MONITORING OF SMALL AND ENDANGERED BIRD POPULATIONS, WITH SPECIAL REGARD TO THE SHORE LARK *EREMOPHILA ALPESTRIS*

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Särtryck ur: Bird Numbers 1992. Proceedings of the 12th International Conference of IBCC and EOAC, Noordwijkerhout, The Netherlands, September 14th-18th, 1992. Editors: E.J.M. Hagemeijer & T.J. Verstrael. Statistics Netherlands, Voorburg/Heerlen & SOVON, Beek-Ubbergen, 1994.

ABSTRACT A review of current knowledge of fifteen rare or endangered species in Sweden shows that for most of them it is not possible to identify the key factors that govern population size and distribution. Only for the Kentish Plover the key factor (predation of nests) has been unambiguously identified, thanks to a detailed long-term study of most aspects of the species' demography. This also means that proper management specifically directed to remedy the problem can be implemented.
In many other species it is not even possible to be certain about the phase of the annual cycle during which a key factor acts, and much less then to identify the real cause.
This paper describes a case study on the Shore Lark, a rapidly declining species. A three year study of a local population within an area of decline has not yet been able to identify clearly any deterioration of breeding success. Of course, the key factor causing the decline may operate in the non-breeding season. It is argued, however, that even if the species has declined because of low breeding success, it may be difficult to prove this if the study population happens to be a viable one. The paper is mainly an argument for more detailed long-term studies of endangered species' demographies in conservation research.

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INTRODUCTION

Current general purpose monitoring programmes in different countries efficiently monitor the population trends of only the common species. These programmes are usually not capable of accumulating sufficient amounts of records about the less common and rare species and they are unlikely ever to become comprehensive enough to include any appreciable number of less common species. Some remedy can be achieved by directing efforts into selected habitats, but the monitoring of the rare species will continue to be a special problem. Another shortage of the general purpose programmes is that they only produce information about the numerical changes and nothing directly about the factors causing these changes. In some cases causes can be suggested by correlation analyses, using such variables as weather, habitat, predation and hunting statistics, but usually we remain ignorant or uncertain even after such an analysis. In fact a positive correlation does not do much more than pointing at the necessity of conducting causal research.

When a species declines for a long time it will sooner or later reach such a level that it becomes endangered. The prime need at that stage is no longer numerical monitoring in the strict sense, but detailed knowledge about the demography, population dynamics and the key factors governing recruitment, mortality, dispersal, and age structure.

A wealth of experience about the management of endangered species has been accumulated, and it is now beyond doubt that the application of general ecological or conservation principles or the extraction of information from literature data is not sufficient to turn an endangered population into a viable one. Instead it is necessary to determine the particular demographic characteristics, ecological requirements and environmental key factors for each species separately, often even of different geographical populations separately since the same situation may not prevail for all of them.

Three species have recently gone extinct in Sweden (Ahlén & Tjernberg 1992). The last pair of a local population of the Middle Spotted Woodpecker *Dendrocopos medius* was recorded in 1980, and there has been no indication of any re-establishment since then, the Barn Owl *Tyto alba* bred for the last time in 1984 and a small remnant population of the Crested Lark *Galerida cristata* in the towns of Malmö and Lund disappeared in 1989.

A common characteristic of all three cases is that the exact cause of the extinction could not be determined. For the woodpecker 'loss of habitat' is the overall explanation, but when it comes to the precise key factors there are several alternatives, such as increased adult mortality or decreased recruitment because of food shortage, competition for nesting cavities with Great Spotted Woodpeckers *Dendrocopos major* and Starlings *Sturnus vulgaris*, inbreeding and predation. The disappearance of the Barn Owl is also unexplained with several guesses: pesticides, rat poison, traffic kills, food shortage because of new farming practices, lack of nest sites, and hard winters. Even for the Crested Lark we know little about the key factors in spite of the fact that it lived so close to people. Predation by domestic cats and destruction of nests by lawn-mowers were proposed to be important during the last stage of extinction. A more general explanation is that of food shortage created by the tidier cities of today.

The intention of this paper is to stress that such ignorance prevails in the case of extinction of most other rare or endangered species. The reason for this is lack of knowledge about the fundamental demographic properties of the declining populations. In order to determine the key factors of the declines one must know precisely the demographic bottle-necks of the actual population under consideration.

