

## Sex differences in winter distribution of Long-eared Owls (*Asio otus*) in Denmark and neighbouring countries

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Evidence presented here indicates that in western Denmark, the sex-ratio of Long-eared Owls (*Asio otus*) during the winter months is significantly biased towards females. Museum collections revealed the same phenomenon in the Netherlands and northern Germany, while sex-ratios approached parity in eastern Denmark, Sweden and central and southern Germany. From the literature, it is clear that there is also a significant winter surplus of females in England, Scotland and the Shetland Islands. Present hypotheses for differential migration are reviewed and it is concluded that none explains adequately this pattern. An alternative hypothesis is presented here, in which heavy predation pressure by Eagle Owls (*Bubo bubo*) and Goshawks (*Accipiter gentilis*) on the breeding range in Fenno-Scandia and parts of the Long-eared Owl's wintering range in northern and western Europe is the primary cause of the differential in the observed pattern of winter distribution.

Key words: Long-eared Owl (*Asio otus*), sex-ratio, differential migration, Eagle Owl (*Bubo bubo*), Goshawk (*Accipiter gentilis*).

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### 1. Introduction

Partial migration is a behavioural phenomenon that varies with respect to time, geographical distribution, sex, and age (BERTHOLD 1984). Food shortage in winter seems to be the main stimulus for migration among birds, and if there is not food enough for both sexes, the general pattern is for the dominant sex to remain on or near the breeding grounds and the subordinate sex to migrate (e.g. LACK 1966, GAUTHREAUX 1978, LUNDBERG 1988). Unlike most owls, female Long-eared Owls (*Asio otus*) show a greater migratory tendency than do males, the hole-nesting Tengmalm's Owl (*Aegolius funereus*) being the only other exception in Europe (LUNDBERG 1979). Female Long-eared Owls are larger than males, with a body mass on average 15–17% greater, although female wing length is only 1% to 1.7% larger, with much overlap (GLUTZ VON BLOTZHEIM & BAUER 1980, CRAMP 1985, LUNDBERG 1986). In spite of the large difference in mass, sexual dimorphism in Long-eared Owls is not obvious in the field and generally is only appreciable with the bird in the hand.

There is considerable and confusing variation in sex-ratio among migrating and wintering Long-eared Owl populations in Europe. HARVEY & RIDDIFORD (1990) found 28 ♀ and 8 ♂ among autumn migrant Long-eared Owls ringed on Fair Isle, Shetland, and among 123 dead Long-eared Owls from England and Scotland received at the Institute of Terrestrial Ecology during 1963–1995, there was a ratio of 89 ♀ : 34 ♂ (WYLLIE et al. 1996). In birds killed between October and February, the sex-ratio was even more strongly female biased (42 ♀ : 8 ♂), whereas between May and September, the ratio was close to parity (12 ♀ : 10 ♂). In the Netherlands, WIJNANDTS (1984) found a sex-ratio among traffic casualties of 17 ♀ : 8 ♂. Further north, the situation is very different. An examination of traffic victims collected by the Norwegian Institute for Nature Research during 1987–1992 revealed a winter sex-ratio of 13 ♀ : 23 ♂ (OVERSKAUG & KRISTIANSEN 1994), a pattern already noted in Finland many years ago (HORTLING 1929 p. 356). Most migrant Long-eared Owls are first year birds e.g. on Heligoland, of 79 birds ringed in October and November, 74 were birds of the year, some still with down on their feather tips (MORITZ & SCHONART 1976).

It therefore seems clear that sex-ratios in wintering Long-eared Owl populations vary geographically, some areas showing a strongly female-biased sex-ratio, others exhibiting near parity. Which environmental factors or other selective pressures may have given rise to this marked intersexual difference in migration strategy and the complex pattern of winter female distribution?

As patterns of movement and distribution outside the breeding season are often influenced by breeding behaviour and intersexual role allocation (MYERS 1981), a few basic biological data are necessary. The Long-eared Owl is a Holarctic species, in the Palearctic found from western Europe to Japan and China (MIKKOLA 1983). The breeding season in Denmark is from early March to May (OLSEN 1992). Males defend what is often only a very small territory, for instance three pairs were found breeding in an area little over two hectares in Denmark (TRAP-LIND 1965, GLUTZ VON BLOTZHEIM & BAUER 1980, CRAMP 1985). Disused Carrion and Hooded Crow (*Corvus corone*) or Common Magpie (*Pica pica*) nests are favoured; females incubate and rear the nestlings, while males bring food to both the young and the female (MIKKOLA 1983).

