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Diurnal exposure as a risk sensitive behaviour in tawny owls *Strix aluco*?

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Sunde, P., Bølstad, M. S. and Desfor, K. B. 2003. Diurnal exposure as a risk sensitive behaviour in tawny owls *Strix aluco*? – J. Avian Biol. 34: 409–418.

Tawny owls *Strix aluco* generally roost in cryptic locations during the day. To test the hypothesis that this cryptic behaviour is an effort to avoid mobbers or avian predators, we measured diurnal behaviour and cause-specific mortality of radio-tagged birds. Non-breeding adults (assumed to be well fed individuals, optimising their own survival) roosted in less exposed locations than adults with young and newly independent juveniles. Parents roosted in the most exposed sites when their young were immature and vulnerable to depredation, probably to guard offspring. Newly independent juveniles apparently selected roosting sites in exposed places to get access to food, as this behaviour was associated with lower perching heights and higher prey abundance beneath their roosting sites. They also perched in more exposed sites, closer to the ground, in summers with low prey abundance compared to summers with high prey abundance. After previous encounters with goshawks *Accipiter gentilis*, dependent juveniles roosted in less exposed places compared to other young. The increased risk of being mobbed was highly significant with increasing roosting exposure. Once an owl was mobbed, the intensity of the mobbing correlated positively with the mass of the mobbers, but mobbing birds never killed any owls. In contrast, diurnal raptors caused 73% of natural owl deaths ($n = 15$) and the depredation rate by raptors was 3.8 times higher in population classes that generally roosted in more exposed locations than did non-breeding adults. We therefore suggest that depredation by diurnal raptors is the main factor shaping the diurnal behaviour of tawny owls.

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While adapted for nocturnal hunting, owls can acquire additional prey by hunting in daylight. Nevertheless, most owls have a very cryptic diurnal behaviour (e.g. Hayward and Garton 1984, Belthoff and Ritchison 1990, Carey et al. 1992), indicating high costs associated with diurnal activity. Mobbing might be such a cost in terms of lost rest or foraging opportunities, or even injury or death (Curio 1978, Harvey and Greenwood 1978). Depressed diurnal activity may also be an anti-predator behaviour, as owls, because of their slow flight, may be particularly vulnerable to depredation by diurnal raptors (Mikkola 1983). Alternatively, thermoregulatory concerns (Walsberg 1986, Kortner and Geiser 1999) or avoidance of insects transferring blood parasites (Rohner et al. 2000) might also influence the

diurnal behaviour of nocturnally active birds.

This paper investigates whether the activity period of radio-tagged tawny owls *Strix aluco* is restricted to the dark hours as a result of disproportionately high costs of diurnal exposure. Examination of diurnal roosts of tawny owls revealed variation in the sites, and in exposure of the owls to mortality by depredation and harassment by mobbing. We considered what countervailing benefits might be associated with roosting in exposed sites. We predicted that the cost of increased exposure might be counterbalanced by the benefit of improved opportunities for offspring guarding and diurnal foraging, and therefore, we investigated these potential costs and benefits. We expected to find that parents guarding predation-vulnerable offspring

should take greater risks in selecting diurnal roost sites adjacent to their young. Similarly, we expected to find that population classes of owls that are in greater need of food should take greater risks in selecting diurnal roost sites to get access to food.

By pinpointing the probable costs and benefits of diurnal exposure in this owl species, normally considered to be highly nocturnal, we hope to provide a hint about which factors that are likely to cause the cryptic diurnal behaviour, a behaviour that appear to be widespread among many species of owls and other nocturnally active birds.

Materials and methods

Study species

The tawny owl (400–600 g) is a crepuscular (Martin 1990) predator that attacks vertebrate prey from perches in trees (Redpath 1995). Occasional reports exist of diurnal hunting during the breeding season (Cramp 1985 and references therein), but detection by passerines usually results in vigorous mobbing (Mikkola 1983, Cramp 1985, Martin 1990). Mobbing may be dangerous as corvids can kill immature juveniles (Overskaug et al. 1999), but diurnal avian predators, particularly goshawks *Accipiter gentilis*, appear to be prominent mortality agents to owls of all ages (Mikkola 1983). Owls possessing territories have high annual survival rates (80–85%; Hirons 1985, Sunde 2001), even in years of poor food conditions. Juveniles, in contrast, may suffer high mortality associated with food limitation during their first months of independence (Hirons 1985, Coles and Petty 1997).

