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## Survival of male Tengmalm's owls under temporally varying food conditions

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**Abstract** We analysed whether annual survival of male Tengmalm's owls in western Finland varies according to changes in the abundance of their main prey, *Microtus* voles. Our analyses were based on capture-recapture data over five 3-year population cycles of voles from 1981 to 1995, each cycle consisting of consecutive years of low, increasing and decreasing vole abundance. Survival estimates of males in the increasing vole years (ca. 55%) were higher than in the decreasing vole years. In the latter case, males faced a drastic crash in *Microtus* vole numbers, and only about one-third of males survived over this crash. After the crash of vole populations, male survival increased rapidly (up to 76%) according to the recovery of *Microtus* vole populations. These results show that temporal variation in the abundance of their main prey modifies the survival of male Tengmalm's owls. In addition to survival, recapture rates also varied, largely due to the fact that in poor vole years a majority of males skipped breeding. The large among-cycle phase variation in survival (25–76%) probably creates selection for phenotypic plasticity in life-history traits related to survival and reproduction.

**Keywords** Recapture · Prey abundance · Three-year vole cycles · *Microtus* voles

### Introduction

Adult survival is an essential component of fitness, and may trade off with investment in reproduction (Williams 1966; Endler 1986). The existing literature on life-history traits of organisms is apparently biased towards estimating the reproductive success of individuals, as reproductive traits are easier to estimate than survival. This is because accurate survival estimates generally need long-term follow-ups of marked individuals. In addition, measuring survival is troublesome, as the time of death is often unknown (e.g. Clobert and Lebreton 1991; Lebreton et al. 1993; but see Daan et al. 1996). Despite the difficulties in estimating survival, it is important to analyse it through time to better understand differences in life-history traits and the behaviour of animals. Especially studies performed in variable environments seem to be lacking (Murphy 1968; Charnov and Schaffer 1973; Schaffer 1974; Schaffer and Rosenzweig 1977; Stearns 1977; Clutton-Brock et al. 1992; Cooch and Ricklefs 1994; Marrow et al. 1996). For example, if survival probabilities vary over time, phenotypic plasticity in essential life-history traits should be favoured by natural selection (Bradshaw 1965; Stearns 1992). In accordance with this, the reproductive effort of red foxes *Vulpes vulpes* (Lindström 1988) and Tengmalm's owls *Aegolius funereus* (Hakkarainen and Korpimäki 1994a, 1994b, 1994c) seem to vary as a response to annually varying food conditions and survival prospects of their offspring.

Earlier analyses of the survival of birds have mainly concerned species that live under relatively stable environmental conditions, and the main question has been on age-related changes in annual survival. Such capture-recapture studies have included various long-lived seabirds [e.g. Manx shearwater *Puffinus puffinus* (Perrins et al. 1973); kittiwake *Rissa tridactyla* (Coulson and Wooller 1976; Aebscher and Coulson 1990); herring gull *Larus argentatus* (Chabryk and Coulson 1976); fulmar *Fulmarus glacialis* (Dunnett and Ollason 1978); Adelie penguin *Pygoscelis adeliae* (Ainley and DeMaster 1980); common eider *Somateria mollissima* (Coulson 1984);

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shag *Phalacrocorax aristotelis* (Aebischer 1986; Harris et al. 1994); short-tailed shearwater *Puffinus tenuirostris* (Bradley et al. 1989); wandering albatross *Diomedea exulans* (Weimerskirch 1992); common murre *Uria aalge* (Sydeman 1993)], waders (e.g. Temminck's stint *Calidris temminckii*) (Hilden 1978), small passerines [e.g. black-capped chickadee *Parus atricapillus* (Loery et al. 1987); collared flycatcher *Ficedula albicollis* (Gustafsson and Pärt 1990)], and raptors [sparrowhawk *Accipiter nisus* (Newton et al. 1983, 1993, 1997)]. Studies on species living under temporally varying environmental conditions are clearly under-represented.

