Partial albinism in a semi-isolated population of great reed warblers

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Albinism in birds is thought to result from the expression of recessive alleles that disrupt melanin pigmentation at feather development. We have studied great reed warblers *Acrocephalus arundinaceus* in a recently founded and increasing population in Sweden during 15 years for the presence of birds with albinistic feathers. The study population was founded in 1978 and the few cases of albinism was exclusively recorded during the first five years of our study (1985–1989). This fits to the expected pattern if albinism is governed by recessive alleles; we have previously demonstrated that the population suffered from inbreeding during the first years of our study. The albinistic birds experienced a similar lifetime reproductive success as normally coloured birds.

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In birds, the absence of normal colour pigmentation, albinism, is common among domesticated species and in populations bred in captivity (SAGE 1963). It is believed to result from the expression of recessive alleles that offset the normal melanin pigmentation at feather development (SAGE 1962). Plumage albinism occurs infrequently but regularly also in natural populations (SAGE 1963; SLAGSVOLD et al. 1988; ELLEGREN et al. 1997), often affecting just some feather tracts, a phenomenon called partial albinism. In natural populations, a few studies have reported that partial albinistic individuals are particularly frequent in small and isolated populations as compared to large continuous populations, both in birds (HOLYOAK 1978) and in mammals (PARSONS and BONDRUP-NIELSEN 1995). Such a pattern is expected because inbreeding is more likely to take place in small populations than in large populations, and inbreeding increases the chance of recessive alleles turning up in double copies in individuals (homozygotes) and hence being expressed.

The great reed warbler *Acrocephalus arundinaceus* has recently become established as a breeding bird in Sweden, and the total Swedish population has increased from about 10 males in the late 1960ies to about 500 males in the 1990ies (HOLMBRING 1973; BENSCH et al. 1994). Since 1983, we have studied the species breeding biology and behaviour at Lake Kvismaren which was colonised by great reed warblers in 1978 (BENSCH et al. 1987). The population of great reed warblers at Kvismaren increased slowly to 10 males in 1984. In most years since 1988, the population has consisted of 25–30 breeding males and 30–35 breeding females (HANSSON et al. 2000).

The colonisation of Sweden by great reed warblers first started at Lake Tåkern, and then later at several other marshes and reed lakes in the southern part Central Sweden (HOLMBRING 1973; 1979). This pattern of repeated colonisation most likely took the species through several population bottlenecks. Hence, the effective number of breeding birds has repeatedly been as low as a couple of dozen birds. Such low population sizes strongly contribute to loss of genetic variation, which on average increase the level of homozygosity. Assuming that recessive alleles are causing disturbance in melanin production, we expect increased levels of expressed partial albinism in Swedish great reed warblers.

At lake Kvismaren we have found that breeding pairs with similar DNA-fingerprinting profiles, but which appear to be unrelated according to our pedigree data, suffer from an increased risk of egg hatching failure (BENSCH et al. 1994). By using DNA-fingerprinting and microsatellite DNA markers we have shown that the degree of genetic similarity between males and females in a breeding pair has decreased during the study period (HANSSON et al. 2000). This suggests that inbreeding was more severe in the early years following colonisation and that later immigration has brought in novel genetic material, hence increasing the genetic variation over time. Thus, we expected partial albinism to have been particularly frequent in the first years of our study.

METHODS

Each year between 1985 and 1999, most (>95%) adult males and females at Lake Kvismaren (59°10′N,

Table 1. *Individual great reed warblers with partial albinistic feather tracts*

Individual	Sex	Year	Left wing	Right wing
H-53	male	1985	?	?
H-53		1986	One SS	?
H-17[a]	female	1986	?	SS2 (partial, inner web)
H-42	female	1986	GC6 and some MC	?
H-42		1987	GC6 and one PC	One LC
H-42		1988	GC6 and one PC	One LC
H-42		1989	GC6 and PC2	PC1
H-42		1990	GC6 and PC2	PC1 and one MC
H5–25[b]	female	1989	PC2	–
H5–25[b]		1990	PC2	–
V-14	female	1989	PC2	PC4
V-14		1990	PC2	PC4

