

FLEDGLING BEHAVIOR AND SURVIVAL IN NORTHERN TAWNY OWLS¹

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Abstract: Telemetry studies of Tawny Owl (*Strix aluco*) fledglings ($n = 53$) were conducted from May to August in central Norway, where the species is at the northern limit of its range and its density is generally low. Mortality before dispersal was 61% due to starvation and predation by red fox (*Vulpes vulpes*), pine marten (*Martes martes*), and *Corvus* spp. Mortality was highest during the first 10 days after leaving the nest box, when fledglings were small and had poorly developed locomotion. Fledglings that died or disappeared during the first 10 days after leaving the nest box were significantly lighter than those that survived. Mean distance between fledglings and nest box increased during the summer, but fledglings remained relatively close to siblings and their mother until dispersal. The average area used by fledglings that survived to dispersal was 26 ha ($n = 15$), which is a figure larger than reported elsewhere for this species. Dense forest habitats were preferred, and roosting sites offering good vertical and horizontal concealment were used frequently. We propose that observed habitat and area use reflect antipredator strategies and generally low density of this strictly territorial species.

Key words: area and habitat use, fledglings, mortality, *Strix aluco*, Tawny Owl.

Data on survivorship and causes of death are important to studies of population dynamics (Lack 1966). For most bird species, however, few data exist on the survival of dependent fledglings (Sullivan 1989). Recent studies of raptor fledglings report predation and starvation as frequent causes of death (McFadzen and Marzluff 1996, Rohner and Hunter 1996). Body condition at fledging also may affect predation risk later on, with predation as the ultimate cause of mortality for individuals that are already nearly starved. Furthermore, to understand a species' overall behavioral and survival pattern, studies in climatically different parts of its range are needed (Marti 1994).

In the Tawny Owl (*Strix aluco*), one of the most widespread European owl species (Cramp 1985), previous reports on fledgling survival are from the central

part of its range (Southern et al. 1954, Petty and Thirgood 1989). Herein we present data on the survival of Tawny Owl fledglings near the northern limit of the species' distribution, in central Norway. In this area, with relatively harsh climatic conditions, one may expect generally high population turnover (Marti 1994, 1997), and we therefore predicted that (1) Tawny Owl fledgling mortality would be high at the species' northern limit, and (2) fledgling survival will correlate with body condition.

METHODS

STUDY AREA

The study was performed in central Norway, near Trondheim (63°20'N, 10°45'E). Both the occurrence of nesting birds in relation to available nest-boxes (normally 10–30% occupancy) and play-back surveys undertaken in spring 1997, mid-winter 1997/1998, and spring 1998 (20–30% response rate), indicated that Tawny Owl populations in the study area are generally low (Redpath 1994). Furthermore, according to Galeotti and Pavan (1993) and Redpath (1994), Tawny Owls respond faster to play-backs at low density and are more actively encountered; we had similar experiences in our study area.

Vegetation in the study area is dominated by agricultural land, deciduous woodland on the coast near Trondheimsfjord, and boreal spruce forest in inland areas. Tawny Owls occur mainly in the deciduous-dominated areas close to rivers and cultivated land. The climate is characterized by a short summer and a long winter (snow present September–April). Pellet analysis indicates that short-tailed voles (*Microtus agrestis*), bank voles (*Clethrionomys glareolus*), common shrews (*Sorex araneus*), and various species of passerines are important prey for Tawny Owls in the study area.

Potential harmful mobbers on Tawny Owls include various *Corvus* species; potential predators include red fox (*Vulpes vulpes*), pine marten (*Martes martes*), and Northern Goshawk (*Accipiter gentilis*).

FIELD PROCEDURES

Between 1995 and 1997, mostly during May, 53 chicks from 22 broods were weighed 1–2 days before nest departure and tagged with leg-mounted radio trans-

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mitters (Biotrack Ltd., Dorset, United Kingdom) weighing 3.5 g. Survival, area use, and habitat use were monitored until dispersal in August–September. The adult female of 14 broods was tagged with a backpack transmitter weighing 20 g and tracked in order to observe average distance from their broods as a possible expression of a behavioral strategy during summer, a measure of the extent to which she could protect her fledglings from predators. Birds were tracked using a hand-held, 4-element, yagi antenna and a Televilt receiver. They were located at least every third day, if possible, mainly by ground triangulation, but occasionally from aircraft. We often observed fledglings directly, thus enabling an accurate habitat description.