SMALL AND ENDANGERED POPULATIONS IN SWEDEN

This is a brief review of the rarest and most endangered bird populations in Sweden, namely those with less than one hundred breeding pairs in the whole country, and I have excluded a few recent newcomers that are increasing in numbers and seem to have a promising future although they have not yet reached the population size of one hundred pairs, such as the River Warbler *Locustella fluviatilis* and the Greenish Warbler *Phylloscopus trochiloides*.

Black-necked Grebe *Podiceps nigricollis*
Usually breeds a few years at a time at several widely scattered localities. The total population has been between 5 and 20 pairs in recent decades. Key risk factors have been assumed to be food shortage because of competition with fish, and predation. Most breeding sites of the Black-necked Grebe have been closely tied to Black-headed Gull *Larus ridibundus* or Common Tern *Sterna hirundo* colonies, probably because of the predator protection they provide. The Black-headed Gull is presently rapidly declining in Sweden.

Lesser White-fronted Goose *Anser erythropus*
From having been common in the fjelds of Lapland the Lesser White-fronted Goose has declined to a present population of only about ten pairs. The cause of the decline is unknown but overhunting in the breeding as well as in the winter quarters, predation by an increasing population of the Red Fox *Vulpes vulpes* and habitat deterioration of migration or wintering

sites have been advanced as explanations. Introductions of captive-bred birds in combination with an effort to change the species' winter quarters from southeastern to western Europe have been made. Some success has been reported but the final outcome of the experiment is not yet known.

Montagu's Harrier ***Circus pygargus***

About 70 pairs are breeding, most of them on the island of Öland. The population of Öland (about 50 pairs in 1981) is assumed to be stable but no recent count is available. A slow increase in mainland Sweden has been recorded (18 pairs in 1990), but the future of the species outside Öland is uncertain because of the very long distances between suitable localities.

Peregrine ***Falco peregrinus***

From having been almost extinct the population has increased to about 50 pairs, partly because of captive breeding and introductions. Contemporary population increase in Norway and Finland makes it likely that the population size will continue to grow naturally, and the species may soon be out of danger. Both population size and breeding success are presently carefully monitored by a special conservation project (Lindberg 1985). As the need for more releases of captive-bred Peregrines declines, the funding bodies will probably wish to reallocate money to cover other urgent conservation needs. At that stage it is important to find a suitable combination of demographic variables for future monitoring, at a lower economic level but still sufficient to provide information of the causes if a new population decline should begin.

Quail ***Coturnix coturnix***

The average number of records per year was 41 (range 20–86) during the period 1970–1980 and 91 (27–145) during 1981–1988. A considerable increase was observed in 1989 and 1990 with 435 and 280 records. An increase during 1970–1988 is probably only apparent since it disappears completely if correction is made for the contemporary increase of the number of ornithologists. Hence, the high numbers in 1990 and 1991 seem to be a deviation from a long term steady state situation (at least 1990 was a year with a huge invasion-like occurrence in north-western Europe).

Kentish Plover ***Charadrius alexandrinus***

Twenty pairs bred in 1984 on the Falsterbo peninsula, the only Swedish site, but the population has since declined to only 11 males and 7 females in 1991. Survival (return rate) is high, about 80% (but declining), production of fledged young is only about 0.3 per adult, mainly because of nest predation, but survival of young after fledging is usually 60–80%. The disappearance of the species from most of Denmark has made the distance to the nearest other population so long that virtually no immigration occurs. A detailed study with all birds individually ringed is going on since many years. Management involves fencing to exclude Red Foxes, shooting of crows and Minks *Mustela vison*, and use of cages to protect nests. All data from Jönsson (1992b).

Bar-tailed Godwit ***Limosa lapponica***

The population size is probably below 25–50 pairs at a few widely scattered localities in Lapland. Nothing is known about the demography of the population and little about its numerical trend.

Kittiwake ***Rissa tridactyla***

The only Swedish colony was established in 1967 by an adult female from a Danish colony. The size of the colony rose rapidly to 14 pairs in 1971, 45 pairs in 1975, and 60 pairs in 1980. In 1981, 52 pairs produced only 2 fledglings, and colony size dropped to only 15 pairs in 1982. From 1985 the colony has been stable with 25–28 pairs. The number of fledglings has been recorded at least since 1980. Most of the birds have been ringed. These fine data have regrettably not yet been analyzed and published.