In earlier studies, we have shown that essential life-history traits of vole-eating Tengmalm's owls, such as clutch and egg size, laying date, number of fledglings produced per breeding attempt and lifetime reproductive success, vary in the course of the vole cycle (Korpimäki and Hakkarainen 1991; Korpimäki 1992; Hakkarainen and Korpimäki 1994a). Annual changes in vole density also have drastic effects on owl breeding density (Korpimäki 1994). As large variation seems to be present in Tengmalm's owl populations, we sought to examine whether temporal changes in the abundance of their main prey, *Microtus* voles, affect the survival of resident male Tengmalm's owls.

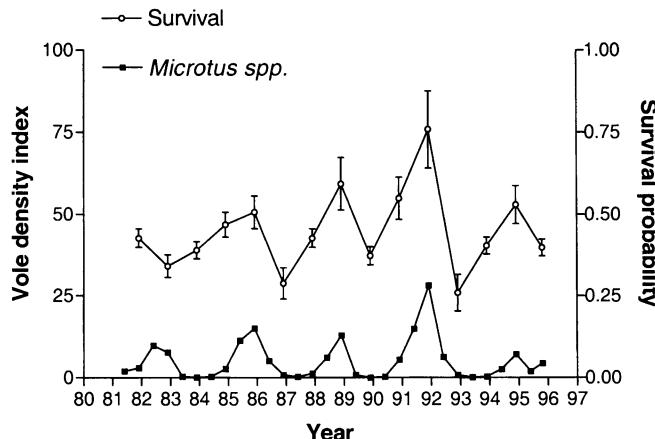
## Materials and methods

### Study area, study population and vole cycles

The study was carried out in the Kauhava region, western Finland (approximately 63°N, 23°E), where a breeding population of Tengmalm's owls has been studied for >25 years. The study area mainly consists of coniferous forests (46%), agricultural land (27%) and peatland bogs (23%). In this study, we used data collected over 15 years (1981–1995) in an area of 800–1,200 km<sup>2</sup> (30×40 km). The study area contained 395–450 nest-boxes prior to 1987, but in 1988 the count was increased to 500 nest-boxes. In addition, there were about 30 natural cavities (their number was low because of modern forestry) suitable for Tengmalm's owls. The density of erected nest-boxes (approximately 0.5 km<sup>2</sup>) is about the same as the density of suitable natural cavities for Tengmalm's owls (0.5–1.5 km<sup>2</sup>) in natural pristine coniferous forests in southern Finland (Pouttu 1985; Virkkala et al. 1994).

Each year, we checked the nest-boxes and natural cavities at least twice per breeding season to find all owl nests. These nests were then visited to determine the main parameters of breeding performance [laying date, clutch size and number of fledglings produced; for further details see Korpimäki (1987, 1992)]. Parent owls were trapped, measured (body mass and wing length to the nearest 1.0 g and 1.0 mm, respectively) and ringed when nestlings were 1–2 weeks old. In some cases, nesting attempts failed before individuals could be identified. Despite this, 80–90% of breeding parent owls were ringed or retrapped in each year of the study [see Korpimäki (1987, 1992); Hakkarainen et al. (1996) for further details]. Each year we used about the same total effort for owl trapping. No detectable ring wear occurred even on the oldest owls [maximum lifespan 10 years; Korpimäki (1992) and unpublished data.], and we assumed that there were no ring losses.

Males were captured by a swing-door trap attached to the entrance hole of the nest-box when they were feeding their 1- to 2-week-old nestlings (Korpimäki 1987). Because voles of the genera *Microtus* are the main (e.g. Sulkava and Sulkava 1971; Korpimäki 1988) and preferred prey of Tengmalm's owls (Koivunen et al. 1996), their densities were estimated by snap-



