

The Dispersion Dynamics of Tengmalm's Owl *Aegolius funereus* in Central Europe

Ortwin Schwerdtfeger

ABSTRACT

In the course of population ecological studies on Tengmalm's Owl in the Harz mountains the species' distribution and its changes in space and time have been investigated. In an area of 200km² nearly all nests have been recorded and nearly all owls marked since 1978. In 1988 the results were summarized in a model of dispersion dynamics for the insular distributional pattern of Tengmalm's Owl as is typical for Central Europe. Further results permit the procedure of emigration and immigration in connection with reproduction and mortality-rates to now be quantified and characterized by their dependence on fluctuating food conditions. Thus we get a survey of how a population of Tengmalm's Owl consists of owls with fidelity to birth-place, fidelity to area and nomads. This is valid for both sexes and for different age groups.

Considering the long period of study, the size of the investigated population, its age structure, its reproduction as well as recapturing rates, we can assume that the results are representative for Central Europe. The phenology of dispersion dynamics differs from that of Scandinavian investigations.

INTRODUCTION

In order to take advantage of the specific resources of a bird species for its own existence and reproduction, a suitable dispersion of the individuals is very important. This applies to global dispersion in suitable habitats as well as within the local distribution of a fixed breeding area. Pattern and dynamics of a species' dispersion are determined by its system of behaviour and are regulated by environmental factors. By marking as many individuals as possible, such systems can be documented and analysed.

In the course of population ecological studies on Tengmalm's Owl in the Harz mountains nearly all broods have been recorded and nearly all owls have been marked since 1978. Thereby its distribution and changes in space and time have been investigated. The results were summarized in a model of dispersion dynamics (Schwerdtfeger 1988b). This model has been confirmed by further investigations.

Moreover, by an analysis of the age-structure of the population the mortality-rates could be estimated (Schwerdtfeger 1991). Utilising these rates it is possible to quantify the rates of emigration and immigration, and to characterise them in their dependence on fluctuating food conditions.

MATERIAL AND METHODS

The study area of 200km² situated at 51°38'N 10°33'E to 51°53'N 10°14'E, mainly consists of spruce forests and its altitude ranges from 450 to 850m a.s.l. Because of the lack of natural nest holes, nearly all broods occupy the 250 nest-boxes that are spread uniformly about the area.

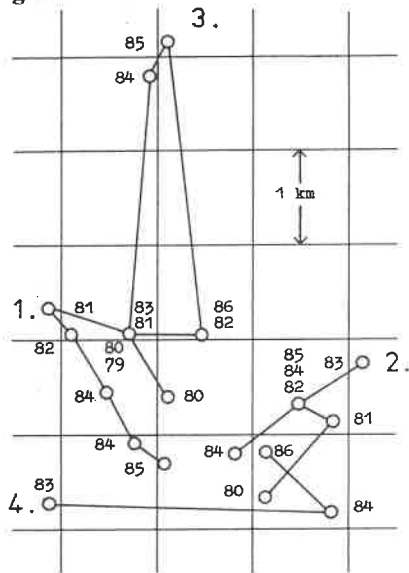
The broods of the Tengmalm's Owls are frequently controlled to register the breeding data and the stored prey. Adult owls are caught at the nest-boxes: the females with a long-handled net, the males with a nylon net, while they bring in the prey, and single males with traps while investigating holes. The captured owls are aged according to the moult pattern of primaries (Schwerdtfeger 1984, 1988a, 1991).

From 1979 to 1991, 390 broods with 1,120 fledglings were systematically controlled, and 84% of the male and 98% of the female breeding birds were caught.

LOCAL DISPERSION DYNAMICS

First viewed were the dispersion dynamics in a 15 km² section of the study area, where four males were resident for several years, utilizing 18 different nest-boxes for their 24 broods. Figure 1 shows the sequence and spacing of the breeding sites with 16 different females (see Schwerdtfeger 1990).

Figure 1. Shift of breeding site of four males.

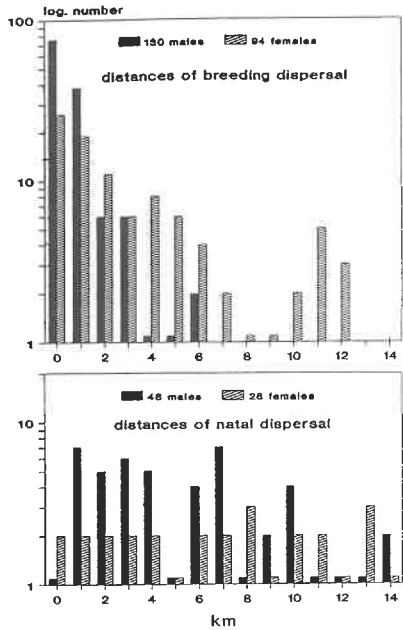


This reveals that neighbouring males shift their breeding sites from year to year, that females fluctuate more than males, and that therefore mate fidelity occurs very rarely.