Puffin ***Fratercula arctica***

As a naturally breeding bird the Puffin went extinct in 1970 after having declined for many years. Predation by Minks was the most likely reason. Between 1981 and 1985, 134 juveniles from the Faroes were released at the old breeding site. Indications of breeding (adults in summer and juveniles in August) have been recorded from 1985. Since Puffins begin to breed when they are 5–6 years old, this delay is what one would expect. There was a new release in 1990, but there is no monitoring of the breeding performance of the birds. Data from Nordin (1992).

Hoopoe ***Upupa epops***

The number of records has increased slowly (within the range 50–130 since 1974), but this increase may be a result of an increasing number of observers. It is likely, however, that the present level of visitation in our country is higher than it was before 1960. There are few breeding records, and not every year. It is too early yet to consider the species as truly re-established.

White-backed Woodpecker ***Dendrocopus leucotos***

The present population is estimated at approximately 60 pairs and it is declining. A long term research and monitoring project has been active (see also Aulén, this volume) but so far it has not been possible to determine the exact cause of the decline. Habitat loss seems to be the most important factor, but the demographic consequences have not been determined certainly. It has been assumed that clutch size has declined from 4–7 eggs in the 19th century to 3–4 eggs to-day, but the old clutch data are doubtful, and recent brood size does not differ from that found in Norway, Finland and Poland. Only 60% of the adult territorial birds breed successfully. Although adult survival is 77% only 16% of the young survive to the age of three years, when they are supposed to start breeding. Much is known about habitat and food choice but too little about demography. Data from Aulén (1988) and Aulén & Carlson (1990).

Arctic Warbler ***Phylloscopus borealis***

Some decades ago it was thought that this species would expand as a permanent breeder in Sweden, but it is still very rare with only a few records every year. The species must be considered endangered in our country though not because of any known factor operating there.

Golden Oriole ***Oriolus oriolus***

The number of records has been between 100 and 150 in recent years, mainly singing males. It has probably a rather stable population of 50–100 breeding pairs although we know little about the true ratio of breeders versus total numbers. Still less is known about its breeding success and survival.

Serin ***Serinus serinus***

After having established itself in the 1940s, it increased in numbers, particularly in the 1970s. A maximum was reached around 1980 when at least 50 pairs were assumed to breed only in the province of Scania, and there was more than 20 records in the rest of Sweden. In 1990 the total number of records in all Sweden was about 35. The number of nest finds is very low in comparison with the number of records, and almost nothing is known about the breeding success or demography of the small population.

Corn Bunting ***Miliaria calandra***

From having been a rather common farmland bird in many parts of southern Sweden, this species is now the most endangered of all, likely to become extinct within a few years time. A conservation project was started in 1988, involving an annual census, studies of breeding success and habitat choice, and some efforts to protect and manage the last breeding sites. The number of singing males has been about 17, 16, 15 and 11, respectively, in 1988–1991. It seems that most of these males are single. In 1990 only 7 females were observed. Five of them bred but only three successfully, producing 10 fledged young. In 1991 the number of females had declined to 5, and only two of them bred, one of them successfully with four fledged young. The production of young is clearly far below what is needed to maintain population size. The key factors for the low breeding success are not yet known. All data from Jönsson (1992a) and references therein.

A summary of the quality of the demographic data available for the species mentioned above is given in table 1.

STATUS AND DECLINE OF THE SHORE LARK *EREMOPHILA ALPESTRIS*

Little is known about the breeding history of the Shore Lark in Sweden. Much must be inferred from records during migration and wintering (Svensson 1990), and from the development in Finland (Hildén 1987). The species increased from about 1850 at least until about 1900. Finnish data then suggest stepwise declines with the most recent heavy declines in the 1950s and in the last one or two decades. As late as in the 1940s several thousand pairs were estimated to breed in Finland (Merikallio 1958), although the sample was small (only 12 birds on line transects, multiplied with the assumed total distribution area). The Finnish atlas (1976–1980) produced

Table 1. Survey of current knowledge and research and management activities for endangered and rare species in Sweden. The number of plus signs scores the level of knowledge or the level of activity.
Pop = total population size;
Tre = current trend;
Bre = number of breeding pairs;
Clu = clutch size;
Hat = hatching success;
Fle = number of fledglings;
Rec = recruitment of new breeders;
Mor = adult mortality;
Key = key factors;
Res = ongoing research project(s);
Man = active management.