Most Long-eared Owls stay on their breeding grounds throughout the year when food supply is adequate, but in years with fewer prey, large numbers of owls move from Fenno-Scandia to central and western Europe (GLUTZ VON BLOTZHEIM & BAUER 1980). In Finland, about 80% of all birds are nomadic and only breed when and where food is abundant (JUVONEN 1976 cited in CRAMP 1985). This is consistent with the results of a theoretical analysis predicting that partial migration will be most frequent in regions where climatic variability is high (COHEN 1967, cited in LUNDBERG 1988). These data also support the hypothesis that predicts an increasing proportion of partially migratory birds with increasing latitude (LUNDBERG 1988).

#### Differential migration hypotheses

Various hypotheses for the latitudinal segregation of sexes in winter have been presented (review in CLARK et al. 1978, MYERS 1981, KETTERSON & NOLAN 1983, BERTHOLD 1984, KJELLÉN 1994). Below is brief summary of each of the main hypotheses, with comments regarding the applicability of each to the Long-eared Owl system as described above:

(1) Intersexual competition for food in winter impels the smaller, subordinate sex to migrate (GAUTHREAUX 1978, KETTERSON 1979, KETTERSON & NOLAN 1979).

This hypothesis is not supported by the Long-eared Owl since the much larger female migrates in the winter months from parts of Fenno-Scandia and Denmark to England and other parts of northern Europe, while the smaller, subordinate male remains nearer the breeding grounds. However, food shortage in winter probably is the major factor controlling ultimate densities of temperate bird populations (LACK 1966), here confirmed by a greater immigration to England and Denmark in years with low vole populations further north (cf. WYLLIE et al. 1996, pers. obs.).

(2) If there is competition for breeding resources, it is an advantage for the individuals of one sex, usually males, to winter closer to the breeding grounds, because they can arrive earlier in the breeding season (KETTERSON & NOLAN 1976).

There is no evidence for strong territoriality or competition for breeding resources in the Long-eared Owl; there are very few reports of aggressive encounters and the species is well known for its communal roosting behaviour in winter (CRAMP 1985, SCOTT 1997). In view of the fact that nests are regularly placed very close together, and the lack of apparent territoriality in this species, this hypothesis is not supported by the pattern of differential migration exhibited by Long-eared Owls.

(3) Physiological limitations related to body size (greater cold tolerance and ability to fast) permit the larger sex to winter in harsher climates (KETTERSON & NOLAN 1976, KETTERSON & KING 1977, KETTERSON & NOLAN 1979, cf. BERGMANN'S rule).

BERGMANN'S rule predicts that birds of the same species or group of species are larger at higher than lower latitudes, because birds in colder climates need greater volume to area relations to maintain body temperature. The winter distribution of the differential migration of the two sexes of the Long-eared Owl is a clear exception to this rule and the data do not support this hypothesis.

(4) Risk of mortality on migration may vary intersexually, leading to one sex becoming sedentary while the other is migratory (KETTERSON & NOLAN 1983).

That migration carries a high risk of mortality, the generally accepted rule for migrating species, seems also to apply to the Long-eared Owl in normal years. Finnish migrants of all ages, except first calendar year birds, exhibit a higher mortality rate than their non-migrating conspecifics (Finnish recovery printouts). If mortality risk on migration is indeed different between sexes in the Long-eared Owl, the larger and less manoeuvrable female is likely to be at greater risk, particularly in relation to traffic accidents, and therefore less likely to migrate than the male. This hypothesis can also be rejected.

None of the existing hypotheses seems adequately to explain the pattern of differential migration found in the Long-eared Owl. This study will use sex-ratio data from European Long-eared Owl wintering populations to examine more closely the distribution of the sexes in winter and seek a suitable explanation.

## 2. Material and methods

New information is here presented on sex-ratios of accident victims among Long-eared Owls in Denmark based on eleven years of study, and of birds in England, Germany, the Netherlands and Sweden through study of museum material from the larger collections in northern Europe.

