Winter starvation in Danish Barn Owls

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(Med et dansk resumé: Vinterdødelighed blandt danske Slørugler)

Abstract Winter conditions can affect both survival and reproduction, and are often limiting factors for populations especially of species at the northern edge of their breeding range. Here, we investigate the effect of winter temperatures on the survival of Barn Owls *Tyto alba* in Denmark. A sample of 124 Barn Owls found dead during 1992-2010 were categorized as either 'presumed starved' or as having died from 'other causes'. We then tested whether the juvenile/adult ratio and male/female ratio differed between the two categories, and from the ratio in the total population. Parameters influencing the numbers of dead owls and parameters influencing the weight of the owls were identified. We found 1) that lower mean monthly temperatures led to more owls being found dead, and 2) that the male/female and juvenile/adult ratios among dead owls did not differ between the different death causes, nor did juvenile/adult ratios differ from the total population. These findings could mean that all individuals are equally at risk of dying from starvation during severe winters like the winter of 2009/10, contrary to the general assumption that juveniles have a higher winter mortality compared to adults. Similarly interesting is the finding that the temperature/death relationship was non-linear, suggesting that there is a temperature threshold, below which Barn Owls are simply no longer able to cope.

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Introduction

Winter conditions can affect survival and reproduction of raptors and owls (Marti & Wagner 1985, Sunde 2002, Solheim 2009). Barn Owls *Tyto alba* in Denmark are at the northern limit of their breeding range (Roulin 2002), and during the winter of 2009/2010, the coldest winter in 14 years (DMI 2010), the Danish population suffered an almost 90% mortality (Nyegaard *et al.* 2014).

The Barn Owl is a widely distributed species (Everett *et al*. 1992) preying on small vertebrates, primarily rodents (Massemin & Handrich 1997). Like other raptors and owls, females are slightly bigger than males, although this reversed sexual dimorphism is rather weak (Marti 1990). The Barn Owl used to be a rare breeding bird in Denmark, but between 1998 and 2009 the population increased from 38 to 492 breeding pairs (Nyegaard *et al.* 2014). However, the winter mortality in 2009/2010 reduced this number to only 52 known pairs (Nyegaard *et al.* 2014).

That starvation during severe winters can limit Barn Owl populations is well known (Stewart 1952, Marti 1994, Altwegg *et al*. 2003, Toth *et al*. 2005). Barn Owls are believed to be less resilient to cold temperatures than many other middle-sized raptors and owls, and it has been suggested that this is because they do not store much body fat (Marti & Wagner 1985, Handrich *et al*. 1993, but see Massemin & Handrich 1997). They also have a rather narrow thermo-neutral range (25-33 °C; Marti & Wagner 1985, Toth *et al*. 2005) and, consequently, a high energy expenditure for thermoregulation under cold conditions (Marti & Wagner 1985, Massemin & Handrich 1997).

In the present study, we investigated the factors causing winter mortality in Barn Owls by looking at possible differences in sex and age ratios in birds having died of starvation, and birds having died in accidents. We examined the effect of temperature on the number of owls having died during the winter months, and explored possible effects of weather parameters, location (North/South), sex and age on the body weight of these owls.

Methods

During spring 2010, data on 124 dead Barn Owls from the period 1992-2010 were obtained from taxidermists, mainly in Jutland, from the Copenhagen Zoological Museum, and from ringing data for Barn Owls reported to the Copenhagen Bird Ringing Centre. The data, to the extent possible, included date and approximate position at time of death, presumed cause of death, weight, ringing information, sex and age (juvenile or adult). Sex was determined through dissection by the taxidermists, and age was obtained from ringing information. In the absence of ringing data, the age of females was determined by inspection of the oviduct; a straight and thin oviduct indicating an immature bird (Newton *et al*. 1997). Finally, we obtained annual numbers of breeding pairs in Denmark from *Project Barn Owl* (Tytoalba 2010) and used it as a proxy for population size.

Temperature is a good indicator of winter severity, because it affects the hunting success of Barn Owls and has a metabolic cost (Taylor 1994, Altwegg *et al*. 2003 and references therein). Weather data for 2004-2010 (precipitation, wind and temperature from two weather stations) were collected online from the Danish Meteorological Institute (DMI), and Peter Sunde (Department of Bioscience, Aarhus University) kindly provided similar data for the years 1994-2000. Owls from years without weather data were treated as 'missing data' in the analyses.

