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Breeding success, dispersal, and long-term changes in a population of Eagle Owls *Bubo bubo* in southeastern Sweden 1952–1996

VIKING OLSSON

Abstract

In 1950 when the Eagle Owl became legally protected in Sweden, the species was nearly extinct in most parts of the country and survived only with a small population in the southeastern part of the country, along the Baltic Sea coast. This population has been studied in 1952–1996. Recoveries of birds ringed in the study area demonstrated that dispersal was limited; post-fledging dispersal was on average 56.8 km in the first year of life. In birds older than one year the mean distance from the hatching site to the site of recovery was 47.7 km. The mean brood size in successful nests was 1.47 young. However, the mean reproductive success calculated for all occupied territories was only 0.68 young per pair and year. Among all pairs, 43.7% bred successfully and 24.7% failed. Thus, each year 31.6% of the pairs stayed in the territory without breeding. For an extended part of this long term study, reproduction seems to have been just enough to maintain a stable population size in the study area. Only in the years 1986–90, there seemed to be a surplus of young produced in the study population resulting in new breeding pairs, predominantly outside the old study area.

From a national project with captive breeding, 2759 young Eagle Owls have been released in nearly all parts of Sweden. Around 1982, the number of pairs originating from the released birds was in equilibrium with the original "wild" population, and in 1995 the released birds and their descendants were about twice as many. In recent years probably many pairs are of mixed origin, and the mixing of the two populations is likely to increase in the future. In total, there were about 400 territories occupied by Eagle Owls in Sweden in 1996.

Viking Olsson, Stigarvägen 1, S-611 65 Nyköping, Sweden.

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Introduction

During the first half of the 20th century the Swedish Eagle Owl population declined sharply. The main reason for this was probably an extensive intentional persecution in most parts of the country (Curry-Lindahl 1950). In order to stop the decline the Eagle Owl was protected by law in 1950. At that time another threat emerged. Many Eagle Owls were found dead or dying with high pesticide residues in their body tissues. In 1966 the use of mercury in seed dressings was banned, and in 1975 there was a law also against the use of DDT. However these protection measures came too late and the wild population declined to a minimum around 1985. The numbers had then decreased with 50% as compared with the population size two decades earlier (Olsson 1986).

The Eagle Owl had by then been more or less exterminated in most parts of Sweden and remained as a sustainable population only in a small area in the southeastern part of the country, along the Baltic Sea coast (Figure 1). Changes in breeding success in the central part of this area have been studied 1952–1996. From 1952 to 1972 the number of territories studied, mainly in Östergötland, slowly increased from three to about ten. After this year the study area was enlarged with a number of territories in Södermanland to the north and some in northeastern Småland to the south. In 1972–1996, 20–25 territories were investigated each year. Earlier studies on this population focused on choice of habitat and nest sites, and on prey choice and its relationship with the intake of pesticides (Odsjö & Olsson 1975, Olsson 1979). These issues will only be dealt with briefly in this paper. Here I will focus on long-term trends in breeding success and population dynamics of this population of Eagle Owls in southeastern Sweden.

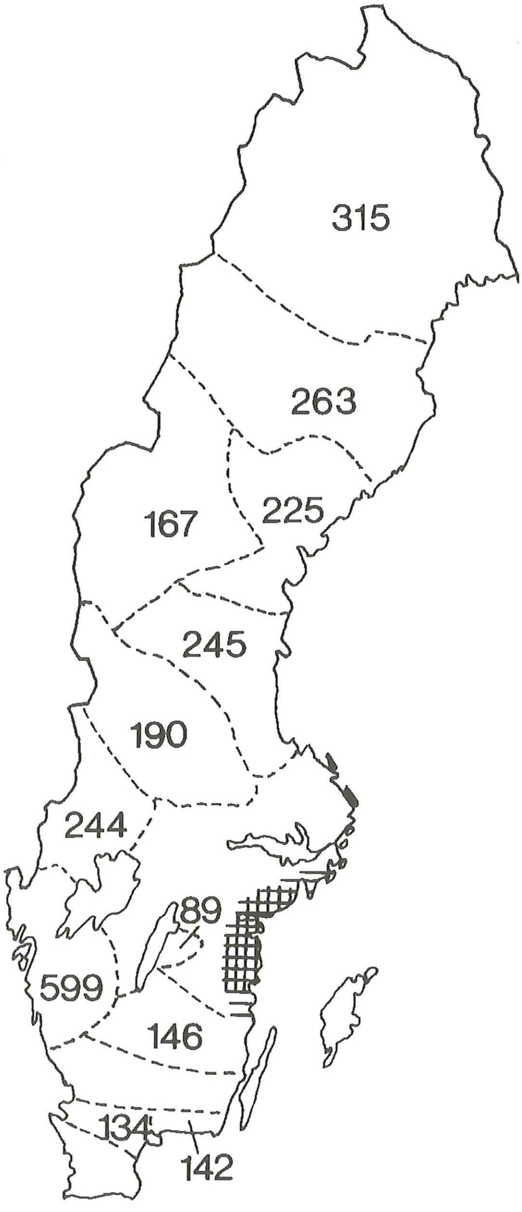


Figure 1. The study area (cross-hatched) in the centre of the region (horizontal hatching) where the Eagle Owl survived after being exterminated in other parts of Sweden. Values indicate the number of released Eagle Owls in different parts of the country up to and including 1995 (UV69-IR).