These data were reconfirmed in the whole study area. Breeding-hole fidelity is rare: repeatedly caught males took an already used nesting hole in 30% out of 106 cases. With females this was only found in 5% out of 123 cases. Figure 2 depicts breeding dispersal distances. The logarithmic frequency distribution for the males results in a nearly linear decline within a few kilometres, which is considerably smaller for the females. Thus both sexes show an almost exponential distribution within about 15km. Added to that are 18 distances between 10 and 30km in the case of the females, while there is only one case of a male movement of 26km. All in all, the determined differences of the distances between males and females are significant ($p < 0.001$, U-test).

Figure 2 also shows the distribution of the dispersal distances of juveniles. With the females this distribution is nearly uniform, while for males it declines with distance.

Figure 2. Breeding and natal dispersal.



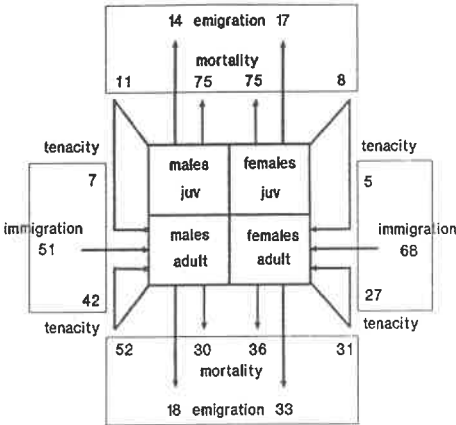
GLOBAL DISPERSION DYNAMICS

The fact that the biggest part of the captured adults had not been ringed indicates a high rate of immigration. How many owls are there with fidelity to birth area and fidelity to breeding area and how extended are the fluctuations, considering different breeding seasons?

The number of owls with fidelity to their area was determined by capture and ringing. By an analysis of the age structure, the mortality rates were estimated (Schwerdtfeger 1991) to be 30% for adult males, 36% for adult females and 75% for fledglings during their first year (assuming a sex ratio of 1:1). These parameters are concise in this study, for they make it possible to estimate the rates of emigration and immigration.

Out of 850 ringed juveniles, fledged in the study area from 1979 to 1990, only 11% of the males and 8% of the females were recaptured in the area (Fig. 3). Utilising the average mortality rate of 75%, the remaining owls, 14% of the males and 17% of the females, must have survived their first year outside the area.

Figure 3. Average fluctuation between breeding seasons.



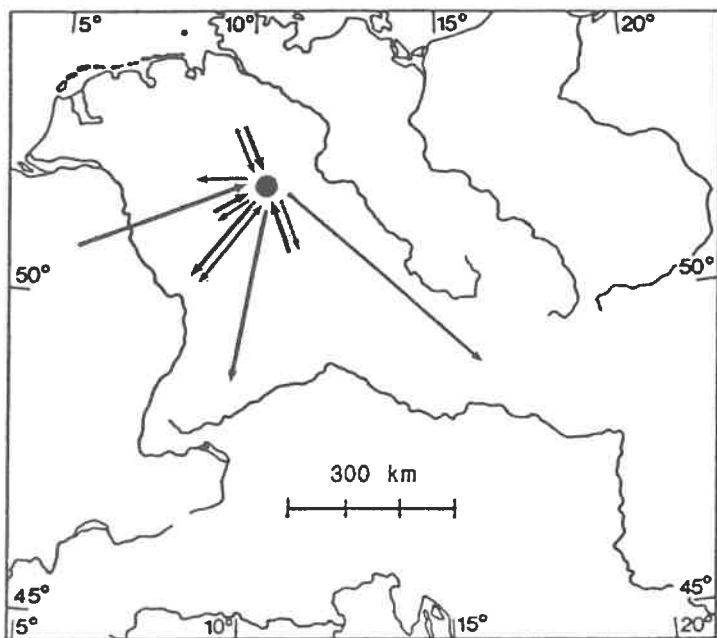
During the 12 years of investigation, on average this breeding population has been structured as follows:

Among the males 7% are juveniles fledged in the study area and 42% are adults previously caught in the area. Among the females the corresponding values are 5% and 27%. The remaining owls, that is 51% of the males and 68% of the females, must have immigrated (Fig. 3, left and right). The difference is statistically significant ($p < 0.025$, chi-square-test). How does the population change before the next breeding season? Among the captured breeding population 52% of the males and 31% of the females were captured in consecutive years, which means they were tenacious to the area.