Predictions

In the following analyses, we compared three categories of owls with differences in their predicted benefits of daytime activity. (1) Non-breeding adults were assumed to be well fed and should minimise any cost during the day as opposed to (2) breeding birds that guard and defend their young offspring against potential predators (Wallin 1987, Sunde et al. 2003) which kill a large fraction of the young within the first weeks after fledging (Coles and Petty 1997, Overskaug et al. 1999, Sunde 2001). (3) Newly independent juveniles comprised another population class that might benefit from diurnal exposure by being able to forage. If daytime exposure is costly, we predicted that non-breeding adults should roost in less exposed places compared to the other two status classes. If one benefit of roosting in an exposed site is improved offspring defence, we predicted parents to roost in the most exposed places during those breeding stages when the young are most vulnerable. If

roosting in exposed places is motivated by improved opportunities for hunting in hungry individuals, we predicted that juveniles should roost in more exposed sites during years with less abundant food. We also expected higher prey abundance beneath exposed roosts. Finally, as owls appear to perch closer to the ground when hunting compared to when resting (Bye et al. 1992, this paper), we would expect exposed roosting sites to be closer to the ground if the owls searched for prey.

If the ultimate cost of diurnal exposure is an increased mobbing risk, we expected this risk to increase with the exposure of the owl and, in an appropriately large sample of deaths, cause some fatalities. If the cost is depredation, we expected some deaths to be caused by diurnal raptors, particularly in those population classes most inclined to roost in exposed sites. Alternatively, if roosting in exposed places is costly in terms of heat stress or insect harassment in summer, or cold temperatures in the winter, we should expect roost site selection to vary with seasons and temperature.

Study area

The study was carried out during 1998–2002 in the Gribskov Forest and Strødam Scientific Reserve (55° 57' N, 12° 16' E), Denmark. The typical habitats of residential as well as dispersing owls were woods consisting of managed stands of 15–150 year old beech *Fagus sylvaticus*, spruce *Picea abies* and oak *Quercus robur*. Most owls were radio-tagged within a 7.6 km² area comprising 11 exclusive territories (1.4 pairs km⁻²), but as juveniles dispersed, the radius of the study area was enlarged by 10 km. The density of goshawks was 0.14 pairs km⁻² (eight pairs in 56 km² monitored 1987–1997 B. Jensen, unpubl. data). Throughout the study period, rodents (primarily yellow-necked mouse *Apodemus flavicollis*, bank vole *Clethrionomys glareolus* and field vole *Microtus agrestis*) comprised most of the diet (Sunde 2001). The abundance of rodents (trapping-indexed every two or three months from March 1998 to August 2000) reached a seasonal peak in early autumn (Bølstad 2001, see also Jedrzejewski et al. 1996). On an inter-annual basis, a major beech mast crop in the autumn of 1998 resulted in 2–3 times higher trap-indices in the summer of 1999 compared to 1998 and 2000 (Bølstad 2001, P. Sunde unpubl. data). A new large beech mast crop emerged in the autumn of 2000, and even though no trapping data are available for 2001, prey abundance during the summer and early autumn was considerably higher than in years with no beech mast crop (see also Jedrzejewski et al. 1996; Fig. 2). Accordingly, of 16 pairs checked annually for reproduction, all attempted to breed in 1999 and 2001, as compared to 69%, 25% and 56% in 1998, 2000 and 2002, respectively.

Radio tagging of owls and definitions of life history groups

Territory-holding owls were caught and surveyed with telemetry during 1998–2000, juveniles during 1998–2002. The adults were caught throughout the year and the juveniles were tagged when four weeks old, a few days before leaving the nest. The backpack tags (7.5–13 g including harness, Biotrack Ltd., Wareham, UK) transmitted for 9–12 months and were renewed or removed when recapture was possible. Behavioural data were collected from April 1998 to August 2001 and survival data until 1 January 2003.

The breeding status of adults was divided into 'non-breeding', 'incubation' and 'late breeding'. The start of incubation was determined by radio-tagged females staying in their nests or by backdating based on nestling age. The late breeding phase began when the female left her nest by day, two weeks after hatching and lasted until the young either died or grew independent, 3–4 months after hatching. We further subdivided this period into a nestling phase, followed by an initial (day 1–10 after fledging), middle (day 11–45 after fledging) and late post-fledging phase (day 46 after fledging until independence). During the initial post-fledging phase, the young had poor flying skills and were subject to 10–20% depredation (Overskaug et al. 1999, Sunde 2001). In the middle phase, the flying skills of the young had improved, but the depredation mortality was still considerable. During these first two phases, the parents usually roosted near their young (Sunde et al. 2003). At the last post-fledging stage, the juveniles could no longer be discriminated from adults by their plumage or appearance, and no longer roosted in association with their parents. They were considered independent when they ceased begging for food at

55–83 days after fledging. This was monitored by locating the broods every 1–2 nights and listening for begging calls.