Det område av Sverige där denna studie utförts (kryssmarkerat) i centrum av den region (vågrätt linjerat) där berguven fanns kvar efter den nästan totala utrotningen i övriga landet under 1900-talet. Siffrorna anger antalet utsläppta uvar t.o.m. 1995 i olika delar av Sverige (UV69-IR).

Methods

Studies on Eagle Owls are strongly hampered by their nocturnal habits, their vulnerability at breeding sites, and the consequences of legal protection. Breeding is carried out from March to September (Olsson 1979). Visits to the nest sites have to be avoided during the first three months of breeding due to the high risk of females deserting when disturbed close to the nest. Hence the nests were not checked before the young were about three weeks old, that is not before 20 May in southeast Sweden. Events that had occurred in the preceding months could only be verified from careful observations in and around the nest scrape.

I have made efforts to bring legal protection to nesting places particularly exposed to disturbance by humans. All visits to protected nests have been performed under necessary legal permissions.

Occupied territory or not?

Censusing Eagle Owls by detecting calling individuals in early spring is not a reliable method. In a German study 30% of the occupied territories were missed with one visit, and 13% were still missed after two visits (Bergerhausen & Willems 1988). At least four visits were needed to detect all occupied territories. In this study, I only used the method of censusing calling Eagle Owls as a complement.

Each year I made very careful visual controls at potential nesting sites, also in territories without any sign of breeding activity in the usual nest scrapes. In an active nesting area, there are always obvious signs of Eagle Owls, such as feathers, down, pellets, prey remnants, and droppings. With experience it is easy to find the rather few perches where birds prefer to rest and where these signs accumulate. If there were no such signs in a potential nesting area this was a clear indication that no Eagle Owl had visited the territory the actual spring. The group "occupied territory" involves all territories with at least one regularly visiting Eagle Owl, including sites which may have been occupied by single birds.

Breeding attempt or not?

The Eagle Owl does not build a nest but instead scrapes out shallow hollows, often several, in early spring. However, fresh nest scrapes do not prove that breeding was initiated that season; nest scrapes can be done also by single males. At egg-laying the female adds small feathers and down into the nest

Table 1. Estimated average date of start of egg-laying (divided in 10-day periods) in southeast Sweden. Data are presented for two general periods, 1952–1977 and 1978–1995, and also separately for the period 1985–1991 when breeding success was exceptionally good.

Medeldatum för äggläggningens inledning under 10-dagars perioder, redovisade dels för åren 1952–1977 och 1978–1995, samt separat för 1985–1991 då häckningsframgången var speciellt god.

Ten-day periods *Tiodagars perioder*	Number of broods in % *Antalet kullar i %*		
	1952–77	1978–95	1985–91
20 February–1 March	4.8	1.6	3
2–11 March	6	4.9	3
12–21 March	18.0	12.2	15
22–31 March	38.6	36.6	45
1–10 March	16.9	28.5	19
11–20 April	7.2	11.3	9
21–30 April	4.8	4.9	4.5
Total *Total*	83	123	66

scrape. In most cases, egg-laying starts in early March (Table 1). During incubation the female stays at the nest and during this period she is fed by the male. As a result, prey remnants and pellets accumulate around the nest scrape. If the nest is preyed upon or deserted already at this early stage, it is still possible to tell from these signs that there has been eggs in the nest.

Successful breeding or not?

From hatching onwards, pellets and prey remnants will gradually accumulate at the nest. If the young are preyed upon it is often possible to estimate approximately at which age this happened by the amount of prey remnants. If the young disappear when 1–3 weeks old they are easily removed by the predator and no remnants of the young will then be found. When 3–4 weeks old the young seem able to defend themselves against a predator, and then down, feathers and even parts of the young are found in or near the nest (Figure 2). To avoid disturbance, nests were in most cases only visited once, if possible when the young were 4–6 weeks old. If any young was found alive at this visit the breeding was recorded as successful; nestling losses after this age are

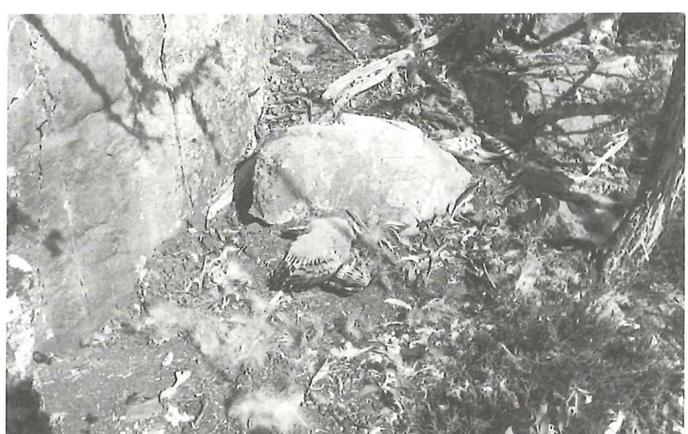
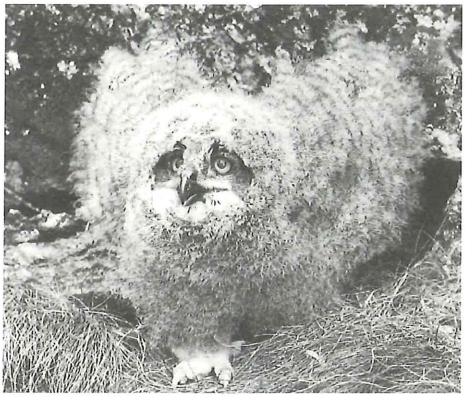


Figure 2. A nest site where the two young birds have been killed and torn apart by some predator, probably a fox or badger. The young were then about six weeks old. 19 June 1978.