Again, using the mortality rates as given above, 18% of the males and 33% of the females must have left the study area (Fig. 3). The difference between the sexes is significant ($p < 0.01$, chi-square-test).

Where the many dispersing owls come from and where they fly to, has been assessed by 48 recaptures and two owls found dead. Half of these recoveries suggest a continuous exchange of owls between other areas in the Harz mountains (i.e. up to 40km distant). Figure 4 depicts the other half on more distant recoveries (i.e. 50-490km). Natal and breeding dispersal are shown as thin or bold arrows respectively. Among these recovery distances just two above 195km stem from young males (Schwerdtfeger 1988b).

Figure 4. Long distances of breeding and natal dispersal.



Corresponding recapture data are known between nearly all intensively investigated breeding areas of Tengmalm's Owls in Central Europe showing that a considerable exchange of individual owls takes place between those breeding areas which are geographically and ecologically fairly isolated; thus this dispersal is mainly due to juveniles and females (Schwerdtfeger 1988b).

INFLUENCE OF FOOD CONDITIONS

Having quantified all fluctuations so far, I now consider the influence of food conditions. Various factors in the breeding cycle of Tengmalm's Owl are influenced by variations of the main prey populations, i.e. *Microtus* and *Apodemus* species. In the study period from 1979 to 1991 the

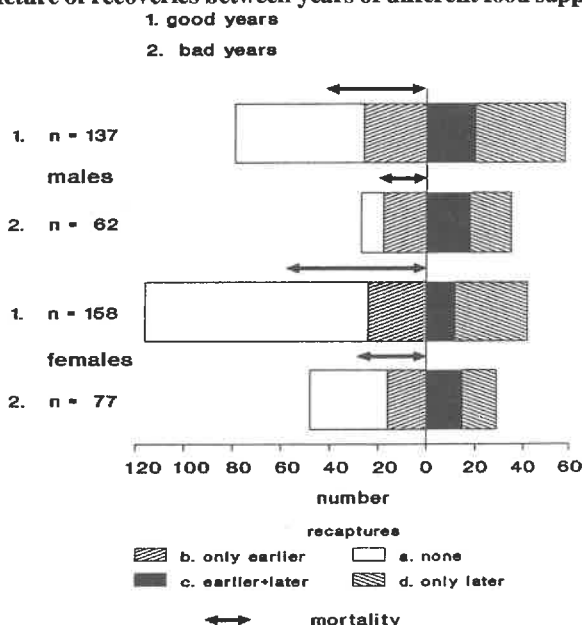
number of broods corresponded to the number of stored prey ($r = 0.835$, $p < 0.001$) (see Schwerdtfeger 1988a), thus suggesting that the fluctuations of owls could be influenced by food conditions.

In order to examine this, I compared the four "best" years with the highest average clutch size (1981, 84, 86, 88) and the four "worst" years with the lowest average clutch size (1982, 85, 87, 89) (see Schwerdtfeger 1991).

In Figure 5 the owls caught in these years were divided into four classes according to their capture series in the study area:

- a. no further capture, neither earlier nor later
- b. caught earlier, but not later
- c. caught earlier and later
- d. only caught later

Figure 5. Structure of recoveries between years of different food supply.



