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Population Structure and Mortality of Eleonora's Falcon *Falco eleonorae*

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INTRODUCTION

Eleonora's Falcon breeds on small islands in the Mediterranean. The centre of its distribution is the Aegean Sea, with colonies of up to 300 pairs. One of these colonies has been visited regularly since 1965, and yearly since 1979. By systematically ringing the young falcons, it has been possible to lay the foundation for a detailed investigation, carried out in 1985, of the population structure and mortality of this species. It would be very difficult to obtain the data necessary for such a study from a solitary breeding species, and little is known about age structure and mortality of raptor populations. Newton (1984) summarises: "Mortality has proved the most difficult aspect of raptor biology to get unbiased information on", and "in my view, a pressing need in the study of raptors is for more research involving marked birds, especially breeders". Detailed investigations, based on large numbers of marked breeding birds trapped and identified in successive years, have been published for the Sparrowhawk *(Accipiter nisus)* and the Peregrine *(Falco peregrinus)* (Newton *et al.* 1983; Newton 1985; Mearns & Newton 1984). In this paper we summarise the results of our work on Eleonora's Falcon covering a period of 21 years. We include some data on the relative abundance of the two morphs (light/dark), confirming earlier results. Necessary preliminary work, in particular regarding breeding success, had been carried out earlier (Wink *et al.* 1982) and for general information about Eleonora's Falcon we refer to Walter (1979).

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MATERIAL AND METHODS

The falcon colony is situated on a small rocky island and comprises about 275 breeding pairs. Since 1965 the following numbers of nestlings have been ringed: 1965: *ca.* 200; 1969: 127; 1976: *ca.* 110; 1977: 174; 1979: 224; 1980: 300; 1981: 200; 1982: 194; 1983: 175; 1984: 111. Since 1980 we have, in addition, colour-ringed the nestlings, using eloxied aluminium rings with a different colour for each year. About 140 adult falcons (mainly female) were marked during these years. Because of their low mortality, they made a significant contribution to our model computations. In late summer 1985 we examined the falcons using several telescopes and determined whether they wore a ring and, if so, which colour. Additionally, the falcons of a neighbouring colony (about 5km distant) were checked in the same way. These observations were very time-consuming, one of us being taken up exclusively with this work for almost two weeks, with another spending more than

one week on it. Additional data were obtained by retrapping several breeding birds ringed in earlier years. In 1986 the observations were repeated on a somewhat smaller scale. The results of 1985 were confirmed but we did not gather any essential new information.

RESULTS

Fidelity to the birth site

For our investigation it is important to have some knowledge of the emigration and dispersion rates, because one has to estimate to what extent (unmarked) falcons from neighbouring colonies can be expected to join the colony as breeding birds. In 1985 we checked 149 falcons out of about 200 pairs in a neighbouring colony (5km distant). We found only one (perhaps two) ringed bird, a 2-year old which probably did not breed. This confirmed our earlier impression that the falcons return almost exclusively to their natal colony (see Wink *et al.* 1987 for more details).

Relative abundance of the two morphs

The relative abundance of the two colour morphs (light denoted by ♂, ♀, and dark by ♂,♀) can be read from Table 1. The results for 1985 agree with earlier ones (Wink *et al.* 1978). In 1986 we found a considerable shift in favour of the dark morph, which we cannot explain. The morph distribution of 102 pairs in 1985 and 36 pairs in 1986 agrees with the numbers expected under the hypothesis of random pairing (Table 2). On the neighbouring island we found the ratio: 120 light, 50 dark, i.e. 71% and 29%. It seems that the relative abundance has not changed during the past 20 years (see Walter 1979).

Table 1. Frequency of the two plumage morphs in an Aegean colony of Eleonora's Falcon.

	light		dark		light		dark	
	1985	1986	1985	1986	1985	1986	1985	1986
♂	107	27	46	21	70%	56%	30%	44%
♀	120	34	43	18	74%	65%	26%	35%
	227	61	89	39	72%	61%	28%	39%

Table 2. Composition of breeding pairs with respect to morphs. Comparison of observed and statistically expected numbers, based on random mating.

	observed		expected	
	1985	1986	1985	1986
♂ ♀	60	10	53	13
♂ ♀	21	13	23	10
♂ ♀	14	7	18	7
♂ ♀	7	6	8	6

Age at first breeding

Our previous work had shown that generally the female falcons breed for the first time at age 2 years, while the males begin to breed at 3 (Ristow *et al.* 1983). In essence, this could be confirmed. However, a few remarkable exceptions were observed.