In order to couple owls to various weather parameters, we used two Danish weather stations: a northern in Viborg (56°27'N, 9°23'E) and a southern in Tønder (54°56'N, 8°51'E). We then divided the owls in our sample into a northern and a southern group depending on where they had been found. For use in our investigation of the number of dead owls during winter in Denmark, mean monthly temperatures for the whole of Denmark were obtained from DMI for 1998-2010. We could not obtain mean monthly temperatures for all of Denmark from years before 1998, since these were not available online. Again, owls from years with missing temperature data were excluded from the subsequent analysis. We restricted our analysis to December-March, the coldest months of the year in Denmark and thus the main period during which starvation occurs. Unfortunately, data on snow cover, wind and precipitation for all of Denmark could not be obtained.

We considered two categories of owls: 1) Those having died from accidents representing the healthy part of the population, and 2) Birds found dead, largely representing the starved part (Sunde 2002). Inevitably, there was some uncertainty regarding cause of death, and this made it necessary for us to use a more objective parameter. We therefore used a two-sample t-test to test whether there was a difference in the weight between the owls reported as 'found dead' and the owls reported as having died in 'accidents'. It turned out that birds in 'accidents' were significantly heavier than those in the 'found dead' group ($t_{104} = 8.47$, $P < 0.0001$). Looking at the weight distribution of the two categories, we therefore defined a threshold value of 250 g to reclassify the cause of death as 'presumed starved' and 'other causes' (Fig. 1). Other authors have used a threshold of 240 g to identify starved Barn Owls (Newton *et al*. 1991, 1997),

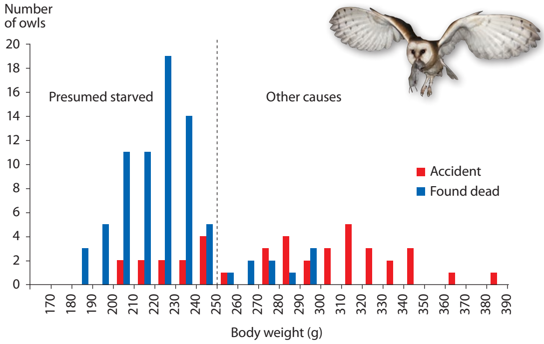

Fig. 1. Body weight distribution of Barn Owls killed in accidents or just found dead. All birds having a weight below 250 g were assumed to have died from starvation, while heavier birds were grouped as having died from 'other causes'. Photo: Klaus Dichmann.
*Fordeling af dødsårsager for Slørugler med forskellige kropsvægte (*Body weight*). Hver fugl var oprindeligt blevet kategoriseret som enten fundet død (*Found dead*) eller død pga. ulykke (*Accident*). På basis af kropsvægten blev de siden reklassificerede som 'formodet sultede' (*Presumed starved*; alle der vejede under 250 g) eller 'andre årsager' (*Other causes*; alle over 250 g).*

but since Denmark is at the northern limit of the species distribution (Roulin 2002), Barn Owls might be heavier in this area. The reclassified cause of death was used to investigate if there were differences in the effects of various parameters on the number of dead owls within the two groups.

We used χ^2-tests to see, if proportions between juvenile and adult owls within each mortality group differed from the adult to juvenile winter ratio of 1:2.7 found in an American population study (Marti & Wagner 1985). No age ratio was available for the Danish population (see discussion for further remarks). Similarly, χ^2-tests were used to test whether there were differences between the age and sex classes in the proportion of the two death causes. We used Yates' correction in cases with only two groups.

A Generalized Linear Mixed Model (GLMM; PROC GLIMMIX procedure in SAS 9.1.3) was used to test, which parameters influenced the number of dead owls, using a logit-function and keeping year as a random factor. We wanted to see, if the number of dead owls was affected by 1) Cause of death, 2) Number of breeding pairs in a given year and 3) Mean winter temperature for the whole of Denmark. Temperature was also added as temperature squared to see if there was a non-linear effect. A parabolic relationship between temperature and number of deaths could mean a steeply rising mortality at temperatures below a certain threshold. The best model was selected through backwards selection and verified by forward selection.

We used a Mixed Model (PROC MIXED SAS 9.1.3) to examine if there was a linear relationship between the fixed effects and the dependent variable weight. The fixed effects were mean monthly temperature at the location, precipitation at the location, wind at the location, location (Viborg/Tønder), sex, age, cause of death and month. Years were used as a random factor. We did not have enough degrees of freedom to test all of the parameters together, and therefore used univariate tests to find the parameters with the highest significance level.