In total, the analyses were based on 27 radio-tagged birds caught as territorial adults and 56 juveniles surviving to the last post-fledging stage. Depending on the year, the juveniles fledged between 1 April and 2 June, and they became independent between 12 June and 18 August. As several juveniles reproduced the following spring and no transient behaviour was recorded after 1 January, the 23 juveniles that were still surveyed after this date were subsequently categorised as adults. The entire sample of "adults" was thus comprised of a total of 50 individuals. However, as the transmitters of the former juveniles expired before May, almost all data on adults from the period May–December originate from paired, territorial individuals.

Observations of roosting owls

Point observations of roosting tawny owls were made in daylight throughout the year, but the observation frequency was particularly high, up to one per day, around fledging and independence of the juveniles. Radio tracking was done with a hand-held receiver (RX8910 or RX98, Televilt Int.) with collapsible antennae. The owls were first located by triangulation, then located in the canopy and visually observed whenever possible. Before advancing towards the roost for a more precise location, the observer carefully listened for mobbing birds. Mobbing was distinguished by intense alarm calls targeted towards the owl. Once identified as a mobbing event, the intensity of the mobbing was scored on an index from 1 (weak alarming) to 4 (physical attacks; see Table 1), and the numbers of mobbing

Table 1. Definition and coding of parameters of roosting sites and mobbing intensities measured in the field.

Parameter	Definition/coding
Exposure	0: hidden in solid objects (inside tree cavities, nest boxes etc.). 1: hidden by thick and dense vegetation cover (difficult or impossible to observe from any angle even at a few metres' distance). 2: partly covered by vegetation (partly covered by vegetation, but not hidden as such). 3: relatively exposed (no or negligible leaf cover around or in front of the owl, but background [typically a tree trunk or canopy] provides decent camouflage). 4: completely exposed (easily visible from afar: no concealment whatsoever).
Height	Height above the ground. 99% of the observations were in the interval 0.2–25 m. Square root transformed in the statistical analyses.
Vegetation type	Dominating tree vegetation type within 15 m of the roost: A: beech, B: other deciduous trees than beech (oak, maple, birch etc.), C: coniferous tree stands (mainly Norway spruce) and D: other habitats (gardens, parks, etc.).
Light intensity	1: bright daylight (sunlight). 2: moderate daylight (overcast), 3: weak daylight (heavily overcast or dusk/dawn).
Canopy density	1: open land (> 40 m between the trees), 2: open wood and woodland (thinned mature tree stands, parks or forested meadows), 3: moderate (continuous canopy with frequent gaps as found in most tree stands in the area), 4: closed canopy (8–20 m visibility: un-thinned tree stands with homogeneous age) and 5: very closed canopy (less than 8 m visibility: young, un-thinned spruce plantings or willow shrubberies).
Intensity of mobbing	1: weak alarm calls (alarm calling at > 4 m distance), 2: passive mobbing (repeated vigorous alarm calls at 1–4 m distance), 3: active mobbing (alarm calls at less than 1 m distance, but no physical attacks), 4: aggressive mobbing (physical attacks).

birds were recorded and identified to species. The weights of the mobbers were obtained from data in Cramp (1992) and Cramp and Perrins (1993–1994). Once located with an appropriate ($\pm 0\text{--}3$ m) precision, the vegetation type and canopy density (Table 1) of the roosting site were registered, the owl's perching height estimated and its exposure scored on a scale from 0 (hidden within tree trunks) to 4 (easily visible from afar, see Table 1). As far as possible, the exposure score was estimated from the point of view of an avian predator/mobber, i.e. horizontal exposure was considered more important than visibility from the ground. Most mature tree stands were thinned, so when owls perched high in the canopies, it was usually still possible to score the exposure from a distance (20–50 m). If the exposure could not be estimated with any certainty, no scoring was done.

Analyses of roosting choice

Measures of roosting choice

The owls' exposure scores (hereafter referred to as "exposure") were used as a predictor of their activity levels as well as the detection risks from potential mobbers and raptors. For the different owls (or broods) this was indexed as a mean exposure of at least three individual point observations. Since many adults, but very few juveniles, often roosted in cavities, we modified the initial scale by combining the two lowest categories (score 0–1 in Table 1, both scored to 1) before calculating the mean exposure. A homogeneity analysis on mean exposure assigned to 18 non-breeding adults during May–October by the two authors responsible for most of the radio tracking (PS, MSB) and by volunteers (all lumped into one group), gave no indications of any observer bias but indicated significant differences among the owls (2-way ANOVA; Observer: $F_{2,20} = 1.69$, $P = 0.21$; Owl: $F_{17,20} = 2.60$, $P = 0.02$).

Low perching height (hereafter "height") was assumed to be an indicator of foraging behaviour (Bye et al. 1992). We tested this assumption by comparing mean heights by day and by night of 22 owls. Heights by night were primarily recorded when owls were surveyed while hunting in open, moonlit habitats. This test showed that the mean heights of adults were higher during the day than during the night (7.5 m as opposed to 4.9 m; Wilcoxon's signed rank test: $Z = -3.328$, $N = 22$ adults, $P < 0.001$), indicating generally lower perches for hunting than for roosting.