When we located dead fledglings, cause of death was determined by interpreting signs left on the carcass and surroundings; for example, predation was assumed if fledglings were found at red fox and pine marten dens. Intact carcasses and remains were X-rayed and a veterinarian performed autopsies to determine the general condition of the birds and possible diseases.

When calculating daily mortality rate, we divided the period from nest departure to when young dispersed from their natal home range into four stages, corresponding to the development of behavioral traits. Phase 1 (day 1–10) spanned the period from nest departure until fledglings enter safe positions above the ground. Phase 2 (day 11–30) covered the period when flying ability improved until they could escape from the observer without difficulty. Phase 3 (day 31–about 90) covered the following 2-month period until dispersal. A fledgling was judged to have dispersed (phase 4) when its distance from siblings and natal area rapidly increased.

We mapped the total area used by individual fledglings that survived through phase 3. To provide more information about movements within the home range, we measured mean distances between fledglings and their nest box, between fledglings and their siblings during phases 1–3, and between fledglings and their mother. We divided the landscape into four habitats: (1) spruce-dominated (*Picea abies*) forest, (2) deciduous-dominated woodland, (3) mixed deciduous-coniferous forest, and (4) open country. The availability of these four habitat categories within each fledgling's home range was estimated by comparison with vegetation maps (1:5,000). When we could observe a fledgling at its roost, the degree of shelter was recorded as whether the roost site was (1) more open than the surrounding (10-m radius) vegetation, (2) about the same as surrounding vegetation, or (3) more sheltered than the surrounding vegetation.

DATA ANALYSIS

Differences in survival rates and mortality were tested using Micromort ver. 1.3 (Heisey and Fuller 1985a, 1985b), and by calculating a Kaplan-Meier curve of the estimated cumulative survival. Cox regression (forward, stepwise, and LR selection, Norusis 1994) was used to explore possible effects of age, body weight before departure from the nest box, and year of tagging on survival through all four phases.

Individual area use was calculated by the minimum

convex polygon method (Mohr 1947) and Ranges V software (Kenward and Hodder 1995). The stability of home ranges was tested with Schoener's ratio (Swihart and Slade 1985), where ΔT is the minimum time interval between independent, consecutive fixes. The test denotes the shortest independent time interval in days ($t^2/s^2 \geq 1.96$) followed by two independent intervals. Thus, ΔT verifies the time necessary between fixes to avoid autocorrelation. Because several individuals were monitored through two or more phases, a repeated measures ANOVA was used to determine the mean distances (during phases 1–3) between the fledglings and their nest box, between fledglings and their siblings, and between fledglings and their mothers.

Habitat selection within home ranges at the third order selection level (Johnson 1980) was analyzed by compositional analysis (Aebischer et al. 1993). If adequate data were available, siblings that survived through phase 3 were treated as one observational unit because individuals within sibling groups did not differ in habitat use, and radio locations within each sibling group were pooled to estimate the percentage of habitat use. The relative proportions of use and availability of habitat were summarized in a compositional analysis using log-ratio transformations and analyzed by SAS, version 6.12 for Windows (SAS Institute 1996). The level of significance (0.05) was obtained with 9,999 randomizations. The degree of concealment at roosting sites was analyzed by binomial tests based upon comparison of two groups of observations: roosting site with less cover than available in surrounding 10-m radius, and roost sites with more cover.

RESULTS

Twenty-five fledglings were verified ($n = 20$) or assumed ($n = 5$) to have died during the period after they left their nest box and before dispersal (phases 1–3). After dispersal (phase 4), four more fledglings were recorded as dead. Mortality rate was highest just after fledglings left their nest box (phase 1), but mortality occurred continuously until dispersal (Fig. 1). Starvation and predation were the primary causes of death. Starvation was most frequent in phase 1, but predation increased in phases 2 and 3 (Table 1). The red fox was the most important predator ($n = 5$ cases), followed by corvids ($n = 2$ cases) and pine marten ($n = 1$ case). Cox regression revealed no effect of age ($P > 0.6$) or study year ($P > 0.05$) on survival, but a significant negative effect of fledgling mass on the probability of survival ($P = 0.04$). Fledglings that died or disappeared during the first 10 days after leaving their nest box had a 16% lower body mass ($t_{46} = 2.67$, $P = 0.01$) than those that survived that period.