**Fig. 1** Annual survival probabilities ( $\pm$ SE) of male Tengmalm's owls and density fluctuations of *Microtus* voles in the study area in western Finland during 1981 to 1995. Trapping censuses were conducted with similar methods in May and September of each year. Each symbol is based on the number of voles snap-trapped during ca. 1,000 trap nights. Vole density index describes the number of *Microtus* voles snap-trapped per 100 trap nights

trapping in the main habitat types (farmland and woodland) in May and September each year (Korpimäki and Norrdahl 1989; Korpimäki 1994; Klemola et al. 1997; Korpimäki and Wiehn 1998). According to the results of the spring and autumn snap-trapping, three biologically meaningful and regular phases of the population cycle of voles were identified (see Fig. 1). In the low vole years (1981, 1984, 1987, 1990, 1993) there was a scarcity of *Microtus* voles throughout the breeding season of Tengmalm's owls, but vole populations started to recover slowly after the breeding season, and continued to increase in the following winter due to winter reproduction of *Microtus* voles (e.g. Hansson 1984; Norrdahl and Korpimäki 1993). In the increasing vole years (1982, 1985, 1988, 1991, 1994), *Microtus* vole abundance was moderate during the breeding season of owls but their numbers quickly increased, and peaked in the next autumn. In the decreasing vole years (1983, 1986, 1989, 1992, 1995), *Microtus* vole densities were moderate to high in the early breeding stage of owls, but during the late spring, and next summer and autumn, their number crashed to a very low level. Therefore, regular 3-year population cycles of *Microtus* voles that consisted of consecutive low, increasing and decreasing vole years occurred in our study area (Fig. 1; see also Korpimäki 1994; Klemola et al. 1997; Korpimäki and Wiehn 1998).

We only examined the survival of male Tengmalm's owls, because females may disperse by up to 500 km between successive breeding seasons [Korpimäki et al. (1987); see Schwertfeger (1984), Löfgren et al. (1986), Sonerud et al. (1988) for other areas], whereas males are sedentary after the first breeding attempt, moving only up to 7.5 km between successive breeding seasons [(median 1 km; Korpimäki (1987, 1993)]. Annual breeding dispersal distances of males seem to differ a little bit between the increasing and decreasing vole years [medians 0.8 km and 1.5 km, respectively; Korpimäki (1993)]. This difference, however, is small compared to the extent of our study area (30×40 km) and therefore may not have biased our survival estimates. The recent data on breeding dispersal distances of male owls show similar values [mean+SD, 861+927 m; Hakkarainen et al. (2001)]. After the first breeding attempt males use one to five nest-boxes for breeding in an area covering 2–5 km<sup>2</sup> during their lifetime (Korpimäki 1992). Some males, especially those occupying territories near the edges of the study area, may have moved from the study area, but this proportion is likely to be very small. Only two males moved >5 km inside our large study area, and only one breeding male was later reported to have bred outside our study

area (Korpimäki 1987, 1993; Hakkarainen et al. 2001), although in the vicinity of our study area there are about 1,000 nest-boxes suitable for Tengmalm's owls. These nest-boxes are annually checked and parent birds trapped by bird ringers (see e.g. Hakkarainen et al. 1996). In addition to this, our nest-searching efficiency has been very high, as we have also tried to detect non-breeding males in our study population (Hakkarainen and Korpimäki 1998). Therefore, our survival estimates are probably not confounded to a large extent by emigration or lost individuals.

Survival analyses were performed using the capture history of 459 males that recruited to our breeding population in 1981 to 1995. At that time, on average, 15% (SD 13%) of nest-boxes were occupied by Tengmalm's owls, but between-year variation in breeding frequency was high (range 3–34%) because of a large annual variation in vole abundance.