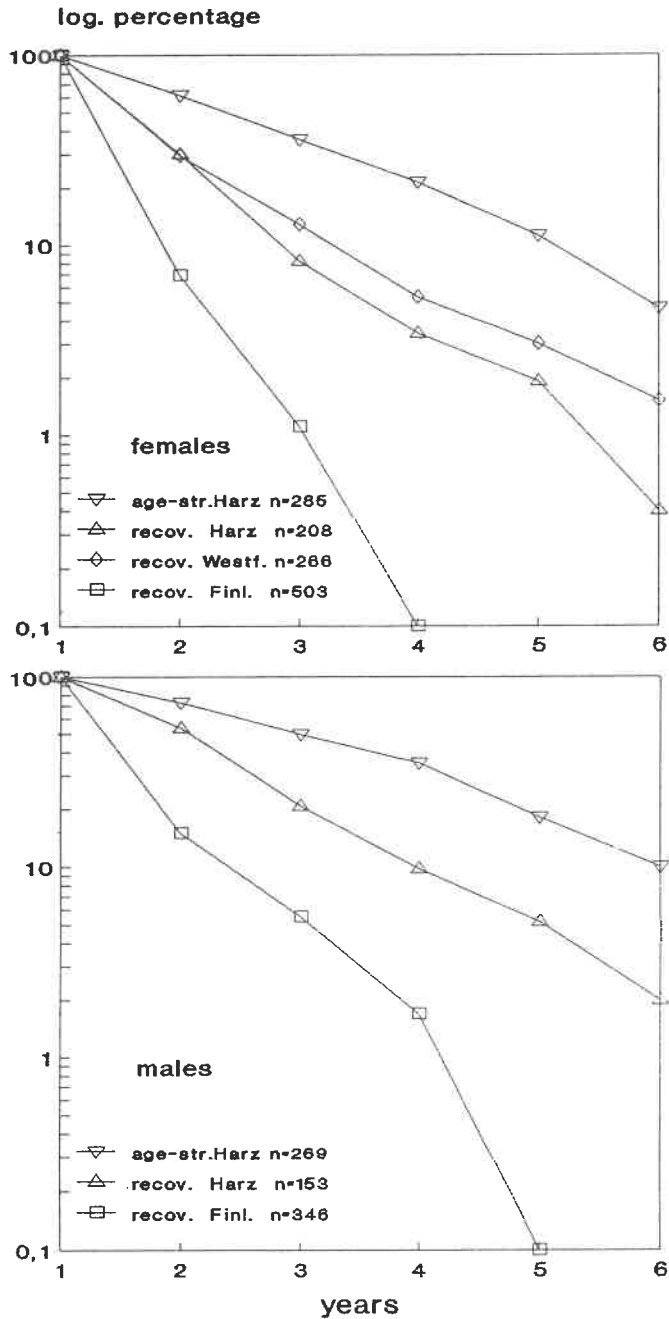
The number of owls caught earlier and later (c.) was nearly equal in good and in bad years. The numbers of owls caught only in the considered year (a.) was in good years six times and three times larger than in bad ones for males and females respectively. The number of females in this recapture class is 20% larger as compared with males.

These differences of dispersal between good and bad years are significant both for males and females ($p < 0.01$ and $p < 0.025$, chi-square-test). The same applies to differences between the sexes in good and in bad years (both $p < 0.01$). The owls of the classes (c.) and (d.) were still alive in consecutive breeding seasons. The owls not recaptured must have died or emigrated. In Figure 5 the expected mortalities in the following year are marked by arrows. The allocation of mortalities among the classes (a.) and (b.) is impossible. It is remarkable, however, that the disappearance rate is only slightly bigger than the mortality rate in bad years alone and for the males only. This suggests that all surviving males remain in the breeding area if the food conditions improve.

A dependence on the quality of food conditions was also indicated for the dispersal behaviour of juveniles fledged in this area. Within both sexes the percentage among these owls recaptured in the study area correlates to the average number of prey items deposited in the nest boxes in the year following birth ($p < 0.025$ for males and $p < 0.05$ for females, Spearman-rank-correlation). When food conditions are getting worse, of the fledged juveniles only 7.3% of the males and 6.8% of the females settled in the study area, whilst with improving food conditions the corresponding

values were 37% and 32%. As these percentages are higher than the estimated average survival rates of juveniles, all surviving juveniles seem to breed in the year following their birth if the food conditions improve.

Figure 6. Age structure and recovery rates as compared to other studies.



DISCUSSION

It has to be stressed that this survey on the fluctuations of the studied population is based on several assumptions. Some circumstances could not be considered sufficiently, e.g.

- a. The estimated mortality rates are means over the 12 years. It is unknown how these rates vary between years as well between owls tenacious to their area and nomadic ones.
- b. Data of years with good food conditions especially influence the given percentages in Figure 3, as most adults were caught in such years.
- c. Non-breeding adults could not be sufficiently considered: only half of the unpaired, courting males were caught, and the few caught females do not allow a conclusion as to the size of a "breeding reserve" and its yearly variation.
- d. Investigation is needed into how the dispersion dynamics depend on the size of a breeding area, on its position relative to neighbouring areas and on ecological factors (Schwerdtfeger in prep.).

A summarising presentation of the fluctuations of juveniles and adults is not available from any other breeding area of Tengmalm's Owl. It is also difficult to compare basic data, as is necessary, with other breeding areas in Central Europe, due e.g. to:

1. a sufficient number of data entries, especially for males,
2. an ambitious mode of registration and
3. different ways of analysis.