The mean distance among siblings did not differ among the first three phases (ANOVA, $F_{2,34} = 0.16$, $P = 0.85$), and normally siblings could be observed within a 50-m radius of each other. Mean distance between fledglings and mothers did not vary from phase 1 ($n = 14$ family groups) to phase 3 ($n = 10$ family groups; ANOVA, $F_{2,36} = 2.21$, $P = 0.13$). Mean distance between fledglings and their natal nest box, however, increased from phase 1 ($n = 114$ fixes) to phase 3 ($n = 281$ fixes; ANOVA, $F_{2,558} = 4.13$, $P < 0.02$), reaching an average of 320 m in phase 3. For individ-

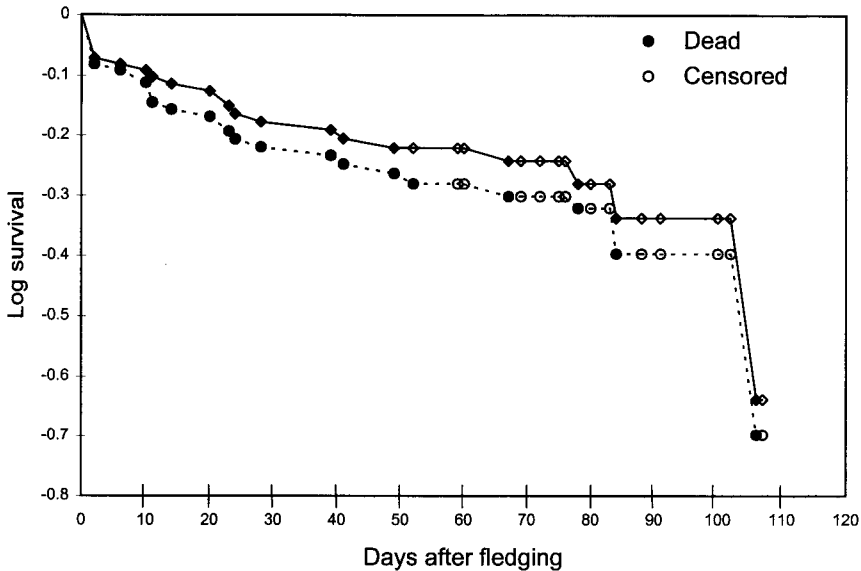


FIGURE 1. Survival rate of radio-tagged dependent Tawny Owl fledglings in central Norway. Two estimates are given, one based on verified cause of deaths (solid line) and a more realistic estimate which includes birds assumed dead because they disappeared shortly after nest departure (dash line). Filled dots denote verified and assumed deaths, open dots denote censored cases (individuals registered as alive just prior to dispersal late in summer and assumed to have dispersed). About half the fledglings died before dispersal, with a peak in mortality just after leaving the nest box. The drop in the cumulative survival at the end of the monitoring period is a result of few individuals being left in the sample at that stage (see also Table 1 for details).

uals ($n = 15$) which survived through phase 3, and for which there were sufficient fixes not showing autocorrelation ($n > 20$), average home range of fledglings was 26 ha (6–119 ha).

Overall habitat use was disproportionate with availability at the third order selection level ($n = 8$ sibling groups; Wilks' $\lambda = 0.13$, $df = 3$, $P < 0.01$). Forest habitats were highly preferred compared to open country ($P < 0.05$). Mixed deciduous-coniferous forest was used significantly more than pure spruce forest (Table 2). Concealment at roosting sites was significantly better than the vegetation otherwise could offer within a radius of 10-m around the site ($n = 278$ fixes, lower horizontal visibility; binomial test, $P < 0.001$, and vertical cover; binomial test, $P < 0.001$).

DISCUSSION

Southern et al. (1954) monitored 71 Tawny Owl fledglings by their persistent call and reported only 2.8% (2/71) mortality before dispersal. In contrast, a telemetry study of 12 Tawny Owl fledglings revealed a mortality rate of 91.7% (11/12) resulting from predation and starvation (Petty and Thirgood 1989). Belthoff and Ritchison (1990) found 18.2% (4/21) mortality in 21 Eastern Screech-Owl (*Otus asio*) fledglings, 75% from predation and 25% through unknown causes. Bendel and Therres (1993) found 55% (19/34) mortality in 34 Barn Owl (*Tyto alba*) fledglings, mostly from drowning. Finally, Rohner and Hunter (1996) found 41% (23/55) mortality during the summer in 55 Great-

Horned Owl (*Bubo virginianus*) fledglings, 33% due to anemia, 28% to predation, 15% to collision with vehicles, and 23% to unknown causes. Thus, our study is consistent with previous telemetry investigations.