Statistical procedures and considerations

To ensure homogeneous environmental conditions (full leaf cover) and temperatures within the thermo-neutral zone, we primarily used data from May–August. As variance homogeneity was not always achievable, we

used non-parametric statistics in all univariate tests. Where parametric methods were used for multivariate comparisons, the conditions were met. When calculating mean exposure and mean height, we generally used the individual owl as the statistical unit, but in dependent and newly independent juveniles, the brood was used as the observation unit, as sibs usually roosted together throughout the dependency period, and occasionally, later. For the different owls, we also correlated exposure against height and temperature, and in parents, distance to nearest young. We then analysed whether any consistent relation existed between exposure and a given factor, as tested with a binomial test on the signs of the correlation coefficients of correlations based on 10 or more point observations. In the correlation analyses including parents, the pair was used as the observation unit because the mates differed in proximity to offspring (Sunde et al. 2003).

Analyses of roosting choices in relation to prey abundance

To test whether owls roosting in exposed sites were perching for prey, we assessed the density of small mammals beneath previously used roosts in August–September 1998. Small mammals comprised about 90% of the ingested prey mass of juveniles and adults during this period (Sunde 2001). The roosts in question were evenly spread among the six adults and four independent juveniles studied during this period. For each individual owl, the indexed roosts were randomly selected among the total number of point observations. A few days after the owl had used a site, we placed a grid of 25 "Ugglan" live traps (Grahnb, Hillerstorp, Sweden) covering a 20 m \times 20 m area for two nights, resulting in 50 trap nights. The traps were supplied with bedding and wheat grains to compensate for lost foraging. Since the captured mammals varied extensively in body mass (3–40 g), we used the mass rather than the number of individuals as an index of prey abundance. To homogenise variances, the prey mass was square root transformed before analysis. First, we tested the variation between adults and juveniles and between individuals in a nested ANOVA. Since no significant individual differences appeared, the roosting site was then treated as an independent observation in ANCOVA analyses of the relations between prey mass, age group, exposure and height.

Analyses of mobbing and predation risks

Mobbing risk and mobbing intensity

The probability of a roosting owl being mobbed was analysed by means of multiple logistic regression, using the maximum likelihood criterion to select explanatory variables (Hosmer and Lemeshow 1989). Because mob-

bing was a rare event, the individual point observation was used as an observation unit. To avoid dependency between close positions, we randomly discarded all but one of the observations, if two or more owls were registered roosting within 100 m of each other on the same day. We also tested the between-owl variation in the model to assure that no owls differed in mobbing risk. In all analyses, forward selection as well as backward elimination procedures resulted in the same models. The intensity of the mobbing was correlated (r_s) with the owls' exposure, and the number and mass of the mobbers.

Cause-specific mortality

The radio tags enabled us to find owls that had died and to establish the cause of death. Mortality induced by avian predators was distinguished from other causes of death by the presence of beak or claw marks on the skeleton and/or by feathers being systematically plucked. The predation rates of raptors on the different subgroups of owls were based on the numbers of deaths occurring during the entire duration of the survey ("radio days") summed over all individuals (Heisey and Fuller 1985).

Results

Roost site selection

General pattern

The owls often repeatedly used the same few tree stands for roosting, particularly in the winter. As a rule, exposed roosting sites were used only once or a few times, whereas roosts in dense vegetation or cavities could be used for months. The presence of excrement and regurgitated pellets beneath the roosts indicated that even exposed roosting sites were normally used throughout the day. Regardless of season, non-breeding adults roosted in much less exposed sites than parents with offspring (Fig. 1a), but the two groups did not differ in perching heights (Fig. 1b). During the summer, (newly) independent juveniles roosted in considerably more exposed locations (Fig. 1a) and closer to the ground (Fig. 1b) than did non-breeding adults. As the autumn progressed, this difference was diminished as the juveniles gradually approached the same values as the non-breeding adults.

Roost site selection of adults

Non-breeding adults followed a very cryptic roosting habit throughout the year, in particular during November–April (Fig. 1a, Friedman test for seasonal differences in mean exposure, $N = 10$, $\chi^2_3 = 11.000$, $P = 0.01$). The mean height during the day did not differ among