[a] Additional abnormality: upper mandible 3.5 mm shorter than lower mandible
[b] Daughter to H-42

15°25′E) have been captured in mist nets. At capture, we collected standard morphological measurements (BENSCH et al. 1998) and routinely evaluated the birds for plumage wear, missing feathers, presence of feather ectoparasites, and miscellaneous abnormalities. Hence, remiges, rectrices and the larger coverts have been carefully inspected on all handled birds, and particularly in the latter half of the study, it is very unlikely that partial albinistic birds have escaped our attention. The naming and numbering of the feather tracts follows Svensson (SVENSSON 1992). To test whether the annual proportion of albinistic birds among first time breeders changed over the study period we employed logistic regression in SAS genmod module (SAS 1990). We used the annual number of albinistic first time breeders as the dependent variable, the annual total number of first time breeders as the binomial denominator and year as the independent variable.

RESULTS

Of 432 examined birds, one male and four females showed one or more albinistic feathers (Table 1; Fig. 1). These included secondaries (SS, 2 birds), greater coverts (GC, 1), primary coverts (PC, 3), median coverts (MC, 1) and lesser coverts (LC, 1). Three of the birds were handled in more than one year, two of them showing the same albinistic feathers both years they were examined. The female H-42 was examined each year between 1986–90. Though the same greater covert in the left wing (GC6) was scored to be albinistic in all five years, the affected feathers in the right wing was not the same in all years. It is worth pointing out that the female H5–25 was the daughter of H-42, and that both showed left wing albinism involving the same primary covert. These two birds were the only locally hatched among the five encountered albinistic birds. None of the parents of H-42 were scored to be albinistic.

All five birds encountered with albinistic feathers entered the local population during the 1980ies (Fig. 2), however two lived up to 1990 (Table 1). This distribution is significantly different from the null

Fig. 1. Female great reed warbler showing partial albinism (individual V-14 in Table 1).

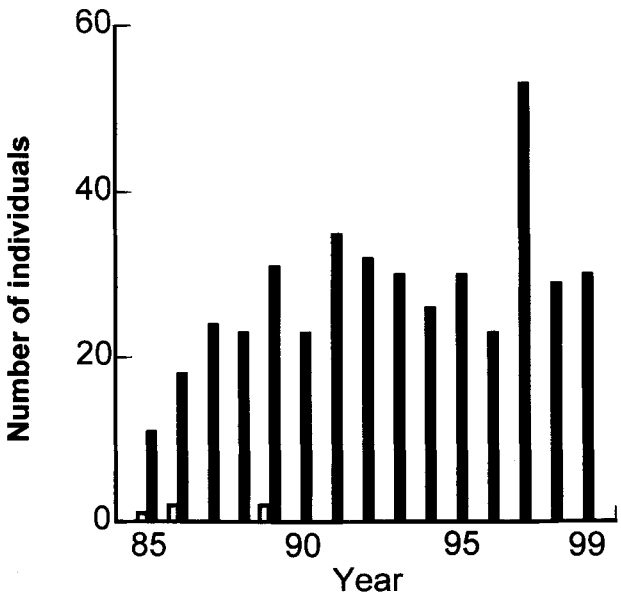

Fig. 2. Number of albinistic (open bars) and normally coloured (filled bars) great reed warblers among first time breeders at lake Kvismaren between 1985 and 1999.

hypothesis of a random distribution of albinistic birds over the study period ($F_{1,13} = 21.7$, $P = 0.0004$).

To test whether birds with albinistic feathers are less fit than normally coloured birds we compared their life span and lifetime number of fledglings. As comparison we used the normally coloured birds that entered the breeding population in 1985, 1986 or 1989 (i.e. birds from those years when the albinistic birds entered the population). Partial albinistic birds ($n = 5$) lived longer (3.0 ± 0.7 versus 2.4 ± 0.2 years) and produced more fledglings (9.8 ± 3.7 versus 7.0 ± 1.1 young) than the normally coloured birds ($n = 60$), however none of these differences are significant ($F_{1,63} \leq 0.6$; $P > 0.4$).

