

A characterisation of the homozygous dark morph of Eleonora's Falcon

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The homozygous dark morph in Eleonora's Falcon *Falco eleonorae* occurs with a frequency of 2% in the wild. Males of the corresponding fledglings possess a barely discernible moustachial stripe, but female fledglings do not. Adults of the homozygous dark morph are only distinguishable from the more common heterozygous dark morph by the greater extent of black on the bill. This paper is part 25 of a series on Eleonora's Falcon.

INTRODUCTION

POLYMORPHIC PLUMAGE COLORATION IN ELEONORA'S FALCON *Falco eleonorae* is usually simplified as consisting of light and dark morphs. The character is inherited according to Mendelian laws. We consider morphs to be controlled by a single gene locus consisting of the alleles D (dominant dark) and l (recessive light) (Wink *et al.* 1978). Three genotypes are distinguishable: the homozygous dark morph 'DD', homozygous light morph 'll', and heterozygous dark morph 'Dl', their abundances being 2%, 70%, and 28%. It is beyond our scope here to explain selective factors governing this balance between the three genotypes in nature. A requirement for such analysis is the recognition of these genotypes, both at nestling and adult stages. We report new observations on the rare 'DD'-genotype. While 'DD'-fledglings have been described in the literature, plumage differences with respect to sex were previously unavailable, and the 'DD'-adult is undescribed (Ristow *et al.* 1998). A conventional way to address these problems is through captive breeding, but our approach is based on field observations, ringing data and DNA analyses.

IDENTIFICATION OF MALE AND FEMALE HOMOZYGOUS DARK FLEDGLINGS

During long-term observations of a large colony of Eleonora's Falcon off Crete we studied more than 40 'DD'-chicks. They can be recognised at a relatively early age by their wholly black bills (Plate 1), whereas 'll' and 'Dl'-chicks have grey bills. When analysing these chicks, just prior to fledging, c. 50% had a just-discernible moustachial stripe, not evident among the others (Plate 2). The first group develop black bills at 16 days and the mantle, wing, tail and breast feather tips are paler brown compared to the second group, which are marginally larger and develop an even blacker bill at 13 days. Size differences suggest the latter are females (Wink *et al.* 1982). This assumption was confirmed by molecular sex determination. From 28 individuals sampled between 1990 and 1999, a drop of blood was taken to determine the sex by laboratory DNA-analysis. Total DNA was extracted and sex-specific DNA fragments were generated by polymerase chain reaction (PCR) (Wink *in press*). ³²P-labelled PCR products were separated by high-resolution polyacrylamide electrophoresis and detected by autoradiography. These sexing data were used to reanalyse plumage differences observed in the field. The analysis revealed 14 males and 14 females, precisely a 1:1 sex ratio.

In retrospect, with knowledge of feather-tip coloration, it is now easy to identify the individual in Plate 1d, *Sandgrouse* 20: 57, as a female. Generally, adult males of all morphs have grey-blackish plumage, which is blacker than in females of the respective morph (Ristow *et al.* 1998). Therefore, it is surprising that 'DD'-males are paler than females. However, the paler appearance of 'DD'-males is created by the buffish feather tips, which are unique to fledglings. Also, among 'II' and 'DI' morphs, male fledglings have paler feather tips than females, albeit the difference is minute.

SPOTTING A PERFECT HOMOZYGOUS DARK PAIR

The reason why so few 'DD'-nestlings are found is a consequence of morph frequencies: both parents must be dark to produce a 'DD'-genotype. As 'DI' is the common dark genotype, with a frequency of 28%, the chance of a D x D-pair is $c. 0.28 \times 0.28 = 7.84\%$. According to Mendelian laws, $1/4$ of their offspring are 'DD'-genotypes, hence 7.84:4 is broadly the 2% frequency observed in chicks. Similarly, the probability to find a pair with one partner 'DI' and the other 'DD' is $0.28 \times 0.02 = 0.56\%$; 50% of the offspring of such a pair would be 'DD'-chicks. Finally, the probability of finding the perfect black pair, i.e. 'DD' paired with 'DD', is $0.02 \times 0.02 = 0.04\%$, or 1 in 2500; such a pair would produce only 'DD'-chicks. This simple calculation is based on the assumption that all survival and partnership factors with respect to morph and sex are not biased, a condition unlikely to be met. But, this crude calculation provides an estimate of the chances of locating a pair that produces only 'DD'-chicks. We found one such pair in the Cretan colony and trapped the female.

In 1996, a pair of dark morph Eleonora's Falcon was located in an area where such a pair had not been noted the previous year. As evidence that the same individuals were involved during subsequent years, we should note that territorial site tenacity and pair-bond have been demonstrated to be the rule for the species (Ristow *et al.* 1979, Swatschek *et al.* 1993), and that the territory where the two perched was the same in 1996–1999, at the upper end of a south-facing slope. In this area of $c. 60$ metres x 20 metres, no other adult falcons were seen perching in 1996–1999. Nest locations within the territory differed, but were always $c. 5$ metres below the ridge. In 1996, the first year, the nest site was almost completely exposed to the sun, suggesting that the pair were inexperienced. In 1997–1999 other eyries 10, 15 and 20 metres west of the first site were occupied, all within a horizontal rock crevice with a large stone providing the nest with permanent shade. Each year the pair raised two chicks, indicating that adults of unchanged fitness were involved. The hatching date of the first chick, derived from weight and wing length ($c. 10$ September 1996, 6 September 1997, 30 August 1998, 28 August 1999), was always later than the colony median (24 August), although a trend towards earlier laying is noticeable during the period. DNA-fingerprints of the chicks, obtained using oligonucleotide probes in 1998–1999, and the female confirm the genetic parentage of this adult and also demonstrate that only one male fertilised the eggs. The pair produced eight consecutive 'DD'-chicks. The 8:0 ratio compares favourably with a 4:4 or a 2:6 ratio expected of other 'DD x DI' or 'DI x DI' dark morph pairs (4-field chi-square test, $n=15$; $p<0.05$). From this evidence, we conclude that the pair involved is a 'DD x DD' pair.