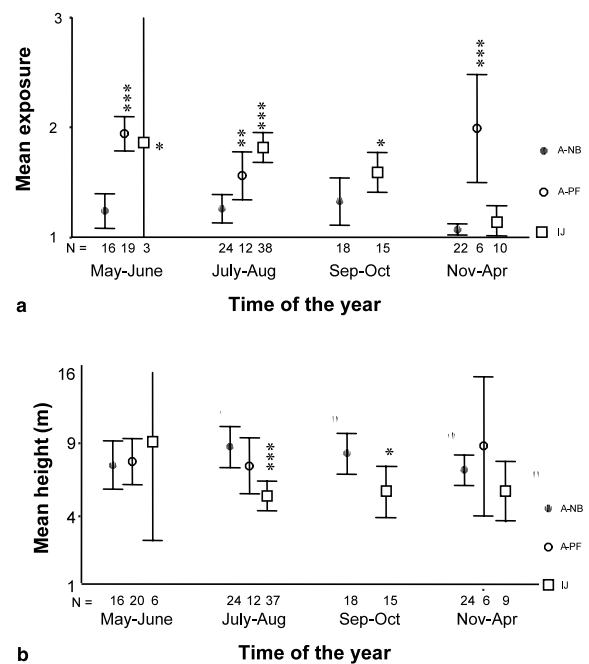


Fig. 1. Means and 95% confidence limits of mean exposure (a) and mean height (b, note that the scale of the abscissa is square root transformed) at different times of the year for non-breeding adults (A-NB), parents during the post-fledging period (A-PF) and independent juveniles (IJ). For each of the four periods of the year, the mean exposures and mean heights of breeding adults and independent juveniles are tested against the baseline of non-breeding adults with the Mann-Whitney's U-test, as indicated above the error bars (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$). N = number of owls point observed at least thrice allowing a mean value to be calculated

seasons (Fig. 1b, Friedman test, $N = 10$, $\chi^2_3 = 0.840$, $P = 0.84$). We found no significant patterns in the correlations between exposure and ambient temperature or height during any time of the year (Table 2).

Adults with young roosted in more exposed places before day 45 after fledging than later (Friedman test of mean exposure between the four sub-phases of the late breeding period: $N = 10$, $\chi^2_3 = 20.04$, $P < 0.001$). Hence, from day 46 after fledging to independence, the mean exposures of the parents were similar to their mean exposures the first month after independence of their offspring (Wilcoxon's test signed rank test: $N = 14$, $Z = -0.204$, $P = 0.84$).

Before day 45 after fledging, 11 out of 12 pairs increased exposure due to their proximity to the nearest offspring (data from May–August, sign test, $P = 0.006$), suggested they selected roosting sites in exposed places to guard their young. The within-pair correlations revealed no trends between exposure and temperatures or heights (Table 2).

Roost site selection of juveniles

Newly independent juveniles selected more exposed roost sites that were closer to the ground in 1998 and

Table 2. Distribution of signs of Spearman's r_s of correlations between exposure and ambient temperature ($^{\circ}\text{C}$) and height. The correlation analyses were done for individual non-breeding owls or pairs of breeding adults represented by a minimum of 10 point observations each. The P-values represent the outcomes of two-tailed binomial tests (ignoring observations with $r_s = 0$).

Status group	Season	Exposure – Temperature				Exposure – Height			
		+	–	0	P	+	–	0	P
Non-breeding adults	May–Aug	10	3	2	0.09	9	2	-	0.07
	Nov–April	5	2	2	0.45	2	5	2	0.45
Adults with young †	May–Aug	4	8	-	0.39	5	7	-	0.77
Independent juveniles	May–Aug	10	11	-	1.00	1	19	-	<0.001

† Based on observations from the late nestling period until 45 days after fledging. Pairs used as observation units.

2000 than in the post-mast years of 1999 and 2001 when rodents were more abundant (Fig. 2a,b). In almost all independent juveniles, exposure increased with decreasing distance to the ground, but did not correlate with temperature (Table 2).

The commencement of independence did not lead to an increase in mean exposure compared to the late dependence period (Fig. 2a; Wilcoxon's test: $N = 20$ broods. $Z = -0.709$, $P = 0.48$), as would be expected if the start of independence leads to a higher diurnal hunting effort due to food stress. However, the mean height dropped significantly after independence (Fig. 2b, $N = 20$ broods. $Z = -2.800$, $P = 0.005$) as expected for birds that increasingly select roosts for hunting purposes.

Roosting choice in relation to experience with goshawks

Three broods of juveniles exposed to goshawks during the last weeks of the dependency period, subsequently roosted in significantly less exposed locations than did 19 broods not known to have been in contact with avian predators (Mann-Whitney U-test, $U = 4.5$, $P = 0.02$). The two groups did not differ in roosting heights ($U = 14$, $P = 0.16$). The first group consisted of two broods losing a sib to goshawk depredation in 1998 and 2001 and a brood roosting close to a goshawk nest in 2001. In the first two cases, the survivors probably observed the killing of their sib as they roosted together before the attack. In the latter case, a fledged goshawk brood resided within the same $250\text{ m} \times 250\text{ m}$ area as the owl brood.