As winter is the critical period for testing sex-ratio with respect to partial migration, specimens taken during breeding months were eliminated. Any gross intersexual difference in winter detectability through differential mortality was considered unlikely, given that both sexes hunt in winter, unlike during the breeding season when mainly the male hunts (e.g. MIKKOLA 1983, CRAMP 1985). All Long-eared Owls brought to JE in Taps, Jutland, Denmark, between 1 November and the end of February over an eleven year period (1986–1997) were examined by gonadal inspection and aged using the criteria described in PIECHOCKI (1979). In addition to sex and age, the date, locality and cause of death were recorded for each specimen. A total of 45 owls was studied by JE, with two additional birds examined by HUGO CHRISTENSEN. The same information was collected from skins taken between November and February in Denmark housed in the Zoologisk Museum in Copenhagen ( $n = 30$ ) and Naturhistorisk Museum in Århus ( $n = 5$ ). This amounts to a total of 82 birds examined in detail. In addition, winter sex-ratios of Long-eared Owls in England, Germany, the Netherlands and Sweden were estimated, using the collections of native birds in the Museums of Natural History in Tring, Berlin, Bonn, Frankfurt, Dresden, Halberstadt, Wuppertal, Leiden, Stockholm, and Malmö. Data on body mass of Danish owls examined by JE were taken, and body masses of Swedish owls were abstracted from specimen labels in the Malmö collection.

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## 3. Results

Data on Long-eared Owl winter sex-ratios are presented in Table 1. In all cases we used a G test with the appropriate Williams' correction (FOWLER & COHEN 1996) to examine the data for significant relationships. The sex-ratio amongst wintering owls in western Denmark (Jutland and Funen) was strongly female-biased ( $48 \text{ ♀} : 10 \text{ ♂}$ ,  $G_{\text{adj}} = 26.4$ ,  $p < 0.01$ ), whereas eastern Danish populations (Zealand, Falster, Anholt and Bornholm) exhibited parity. The difference between these populations was highly significant ( $G_{\text{adj}} = 8.51$ ,  $p < 0.01$ ). The sexes and locations of the 82 Danish specimens are mapped in the figure. JE resides in southern Jutland, hence the concentration of records there.

Table 1: Sex-ratio of Long-eared Owls from Germany, the Netherlands, England, Sweden and Denmark. Data are arranged in geographical order from northeast to southwest.

Tab. 1: Verhältnis der Geschlechter der Waldohreulen in Deutschland, Holland, England, Schweden und Dänemark. Die Daten sind geografisch von Nordost bis Südwest aufgelistet.

	♀	♂
Stockholm (RMS)	105	96
Malmö (MM)	27	39
Eastern Denmark (Zealand, Falster, Anholt and Bornholm)	12	12
Western Denmark (Jutland & Funen)	48	10 (**)
Northeastern Germany	15	5 (*)
Eastern Germany	10	9
Western Germany	21	24
Southern Germany	1	0
Netherlands	27	10 (**)
Tring (BMNH)	9	4

(\*) sex-ratio significantly female biased at the 5% level ( $p < 0.05$ , G test)

(\*\*) sex-ratio significantly female biased at the 1% level ( $p < 0.01$ , G test)

Like eastern Danish populations, Swedish owls exhibited near parity (132 ♀ : 135 ♂,  $G_{adj} = 0.03$ ,  $p > 0.05$ ). A similar result was found for Germany as a whole (47 ♀ : 38 ♂,  $G_{adj} = 0.94$ ,  $p > 0.05$ ), although a significant female bias was found among owls collected in the northeast of the country (15 ♀ : 5 ♂,  $G_{adj} = 4.87$ ,  $p < 0.05$ ). Owls from the Netherlands also demonstrated a female-biased sex-ratio (27 ♀ : 10 ♂,  $G_{adj} = 7.8$ ,  $p < 0.01$ ), as did UK birds, although sample sizes of the latter were too small for statistical significance (9 ♀ : 4 ♂,  $G_{adj} = 1.77$ ,  $p > 0.05$ ).

Body mass data are presented in table 2. Note the larger mass dimorphism (16.9%) in the Netherlands than in Sweden (12.4%) and Denmark (11.0%).

#### 4. Discussion

As described above, none of the existing hypotheses accounts well for the differential migration patterns observed in the Long-eared Owl. On the basis of the results of our study, we suggest a new hypothesis:

Where a sexually dimorphic population is under heavy predation pressure, the more vulnerable sex is more likely to migrate in winter to areas without or with fewer of the main predator(s).