Boplats där två sex veckor gamla uvungar dödats och slitits i bitar, troligen av räv eller grävling.



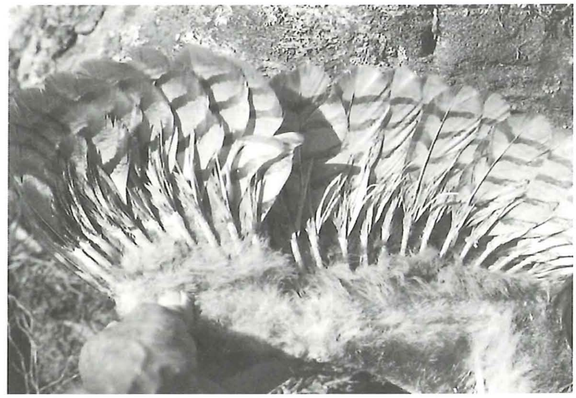


Figure 3. A young Eagle Owl at the age of 32 days (left) and the development of a wing of a young at the age of about 45 days (right). The best time for nest control and ringing is between these two ages.

Två uvungar i inledningen respektive avslutningen på den period då bokontroll och ringmärkning är lämpligast: till vänster 32 dagar gammal, 22 juni 1965, och till höger ca 45 dagar gammal, 28 juni 1988.

very rare. In some cases the first visit to a nest was made in June or July. At this time of year absence of young does not prove that breeding was unsuccessful; long before being able to fly properly the young often move away from the nest. To find the young at this age the behaviours of the adults must be studied, and an intense search be performed for prey remnants, pellets, and the typical downs of the juveniles.

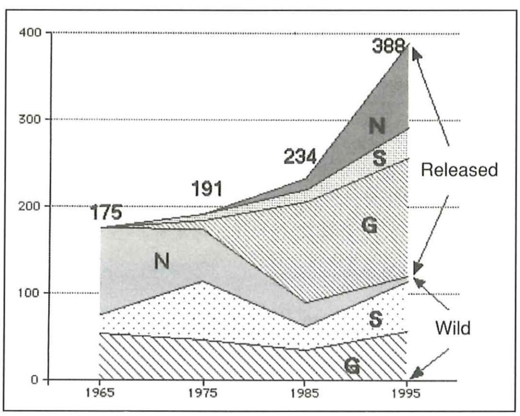


Figure 4. Changes in the Swedish Eagle Owl population 1965–1995. The three areas N-S-G at bottom show number of pairs in the wild original population – at top the same N-S-G with number of breeding pairs from released birds and their offspring. N = North Sweden (Norrland), S = Mid-Sweden (Svealand), and G = South Sweden (Götaland).

Förändringar i det totala uvbeståndet i Sverige 1965–1995. Antal häckande uvpar från den vilda ursprungliga populationen (i de tre undre fälten N-S-G = Norrland, Svealand och Götaland), i de tre övre (N-S-G) antalet häckande par som har sitt ursprung från utsläppta uvar.

Because visits to the nest during the early breeding period had to be avoided, the start of egg-laying had to be estimated on the basis of examination of the young at a later stage of the breeding cycle. The young have been aged at ringing according to the length of the wing feathers and general appearance (Figure 3), and as a routine they have also been photographed. From this estimation of age at ringing, an approximate incubation period of 33 days and the clutch size, I estimated the date when egg-laying started. Ringing and recapture of the adults is impossible for security reasons. However, in a long term study ringing of nestlings can accumulate useful information on lifespan, mortality, post-fledging dispersal, and the distance between site of hatching and final site of breeding. Up to and including 1996, 347 young have been ringed and 64 of these have later been recovered (19%).

The project UV-69 and its successors.

To restore Eagle Owl populations in the parts of Sweden where it had been exterminated, a national captive breeding project was started in 1969. Unfortunately only limited information has been published from this project and for the present study I had to extract information from their internal annual reports (UV-69-IR). In this project up to 1995, 2759 juvenile birds have been released (Figure 1) resulting in 268 pairs breeding in the wild (up to 1995). In the early 1980s the number of free-living breeding birds with captive origin exceeded the number of birds hatched in the wild (Figure 4). These data are mainly based on three national surveys of Eagle Owls, 1966, 1975, and 1985 (Olsson 1967, 1976, 1986), and I have also included information on number of released birds that have become breeders in the wild (UV69-IR). Due to differences in the information available from different groups in the captive breeding project, data presented in Figure 4 are minimum values.

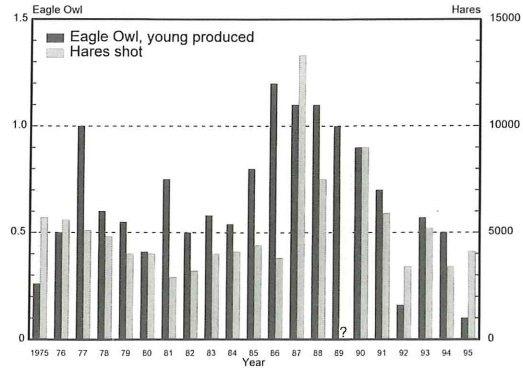


Figure 5. The mean productivity (young/pair and year) of all the Eagle Owls in occupied territories in 1975–1995 (left scale), compared to the number of shot hares in the county of Södermanland in the same years (right scale).

En jämförelse mellan produktiviteten hos uv (ungar/par och år; svarta staplar, vänstra skalan) inom de besatta reviren 1975–95, och harstammens storlek (mätt som årlig avskjutning i Södermanlands län; grå staplar, högra skalan) under samma årsserie.