Roosting choices related to prey availability

On average, three times more prey mass was indexed beneath the roosting sites of independent juveniles than beneath sites used by non-breeding adults (Nested ANOVA; age effect: $F_{1,16} = 9.06$, $P = 0.008$; within-owl effect: $F_{8,16} = 1.87$, $P = 0.21$). Prey mass correlated positively with exposure (Fig. 3a; $r_s = 0.483$, $N = 26$, $P = 0.012$) and negatively with height (Fig. 3b, $r_s = -0.419$, $N = 26$, $P = 0.03$). However, neither of the two covariates explained any significant additional

variation in prey mass when compared with the general difference among age groups (exposure: $F_{1,23} = 0.73$, $P = 0.40$; height: $F_{1,23} = 0.23$, $P = 0.64$).

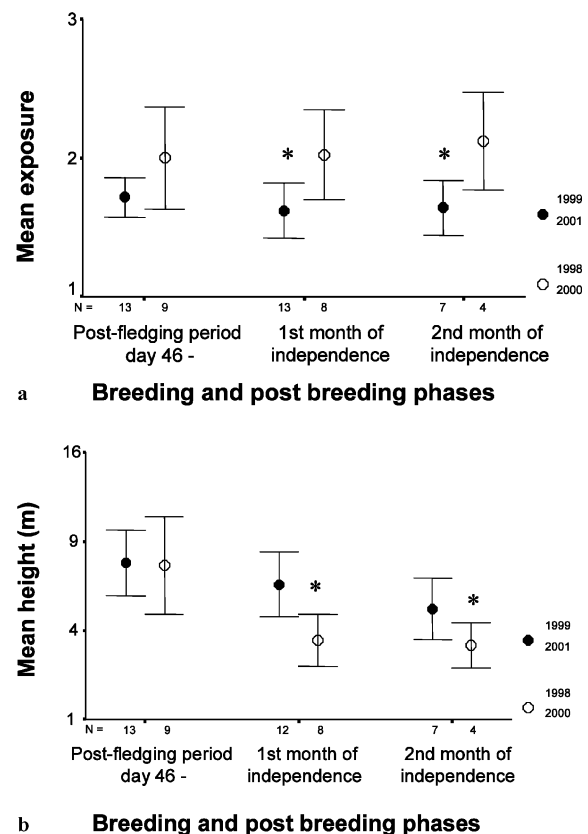


Fig. 2. Variation during May–August in (a) mean exposure and (b) mean height (note that the scale of the abscissa is square root transformed) of juveniles ($N =$ number of broods) from the last phase of the post-fledging period through the first two months of independence. The data are subdivided into two annual categories, 1998/2000 of intermediate food conditions and 1999/2001, which were preceded by autumn of large beech mast crops resulting in abundances of rodents. For each phase, the difference between broods from different annual categories is tested with Mann-Whitney's U-test (*: $P < 0.05$).

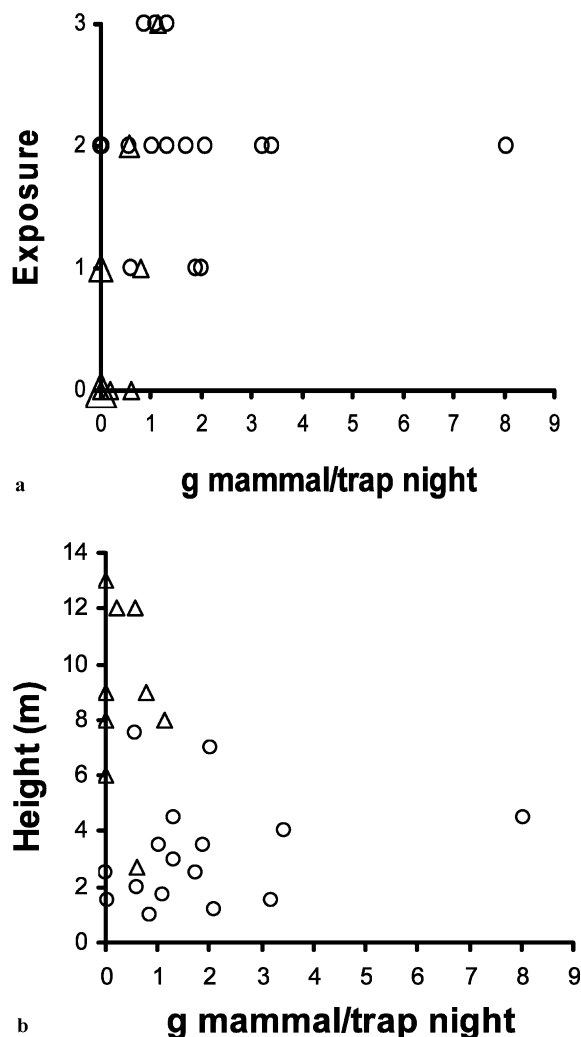


Fig. 3. Exposure (a) and height (b) of roosting owls plotted against prey abundance (g mammal biomass/trap night) at the roosts. Data were gathered during August–September 1998, i.e. the first 2 months after juvenile independence. Triangles indicate adults, circles juveniles. The enlarged triangles in (a) indicate ties of 2 and 3 observations.