In 1985 we found a pair consisting of a 1-year old female and a 2-year old male. Both birds were repeatedly observed defending a territory. On checking, we found a nest and, about 40cm away, fragments of an egg destroyed by rats. It seems that the pair attempted to breed but lost their clutch before our arrival. The birds then gradually abandoned the territory, being seen less frequently and finally disappearing. A similar observation was made the following year. Again, a pair consist

ing of a 1-year old female and a 2-year old male had occupied a territory; they were seen to copulate but no breeding attempt was undertaken. These observations agree with those of Clark concerning the presence of 1-year old females in a Moroccan colony of Eleonora's Falcon (Clark *et al.* 1977). It is well known that 1-year old Peregrine females sometimes breed successfully.

As can be seen from Table 3, we observed six 2-year old males in 1985. Apart from the one mentioned above, at least 4 of these were paired. Several were observed transferring prey to their mate, indicating successful breeding. We have to conclude that (at least in 1985) a number of the 2-year old males started to breed. This augments and slightly changes our previous findings.

Table 3. Age structure of an Aegean colony of Eleonora's Falcon.

	♂	♂	m	♀	♀	f	sum
1-yr old	-	-	-	1	-	1	1
2-yr old	4	2	6	10	1	11	17
3-yr old	5	4	9	4	2	6	15
4-yr old	6	-	6	4	4	8	14
5-yr old	12	2	14	6	1	7	21
6-yr old and older	16	5	21	5	4	9	31
not ringed	51	29	80	71	24	95	175
sum	95	41	136	100	38	138	274

Presence of young birds in the colony

In successive years we found quite different numbers of 1-, 2- and 3-year old falcons (breeding or non-breeding) present in the colony (see also Ristow *et al.* 1983). In fact, no other aspect of the population and age structure of our colony is as confusing. We know from recoveries of ringed birds that 1-year and also 2-year old falcons disperse widely over the Mediterranean basin. Therefore one would expect only a (perhaps small) proportion of these birds to show up in the colony. Our findings are as follows:

1981/'82: no 1-year old falcons seen,
1983: *ca.* 8 1-year old birds (*ca.* 3% of the population),
1985: *ca.* 2-3 1-year olds,
1986: 4 1-year old females and 2 males.

The annual variation in the number of 2-year old birds was also considerable: in 1982 we found 10 in a sample of 33 breeding females, whereas no 2-year old male could be seen (the number of males checked was quite low, however). One year later there were only 7 2-year olds among 89 breeding females, and again no males. (These figures cannot be compared directly because of different numbers ringed in previous years; the difference, however, is significiant). In 1985 we had a similar situation for the females, namely 11 2-year olds out of 138, but, as mentioned above, there were also 6 males present.

Concerning 3-year old birds, we can compare only the numbers for 1983 and '85 which were quite different: 1983 - 7 males, 16 females; 1985 - 9 males, 7 females. Nevertheless, we believe that most birds breed at this age, in particular the females.

For a detailed interpretation, we need more observations. At present, we can only note that the situation seems to change from year to year.

Age structure

The data on age structure collected in 1985 are presented in Table 3: 99 marked birds were counted, i.e. 36% of the total colony. We trapped 14 birds, 6 of which (43%) were ringed. The count of 1986 with 83 birds checked, 30 of them ringed, is roughly in line with the results of 1985. In particular the marked section of the population was again 36%.

In order to discuss the numbers in Table 3, we use a simple population model taking into account three parameters, namely:

a = reproduction rate = young/breeding bird/year
s = mortality prior to breeding age
t = yearly mortality of adult birds.

In a stable population, these parameters correspond to the equation a(1-s) = t (see Ricklefs 1973).

In Eleonora's Falcon, a = 0.6 (Wink *et al.* 1982). On the basis of a preliminary study we had estimated the mortality rates as s = 0.78 and t = 0.13. Starting with a total population of 550 breeding birds, these parameters lead to the expected age structure of Table 4, line 3. We assume for simplicity that 2-year old birds breed; this may lead to errors, but in 1985 we found a rather large number of 2-year old breeders. Thus we get the following numbers in line 3: 550 x 0.6 x 0.22 = 72, 550 x 0.6 x 0.22 x 0.87 = 62, etc. Taking into account the differing yearly ringing rates, the expected number of marked birds of every age can be computed (line 4). Since exactly half of the population was checked by telescope, half of these numbers are the expected observation numbers (line 5). These can now be compared with the numbers of actual observations (line 6).

Table 4. Model computation for the age structure under the assumption of 275 breeding pairs, 13% adult mortality, 78% juvenile mortality.

year of birth	83	82	81	80	before 80
age in 1985	2	3	4	5	older than 5
expected no. of breeding birds	72	62	54	47	315
expected no. of ringed birds	37	37	33	44	62
expected observation no.	18	18	16	21	44
actually observed	17	16	14	21	30

We find an excellent agreement between expected and observed numbers for falcons aged 2-5 years. For older birds, there is a noticeable but acceptable difference (44 and 30). Altogether, our assumptions concerning the mortality rates are convincingly supported. Similar computations with different s and t lead to numbers much less in agreement with the actual observations.