Results

Of 250 successful Eagle Owl broods in my study area, 50% contained one, 44% two, 5% three, and 1% four young. The mean number of young in successful broods was 1.57. This value, however, is not a good estimate of the production of young when investigating if the population is in balance. Also in years when breeding is not initiated or the breeding attempt fails, the pair stays in its territory. Hence, for an analysis of the balance of the population a better estimate is the mean annual number of young produced in all occupied territories, which in the period 1952–1996 was on average 0.68 young per pair. This value showed considerable variation between years (Figure 5). In the years 1952–85 the average production was close to 0.5 young/pair, in 1986–90 the production was higher (1.0 young/pair), and in 1991–1995 production of young was very low (less than 0.5 young/pair). The year 1995 was exceptionally bad with only one successful breeding producing one single young from a total of 23 occupied territories. In 1996 and 1997, however, a clear improve-

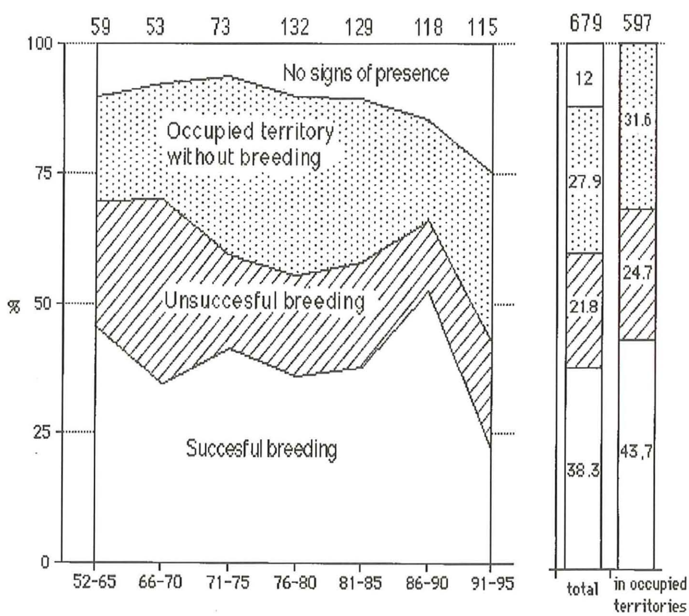


Figure 6. Occupancy and breeding success in Eagle Owl territories 1952–1995. Breeding results are means of 5-year periods (except for the mean for the whole period 1952–1965). The values above the upper line are number of checked nests.

Besatta revir och häckningsresultatet hos berguv 1952–1995. Figuren är baserad på medelvärden av 5-årsserier, utom under de inledande åren 1952–1965 (där medelvärdet är för hela denna period). Antal kontrollerade boplatser på linjen överst. No sign of presence = *inga tecken på närvaro.* Occupied territory without breeding = *besatt revir utan häckning.* Unsuccessful breeding = *misslyckad häckning.* Successful breeding = *lyckad häckning.* In occupied territories = *i besatta revir.*

ment of the production of young has been recorded.

A more general picture of the breeding results 1952–1995 is presented in Figure 6. In 12% of 679 territory visits (one visit per territory and year) I found no signs of Eagle Owls. This value, however, may be affected by differences in my efforts to visit nests where the birds have been absent in preceding years. In 597 occupied territories, breeding was successful in 43.7%, breeding failed in 24.7%, and there was no sign of breeding in 31.6%. Thus, breeding was initiated in at least 68.4% of the territories that was occupied by Eagle Owls.

During my long term study, it has become obvious that both the quality of the territory as well as the nest site itself are of critical importance for breeding success and the attachment to a territory. In one territory breeding was performed in a single well sheltered nest scrape (cf. figure 11 in Olsson 1979) 31 years in a row with a high degree of success. In another territory with three different scrapes all on the same cliff ledge, 27 young were raised in 26 years. A third territory occupied in many years had a very good supply of prey but no good nest sites (cf. figure 13 in Olsson 1979). In 24 years 13 unsuccessful breeding attempts occurred there and in total only 9 young were reared. When considering the nest sites occupied more than 4 years between 1975–1996 (N = 37 nest sites), there was a significant positive correlation between the percentage of years with successful breeding (out of years occupied) and the annual production of young (only successful years included)($r = 0.42$, $P = 0.010$; percentage values were arcsin transformed in this analysis).

Nesting success also depends strongly on the accessibility for predators to the nest site. Though being a large and strong bird the Eagle Owl seems to be a rather weak nest defender. Easily accessible nest sites have been depredated several years in a row, probably by Badger *Meles meles* or Red Fox *Vulpes vulpes*. During the last decade the Marten *Martes martes* has increased considerably in the study area increasing the risk also to nests on ledges only approachable with difficulty. At one nest site the birds bred successfully in the years 1986–88 with no successful breeding thereafter. In 1990 I even found faeces of Marten in the nestscrape, and in 1992 and 1993 I found remnants of the half grown young close to the nest. In the following years the territory has been totally abandoned.

Other conditions may also determine breeding success and the attachment of the pairs to the nest site. Eagle Owls sometimes breed on small islands in the outer parts of the archipelago along the southeast coast of Sweden. In nearly all of these territories the birds have disappeared after one or a few years, probably as a result of very low food supply in winter and early spring.

In several cases, brood losses and permanent desertion of territories have been caused by man. In two cases after extensive wood cutting right up to the nesting cliff, the Eagle Owls abandoned these breeding sites for 7 and 9 years, respectively. When heavily disturbed by rock-climbers, a certain cliff was not reoccupied until 10 years later. In most cases of such desertions, it has been impossible to find the pair in any of the surrounding suitable cliffs the next year. Thus it seems probable that it is new pairs which re-establish such sites.