Mobbing and predation

Of a total of 2104 point observations of 72 owls from May 1998 to August 2001, 58 cases of mobbing were registered. The mobbing risk increased with increasing exposure and was greater during May–June than during the rest of the year (Table 3, Fig. 4). Once an owl was mobbed, the mobbing intensity was positively correlated with the body mass of the mobbing birds, but not with the total number of mobbers or the owls' exposure (Table 4).

Of 15 owls that died by natural causes (excluding five traffic deaths and two cases in which only the transmitters were found), 73% (95% CI = 45–92%) were killed by raptors, apparently all by goshawks. The remaining

deaths were caused by starvation (two juveniles) and disease (two adults). The raptorial depredation rate for groups that scored a significantly higher mean exposure than non-breeding adults were 3.8 times higher than for non-breeding adults and groups roosting similarly to non-breeding adults (Table 5).

Discussion

The difference in roosting behaviour between the three population classes which were assumed to differ in their need of daytime activity, indicates that roosting in exposed places is associated with costs as well as benefits. In the reference group of non-breeding adults, these benefits appeared to be outweighed by the costs as these birds selected very cryptic roosts throughout the year. The comparatively higher exposure of adults with young and newly independent juveniles, does on the other hand, suggest that under some circumstances, the benefits of daytime exposure did compensate for the costs.

Benefits of diurnal exposure

Parents appeared to select exposed roosting places in order to be more able to detect and respond to threats to their young, as their exposure was highest when the young were most vulnerable to predators and when the parent-offspring distance was low. This result is in accordance with a previous study (Wallin 1987), suggesting that tawny owl parents trade their own security against the benefit of increased offspring survival through brood defence.

We occasionally observed parents strike prey or feed young during the day, but the lack of correlation between exposure and perching height suggests that diurnal hunting was of secondary importance to brood guarding.

In newly independent juveniles, roosting in exposed sites agreed with the predictions of diurnal foraging, as the difference in exposure between juveniles and non-breeding adults was similar to juveniles selecting sites richer in prey. The association between low perching and exposed roosting sites in almost all juveniles further suggests that exposed juveniles were perching for prey and that the individuals varied their roosting choices on a day-to-day basis in accordance with their foraging needs. The trend among juveniles to select more exposed sites closer to the ground in years of less favourable food conditions also suggests increased diurnal foraging efforts when food was scarce. Diurnal foraging, however, does not explain why juveniles roosted in more exposed places than adults before they reached independence, but maybe they attempted to increase energy intake by daytime foraging even before reaching independence.

Table 3. The influences of various factors on the risk of a roosting owl being mobbed by other birds as analysed by means of binomial logistic regression and tested with maximum likelihood methods. The table shows changes in deviance values of the overall fit by each factor in isolation ("single effects") and when all other significant factors are included in the model ("complex model"). The numbers of cases of no mobbing+owls being mobbed are shown in brackets. Four owls were recorded as being mobbed thrice, 10 owls twice, 26 owls once and 32 owls were never observed mobbed.

Factor	df	Adults only (N = 1103+28)		Juveniles only (N = 943+30)		Combined data (N = 2046+58)	
		single effects	complex model	single effects	complex model	single effects	complex model
Owl	§	21.849	22.617	45.936	46.832	67.133	60.829
Time of the year	3	13.810**	3.898	9.523*	9.180*	17.044***	9.630*
Breeding stage	2	10.601**	2.004	—	—	—	—
Habitat category	3	4.239	4.691	1.480	0.841	1.052	4.141
Canopy density	1	1.082	0.100	0.292	0.014	0.183	0.033
Light	1	0.048	0.805	0.154	0.054	0.148	1.209
Height	1	0.950	0.009	0.334	0.524	0.686	0.347
Exposure ‡	3	31.907***	31.907***	9.747*	10.319**	27.661***	24.422***
Age class †	1	—	—	0.069	0.051	0.084	0.342

§ Degrees of freedom: adults only = 40, juveniles only = 43, combined data = 71.

‡ Treated as a categorical variable. The two highest scores were combined (see also Fig. 4).

† In juveniles: dependent vs. independent juveniles, in the pooled sample: adults vs. juveniles.

*P<0.05; **P<0.01; ***P<0.001.

