

Biology and molecular genetics of Eleonora's Falcon *Falco eleonora*, a colonial raptor of Mediterranean islands*

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ABSTRACT

Eleonora's Falcon breeds colonially on Mediterranean islands, especially of the Aegean Sea. Colonial breeding provides the advantage that intruding raptors (17 species of raptors, owls, and raven have been observed in 23 years) can be successfully warded off in a social mobbing reaction. Eleonora's Falcon is a socially monogamous species. Breeding colonially on islands in close vicinity could facilitate extra-pair paternity. But a DNA fingerprinting study revealed that extra-pair young (EPY) could not be detected; thus social and genetic monogamy is the breeding system in this species. As copulations were observed almost every 30 min during the days prior to egg-laying, sperm competition could be the means to avoid EPY; mate guarding is less efficient, as mates are often separated when away for hunting.

DNA sequences of the cytochrome b gene show that Eleonora's Falcon, Sooty Falcon *Falco concolor*, and Hobby *F. subbuteo* are a closely related monophyletic group. Red-footed Falcon *F. vespertinus* and Amur Falcon *F. amurensis* are sibling species which cluster as a sister group to *eleonora*/*concolor*/*subbuteo*. These species also share a number of ecological and behavioural characters, which they apparently obtained from a common ancestor. These 5 species prey on insects and small birds to a large extent; they winter in Africa south of the Sahara, but breed in Europe or Asia. Some of these falcons live socially or even colonially (*F. eleonora*, *F. concolor*, *F. vespertinus*, *F. amurensis*). In this falcon complex dark and light plumage morphs are apparent; it is likely that the distant ancestor was polymorphic.

INTRODUCTION

Eleonora's Falcon *Falco eleonora* is one of the rarer falcon species with about 3800-4500 breeding pairs on Mediterranean and the Canary islands; the majority (2500-3000 pairs) breed on Aegean islands (Cramp 1990; Wink, 1994a). *F. eleonora* migrates via East Africa to Madagascar where this falcon winters in mixed flocks with Sooty Falcons *Falco concolor*; a detailed summary

*This contribution represents part 24 of a series on Eleonora's Falcon

of all known records outside the breeding season is given in Ristow and Wink (1995). The biology of Eleonora's Falcon has been summarized and reviewed in Cramp (1980) and Walter (1979a).

We have been studying the biology of Eleonora's Falcon in a large South Aegean colony since 1965, and since 1975 we have been working in the colony almost yearly for prolonged periods. In this paper we summarize data obtained over the last 23 years and will discuss the advantages/disadvantages of colonial breeding and the phylogenetic relationships of Eleonora's Falcons with other falcons.

STUDY SITE

The falcon colony we studied is situated on a small, uninhabited rocky island in the South Aegean Sea (the exact site is not given for reasons of conservation). The number of breeding falcons varied between 200 and 350 pairs. Nests were under bushes, on cliffs or in small crevices and about 70% of them were monitored by us (Wink *et al.*, 1982a). Field research was carried out by 1 to 4 scientists every year for periods between 2 and 8 weeks each year. We were thus able to monitor the whole breeding season from May until October. For about 40 nests, breeding, egg laying, hatching, development of the young and fledging have been recorded in detail. In addition to a normal ring, all young falcons were colour-ringed between 1980 and 1990 (each year had a different colour), to enable us to determine their age in subsequent years.

PLUMAGE & MORPHOLOGY

Eleonora's Falcons are polymorphic, showing a light and a dark morph, but intermediate plumage variations have also been described (Wink *et al.*, 1978; Ristow *et al.*, 1998). Plumage morphs are inherited in a Mendelian fashion with dark being the dominant allele. Our description with DD (the dominant and homozygote dark morph), ll (recessive homozygote light morph) and Dl (heterozygote dark morph) represents a simplified model for the observed colour polymorphism (Ristow *et al.*, 1998). Abundance of the homozygote dark morph DD is 3.4%, the heterozygote dark morph Dl 30.1% and that of the recessive light morph ll 66.5% (Wink *et al.*, 1978). A detailed description of plumage variation in immature and adult falcons has been documented (Wink *et al.*, 1978; Ristow *et al.*, 1998). The abundance of the dark morph varies through its range and between years. The dark morph has an abundance of about 20-30% in Aegean colonies (Wink *et al.*, 1978; Ristow *et al.*, 1989; 1998) and appears to decrease to 6-20% in west Mediterranean colonies (Ristow *et al.*, 1998).

Sexual dimorphism

As in all falcons, Eleonora's Falcon also shows a strong size dimorphism (males 327 ± 22 g; females 399 ± 27 g) which is also reflected in other morphological characters (Wink *et al.*, 1982b). Also colouration of the cere is indicative during the breeding season; ceres are orange-yellow in adult males and bluish-green in females (Walter, 1979; Ristow *et al.*, 1998). The orange-yellow colour derives from carotinoids; carotene based colouration is frequent in animals and it has been speculated that the intensity could be a cue for females to select healthy males (Ferry & Bird, 1998).