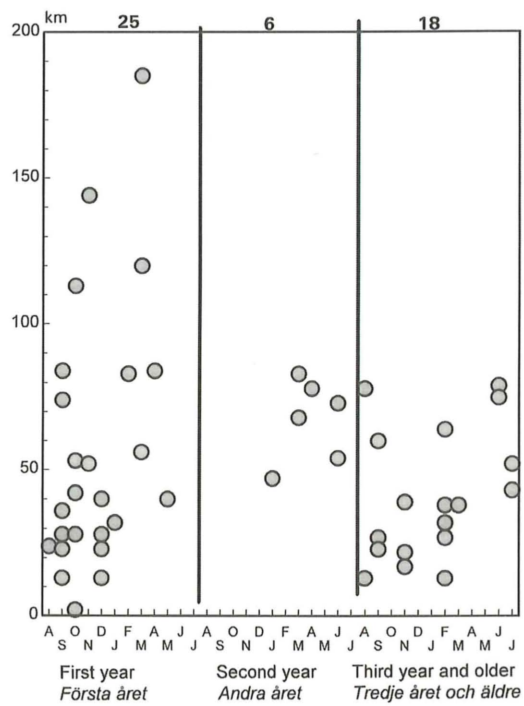


Figure 7. Distance from the hatching site to the site of recovery of ringed Eagle Owls found in their first year, second year, or when older, respectively. On the x-axis are given the month of recovery. The values above the upper line are the number of recovered individuals in each age group.

Avståndet från märknings- och kläckningsplatsen för ringmärkta uvar funna under första levnadsåret (t.v.), andra året (mitten) och samtliga äldre (t.h.). På x-axeln anges den månad individerna återfunnits, och värden ovanför grafen är antal återfunna individer i respektive åldersgrupp.

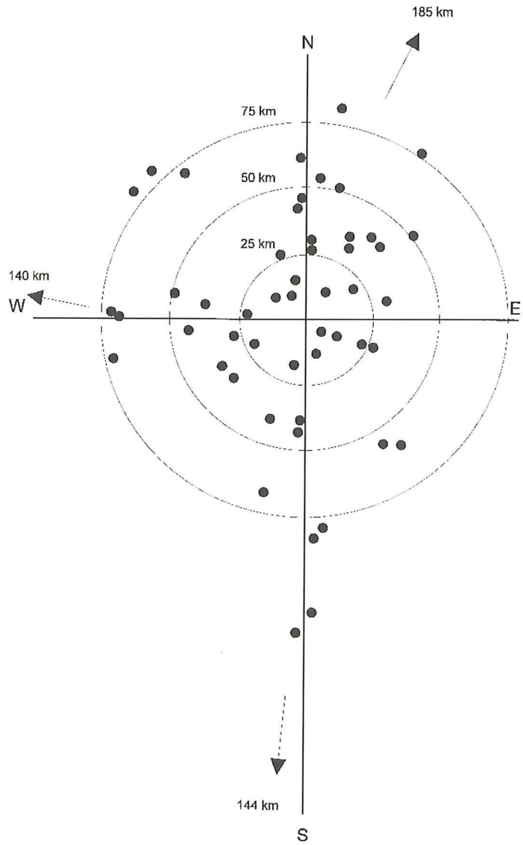


Figure 8. The direction and distance from the ringing site of all recovered Eagle Owls from the study population. Data are combined so that all individuals have the same presumed common starting point. Three birds recovered at greater distances from their hatching place are indicated by arrows and the distance they dispersed given in kilometres.

Avstånd och riktning för alla återfynd av ringmärkta uvar i den undersökta populationen, sammanförda till en gemensam utgångspunkt. Tre längre återfynd har markerats med pil och spridningssträcka angivits i kilometer.

Recoveries of ringed birds

When two months old, the young are able to fly for short distances but they stay in the territory and are fed by their parents until they are four months old. In late August most juveniles become self-supporting and they start their post-fledging dispersal (Figure 7). Based on the start of post-fledging dispersal I have here choosen August as the first month of the year in the calculations of life span. The mechanism by which juvenile dispersal starts is not fully understood. Adult birds may cease feeding their young, in this way forcing the juveniles to leave, or the juveniles leave the territory voluntarily. An incident in 1996 suggests the latter. A juvenile bird that was unable to fly with a broken but healed wing was fed near the nest up to the middle of October. If this bird had not been taken to veterinary care it had probably been fed even longer.

From September onwards juveniles disperse from their hatching site, some moving as far as 100–200 km. However the mean distance of all first year birds was only 56.8 km. For birds older than one year the mean distance between the hatching and recovery site was 47.7 km, and for the 12 oldest individuals 40.4 km. Hence the dispersal distances are rather limited and most dispersing birds have been recovered within the area of the original "wild" population. Dispersal seems to be in all directions (Figure 8), however note that rather few birds move to the east, an effect of the Baltic Sea being situated just east of the study area. Ringing recoveries also give information about life span (Table 2) and the causes of death (Table 3).

Eagle Owls have a higher probability to be recovered along roads and railways, and at electric constructions, because these places are continuously checked by man. This will bias the causes of death towards man-made constructions as compared with more "natural" causes. Unexpectedly, inexperienced

Table 2. Age when recovered for all recoveries of ringed Eagle Owls in the study population.
Åldersfördelning av alla återfunna ringmärkta berguvar från den undersökta populationen.