A source of possible predation pressure on the Long-eared Owl is the Eagle Owl (*Bubo bubo*), sympatric with the Long-eared Owl in large areas of Norway, Sweden, Finland, Germany and Russia (GLUTZ VON BLOTZHEIM & BAUER 1980, CRAMP 1985, HAGEMEIJER & BLAIR 1997). According to TUCKER & HEATH (1994), the breeding population in Norway is between 1,000 and 3,000 pairs, Sweden 250–350, Finland 2,000–3,000, Germany 400–500, Russia 2,000–20,000, Netherlands 0–2, Luxemburg 1–5 and England 0. In Denmark the population is currently estimated at 50 pairs, thanks to recent immigration from Germany and Sweden (KLAUS DICKMAN pers. comm.). Eagle Owls hunt essentially nocturnally and take other owl species more often than their availability warrants (MIKKOLA 1983, CRAMP 1985). MIKKOLA (1983) recorded predation events involving owls in Europe and found that the Long-eared Owl was the most numerous owl prey of the Eagle Owl (118 records). UTTENDÖRFER (1939) studied 118,000 German bird remains taken by birds of prey and owls and found 155 Long-eared Owls killed by Goshawks (*Accipiter gentilis*) and 62 Long-eared Owls killed by Eagle Owls. In northern Bavaria, Germany, 3.7% of all prey taken by Eagle Owls during the breeding season were Long-eared Owls (BEZZEL et al. 1976), and in northeastern Harz Foreland, 21 Long-eared Owls were found among 612 bird-prey items in pellets of 8–10 breeding



Figure: Sex and locality of 82 Long-eared Owls from Denmark during the winter period. Note the preponderance of females from Jutland and Funen (48 ♀ : 10 ♂), compared with the even sex-ratio on Zealand, Falster, Anholt and Bornholm (12 ♀ : 12 ♂).

Abb.: Geschlecht und Fundort von 82 Waldohreulen gefunden in der Winterperiode in Dänemark. Im Vergleich zu Jylland und Fünen, wo die Anzahl der weiblichen Exemplare überwiegt (48 ♀ : 10 ♂), ist der Unterschied zwischen den Geschlechtern auf Seeland, Falster, Anholt und Bornholm gleich (12 ♀ : 12 ♂).

pairs of Eagle Owls (WADEWITZ & NICOLAI 1993). Among 1048 Long-eared Owl ringing recoveries from Finland, Sweden and Russia, 23 were killed by owls or raptors and a further 45 were predated by unknown animals (ringing recovery printouts from Sweden, Finland and Russia). Eagle Owls and Goshawks therefore seem to be important predators of the Long-eared Owl and as such, the degree of predator pressure may contribute to the pattern of differential migration seen in the last species. As the female is heavier but without a correspondingly greater wingspan, it is presumably easier prey for the Eagle Owl and the Goshawk than the more manoeuvrable male.

A prediction arising from our hypothesis is that female Long-eared Owls will be preyed upon more heavily by Eagle Owls and Goshawks than their availability relative to male Long-eared Owls would suggest. However, no information is as yet available on sex determination of predated Long-eared Owls, not surprising in view of the slight intersexual difference in skeleton biometrics (WINDE 1977).

Table 2: Body mass (g) of Swedish (Malmö Museum), Danish (pers. obs.), and Dutch (CRAMP 1985) Long-eared Owls. All Swedish and Danish weights are from the non-breeding period, the Dutch figures from December to March.

Tab. 2: Körpermasse schwedischer (Malmö Museum), dänischer (J.E.) und holländischer Waldohreulen (CRAMP 1985). Alle schwedischen und dänischen Exemplare stammen aus der Winterperiode, die holländischen von Dezember bis März.

		n	Average mass (g)	SD	Range (g)	% difference
Sweden	♂	37	197	11.0	160–262	12.4
	♀	24	225	25.3	180–314	
Denmark	♂	11	258	28.3	242–297	11.0
	♀	25	290	19.5	247–329	
Netherlands	♂	21	256	20.8	221–303	16.9
	♀	24	308	37.4	262–435	

To investigate whether predation pressure by Eagle Owls and Goshawks may be contributing to the pattern of differential migration seen in the Long-eared Owl, one approach is to examine the geographical distribution of all three species. The geographic ranges of Eagle Owls and Goshawks correspond broadly with that of the Long-eared Owl, although they occur at lower densities in regions where female-biased sex-ratios are found: Denmark, northern Germany, the Netherlands, Belgium, Luxembourg, France and United Kingdom (GÉNSBØL 1984, CRAMP & SIMMONS 1980, CRAMP 1985). In Germany the strongholds of the Eagle Owl are in middle and south Deutschland (HAGEMEIJER & BLAIR 1997), areas from which there are few ringing recoveries of Fenno-Scandian Long-eared Owls. In Poland, also a stronghold of the Goshawk, there are only 10 recoveries from Fenno-Scandia and Russia out of a total of 1090 (GLUTZ VON BLOTZHEIM & BAUER 1980 and ringing recovery printouts from Sweden, Finland and Russia). It therefore seems likely that migrant owls from Fenno-Scandia and Russia winter or at least pass through northern Germany, and in general spend the winter where Eagle Owls occur at low density. An additional reason for the female to migrate may be that with thick snow cover in the northern winter it is more difficult for the less manoeuvrable female to catch voles. Table 2 gives body mass data from Sweden, Denmark and the Netherlands. The results indicate a trend for body mass to increase southwards, perhaps indicating a more plentiful food supply in the south, additional reason for female-dominated migration south. If prey densities are indeed higher in southern countries, female Long-eared Owls may be better placed to outcompete both migrant and resident males for food. The greater difference between male and female body masses in the Netherlands may reflect the difficulties faced by males in the south of the wintering range. Norwegian Long-eared Owls appear to be increasing (SCOTT 1997), so differential migration does indeed seem a successful strategy for individuals within this population and it seems probable that natural selection will operate on this trait.