We also investigated the possibility of poisoning among our sampled owls, since during winter, some Barn Owls hunt in barns where there is a risk of catching poisoned mice. However, there was no indication of poisoning in our data set (A. S. Hammer & T. K. Christensen pers. comm.).

Tab. 1. Sample size and mean body weight of Barn Owls 'presumed starved' and having died from 'other causes'. Number of Barn Owls and the mean body weight are given for the two death causes, as well as for sexes and age classes. JM: juvenile males, JF: juvenile females, AM: adult males, AF: adult females, unknown sex/age: either sex, age or both unknown.
Antallet af døde Slørugler (Number) *og den gennemsnitlige vægt* (Mean body weight) *for de to dødsårsager* (Presumed starved: *formodet sultede og* Other causes: *andre årsager) såvel som for de to køn og aldersklasser.* JM: *Juvenile hanner,* JF: *Juvenile hunner,* AM: *Voksne hanner,* AF: *Voksne hunner,* Unknown sex/age: Køn, alder eller begge ukendt.

Sex and age class	**Presumed starved**		**Other causes**	
	Number (Total = 75)	**Mean body weight ± SD**	**Number (Total = 49)**	**Mean body weight ± SD**
JM	16	210.0 ± 12.4	12	280.3 ± 33.4
JF	12	226.6 ± 12.1	12	310.5 ± 38.6
AM	8	216.7 ± 18.5	4	296.4 ± 51.1
AF	11	222.5 ± 9.6	8	285.1 ± 36.4
Unknown sex/age	28	220.9 ± 13.0	13	290.2 ± 39.9

Results

Compared to the proportion (1 adult to 2.7 juveniles) in the American population studied by Marti & Wagner (1985), there were no significant differences in the proportion of juveniles to adults within each mortality group (presumed starved: χ^2_1 = 0.23, P = 0.63; other causes: χ^2_1 = 0.21, P = 0.65). Neither were there any significant differences in the proportion of the sexes (χ^2_1 = 2.40, P = 0.12), age classes (χ^2_1 = 1.41, P = 0.23) or both (χ^2_3 = 2.37, P = 0.50) for the two causes of death (Tab. 1).

The temperature parameter that best explained the data for the starved owls in the GLMM, was temperature squared. There was no significant effect of either temperature or temperature squared when looking at the total number of Barn Owls being reported ($F_{1,80}$ = 2.04, P = 0.16). However, there was a significant interaction between temperature squared and cause of death ($F_{1,80}$ = 6.43, P = 0.013). On this basis, we divided the data set according to cause of death. We found that there were more dead 'presumed starved' birds at higher population sizes (see Tab. 2) and at lower temperatures (Fig. 2), while no effect of population size or temperature was seen for birds having died from 'other causes'.

In our Mixed Model for weight, only the linear effect of temperature was tested. Temperature itself did not have a significant effect ($F_{1,41}$ = 0.43, P = 0.52), but the interaction between temperature and cause of death did ($F_{1,41}$ = 7.6, P = 0.009). On this basis, we divided the data set according to cause of death, as before. Effects were found for 'presumed starved' owls with females weighing more than males, and birds weighing less at higher temperatures (Tab. 3). No effect on weight was found for any of the other parameters tested (precipitation, wind, location (Viborg/Tønder), sex, age and month).

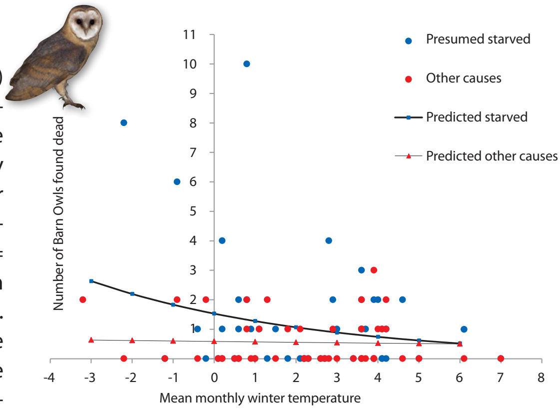

Fig. 2. Numbers of 'presumed starved' Barn Owls and owls having died from 'other causes' at different mean monthly temperatures for the four winter months of 1994-2010. Months for which we did not have temperature data were excluded. The points in the figure show all available data, whereas the graph shows the predicted values for a specific population size (226 breeding pairs – the mean number of breeding pairs during 1999-2010). The predicted values were calculated under the assumption that all dead Barn Owls were reported (this is of course not the case, but see discussion). Photo: Klaus Dichmann.