Year of life *Levnadsår*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Number *Antal*	34	9	4	4	-	-	3	-	-	-	2	-	2	1	-	1	1

Table 3. Death causes of recovered Eagle Owls from the studied population.

Angivna dödsorsaker för återfunna berguvar från den studerade populationen.

Death cause *Dödsorsak*	n	%
Found dead *Funnen död*	21	35
Dead in electric construction *Död i ledningsnät*	18	30
Starved, emaciated *Utmärglad*	7	11.6
Killed in traffic *Trafikdödad*	5	8.3
Injured *Skadad*	4	6.7
Found dead in water *Död i vatten*	3	5
Killed by predator *Dödad av rovdjur*	2	3.3
	60	100

juvenile birds did not dominate among those killed at man-made constructions. Among the 12 oldest birds there is a slightly higher proportion found dead at electric constructions than among 1-year olds and about the same proportion of old and 1-year old birds were killed by traffic. In the group "starved, emaciated" the juvenile birds dominate strongly as many of them have great difficulties in catching there own prey at the age when they become independent.

Discussion

A population in stagnation?

During the period 1952–1985 there was nearly no change in the geographical distribution and the number of pairs in the studied Eagle Owl population. This population has been restricted to the southeast coast of Sweden with pairs breeding at most 50 km inland. To the west of this area, i.e. further inland, there are quite a lot of good territories where Eagle Owls used to breed long ago, however over the last 30 years only occasional pairs have settled in this area. In several cases when ringing data showed that Eagle Owls found dead were old, mature breeding birds, nearby territories remained unoccupied for years. This suggests that there has been a continuous lack of mature birds to fill the gaps in the old area and to colonize new areas. Restricted juvenile dispersal, strong attachment of adults to their territories, and a low production of young may explain this pattern. In 1985–1990 breeding success was higher, both due to a higher proportion of successful nests (Figure 6) and an increase in the number of young per brood (Figure 5). In birds of prey such changes are usually connected with an increased food supply (e.g. Newton 1989).

Prey numbers and breeding success

Eagle Owls breeding in captivity have to a great extent been supplied with a surplus of food. The mean production of young/pair in 340 such broods (1990–1994) was 2.23 young (UV69-IR) as compared with 1.57 young/pair in this study. The importance of food is also obvious from studies on Eagle Owls nesting quite near places with a wealth of prey, e.g. rubbish dumps. This special choice of habitat is quite often chosen by the released birds but also to a lesser extent by birds from the original wild population. Nearly as a rule, 2–4 young (and in one case even a brood of five young), are produced in such territories.

In other species of owls, especially in arctic and subarctic areas, it is well known that breeding is strongly affected by fluctuations in the abundance of small rodents. In south Sweden fluctuations in rodent numbers are not so pronounced (e.g. Erlinge et al. 1983), and there are no data available from my study area. Instead, I have received information from the local wildlife management (A. Lettesjö pers. com) on the annual number of hares (*Lepus* spp.) shot in Södermanland (Figure 5). The Eagle Owls in my study population have demonstrated a great diversity in their choice of prey (Olsson 1979). The investigated prey items (mainly from April–September) were dominated by birds and small rodents (60% and 25% of total prey biomass, respectively). The great abundance of birds in May–September, the main period for food provisioning of young, suggests that food is unlikely to limit breeding success at that time of the season.

Moreover, in years with low supply of small rodents Eagle Owls compensated by including more birds in their diet (see figure 35 in Olsson 1979). A normally low supply of birds during the Swedish winters, in addition with low populations of small rodents, can result in very difficult feeding conditions for the owls in late winter and early spring. In an earlier study, I concluded that hares were very important as food resource for the Eagle Owls during this early, critical period of the breeding season

(Olsson 1979); the density of hares in early spring may then be decisive for the Eagle Owls' possibilities to breed. In accordance with this, I found a significant positive correlation between mean annual breeding success of Eagle Owls and the annual abundance of hares (number of hares shot in Södermanland) (r=0.49, P=0.03, N=20 years; Figure 5).

In a study on *Bubo virginianus* in Canada the hare *Lepus americanus* had a similar important role as prey (Rohner 1995). In a year with low supply of hares the owls compensated by foraging more on alternative preys. However during the winter, food intake from alternative prey was not sufficient for successful reproduction. Rohner (1995) concluded: "Subarctic winter conditions represent a bottleneck and the food situation during this time determines the capacity for the number of territories in the area". In birds in general, females seem to increase their body mass by accumulating fat just prior to the period of egg formation (Perrins 1996). In the Sparrowhawk, it seems necessary for females to accumulate fat up to three weeks before egg-laying, because females that had no fat reserves did not lay any eggs (Newton 1986). Interpreting these results in the light of the breeding ecology of the Eagle Owl, females may be especially vulnerable to shortage of prey in February-March just prior to egg-laying.

Also changes in weather from year to year may affect the abundance of rodents and thus reproduction in Eagle Owls, especially as the owls start breeding very early in the spring when snow often still covers the ground (Olsson 1979). However, the Eagle Owls have not changed start of egg-laying during this study, including the particularly successful years 1986–1990 (Table 1), suggesting that weather factors may have rather limited effect on the timing of breeding in this species. Instead weather, mediated by the quality of the nest scrape itself, e.g. its shelter and drainage, seems to be a more important factor affecting the success of breeding in Eagle Owls (own observations).

In conclusion, the most important reasons for the stagnation of this Eagle Owl population seem to be the difficult feeding conditions during winter enhanced by low dispersal among both juveniles and adults.