Species	Pop	Tre	Bre	Clu	Hat	Fle	Rec	Mor	Key	Res	Man
Podiceps nigricollis	+	+		–	–		–	–			
Anser erythropus	+	+		–	–		–		–		+
Circus pygargus				–	–	–	–	–	–	–	–
Falco peregrinus	+++	+++	+	+	+	+	+	+	+	+++	+++
Coturnix coturnix			–	–	–	–	–	–	–	–	–
Charadrius alexandrinus	+++	+++	+++	+++	+++	+++	+++	+++	+++	+++	+
Limosa lapponica	–	–	–	–	–	–	–	–	–	–	–
Rissa tridactyla	+	+++	+++	+++	+++	+++	+	+	–		–
Fratercula arctica		–	–	–	–	–	–	–	–	–	+
Upupa epops			–	–	–	–	–	–	–	–	–
Dendrocopus leucotos	+	+							+	+++	+++
Phylloscopus borealis	–	–	–	–	–	–	–	–	–	–	–
Oriolus oriolus	–	–	–	–	–	–	–	–	–	–	–
Serinus serinus			–	–	–	–	–	–	–	–	–
Miliaria calandra	+++	+++	+	–	–		–	–	–	+	–
Average no. of plusses	1.5	1.5	0.9	0.6	0.6	0.8	0.5	0.6	0.5	0.9	0.9

only a few records supporting an estimate of about 50 pairs (Koskimies 1990).

For Sweden we have data from only one area, the Ammarnäs region of southern Lapland, where regular counts in suitable habitats have been performed since 1964. About two pairs bred in a special study plot until 1976 but none thereafter, and line transects since 1972 revealed an annual count of about 6 birds through 1977 but only one bird thereafter. Hence it seems that a rather rapid decline hit this area in the mid 1970s. This is supported by migration counts at Falsterbo and Ottenby bird stations (Svensson 1990).

One cannot avoid the conclusion that the species is approaching extinction in Sweden. This caused Ahlén & Tjernberg (1992) to put the Shore Lark in the category 'vulnerable' in the most recent 'Red list' of Swedish vertebrates. It is impossible to estimate accurately the total Swedish population, but it is unlikely that it much exceeds one hundred pairs.

THE CURRENT STUDY OF THE SHORE LARK

The number of individuals of any local population is determined by the classical equation (natality + immigration) < = > (mortality + emigration). Depending on the sign between the two terms the population will decline, remain constant or increase. When dealing with the whole population of a species or with a closed population one can disregard immigration and emigration, which are often very difficult to quantify. It is unknown if the Ammarnäs population has an exchange of birds with neighbouring populations. It is not even known if there are any other populations in the vicinity of our study population since sufficiently large areas have not been surveyed.

The first aim of the study was to determine natality and mortality. Natality was obviously the easiest thing to deal with in spite of difficulty to

Table 2. Number of Shore Larks recorded in 1990–1992 at Ammarnäs, Lapland.
In the lower part of the table the totals of all males and females are given. The size of the searched area was different in different years, but the area of a previous year was always a part of that of a later year.
bp = breeding pairs;
np = non-breeding pairs;
m = single males;
f = single females.

	1990				1991				1992			
	bp	np	m	f	bp	np	m	f	bp	np	m	f
1990 area	4	1	1	1	6	0	4	1	2	1	6	0
1991 area					7	2	8	1	5	2	9	0
1992 area									5	3	9	0

	1990 males	1990 females	1991 males	1991 females	1992 males	1992 females
1990 area	6	6	10	7	9	3
1991 area			17	10	16	7
1992 area					17	8

Table 3. Clutch size and breeding success in the Shore Lark in 1990–1992 at Ammarnäs, Lapland.
E = no. of eggs;
H = no. of hatchlings;
F = no. of fledglings.
Clutch size and no. of hatchlings unknown in one nest in 1992, both assumed to be 4.

Year	1st clutch			2nd/replacement			All clutches		
	E	H	F	E	H	F	E	H	F
1990	4	3	2				4	3	2
	4	4	3				4	4	3
	4	4	3				4	4	3
1991	5	0	0	5	5	5	10	5	5
	4	3	3				4	3	3
	3	3	2				3	3	2
	5	5	5				5	5	5
	3	2	2	3	3	3	6	5	5
	5	3	3				5	3	3
	5	0	0				5	0	0
1992	4	4	0				4	4	0
	4	4	0	4	4	4	8	8	4
	5	4	4	4?	4?	3	9?	8?	7
	4	4	4				4	4	4
	3	3	3	5	5	5	8	8	8
All nests	62	46	34	21	21	20	83	67	54
Per nest	4.13	3.07	2.27	4.20	4.20	4.00	4.15	3.35	2.70
Per female							5.53	4.47	3.60

determine the final production of young leaving the area on migration in late autumn. But the recruitment of new breeding birds in the next season could be assessed if all birds were marked. Mortality among the adult birds would also be rather easy to determine provided that a bird that had bred once always returned to breed at about the same site. There is sufficient support from studies on many other species to permit that assumption, at least for the males.