*Antallet (*Number of Barn Owls found dead*) af 'antaget sultede' Slørugler (*Presumed starved*) og Slørugler klassificeret som døde af 'andre årsager' (*Other causes*) ved forskellige gennemsnitlige temperaturer (*Mean monthly winter temperature*) for de fire vintermåneder i 1994-2010. Måneder uden temperaturdata er ikke inkluderet. Punkterne i figuren viser alle tilgængelige data, hvorimod graferne viser de forventede værdier (*Predicted starved *og* Predicted other causes*) for en specifik populationsstørrelse (her 226 ynglepar – det gennemsnitlige antal ynglepar mellem 1999 og 2010). I beregningen af graferne antages det, at alle Slørugler blev indberettet (dette er selvfølgelig ikke tilfældet, men se evt. diskussionen).*

Tab. 2. Results from the GLMM analysis for 'presumed starved' Barn Owls. The table shows the parameters that had a significant effect on the number of dead owls. Estimates show that more owls were reported dead with higher numbers of breeding pairs. Looking at the squared mean monthly temperature parameter (Temperature squared), the estimate makes little sense on its own. However, taken together with Fig. 2, we see that more owls die with decreasing mean monthly temperature. Year was used as a random factor.

Resultater fra GLMM-analysen for 'formodet sultede' Slørugler. Tabellen viser de parametre, der påvirkede antallet af døde ugler statistisk signifikant. Estimaterne viser, at der døde flere ugler, jo flere ynglepar (Breeding pairs) *der var. Estimatet for den kvadrerede månedlige temperatur* (Temperature squared) *giver ikke meget mening alene, men sammenholdt med Fig. 2 kan vi se, at jo lavere den gennemsnitlige månedstemperatur* (mean monthly winter temperature) *var, jo flere ugler døde der.* År (Year) *blev brugt som en tilfældig variabel.*

Effect	**Estimate**	**SE**	**DF**	**t**	**P**
Intercept	-0.3	0.42	10	-0.73	0.48
Temperature squared	-0.18	0.06	35	-3.04	0.005
Breeding pairs	0.003	0.001	35	2.49	0.02
Covariate parameter					
Year	0.23	0.19			

Tab. 3. Results from the mixed model analysis of weight of Barn Owls in the 'presumed starved' group showing the parameters having a significant effect on the weight of these owls. The estimates show that owls weighed less with increasing mean monthly temperature, and males weighed less than females. Year was used as a random factor.
Resultater fra 'mixed model'-analysen af faktorer der påvirkede vægten af 'formodet sultede' Slørugler. Tabellen viser de parametre, der påvirkede vægten af de sultede ugler signifikant. Estimaterne viser, at uglerne vejede mindre, jo varmere den gennemsnitlige månedstemperatur (Temperature) *var. Desuden ses det, at hanner* (Male) *vejede mindre end hunner.* År (Year) *blev brugt som en tilfældig variabel.*

Effect	**Estimate**	**SE**	**DF**	**t**	**P**
Intercept	227.08	2.92	10	77.7	< 0.0001
Male	-9.78	3.32	30	-2.94	0.048
Temperature	-1.81	0.65	30	-2.78	0.04
Covariate parameters				**Z**	**Pr Z**
Year	11.15	34.12		0.33	0.37
Residual	110.7	30.19		3.67	0.0001

Discussion

Generally, accidents are overestimated as a mortality cause compared to starvation. This is because owls that die from accidents often do so near human activities, and therefore are easier to detect (Sunde 2002). Starved owls, on the other hand, are more likely to be eaten by scavengers or to decompose without being found (Massemin & Handrich 1997, Newton 1998, Sunde 2002, Mikkola 1983 in Solheim 2009). Therefore, numbers of owls 'presumed starved' were probably underestimated compared to owls having died from 'other causes' (mainly accidents). However, the bias in detection probability should not be a problem for our analyses, if we are looking for differences between years, assuming that the detection probability of owls dying of different causes is roughly equal among years (Sunde 2002).

Another constraint for a study like this is if sampling efforts vary between years. Indeed, the sampling effort did vary between years and was particularly high during the winter 2009/2010. However, this bias was corrected for by including year as a random factor.

The ratio of juveniles to adults did not differ from the expected ratio, suggesting that juveniles and adults died in proportion to their numbers in the total population. We also found no difference in the adult/juvenile ratio between the two causes of death. Even though adults could be less prone to accidents because of experience, we assume that death by accidents is equally probable for juveniles and adults in our sample, where most owls killed in accidents had been killed in traffic (irrespective of age, Barn Owls hunt by flying low above the ground and often hunt near roads during winter, making them prone to car accidents; Massemin & Zorn 1998). Since the adult/juvenile ratio was the same in our starved and accidentally killed subsamples, and since the ratio of juveniles to adults did not differ from the expected, we may tentatively conclude that juveniles and adults were equally at risk of dying from starvation during the winter of 2009/2010.

