | 21 | -0.361 | 0.118 | 18 |
| PPA | HVI | 0.590 | 0.016 | 14 | 0.539 | 0.057 | 11 |
| | FMS | -0.145 | 0.607 | 13 | 0.067 | 0.828 | 11 |
| | INC | -0.262 | 0.327 | 14 | -0.042 | 0.863 | 11 |

conducted with nine different radio-collared lynxes, including four different family groups.

The median tolerance distance towards intruding people was 50 m, but it varied considerably (from 8 to 250 m) and was highly correlated with horizontal visibility index (Fig. 2a, Table 3) and forest maturation stage (see Fig. 2b and Table 3). An apparent effect of bed site inclination on tolerance distance disappeared when partial correlation was calculated (see Table 3). The median movement distance of the lynxes after being roused was 300 m, but ranged from 0 (the lynx withdrew 50 metre and returned when the intruders left) to 2,500 m, independently of the habitat parameters (see Table 3). PPA varied from 5 to 170 minutes (median 38 minutes) and tended to be lower in dense vegetation (see Table 3).

The lynxes did not enter steeper terrain for the new rest (SL; Wilcoxon's test: P = 0.55, N = 20) or when resting the next day (SL; Wilcoxon's test: P = 0.45, N = 15). Nor were there any indications of change in the linear walking distance the following night compared with the night before the disturbance (Wilcoxon's test: P = 0.76, N = 18).

No differences in behavioural response were found between females with cubs and lone lynxes (see Fig. 2). However, in two of the experiments, the mother left her cub on a tree before moving away.

## Discussion

There is much empirical evidence indicating that various species of carnivores suffer increased mortality in habitats intersected by roads and habitation (e.g.

grizzly bear *Ursus arctos* (McLelland & Shackleton 1988, Mace et al. 1996), wolf *Canis lupus* (Mech 1989) and Iberian lynx *Lynx pardina* (Ferreras, Aldama, Beltran & Delibes 1992), but see also Weaver, Paquet & Ruggiero 1996). Behavioural avoidance of humans may therefore be of high selective value for the individual and has been found to be maintained for long time after persecution has ceased (Thurber et al. 1994) or over seasons with different hunting pressure (Brody & Pelton 1989). Hence, behaviour alone may restrict the range of individuals and populations, even in periods when they are protected. This may be of relevance for managers of, e.g., urbanised countries or regions with small and protected lynx populations in fragmented habitats that also serve as public recreation areas.

The occurrence of Eurasian lynxes *Lynx lynx* in Norway in the 20th century has been widely regulated by man (Myrberget 1970). In the present study area, hunting-induced mortality of lynxes was found to be considerably higher in the vicinity of roads and habitation (Sunde et al. 1998). However, the rural areas in the lowland also sustained the highest prey densities and the most preferred lynx habitats (P. Sunde, T. Kvam, P. Moa, A. Negård & K. Overskaug, unpubl. data). The present investigation may therefore serve as a case study of a carnivore population where the most preferred habitats lead to a high risk of man-induced mortality.

The Eurasian lynx has, as many other felids, a cryptic behaviour, hiding during the day and hunting by stalking at night, a general habit that implies cover. Because humans and lynxes are active at different times of the day, the limiting habitat require-

ments in areas with human presence probably are available safe covers during the daytime. This is also indicated by the observation that lynxes at night widely used open country and also used roads and bridges as paths (S.Ø. Stener, unpubl. data). The highly significant preference for steep country and forest habitats compared with open land is presumably a general preference for safe hiding places that is also seen in other resting felids (e.g. Anderson 1990).

Habitation and roads, both characterised by a predictable, local occurrence of people, seemed to alter the pattern of habitat use with a zone of avoidance of 0-200 m, compensating with a positive selection for the 200-300 m zone. This avoidance, however, was not very strong, indicating that lynxes cared little about the presence of people. An observation of a breeding den less than 500 m from human habitation (P. Sunde, T. Kvam, P. Moa, A. Negård & K. Overskaug, unpubl. data), further indicates that females may tolerate human activity, even in the presumably most critical phases of breeding. Since lynxes did not avoid human facilities at night (S.Ø. Stener, unpubl. data), it was probably the presence of people rather than the alteration of the habitat (i.e. the presence of the roads or houses) that influenced their behaviour during the day.

In the disturbance experiments, lynxes tolerated quite well people that unpredictably appeared in their vicinity, as indicated by the generally short tolerance distances. Nor did the chases result in short term (same day) or longer term (next day) changes in habitat use or movement patterns. However, the tolerance of resting lynxes towards intruding people was highly dependent upon vegetation cover and forest age. It is noteworthy that habitat inclination (*sensu stricto*) had no influence on the tolerance distance after the effect of vegetation was eliminated statistically. The general preference for steep resting sites, may therefore to some extent be a result of preference for uncultivated forest stands, which are most abundant in steep country, where timber logging is less intensive. High tolerance toward people has previously been reported from a protected lynx population in the Swiss Alps and Jura mountains (Breitenmoser, Kaczensky, Dötterer, Breitenmoser-Würsten, Capt, Bernhart & Liberek 1993). In contrast, the population in the present study was subject to intensive hunting (Sunde et al. 1998). The data therefore support further evidence that lynxes in general may tolerate man at quite high densities as long as sufficient forest habitats are present with lounges of undisturbed refuges with mature forest and dense vegetation.

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