#### Survival models

The survival analyses were made using the MARK program (White and Burnham 1999). This program allows the separate estimation of survival rate ( $\phi$ ) and recapture rate ( $P$ ) (for further details, see Lebreton et al. 1992). This program takes advantage of the information based on capture-recapture history of individuals marked in the population. Our objective was to study whether  $\phi$  and breeding probabilities (an estimate derived from recapture rate,  $P$ ) vary annually due to a large annual variation in *Microtus* vole numbers (see Fig. 1).  $\phi$  describes apparent survival of individuals, including the possible effect of permanent emigration. Recapture rate,  $P$ , decreases with the amount of individuals missed in the trapping process (e.g. due to failed nests, or breeding in a natural cavity unknown to us). Because we trapped almost all (ca. 90%) breeding individuals in our study population, we believe that in this context recapture rate,  $P$ , is influenced by annual changes in breeding frequency of owls rather than a failure in trapping. In accordance with this, the annual number of breeding owl pairs in our study area varied significantly, from ten nests up to 170 nests, because in low vole years the majority of males do not breed (e.g. Korpimäki 1992; Hakkarainen and Korpimäki 1994b). Therefore, recapture rate,  $P$ , in this context describes the breeding probability of male owls. Because of large temporal fluctuations in the abundance of their main prey, *Microtus* voles, survival and future breeding prospects of site-resident males may vary largely depending on whether vole abundance in the field is declining or increasing.

By using MARK we modified the structure and elements of the design matrix to include both time dependency ( $t$ ) and changes

in *Microtus* vole numbers in our survival models (see below). For the latter, we calculated the difference between the autumn (September) and spring (May) trap indices of *Microtus* voles, describing food conditions through the critical winter period. Positive values indicated improving food conditions, whereas negative values showed a steep decline in *Microtus* vole numbers, especially in the decreasing vole years (Fig. 1). We analysed all model combinations in which survival ( $\phi$ ) and recapture probabilities,  $P$ , were allowed to vary or to be constant with respect to time ( $t$ ) and *Microtus* vole numbers (see below). The models were ranked on the basis of Akaike's information criterion (AIC; Akaike 1973). The model of best fit was then compared to the next best model by a likelihood ratio test (LRT; i.e.  $\chi^2$ -test based on differences in deviance between models) or by differences in AIC (i.e.  $\Delta\text{AIC}$ ) between models. When  $\Delta\text{AIC}$  is  $<2$ , then both models have approximately equal weight for the data. If  $2<\Delta\text{AIC}<7$ , then there is considerable support for a real difference between the models, and if  $\Delta\text{AIC}>7$ , then there is strong evidence to support the conclusion of differences between the models. For example, a significant difference in fit between the model  $\phi_{\text{Microtus}}P_t$  and  $\phi P_t$  indicates that survival is related to changes in *Microtus* vole numbers, because the models including *Microtus* vole abundance fitted the data better than the model with constant survival. In this case, we conclude that survival is dependent on changes in *Microtus* vole numbers. An insignificant difference between models indicates that *Microtus* vole numbers did not affect survival. We were also interested in whether recapture is time dependent in our models. Time dependency in "catchability",  $P$ , describes differences in the probability of breeding, because our trapping and nest-searching efficiency did not vary annually. In poor vole years most owls skip breeding and so could not be caught. We assessed the fit of our data using the contingency table tests in the RELEASE program (tests 2 and 3; see Burnham et al. 1987).

## Results

When using the whole data set (15 years) in our RELEASE T 2 and T 3 tests for the goodness of fit, we found that the fit of our data was adequate when using the T 2 test ( $\chi^2=6.03$ ,  $df=9$ ,  $P=0.74$ ) and T 3 test [ $\chi^2=29.32$ ,  $df=23$ ,  $P=0.17$ ; test 2+3,  $\chi^2=35.34$ ,  $df=32$ ,  $P=0.31$ ; see also Burnham et al. (1987); Lebreton et al. (1992)]. Details on recapture histories, model character-

**Table 1** The observed recaptures of male Tengmalm's owls.  $R_i$  The number of recaptures of all recruited males through different periods of the year ( $i$ ),  $M_{ij}$  number of recruited males recaptured in

years following ( $j$ ) the recapture year  $i$ ,  $r_i$  the total number of recaptured males that bred in year  $i$  (see Lebreton et al. 1992)