The study was carried out on a mountain range north of Ammarnäs in 1990–1992. Some of the results of 1990 and 1991 were published in Svensson *et al.* (1992).

Population size

In 1990 an area of about 60 km^2 was searched. In 1991 the area was enlarged to about 100 km^2 and in 1992 to about 115 km^2. Table 2 gives the number of birds recorded. The total number of certainly breeding pairs was 5, 7, and 5. Within the smaller area of 1990 it was 5, 6, and 2, respectively. The numbers are clearly two small, yet to say anything about the numerical development of the population. In both 1991 and 1992 there was a surplus of males. Only 37% and 32%, respectively, were females. Thus, the effective population size is considerably lower than the total number of birds.

Breeding success

Data on breeding success is given in table 3. Although it is stated in the literature that the Shore Lark lays two clutches, we first doubted that this could be the case in our area since the breeding season is short and no other species lays two clutches. But in 1991 one and in 1992 two second clutches after a first successful brood were found. In both 1991 and 1992 one replacement clutch after depredation of the first clutch was recorded. Second clutches may have been missed in 1991, though probably not in 1992. In any case the figures in table 2 must be minimum figures.

The data on reproductive success for the different years were similar. Clutch size was 4.0, 4.2, and 4.1, and the number of fledglings per nest was 2.7, 2.6, and 2.9, respectively. Hence the data for all years can be pooled.

In total, the data come from 15 pairs and 20 breeding attempts. Two pairs failed without laying a replacement clutch, two pairs failed and produced a successful replacement clutch, three pairs produced two successful clutches, and eight pairs produced one successful clutch each. In one case clutch size or number of hatchlings could not be checked but three fledglings were produced (a second clutch). In this case the number of eggs and hatchlings was assumed to be 4 (the mean value).

The overall mean clutch size was 4.15 eggs, and the mean for each female (including replacement and second clutches) was 5.53 eggs. The number of hatchlings was 3.35 per brood and 4.47 per pair. The number of fledglings was 2.70 per brood and 3.60 per pair, the latter figure being the true breeding success. This means that 81% of the eggs hatched, that 81% of all hatchlings fledged, and that 65% of the eggs resulted in fledged young.

Clutch size did not differ much in first versus replacement and second clutches (4.13 in the 15 first clutches and 4.25 in the four replacement and second clutches with known egg number). There was no mortality in these broods so the mean number of fledglings was the same, 4.25, versus only 2.27 in the 15 first clutches. Including the fifth second clutch with three fledglings the figure was 4.00. The difference between 2.27 and 4.00 is significant (t-test, $p < 0.02$). However, if the four first clutches that failed completely are excluded, the average number of fledglings becomes 3.09 ($n = 11$), and the difference is no longer significant. Thus the productivity difference between first and second and replacement broods is caused by fewer complete losses (less predation) among the latter.

Mortality

In 1990 two females were ringed. Both returned in 1991 but failed to do so in 1992. In 1991 two males and three new females were ringed. Both males returned in 1992 but only one of the females. This gives an adult return rate of 100% for the males, 43% for the females, and 56% for both sexes pooled. It is not certain that all surviving females have returned so the estimate is a minimum one for survival rate.

In 1990 eight ringed young fledged and two of them, both males were seen in 1991. In 1991 there was 23 ringed fledglings, and four of them (three males and one female) were seen in 1992. Thus a total of 31 ringed fledglings produced 6 returns one year later, which is 19%. Since first year birds usually disperse much more than adults this figure tells little about survival rate among the young. The fact that five of the six returning yearlings were males may indicate that young males have a higher site fidelity than females. But alternatively, it may be an indication of differential survival or a skewed sex ratio among the fledglings, which both would fit with the skewed sex ratio in favour of males among the adults.