Our findings contrast with other studies that show a difference in resistance to cold weather between juvenile and adult Barn Owls (Taylor 1994, Altwegg *et al*. 2003, Toth *et al*. 2005). However, particularly severe winters have previously been shown to lead to equally high mortality for juveniles and adults (Altwegg *et al*. 2006). We therefore believe that it was the severity of the winter 2009/2010, from which most of our data came, that led to the equal risk of starvation for adults and juveniles.

Assuming an equal probability of females and males dying from 'other causes', the fact that the male/female ratio was the same in both groups (starved and 'other causes') is in agreement with previous studies showing an equal resistance to starvation among the two sexes (Handrich *et al*. 1993).

The non-linear negative relationship between temperature and the number of starved Barn Owls indicates that there might be a temperature threshold, below which Barn Owls will not be able to survive. Further studies should try to test this hypothesis and possibly find the actual threshold, as the data in this study were not sufficient for this purpose. We also found an effect of population size on the number of starved birds, but no such effect on the number of birds that died from 'other causes'. This was probably due to differences in sampling efforts between the two groups.

The Barn Owl is one of the less dimorphic owl species (Handrich *et al*. 1993). In our study, females were heavier than males in the starved part of the population. However, for birds having died in accidents, we did not find this difference in weight between the sexes. This could be caused by varying amounts of body fat masking the small difference in body size.

Dead Barn Owls from the severe winter 2009/10, where almost 90% of the Danish population perished. Photo: Klaus Dichmann.
Døde Slørugler fra isvinteren 2009-10, hvor næsten 90 % af den danske bestand omkom.

Counterintuitively, birds that died from starvation showed a non-linear tendency of decreasing weight with higher temperatures. This might be explained, if all birds having starved to death weigh approximately the same at the time of death, irrespectively of the temperature at which they died. High temperatures might then lead to a faster decomposition, and since starved birds are more difficult to find, they might lose a substantial amount of weight before recovery. This might also explain why the weight of birds killed by 'other causes' show no relationship with temperature, since they are reported immediately. However, if they were not reported immediately, and perhaps also decomposed significantly, some owls would have received a wrong classification. Fortunately, this does not seem to be the case, as lower temperatures led to more 'presumed starved' owls, and not vice versa.

Taken together, our study reveals that winter severity is an important limiting factor for the Barn Owl in Denmark, affecting both juvenile and adult mortality. The winter of 2009/2010 was an unusually severe winter, probably leading to extraordinarily high energy expenditure in this poorly cold-adapted species. This very high energy demand apparently meant that virtually no birds were able to find enough food to sustain life, which would explain why we did not find any difference in risk of starvation between adults and juveniles. However, since we have no data on snow cover, we cannot separate between the effects of temperature itself and reduced hunting possibilities due to snow.

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Resumé

Vinterdødelighed blandt danske Slørugler

Vintervejr kan påvirke overlevelse og reproduktion og er ofte en bestandsbegrænsende faktor, især for arter nær den nordlige grænse for deres udbredelse. Vi undersøgte effekten af vintertemperatur på bestanden af danske Slørugler *Tyto alba*. Vi kategoriserede 124 døde Slørugler fundet i perioden 1992-2010, som 'formodet sultet' eller døde af 'andre årsager'. Vi testede om fordelingen mellem unge/voksne og hanner/hunner afveg mellem de to dødsårsager og fra fordelingen i totalbestanden. Vi identificerede desuden parametre, der influerede på antallet af døde Slørugler, eller på vægten af uglerne. Vi fandt:

1) at den månedlige middeltemperatur påvirkede antallet af døde Slørugler, således at jo koldere det var, jo flere ugler blev fundet døde. Denne sammenhæng var ikke-lineær, hvilket tyder på, at der findes en tærskelværdi for temperaturen, under hvilken uglerne ikke længere er i stand til at klare sig.
2) at fordelingen mellem hanner og hunner var den samme i de to grupper. Fordelingen mellem ungfugle og ældre var også den samme for de to dødsårsager og afveg desuden ikke fra fordelingen i den totale bestand. Disse resultater tyder på, at alle individer var lige udsatte for at dø under isvinteren 2009/10.

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