$i$	$R_i$	$M_{ij}$															$r_i$
		$j=2$	$j=3$	$j=4$	$j=5$	$j=6$	$j=7$	$j=8$	$j=9$	$j=10$	$j=11$	$j=12$	$j=13$	$j=14$	$j=15$	$j=16$	
1	6	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
2	19		6	0	0	0	0	0	0	0	0	0	0	0	0	0	6
3	17			2	1	2	0	0	0	0	0	0	0	0	0	0	5
4	7				4	0	0	0	0	0	0	0	0	0	0	0	4
5	31					13	1	0	0	0	0	0	0	0	0	0	14
6	66						3	5	0	0	0	0	0	0	0	0	8
7	9							5	0	0	0	0	0	0	0	0	5
8	77								18	1	1	0	0	0	0	0	20
9	110									10	9	2	1	1	0	0	23
10	15										3	1	0	0	0	0	4
11	78										25	1	1	0	0	0	27
12	113											3	7	1	1	1	12
13	9											4	0	0	0	0	4
14	34												8	3	0	0	11
15	23													5	0	0	5

**Table 2** Results for different survival ( $\phi$ ) and recapture ( $R$ ) models in 1981 to 1996. Differences in model deviance, number of parameters (NP) and Akaike's information criterion [ $AIC = \text{deviance} + 2 \cdot np$ : Akaike (1973)] and the difference in AIC compared to the model of best fit ( $\Delta AIC$ ) for different models are presented.  $t$  Time dependence.  $\phi_{\text{Microtus}}$  annual change in *Microtus* vole numbers (September–May) in the study area

Models	Deviance	NP	AIC	$\Delta AIC$
$\phi_{\text{Microtus}} P_t^a$	169.66	14	853.21	0
$\phi P_t$	178.59	15	864.24	11.03
$\phi_t P_t$	160.58	26	869.82	16.61
$\phi_t P$	187.98	14	871.53	18.32
$\phi_t P_{\text{Microtus}}$	184.65	16	872.41	19.20
$\phi_{\text{Microtus}} P_{\text{Microtus}}$	216.59	3	877.47	24.26
$\phi_{\text{Microtus}} P_{\text{Microtus}} P_t$	216.48	4	879.39	26.18
$\phi_{\text{Microtus}} P_t P$	225.44	3	886.32	33.11
$\phi P$	256.50	2	915.36	62.15

<sup>a</sup> Model chosen for interpretation of data

**Table 3** Recapture probabilities ( $\pm SE$ ) for 1981 to 1995 describing breeding probabilities of male Tengmalm's owls based on the model  $\phi_{\text{Microtus}} P_t$

Time period	Phase of vole cycle	Recapture probability	SE
1981–1982	Low	Non estimable	–
1982–1983	Increase	Non estimable	–
1983–1984	Decrease	0.26	0.16
1984–1985	Low	0.63	0.19
1985–1986	Increase	0.81	0.14
1986–1987	Decrease	0.22	0.11
1987–1988	Low	Non estimable	–
1988–1989	Increase	0.41	0.10
1989–1990	Decrease	0.22	0.06
1990–1991	Low	0.44	0.12
1991–1992	Increase	0.39	0.09
1992–1993	Decrease	0.12	0.06
1993–1994	Low	0.69	0.15
1994–1995	Increase	0.41	0.12
1995–1996	Decrease	0.63	0.20

istics and survival estimates are presented in Tables 1 and 2, and in Fig. 1.

Male survival was dependent on annual changes in *Microtus* vole numbers, because the model  $\phi_{\text{Microtus}} P_t$  (i.e. survival constrained by changes in *Microtus* vole numbers and recapture probability is time dependent) seemed to fit our data better than the next best model,  $\phi P_t$ , with constant survival ( $\Delta AIC$ , 11.03; LRT;  $\chi^2=8.93$ ,  $df=1$ ,  $P=0.003$ ). This gives strong support for the conclusion that the effects of *Microtus* vole numbers on survival cannot be dropped from the model without significantly reducing the fit of the model. According to these model comparisons, the model  $\phi_{\text{Microtus}} P_t$ , which fitted our data better than the other models, was chosen as the most appropriate model to explain survival and recapture rates of male Tengmalm's owls. Model  $\phi_{\text{Microtus}} P_t$  showed that males in the low and increasing vole years had relatively high survival prospects (mean 50%, see also Fig. 1). However, in the decreasing vole years, males experience a steep decline in *Microtus* vole numbers, which creates a large annual variation in survival:

in the decrease phase of *Microtus* vole populations, survival of males is extremely low (mean 34%), but this increases again after the recovery of *Microtus* vole populations (Fig. 1). This is because after the densities of *Microtus* vole populations peak, their numbers crash within a relatively short time, leading to a decrease in the survival of male owls. In contrast, if the number of *Microtus* voles is at a low level, the expected survival of *Microtus* voles is relatively high for a couple of increasing vole years until the next crash of *Microtus* vole populations (see also Fig. 1). The model  $\phi_{\text{Microtus}} P_t$  also showed that recapture probability (i.e. in this study breeding probability of males) is time dependent. It varies parallel to changes in survival estimates, because after the decreasing vole years with low survival prospects of males, the majority of males do not breed (i.e. in the low vole years of 1984, 1987, 1990, 1993), whereas in the increasing vole years about half of the males were breeders (see also Table 3).

## Discussion

The survival of male Tengmalm's owls varied markedly in the course of the vole cycle. This was mainly because peak *Microtus* vole densities were followed by a steep decline in their numbers, when survival was almost twice as low as in the increasing vole years. After the crash of *Microtus* vole populations, however, survival increased for a couple of increasing vole years. Then males could breed successfully until the next crash of the *Microtus* vole populations.

In addition to the great importance of *Microtus* voles to the survival of male Tengmalm's owls, the most appropriate model,  $\phi_{\text{voles}} P_t$ , included time dependency in recapture probability. This is likely due to the fact that many owl males skipped breeding under poor food conditions. This annual variation in the breeding probability of males apparently has large fitness consequences, because in many long-lived species lifetime reproductive success is mostly affected by the number of breeding attempts rather than by a single reproductive event [for a review see Newton (1989), see also Korpimäki (1992), Brommer et al. (1998), Szep and Moller (1999)].

Our results are in accordance with a radio-tracking study on great-horned owls *Bubo virginianus* in Yukon, Canada (Rohner 1996), which gave high annual survival estimates at peak densities of snowshoe hares, and lower ones during the crash phase of hare populations. Annual survival rates of barn owls *Tyto alba* in Scotland were 80–85% in winters of vole abundance, but decreased to 45–55% in winters of vole scarcity (Taylor 1994). Most experimental studies have also revealed that food-supplemented birds survive winter better than unfed control birds (Krebs 1971; Jansson et al. 1981; Brittingham and Temple 1988; Lahti et al. 1998), underlying the importance of sufficient food resources under adverse conditions. Along with these studies our results suggest that variation in annual survival rates may be large, and

should be taken into account when developing realistic models of population dynamics. Generally, relatively low variation in annual survival has been incorporated into models (e.g. Cooch and Ricklefs 1994) explaining life-history tactics of species living under varying conditions. This is probably because most field studies so far have shown rather low annual variation in survival (e.g. Ricklefs 1973; Perrins et al. 1973; Croxall 1981; Aebischer 1986; Newton et al. 1993). In species dependent on fluctuating food supplies, such as some vole-eating owls in Holarctic regions, a large fraction of the population may die at the time when the drastic crash in vole densities occurs (Mikkola 1983). A large variation in annual survival may also be caused by severe winters (e.g. O'Connor 1991), as in greater flamingos *Phoenicopterus ruber roseus*, in which annual local survival estimates fell from 93% to 76% during exceptionally cold winters (Cezilly et al. 1996).

This study is among the few documenting a large annual variation in the survival of adult birds. The survival of male Tengmalm's owls was dependent on future density changes in their main prey. When the *Microtus* vole abundance in the field was increasing, survival prospects of males were relatively high, whereas after the crash of *Microtus* vole populations male survival was largely reduced. Little empirical attention, however, has been paid to the strength of within-population selection on reproductive effort and life-history tactics arising from environmentally induced variation, although large density variation seems to be present in many animal communities investigated over the "long haul" (e.g. Wiens 1989).

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