Vulnerability probably is highest during phase 1, about the first 10-days after leaving the nest box. During this period, fledglings spend time on or near the ground, before they are able to enter safer positions higher in trees. On the ground, they may be less effective at avoiding rain and cold weather, which can be very harmful to them (Bradley et al. 1997, Steenhof et al. 1997), and are less able to escape from mammalian predators. Mortality decreased in phase 2, but starvation and predation still occurred. We suggest that starvation in phases 2 and 3 was due, in part, to extraordinary circumstances such as several days of cold and wet weather. The adults' ability to feed fledglings also probably decreases in bad weather. Indeed, one female died due to starvation and disease during a period of unfavorable weather in summer 1997 during phase 2 of her fledglings. Her fledglings then starved to death; no male was seen to feed the young.

In accordance with expectations for survival versus body condition in bird fledglings (Gaston 1997), our data indicate that those individuals in good body condition survive better. But, because it normally takes many days to complete clutches in raptors (Newton 1979, Mikkola 1983), individual differences in body weight of nestlings before departure actually reflect age differences; although nest departure seems to be

TABLE 1. Mortality of dependent radio-tagged Tawny Owl fledglings in Central Norway. Mortality rates are calculated on the basis of number of deaths per transmitter day (following Heisey and Fuller 1985b). Assumed rates are based on verified and assumed deaths, whereas verified rates are based on known deaths. CE = censored cases, AD = assumed deaths, VD = verified deaths, pred. = predation, starv. = starvation, acc. = accidents (collisions or drowning).

Time phases	Mortality rate					No. owls	Radio days	CE	AD	VD	Causes of VD (%)		
	Per phase		Per day		pred.						starv.	acc.	
	Assumed	Verified	Assumed	Verified									
Dependence													
Phase 1	0.235	0.200	0.026	0.022	53	454	0	2	10	22	78	0	
Phase 2	0.224	0.179	0.013	0.010	41	715	0	2	7	43	29	28	
Phase 3	0.130	0.160	0.005	0.003	32	863	0	1	3	67	33	0	
Total	0.613	0.528	0.013	0.009	53	2,032	0	5	20	40	50	10	
95% C.I.	0.435–0.736	0.339–0.664	0.007–0.017	0.005–0.013									
Independence													
Phase 4	0.346	0.346	0.009	0.009	28	447	24	0	4	0	25	75	
Whole survey													
Total	0.707	0.635	0.011	0.009	53	2,479	24	5	24	30	48	22	
95% C.I.	0.539–0.814	0.449–0.785	0.007–0.013	0.005–0.013									

fairly synchronous, the youngest and lightest may be least prepared. However, continuing to stay in the nest also is unfavorable because feeding rates by the parents may then be lower.

The reason for the long, dependent period for fledgling owls is unclear (Johnsgard 1988). The yearly variation in numbers of available prey and the need for slow development under the safety of parental care may select for a delay in dispersal (Southern 1970). From the perspective of life-history theory, selection may maximize the time fledglings spend near adults, in line with the safe harbor hypothesis (Clutton-Brock 1991). Thus, we interpret the observed area and habitat

use in fledglings as antipredator behavior, and the benefits of good habitats in providing concealment opportunity and high supplies of prey.

Southern et al. (1954) and Petty and Thirgood (1989) reported that Tawny Owl fledglings used 5–15 ha and 2.2–6.5 ha, respectively. Restrictions on area use in Tawny Owl are explained by strong territoriality and high density (Hirons 1985), although habitat quality also may play a part (Redpath 1995). Fledglings we studied used an average of 26 ha. We propose two factors to explain this high figure. First, density of Tawny Owls probably decreases towards the northern limit of their range, e.g., due to harsh environments (Lack 1966). In our study area, generally low density is confirmed by the relatively low use of nest-boxes and response rate to play-backs. Thus, this low density may permit larger areas to be used for those birds that successfully settled. Second, because predation was frequent, the presence of predators may cause fledglings to roam more. Mothers' close association with fledglings may imply a need to protect them from predators; adult females have been known to drive off pine martens and red foxes (Cramp 1985).