Some criteria suggest, however, that the population's ecological relations, as presented here for the Western Harz, are representative for Tengmalm's Owl in Central Europe:

- a. Due to the continuity of this long-term investigation, the size and location of the study area and the fact that data of nearly the entire breeding population are available, fairly accurate estimates of relevant population parameters were possible.
- b. The data of the breeding biology, as well as of the annual fluctuations in the number of broods, correspond well to those published on other Central European areas (Schwerdtfeger 1988b; Korpimäki 1986).
- c. The pattern of long-distance dispersal corresponds to those of other areas (e.g. Franz *et al.* 1984; Meyer 1991).
- d. The age structure of my population approximately shows an exponential distribution in both sexes, as the average recapture rate follows a linear decline on a half-logarithmic scale. The total Central European population of Tengmalm's Owl should show a similar distribution (Schwerdtfeger 1991).

Comparing my results with Scandinavian investigations they show considerable differences:

- a. The annual fluctuation in the number of broods determined by the coefficient of variation increases from south to north (Korpimäki 1986).
- b. In Scandinavia greater distances of breeding and natal dispersal have been found than in Central Europe (e.g. Korpimäki *et al.* 1987).
- c. The recapture rates there were considerably lower than in Central Europe (Löfgren *et al.* 1986; Korpimäki *et al.* 1987).

ACKNOWLEDGEMENTS

Dinah Thyerlei translated the manuscript into English. Karl Radler reviewed the manuscript and provided useful comments. I would like to thank both for their co-operation.

REFERENCES

- FRANZ, A., T. MEBS & E. SEIBT 1984.** Zur Populationsbiologie des Raufusskauzes (*Aegolius funereus*) im südlichen Westfalen und in angrenzenden Gebieten anhand von Beringungsergebnissen. *Vogelwarte* 32: 260-269.
- GLUTZ VON BLOTZHEIM, U.N. & K.M. BAUER 1980.** *Handbuch der Vögel Mitteleuropas*, Band 9: 533-578.
- KORPIMÄKI, E. 1981.** On the ecology and biology of Tengmalm's Owl (*Aegolius funereus*). *Acta Universitatis Ouluensis, Series A. Scientiae Rerum Naturalium* No. 118, *Biologica* No. 13.
- KORPIMÄKI, E. 1986.** Gradients in population fluctuations of Tengmalm's Owl *Aegolius feunereus* in Europe. *Oecologia* 69: 195-201.
- KORPIMÄKI, E. & H. HONGELL 1986.** Partial migration as an adaption to nest-site scarcity and vole cycles in Tengmalm's Owl *Aegolius funereus*. *Var Fagelvärd* Suppl. 11: 85-92.
- KORPIMÄKI, E., M. LAGERSTRÖM & P. SAUROLA 1987.** Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scandinavica* 18: 1-4.
- KORPIMÄKI, E. 1990.** Low repeatability of laying date and clutch size in Tengmalm's Owl: an adaption to fluctuating food conditions. *Ornis Scandinavica* 21: 282-286.
- LÖFGREN, O., B. HÖRNFELDT & B.-G. CARLSSON 1986.** Site tenacity and nomadism in Tengmalm's Owl (*Aegolius funereus*) in relation to cyclic food production. *Oecologia* 69: 321-326.
- MEYER, W. & B. MEYER 1991.** Erste Ergebnisse der Beringung von Raufusskäuzen *Aegolius funereus*. *Populationsökologie Greifvogel- und Eulenarten 2. Wiss. Beitr. Univ. Halle*: 507-518.
- SCHWERDTFEGER, O. 1984.** Verhalten und Populationsdynamik des Raufusskauzes (*Aegolius funereus*). *Vogelwelt* 32: 183-200.
- SCHWERDTFEGER, O. 1988a.** Analyse der Depotbeute in den Bruthöhlen des Raufusskauzes (*Aegolius funereus*). *Vogelwelt*. 109: 176-181.
- SCHWERDTFEGER, O. 1988b.** Modell zur Dispersionsdynamik des Raufusskauzes (*Aegolius funereus*). In R. Van Den Elzen, K.-L. Schuchmann & K. Schmidt-Koenig (Eds). *Proc. Int. 100. DO-G Meeting. Current Topics in Avian Biology*. Bonn 1988: 241-247.
- SCHWERDTFEGER, O. 1990.** Die Bedeutung populationsökologischer Kenntnisse für den Artenschutz am Beispiel des Raufusskauzes (*Aegolius funereus*). *Vogel und Umwelt* 6: 10-21.
- SCHWERDTFEGER, O. 1991.** Altersstruktur und Populationsdynamik beim Raufusskauz (*Aegolius funereus*). *Populationsökologie Greifvogel- und Eulenarten 2. Wiss. Beitr. Univ. Halle*: 493-506.

Ortwin Schwerdtfeger
Quellenweg 4
D3360 Osterode am Harz
Germany