Three of the albinistic birds, those present in 1987 or later, have been typed for allelic lengths variation at eight autosomal microsatellite markers (HANSSON et al. 2000). The level of heterozygosity in these three albinistic females (mean 0.67) was similar to heterozygosity in a sample of 58 females (mean 0.59) from the same time period ($t_{59} = 0.95$, NS).

DISCUSSION

All albinistic great reed warblers in this study were encountered during the 1980ies, the first decade following the colonisation of our study site. From inbreeding theory and knowledge about the colonisation pattern of Sweden (HOLMBRING 1973; 1979), the occurrence of albinistic birds in the early years of our study is most likely caused by a higher level of homozygosity due to inbreeding during the years following the establishment of the population (BENSCH et al. 1994). Although expected, this is the first time partial albinism has been found to decrease in a natural population recovering from a genetic bottleneck.

The overall level of partial albinism in great reed warblers (1.1 %) was slightly higher than proportions of albinism reported for passerines, which typically is less than 0.5 % (SAGE 1963). During the first five years of our study, however, the proportion of albinistic individuals was considerably higher (4.5 %).

Four of the five partially albinistic birds in this study were females. A similar bias towards albinistic females have previously been reported in domestic pigeons *Columba livia* (NERO 1954) and in house sparrows *Passer domesticus* (ILYENKO 1960, as referred to in SAGE 1963). In birds, there is a genetic explanation to why females may exhibit higher levels of albinism than males. This is because females are the heterogametic sex, having two different sex chromosomes (W and Z), whereas males have two identical sex chromosomes (Z and Z). A recessive allele causing the disruption of normal pigmentation and located on the Z-chromosome, will always be expressed in females, but only expressed in males being homozygote for such an allele. However, partial albinism in females is therefore not expected to decline in response to decreasing levels of homozygosity in the population if the trait is Z-chromosome linked. Hence, our proposed interpretation that the decrease in albinism was due to a decrease in inbreeding is not compatible with a Z-linked expression. There is one observation in our data set suggesting that albinism is not Z-linked. This was exemplified by two birds, a female and her daughter both being albinistic, thus suggesting heritability. Under the hypothesis of Z-chromosome linked alleles for albinism, however, the daughter cannot have inherited the allele from her mother, because mothers give W-chromosomes to offspring that develops into daughters.

In a study of hooded crows *Corvus corone cornix*, Slagsvold et al. (SLAGSVOLD et al. 1988) found that albinistic individuals were on average smaller than individuals of normal plumage coloration. Partially albinistic barn swallows *Hirundo rustica* have been found to exhibit lower between year survival than normally coloured individuals (ELLEGREN et al. 1997). Our data set gave no support for the hypothesis that albinistic individuals experience lower fitness than normally pigmented individuals. A reduced fitness would be expected if partial albinism is the result of inbreeding (BENSCH et al. 1994). However, the present study only involves albinism in adult birds, whereas cost of inbreeding mainly seems to be expressed during early development (KELLER 1998).

Hence, selection may already have removed most of those partially albinistic birds suffering from inbreeding costs.

The present study suggests that information on the frequency of albinistic individuals can be used to identify genetically inbred populations. In barn swallows breeding in Chernobyl, Ellegren et al. (ELLEGREN et al. 1997) demonstrated that the frequency of partially albinistic birds increased during the years following the nuclear accident, suggesting that exposure of radioactive material resulted in an increased mutation rate. Hence, by monitoring partial albinism in long term or geographically large scale studies, we might be able to identify populations exposed either to inbreeding or environmental stress. An advantage with the use of partial albinism as a stress indicator is that museum collections can be used as reference populations (SLAGSVOLD et al. 1988; ELLEGREN et al. 1997) to establish whether the observed level of albinism is atypical relative older samples or samples from other geographical regions.

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