Mixed deciduous-coniferous forest was most frequently used, implying that this environment has favorable qualities for fledgling Tawny Owls. For example, although rodents form an important part of Tawny Owl diet, passerines also are important food (Overskaug et al. 1995, Jedrzejewski et al. 1996), and compared to the other three available habitats, passerines are common in mixed deciduous-coniferous forests (Nilsson 1979). However, fledglings do little foraging on their own. Neither are they free to select the place where they grow up, hence, the adults have selected the area for them, and we may in part affect the adult's choice of preferred habitats depending upon where we put out nest boxes. Nevertheless, habitat use

TABLE 2. Ranking matrix of the mean relative difference in the habitat selectivity index = $\ln(U_1/A_1) - \ln(U_2/A_2)$ (see Aebischer et al. 1993), where U and A are the utilized and available proportions, respectively, of a given habitat for eight sibling groups of radio-tagged Tawny Owl fledglings monitored from when they left their nest box in spring until dispersal in late summer. Habitat categories: SPRU, spruce-dominated forest; DEC, deciduous woodland; DEC-mix, mixed deciduous-coniferous forest; OC, open country. Habitat types are ranked in increasing preference (0 = lowest ranked, 3 = highest ranked). * indicate deviations from random at $P < 0.05$ (- indicates a negative direction); hence, DEC-mix forest is used significantly more than SPRU forest, and OC generally is avoided.

Habitat type	Habitat type				Rank
	SPRU	DEC	DEC-mix	OC	
SPRU		-0.97	-1.56*	3.03*	1
DEC	0.97		-0.59	4.00*	2
DEC-mix	1.56*	0.59		4.59*	3
OC	-3.03*	-4.00*	-4.59*		0

and choice of roosting sites may reflect true selection with respect to the danger of mammalian predation (Janes 1985, Belthoff and Ritchison 1990). Telemetry studies of pine martens and red foxes within the study area indicate a preference for pure coniferous (pine marten) and mixed deciduous-coniferous forests (foxes) (Overskaug et al. 1994, 1995). Thus, the use of mixed deciduous-coniferous forests may be a strategy to avoid the pine marten whose climbing ability makes it a permanent threat. The red fox, despite being frequently present in the mixed deciduous-coniferous forest, is a danger only during phases 1 and 2. The preferred habitat may thus be the lesser of two evils concerning predation (Krebs and Davies 1984).

In summary, northern Tawny Owl fledglings in better body condition survive better, at least during the first days after nest departure, and mortality due to starvation and predation is frequent before dispersal. Thus, behavior traits are in part explained as antipredator strategies. The next step in verifying demographic patterns of Tawny Owl adaptation to its northern limit is to investigate the significance of food supply and potential predation pressure within different habitats and to further examine fledgling survival and behavior traits through mid-winter.

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GENETIC VARIABILITY AND ISOLATION OF CORY'S SHEARWATER COLONIES IN THE NORTHEAST ATLANTIC¹

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Abstract: DNA fingerprinting was used to compare levels of genetic variability within and among eight colonies of Cory's Shearwater (*Calonectris diomedea borealis*) in the Madeira, Azores, Canarias, and Berlenga archipelagoes in the Northeast Atlantic. Fingerprint diversity, as measured by one probe and two restriction enzymes, showed very little correlation with population size, suggesting that genetic diversity reflects historical rather than current population sizes. Mean band sharing between pairs of colonies did not show any relation with between-population geographic distance. However, all between-population similarity indexes were lower than the corresponding within-population similarity index, a trend that suggests a small degree of population structure across the breeding range of this subspecies. Despite banding records suggesting high levels of philopatry, gene flow seems sufficient to prevent considerable divergence at these loci. Alternative and equally plausible explanations for the results also are discussed.

Key words: *Calonectris diomedea*, Cory's Shearwater, DNA fingerprinting, gene flow, island populations, procellariiform genetic diversity.

Avian populations are often considered an enigma with regard to degrees of geographic structure and magnitudes of gene flow. On the one hand, birds migrate long distances between breeding and wintering grounds providing substantial opportunities for admixture of populations. On the other hand, many species show a strong philopatry to breeding localities and even nest sites, and populations often exhibit geographic variation in morphological and behavioral traits, suggesting some degree of differentiation between them (Birt-Friesen et al. 1992).

Cory's Shearwater *Calonectris diomedea* is a socially monogamous species and, as most Procellariiforms, exhibits extreme demographic characteristics; it has low reproductive rates coupled with high life expectancy. The adults (over 5 years old) breed on isolated islands (the only time they come to land) sometimes in dense colonies but more often in smaller and more scattered groups (Cramp and Simmons 1977). Two subspecies are currently recognized, *C. d. borealis* breeding in the Northeast Atlantic and *C. d. diomedea* in the Mediterranean Sea. As for Cape Verde's taxon (*C. d. edwardsii*), there is increasing ev-

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