Costs of diurnal exposure

As no consistent intra-individual correlations between temperature and exposure were detected in any of the status groups, microclimatic concerns (Walsberg 1986) or insect avoidance (e.g. Rohner et al. 2000) did not appear to explain the observed variation in roost site selection. This leaves the hypothesis that the assumed

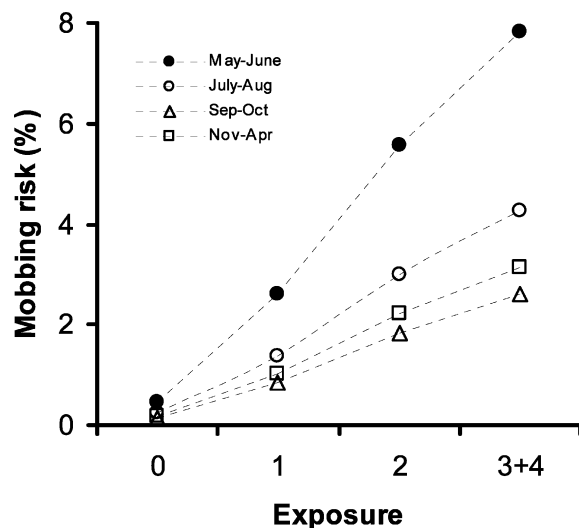


Fig. 4. Graphic presentation of the fitted mobbing risks (logistic regression) of roosting tawny owls as functions of exposure and time of the year (Table 2). The numbers of observations (mobbed/not mobbed) of the different exposure scores are, 0 (in cavity): 1/407; 1 (completely hidden in vegetation): 10/622; 2 (partly covered): 30/751; 3 (relatively exposed): 17/256 and 4 (very exposed): 0/7. Categories 3 and 4 were pooled in the analysis.

cost of diurnal exposure is an increased encounter risk with mobbers or raptors. The increase in mobbing risk with increasing exposure is in line with this suggestion, but even though the intensities of the mobbing bouts were positively correlated with the size of the mobbers, no fatalities due to mobbing birds were recorded. With diurnal raptors being responsible for 73% of the mortality of owls, depredation rather than mobbing appears to be the ultimate cost to be minimised during the day. This is further supported by the 3.8 times higher depredation rate of population classes inclined to roost in more exposed places than non-breeding adults. Finally, juveniles appeared to roost less exposed if they had experienced goshawks. There may still be a link between the risk of being mobbed and preyed upon, however, as mobbers may put owls at risk by advertising their presence to raptors (Curio 1978, Slagsvold 1982). In that case, we might expect the owls to roost in the less exposed places during May–June when the mobbing risk was twice as high compared to the rest of the year (Fig. 2). This did not appear to be the case (Fig. 1). Regardless of the potential role of mobbing for

Table 4. Correlates of intensity of the mobbing of radio tagged owls. The intensity of the mobbing was scored from 1 (weak alarm calling) to 4 (physical attacks, see Table 1). The approximate mass of the mobbing species ranged from 10 g (wren *Troglodytes troglodytes*) to 500 g (hooded crow *Corvus corone cornix*).

Factor	r _s	N	P
Number of mobbing birds	0.197	56	0.15
Weight of the heaviest mobbing species	0.355	56	0.007
Total biomass of the mobbers	0.407	56	0.002
Owl's exposure	-0.040	55	0.77

Table 5. Predation rate (M, 95% confidence intervals are given in brackets) on tawny owls by raptors. Data are sub-divided into different life history phases characterised by different average mean exposure (see Figs. 2 and 3 and text). The annual depredation rate (M) is based on the numbers of depredation events occurring in the total survey period summed over all individuals (radio days): $M = 1 - (1 - [\text{events of depredation}/\text{radio days}])^{365}$. The two groups representing owls at different stages of high and low levels of diurnal exposure differ significantly in raptorial predation risk (log-likelihood test; $\chi^2_1 = 6.180$, $P = 0.013$), whereas the difference between juveniles and adults is not significant ($\chi^2_1 = 3.234$, $P = 0.072$).

Status group		Mean exposure	No. owls†	Radio days	Raptorial depredation	
					Events	M (year ⁻¹)
Adults	A. Day 14 after hatching – day 45 after fledging	2.0	25	1390	1	23%
	B. The rest of the year	1.2	51	11259	3	9%
Juveniles	C. Day 46 after fledging – independence	1.8	56	1420	3	54%
	D. First two months of independence	1.8	45	2466	3	36%
	E. Third month of independence	1.4	39	926	0	0%
	F. Fourth month of independence–31 December	1.3	31	2568	1	13%
Pooled data	A+C+D	≥1.8	81	5276	7	38 (12–57)%
	B+F	≤1.3	57	13818	4	10 (0–19)%

† As most individuals are represented in more than one sub-group, the number of owls in the pooled groups are not additive.

mediating predation, we still find that predation risk appears to be the most likely factor causing tawny owls to hide during the day. Even though the tawny owl might show an extreme example of a cryptic diurnal habit, this result may indicate that depredation by diurnal raptors is an important selective force on diurnal hunting behaviour and habitat choice also in other species of small and medium-sized owls.

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