HOMOZYGOUS DARK ADULT

Observation of the 'DD'-adults, using a telescope, did not provide any clues concerning coloration differences, compared with 'DI'-adults. It was, therefore, decided to trap one adult. Consequently the female was caught, measured, photographed in detail and released over 100 metres away, but within sight, of the eyrie. It circled perhaps 80 metres above the nest and less than ten minutes after



Plate 1 (top). Female Eleonora's Falcon *Falco eleonora* nestling (on right) at c. 15 days, Crete, 11 September 1999. The dark bill is indicative of the homozygous dark morph. The one-day younger sibling (on left) retains the paler bill coloration common to chicks of all morphs. When the nest was visited two weeks later, the latter proved to be a homozygous dark male, its bill having subsequently developed black coloration, albeit with a slightly paler base than the female. (Dietrich Ristow and Ludger Witte)



Plate 2 (middle). Homozygous dark morph siblings of Eleonora's Falcon *Falco eleonora*, 20 September 1998. The 37-day-old male (on right) has paler brown feather tips and a moustachial stripe, a significant sexual character that differs from the two-day younger female. Note the slight difference in mandible coloration. (Dietrich Ristow and Ludger Witte)

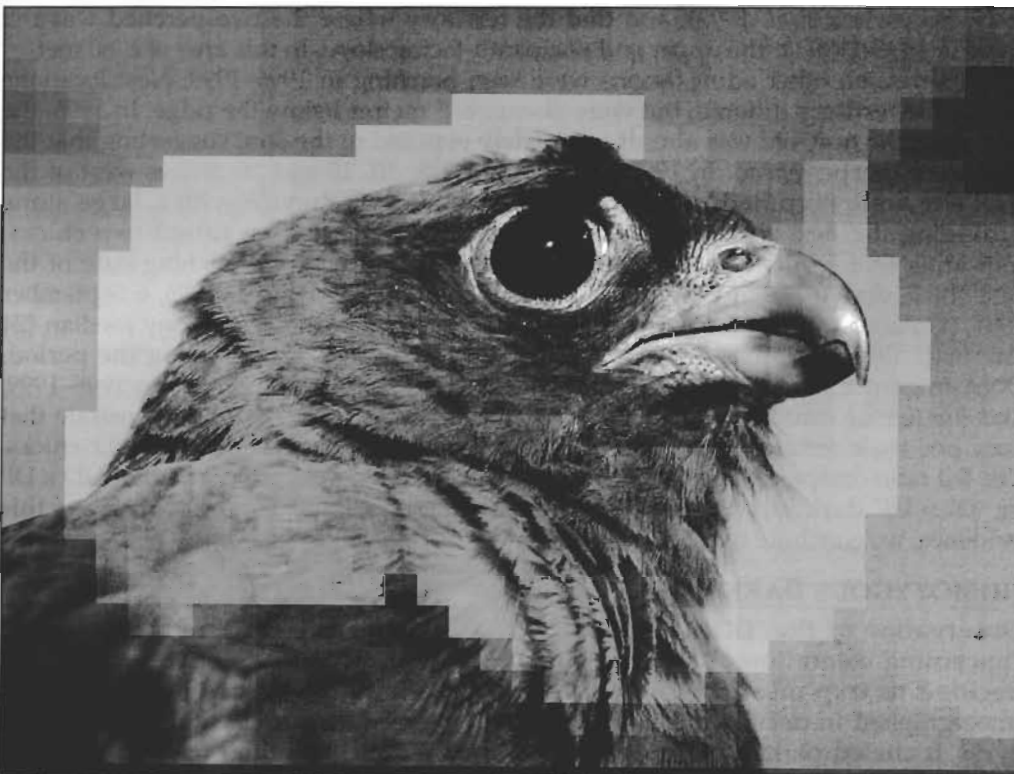


Plate 3 (bottom). Adult female Eleonora's Falcon *Falco eleonora* of the homozygous dark morph ('DD'), at least five-years-old, Crete, 24 September 1999. The black coloration extends from the tip to the cere. (Dietrich Ristow and Ludger Witte)

release perched five metres from the nest to take guard. The plumage coloration of this 'DD'-adult did not differ from that of 'DI'-adult females described in Ristow *et al.* (1998): all underwing-coverts were uniform blackish brown, secondaries and inner primaries had indications of barring on the inner web, especially discernible on the fourth primary (moulted first and therefore most bleached). Tail feathers were barred on the outer web and even the two central retrices had weak barring; the upper and undertail-coverts were barred in typical pattern. Unexpectedly, a single breast feather was yellow buffish and a single undertail-covert rusty pale brown, both throughout their entire length. The only character to distinguish it from normal dark morph birds was the black bill, but even this was bluish grey near the jaws (Plate 3). From Mendelian laws, the similarity of 'DI' and 'DD' adults could largely be expected, but the dissimilarity of juveniles appears unusual. For the observer, the similarity of hetero- and homozygous dark adults presents a problem if the two dark genotypes have to be identified in the field. Unless characterised as a 'DD' and colour-ringed as a juvenile, an adult must be carefully observed with a telescope at close quarters.

'DD x DI'-pairing is >10 times more common than 'DD x DD'-formation. We have evidence that females of two other 'D x D'-pairs were in fact homozygous 'DD'-genotypes, not only from evidence of their offspring but because they match the description of the above individual. One female is now 14-years-old, the oldest known female of the species in the wild.

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