Population balance

For a calculation of the balance between mortality and production of young in this Eagle Owl population there are several basic parameters that have to be approximated. Both the age at which Eagle Owls start to breed and the age composition of the population are uncertain. In captivity there are examples of birds breeding already at the age of one year, and the oldest male died after a successful breeding season when 34 years old (UV69-IR). Under the harsh natural conditions the situation must be quite different. In a well founded study of the Ural Owl *Strix uralensis*, the mean age of first breeding in females was 4.1 years (Saurola 1989). This is more likely to be the age of first breeding also in wild Eagle Owls.

Based on methods in North et al. (1979) and Henny et al. (1970), Hans Ryttman (in litt.) helped me to calculate the balance of this Eagle Owl population, based on wild juvenile birds ringed in the hatched area in Figure 1 (i.e. a somewhat larger area as compared to my original study area). The mean life span was 2 years and 227 ± 94 (SE) days. The percentage of surviving birds in the first year of life was 65.5% ± 3.1%, in the second year 79.4% ± 3.3, and in the following years 88.5% ± 2.4. Using these values the calculations result in a productivity of 0.56 young/year to keep the population in balance if the owls start breeding when 4 years old. With a 95% confidence limit the productivity to maintain a constant population size must be 1.08 young/pair when breeding starts at the age of 4 years.

In the years 1952–1985 the mean productivity was about 0.6 young/pair (Figure 6). During this period the population was stable without changes in geographical distribution or density. When the productivity increased to about 1.0 young/pair 1985–1990 (Figure 5) both density and geographical distribution of the study population were positively affected. These observations suggest that the calculations on survival and mortality in this population seem relevant.

In studies on lifetime reproductive success in birds it has generally been stated that: a) a large fraction of all the fledglings die before they can breed, b) not all individuals that survive to attempt breeding produce offspring, and c) successful individuals vary greatly in productivity (Newton 1989). These general findings are true also for my study population of Eagle Owls. I found that about 77% of the Eagle Owl fledglings died before reaching breeding age, i.e. before 4 years old (Table 2), and similar figures have been found also in Ural Owls (Saurola 1989) and Sparrowhawks (Newton 1989). Each year on average 31.6% of the pairs did not even attempt to breed and 24.7% failed with breeding (Figure 6). In addition, this long term study demonstrates a high variation in productivity between different pairs.

Territories where breeding has occurred in a long sequence of years also tend to have high annual productivity. In particular, territories with a higher proportion of years with successful breeding also had a significantly higher annual productivity of young. This is probably a result of certain territories and nest sites being of superior quality. Newton (1989) states that the most successful individuals raise far more young than are needed to replace themselves and hence contribute disproportionally to the next generation. Thus, there is a tendency for a small fraction of individuals in one generation to produce a large proportion of the next. This may increase the risk of inbreeding, particularly in a small population where birds show limited movements, as in the case of the studied Eagle Owl population.

Interchange between the old population and released Eagle Owls?

Releasing of Eagle Owls bred in captivity has mainly been avoided in a broad zone around my study population at the southeast coast of Sweden (Figure 1). After the long period with stable population size, the subsequent increase in breeding success resulted in new occupied territories inland, but few new sites within the old study area. In Södermanland the number of breeding pairs was probably doubled and in Östergötland new places were established west (inland) of the study area although to a lower extent.

Since 1969 more than 1000 Eagle Owls raised in captivity have been released in south Sweden outside the hatched area in Figure 1. Remarkably few of these birds have later been found in my study area. For security reasons ringing sites of the released birds are not available. However, out of 141 recoveries of released Eagle Owls in 1990–93 (UV69-IR) only five had moved into my study area (one from the west and four from the north or south).

Despite the rather limited dispersal of Eagle Owls there are now probably mixed pairs of released birds and birds from the original "wild" population. Several of the new pairs in the previously unoccupied area between the two populations breed in strange nest sites more typical of released birds. In Södermanland new pairs have been found breeding in man-made constructions, quarries and industrial buildings, some of which have been in full activity.

From now on it will be impossible to separate the breeding pairs into "wild" and "released" birds. Even the small increase among the "wild" birds in Götaland (G) and Svealand (S) between 1985–1995 (Figure 4) may be caused by a restricted immigration of released birds or their descendants. It is likely that the once isolated "wild" population along the Swedish east coast will become more and more affected by immigration of the released birds, for example in their choice of habitat and nest sites. At this point it is hard to say what consequences, positive or negative, this will have on the Swedish Eagle Owl population at large.

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Sammanfattning

Häckningsresultat, spridning och antalsförändringar inom en population av berguv Bubo bubo *i sydöstra Sverige 1952–1996*

Under åren fram till berguvens fridlysning 1950 var förföljelsen i Sverige så hård att arten var i det närmaste utrotad i större delen av landet. Endast inom ett mindre område längs ostkusten (Figur 1) överlevde en sammanhängande och effektivt reproducerande population. Studier inom denna sistnämnda population har bedrivits kontinuerligt under åren 1952–96. För informationer rörande biotop- och boplatsval, födoval mm hänvisas till ett tidigare arbete (Olsson 1979).