We also wish to point out that a more careful evaluation of our data, based on very plausible hypotheses, would result in an even better agreement. First of all, the colony has grown somewhat during the past 20 years (partially as a result of our conservation measures). This results in a lower expected number of older birds. Moreover, it can be assumed that mortality increases (slightly) with age, again leading to a better agreement of the numbers for old birds (and slightly worse for young ones). Finally, even a small emigration and immigration rate would improve the coincidence of the data. Since we cannot quantify any of these aspects, we refrain from a more detailed calculation.

The mortality rate of 13% for adult falcons seems quite low. It is much lower than estimates obtained for related species from recoveries of ringed birds. (Compare the data for Kestrel and Peregrine in Glutz *et al.* 1971). Newton (1984), however, has convincingly argued that this method, based on recoveries by the public, overestimates mortality. He found an adult mortality of 10% or somewhat less in a population of the Peregrine in Scotland. (Mearns & Newton 1984; compare also Kirmse & Kleinstäuber 1977).

Average and maximal age

From the foregoing, we have to assume a low annual mortality of adult falcons (13%). A necessary consequence is that the average age must be quite high. In fact, using the model of the last

section, we have to expect an average age of 1 + 1/t years, in our case 8.7 years. Correspondingly, about half the breeding population should be aged 7 years and older. We want to stress that investigating the average age of a population and using this formula allows an independent determination of adult mortality.

We did not mark a sufficient number of birds in the 1970s to obtain reliable information on the average age. Nevertheless, we have found a remarkable number of older falcons by retrapping breeding birds but, of 14 birds caught in 1985, 6 were ringed: one 4-year old, two 5-year old, one at least 5-year old, one 9-year old and one 16-year old, the last being by far the oldest Eleonora's Falcon so far recorded. In earlier years we recovered three 8-year old, one 9-year old and one 10-year old falcon (Ristow *et al.* 1983).

In our sample of 1986 (telescope checks) we found 20 breeding birds up to 6 years and 10 above 6 years. Since the ringing numbers were much lower before 1980, this indicates a considerable predominance of birds older than 6 years.

Maximal ages of Kestrels living in the wild are reported to be 10, 14 and 16 years; the figures for Peregrines are 15 and 13.5 (Glutz *et al.* 1971). Newton & Mearns mention a Peregrine in its 17th year. Kirmse & Kleinstäuber point out that in a (decreasing) Peregrine population in the GDR a considerable part of the birds must have been more than 20 years old.

Conclusions for protection measures

The following conclusions regarding protection and further survival of this unique species can be drawn from our results:

1. Since the falcons are highly faithful to their natal colony (and territory and partner as well), efficient protection of the existing colonies is most important. This holds true, in particular, for the very few large colonies which harbour a substantial part of the entire world population.
2. Because of the low mortality, the breeding success should be monitored. A decrease in breeding success below a critical limit would not have a significant effect on the size of the breeding population for many years and could thus go unnoticed for a long time. The population would, however, gradually age and eventually collapse.
3. Our colony has been quite efficiently protected from direct persecution for many years. It has also benefited from some additional conservation measures (Ristow & Wink 1985). Nevertheless we could notice only a slight increase of the population (about 2% per year). It may be that the reproductive potential of the species is close to the critical limit. This may be related to its ecological specialisation. We do not believe that the population of Eleonora's Falcon, once collapsed, could recover as spectacularly as the Peregrine's did.
4. It would be desirable also to protect smaller colonies with a potential for growth (sufficient nest sites), so that they could develop positively.

SUMMARY

Our research was carried out on an Aegean colony of about 275 pairs of Eleonora's Falcon. Since 1965 about 2,500 nestlings were ringed; since 1980 about 1,500 were additionally marked with colour rings. By examining the adult falcons in 1982, 1983, 1985 and 1986, data on population structure were collected.

1. At most, a very small fraction of the population settles in colonies of neighbouring islands.
2. Generally, females breed for the first time at the age of 2, males at 3 years.
3. The number of young, often non-breeding birds (between 1 and 3 years) present in the colony seems to vary considerably from year to year.
4. The mortality of young birds between fledging and first breeding is about 78%. The adult mortality is about 13%.
5. A considerable number of the falcons reach a high age. By retrapping, we have so far found three 8-year old, two 9-year old, one 10-year old and one 16-year old falcon, the last being one of the oldest recorded so far among the genus *Falco*.

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