Table 1 indicates that the sex-ratio of wintering Long-eared Owls is female-biased not only in western Denmark but also in the Netherlands and perhaps northern Germany. However, in most parts of Germany, the sex-ratio was near parity. The most likely explanation for this is that part of the wintering population from southern Sweden and Zealand, both with an equal sex-ratio (cf. Table 1), may migrate to more easterly areas in Germany than birds coming from Jutland where females dominate. Indeed, ringing recoveries indicate that most birds moving from Jutland migrate in a southwesterly direction to western Germany, the Netherlands, Belgium and northern France (ringing recovery printouts).

In some avian systems, the larger sex may outcompete the other for food as nestlings, leading to a biased sex-ratio in the population as a whole (LACK 1954, YOM-TOV & OLLASON 1976, both ci-

ted in NEWTON & MARQUISS 1979, but see also NEWTON 1986 and WIEBE & BERTOLOTTI 1992). However, in parts of Denmark (Zealand) and most of Germany, Long-eared Owl sex-ratios exhibited parity, with 12 ♂ : 12 ♀ found in Denmark, and 33 ♂ : 31 ♀ in eastern and western middle Germany. A similar pattern was also found in museum collections in Malmö and Stockholm, which would seem to be evidence against the above mechanism operating in Long-eared Owls. In Norway there is a male-biased sex-ratio during the winter months, presumably because many females migrate south (OVERSKAUG & KRISTIANSEN 1994).

The data presented here seem to support our predation hypothesis – both Eagle Owls and Goshawks are common in the breeding range of the Long-eared Owl in Fenno-Scandia, but rare or absent in the winter range, where female Long-eared Owls predominate.

### 5. Zusammenfassung

Der Artikel zeigt, daß im westlichen Teil Dänemarks in den Monaten November bis einschließlich Februar bei den Waldohreulen ein zahlenmäßiger Unterschied der Geschlechter existiert. Während die Geschlechterverteilung auf Seeland und den umliegenden Inseln in etwa gleich ist (12 ♂, 12 ♀), existiert in Jütland und auf Fünen ein deutliches Überwiegen weiblicher Exemplare (48 ♀, 10 ♂). Auch für Holland und England wurde diese Ungleichheit nachgewiesen. Dagegen sind in Norwegen im Winter überwiegend männliche Vögel anzutreffen. Recherchen in den Vogelbalgsammlungen der größeren nordeuropäischen Museen bestätigen dieses Resultat. Für Schweden und Zentral-Europa ergibt sich allerdings für die Wintermonate eine ausgeglichene Geschlechterverteilung.

Ein Massenvergleich zwischen schwedischen, dänischen und holländischen Waldohreulen zeigt, daß die holländischen Exemplare 25% schwerer sind als die schwedischen und holländische ♂ 17% weniger wiegen als ♀, wohingegen schwedische und dänische ♂ nur 11–12% weniger an Körpermasse aufweisen. Möglicherweise haben die männlichen Eulen in Holland es in den Wintermonaten besonders schwer, mit der Überzahl weiblicher Waldohreulen zu konkurrieren.

Die Mehrzahl der Waldohreulen, die über den westlichen Teil Dänemarks zieht, sind junge ♀. Keine der bisherigen Hypothesen zur Erklärung eines unterschiedlichen Zugverhaltens der Geschlechter kann diesen Befund allerdings befriedigend deuten, was die Verfasser zur Formulierung einer neuen Hypothese veranlaßte: Wo eine Population mit sexuellem Dimorphismus häufig Beute von Prädatoren (z.B. Habicht und Uhu) wird, wandert das stärker gefährdete Geschlecht im Winter in Gebiete mit weniger oder keinen Feinden ab.

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