Artens skyddsbehov gör att informationer om häckningsutfallet måste insamlas vid i stort sett ett enda bobesök. Detta har skett då ungarna beräknats ha uppnått en ålder av 4–6 veckor, som är den av flera skäl lämpligaste tidpunkten. Sammanlagt har 679 sådana bobesök gjorts under åren och vid en stor del av dessa har boplatsen av olika skäl saknat ungar. Endast en mycket noggrann avsökning kan då ge informationer om vårens händelser i och kring boplatsen. En översikt av resultaten redovisas i Figur 6. I medeltal har boplatserna saknat årsfärska spår av berguvsnärvaro vid 12% av kontrollerna. I revir med klart konstaterad närvaro av minst en uv har 31,6% helt saknat spår av påbörjad äggläggning, i 24,7% har häckningen misslyckats och i 43,7% har häckningen lyckats. Antalet ungar i de kullar som lyckats har i medeltal varit 1,57.

För att få en uppfattning om populationens möjlighet att fortbestå är det viktigt att veta hur stor ungproduktionen är i samtliga revir med närvaro av uv. I medeltal har denna siffra legat på nivån 0,68 ungar/par och år vilket i praktiken alltså innebär att ett par producerar lite drygt en unge vartannat år. Ungproduktionen varierar mycket från år till år (Figur 5) men medelvärdet har ändå legat på en i stort sett oförändrad nivå 1952–85 (0,5 ungar/par). Under åren 1985–90 var produktionen betydligt högre (1,0 ungar/par), för att sjunka avsevärt under perioden 1991–1995 (0,3 ungar/par). En klar förbättring av produktiviteten har dock kunnat konstateras 1996 och 1997.

Siffran 0,68 ungar per par kan tyckas mycket låg, men berguven är en långlivad fågel. Återfynden från 347 ringmärkta ungar inom denna undersökning visar att maximiåldern för de vilda uvarna är 18–20 år (Tabell 2). Betydligt högre ålder har konstaterats hos uvar i fångenskap. Det är inte känt vid vilken ålder de vilda uvarna börjar häcka, men 4 år förefaller av olika skäl vara ett troligt medeltal. Det åldersuppdelade återfyndsmaterialet antyder att ca 77% av uvarna aldrig når häckningsduglig ålder. Även bland de revirhållande paren har denna långtidsstudie visat att den totala ungproduktionen är avsevärt högre vid vissa boplatser. Bakom sådana skillnader ligger med all sannolikhet högre kvalitet i revir och boplatser liksom hos de uvar som behållit kontrollen över dessa attraktiva revir.

Rörligheten inom populationen är mycket begränsad. Medelavståndet mellan kläckningsplats och deras slutgiltigt besatta revir var hos de tolv äldsta återfunna fåglarna endast 40,1 km. Något större rörlighet verkar förekomma hos ungfåglarna när de lämnar sin födelseplats; i genomsnitt har de flyttat sig 56,8 km till den plats där de återfunnits. Denna spridning verkar ske i alla riktningar (Figur 8) under september och de närmast följande månaderna (Figur 7). Den ringa rörligheten kombinerad med ett litet antal häckande individer som producerar ungar borde öka risken för inavel.

Under åren 1952–85 har förändringarna inom den studerade populationen varit obetydliga. Antalet par och tätheten mellan dem har ej förändrats nämnvärt och någon tydlig spridning resulterande i nya häckningar i de kringliggande områdena har ej förekommit. När en äldre uv anträffats död nära en boplats har boplatsen i flera fall kommit att stå utan uvar många år efteråt. Dessa observationer tycks tyda på att förökningen nätt och jämt kunnat kompensera dödligheten i populationen, och att antalet könsmogna icke-revirhållande fåglar varit starkt begränsat.

Den ökande produktionen av ungar under perioden 1986–90 (Figur 5) tycks ha resulterat i en ökning i antalet häckande par framför allt i omgivande, tidigare uvtomma, områden. Bakom de goda åren 1986–90 tycks en exceptionell ökning av harstammen ha haft speciell betydelse, framför allt under den näringsfattiga årstiden vid häckningens tidiga inledningsskede. Denna ökning har däremot inte varit alls så påtaglig inom det gamla utbredningsområdet. Inom Sörmlands län blev antalet par i det närmaste fördubblat, medan ökningen i Östergöt-

Berguv *Bubo bubo*. Foto Viking Olsson/N.

land verkar ha varit något mindre. Totalt i Sverige fanns det 1996 ca 400 par berguv (Figur 4).

År 1969 inleddes i Sverige ett projekt för buravel och utsläpp av ungfåglar av uv, först i Götaland, senare följt av delprojekt i Svealand och Norrland (Figur 4). En bred zon väster om den här undersökta populationen med uvar av "vilt" ursprung har i stort sett hållits fri från uvutsläpp (Figur 1). Även de utsläppta uvarna har som regel haft en begränsad rörlighet i förhållande till platsen för frigivningen. Med tiden har dock denna utsläppsfria zon fått mottaga ungfåglar som spridit sig långt både från väster (utsläppta uvar) och öster (från den "vilda" ursprungspopulationen). Flera av de nyetablerade paren i detta tidigare uvtomma området är nu med stor sannolikhet blandpar. Ökningen av den "vilda" populationen åren 1985–1995 (Figur 4) får därför sannolikt också ses som ett resultat av dessa nya blandpar. För detta talar också ett inte så litet fall av okonventionella boplatsval under de senaste åren t. ex. i Södermanlands inland. Tillhåll har valts på hyggen, i stenbrott och sandtag i full drift, och i industribyggnader. Sådana boplatser förekom knappast alls i den ursprungliga populationen, men är inte ovanliga hos de utsläppta s.k. urbanuvarna och deras avkomma. I framtiden kan man förvänta sig att genutbytet mellan urbanuvar och "vilda" uvar ökar ytterligare, vilket sannolikt kommer att förändra den svenska uvstammen till exempel med avseende på häckningsbeteenden och boplatsval.