If the return rate of 56% accurately reflects adult survival a breeding pair must produce 0.88 recruits to return next year. A yearling survival of only 19% is not sufficient (0.19 x 3.6 young = 0.68). But the difference is not large, only 0.20 young, which means that if yearling survival rate is only a little higher than the return rate or 25% it would balance adult mortality. However, a further problem is that in order to maintain population size the breeding pairs must also produce a sufficient number of young to account for the deaths among the non-breeding birds. During all three years only 70% of the females are known to have bred. This means that the number of fledglings per female in the whole population was only 2.6, which requires a yearling survival of c. 35% to maintain population size. This is still a fairly low figure to be a realistic estimate of yearling survival if one compares with that of many other passerines. But if the skewed sex ratio observed among the adults is a primary one (i.e. if only 40% of the fledglings are females) and if adult female survival is lower than that of the males (e.g. the one recorded as return rate, 43%), this figure must be much higher or at least 55%, which is then unrealistically high.

These considerations show that one cannot tell yet if the population produces enough fledglings to balance mortality. Consequently, it can still not be excluded that factors during the breeding season are responsible for the decline of the population, all against the assumption that immigration and emigration are of no importance.

The non-breeding season

Records of migrating Shore Larks show that they stay rather late in the breeding habitat. In south Sweden they almost never arrive before 1 October, and it is not until 10 October that the numbers begin to rise. The main migration period is the second half of October and the first week of November. This means that there are almost two months, between the end of the breeding season in July or early August and early October when they leave the fjelds, that nothing is known about. Both young birds and adults perform a complete moult during this period. This takes 2–3 months. Since they do not seem to start migration until they have completed the moult, this explains why they do not appear below the breeding habitats until early October.

The factors that have caused the decline of the Shore Lark population must be connected either with impaired breeding success or winter survival. Consequently, if no conclusive signs of impaired breeding success in Lapland will be found, the search for an explanation must be directed to the wintering areas.

CONCLUSIONS

Table 1 shows that reliable information about both population size and demographic properties is available for only three of the fifteen species. For two of the species this is a result of specific long term and detailed research projects explicitly designed to reveal information relevant for conservation (Peregrine Falcon and Kentish Plover). In one case (Kittiwake) the data have been obtained because the only Swedish colony happened to establish itself on an island which was also the site of a bird station. The White-backed Woodpecker has been the object of intensive conservation research and management for many years (Aulén 1988, Aulén & Carlsson 1990). In spite of this the demography of the species is not yet understood, mainly because of the great practical difficulties that this widely dispersed species presents. A new study has been initiated recently on the Corn Bunting, but apart from a detailed knowledge of the population size, the information on its demography is yet not sufficient for identification of the bottle-necks in the life cycle.

This means that for a majority of the fifteen rare or endangered species much of the essential information about recruitment, mortality and dispersal that is necessary for constructing predictive population dynamics models is lacking. It is also evident from table 1 that the key factors governing the different demographic variables or population size is known only for a few species. It is really only for the Kentish

Plover that the information needed is actually available. It is known that the only important factor is nest predation in conjunction with the long distance to the nearest neighbour population which prevents immigration. The rest is management of a practical kind. Continued monitoring of population size and demography is of course necessary for the evaluation of the efficiency of the management measures.

For the Peregrine Falcon good basic data on demography exists but it is not yet fully understood whether human persecution or toxic chemicals were (are) most important for the decline. This project shows, however, that full knowledge is not always necessary. If one wants to take the risks (and the costs) in a critical situation, this may none the less lead to success. For some other species it is assumed, in general terms, that habitat loss or deterioration of habitats are important. This is the case particularly for the White-backed Woodpecker and the Corn Bunting. In the former much is known about habitat utilization and food choice (Aulén 1988) and a conservation scheme based on habitat management and protection has been implemented in spite of the paucity of demographic data. Such data are, however, now being collected within a continuation of the research programme. In the latter it has not yet been possible to implement a concrete management plan.

The Shore Lark studies at Ammarnäs will almost certainly provide the data needed to describe in detail the performance of the species during the breeding season. It is important, however, to keep in mind that this information comes from one local population and that this population has survived a general decline of the species. It is of course possible that the conclusion to be drawn within the next few years will be that there is a local balance between recruitment and mortality. In order to learn about the key factors forcing a decline it is, logically, necessary to monitor a declining population.

These considerations are important in any strategic discussion about conservation research. Some people argue that one should use common species or at least viable populations of a declining species in the search of the demographic bottle-necks and key factors. To some extent such data will be helpful, since it is likely that phases of the life history that can be identified as critical already in a viable population will be the real key factors in a declining population. However, when mapping the life history and demography of a species at an early stage of its decline or in a 'profylactic' study, one should try to use a declining population, at least for parts of the analysis.