BREEDING BIOLOGY

Adult falcons always return to their breeding colony once they have started breeding there. In several instances adults maintained their breeding territory through consecutive years, indicating a high degree of site tenacity (Ristow *et al.*, 1979). Also mate tenacity could be confirmed by trapping and retrapping for several pairs (Ristow *et al.*, 1979).

Egg-laying and Clutch size

Eleonora's Falcons return to their breeding colony in May and occupy territories (20-50 m in diameter) which later hold their nests. From May to the middle of July most of the falcons are absent during the day, because there is hardly any food near the colony and only a minor portion returns to the territories for roosting each night.

Egg-laying in a colony is synchronized and starts in the second half of July ($24.5 \text{ July} \pm 3.3 \text{ days}$ for the first egg) with laying intervals of 2.6-2.9 days between first and second, and second and third egg, respectively (Wink *et al.*, 1985, 1993). Generally, by the beginning of August almost 95% of all eggs are laid. There is no replacement clutch upon egg loss. Also hatching is a synchronized process and falls in the same time period each year: Hatching starts at August 14 and reaches a maximum between August 23 and August 28 (Wink *et al.*, 1993). Mean clutch size was 2.28. 3-egg clutches were started earlier than 2- or 1-egg clutches, a circumstance which results in a negative correlation between laying date and clutch size. Within a clutch, 3rd eggs are significantly smaller and darker than 1st and 2nd eggs (Wink *et al.*, 1985). Egg size was positively correlated with female weight (Wink *et al.*, 1985).

Basically, insects represent the major food in winter, spring, and early summer. A shift in diet begins prior to egg laying, when the first migrants, although scarce, can be caught. Males with a higher weight have a better hunting success (Wink *et al.*, 1980b) and deliver more food during courtship feeding than smaller males. Clutch size is correlated with the number and total weight of prey items delivered by the male before and during the time of egg laying (Wink *et al.*, 1980b). Interestingly, male weight increases during the first years of life and gains a maximum between 6 and 8 years (Wink *et al.*, 1993), indicating that the experienced and older males sire more young than inexperienced males which breed for the first time at an age of 3 or 4 (Wink *et al.*, 1987b). On the other hand, female weight decreases with age; females reach their maximum weight during the first 2 to 5 years (Wink *et al.*, 1993) and 30% start breeding when 2 years old (Ristow *et al.*, 1983b).

After 28-30 days of incubation the first two young hatch within 36 h, whereas the third chick, deriving from the smallest 3rd egg, hatches 2-3 days later. Whereas growth of the two first-born chicks is very similar, the 3rd young usually lags behind. Young falcons are able to fly between 30 and 40 days and are fully fledged after 35 days. In the second half of October Eleonora's Falcons leave the breeding colony and depart for East Africa and Madagascar, their wintering quarters (Ristow and Wink, 1995).

In a total of 1016 nests studied between 1985 and 1990 a mean clutch size of 1.92 was found, 1.58 young hatched (egg loss due to predation by rats, sun irradiation, or other factors amounted to 17.5%) and 1.51 young fledged per nest. Later losses are due to siblicide, disease or predators (Wink *et al.*, 1993). These figures result when assessments were made in September, when earlier egg losses could not be recognized with certainty. If the whole season was evaluated, a clutch size of 2.3 and 1.2 fledged young per nest was found (Ristow & Wink, 1985).

Food and feeding

Eleonora's Falcons raise their young at a time (September-October) when food abundance is high because of the autumn migration of palaearctic migrants (Walter 1979). Migrants usually start on the mainland in the evening and reach the breeding islands of Eleonora's Falcon in the early morning hours. The island operates like a funnel and attracts the migrating birds close to the island where a phalange of falcons usually surf in the wind waiting for the prey to come. Prey items include: *Phylloscopus trochilus* (29%), *Lanius collurio* (10.5%), *Saxicola rubetra* (9.6%), *Muscicapa striata* (9.6%), *Anthus trivialis* (4.3%), *Sylvia communis* (4.2%), *Calandrella brachydactyla* (3.5%), *Oenanthe oenanthe* (3.4%), *Phylloscopus sibilatrix* (3.2%), *Hippolais icterina* (2.9%), *Motacilla flava* (2.2%), *Ficedula hypoleuca* (1.6%), *Luscinia megarhynchos* (1.2%), *Passer domesticus* (1.5%), *Oriolus oriolus* (0.85%), *Lanius minor* (0.8%), *Jynx torquilla* (0.65%), *Streptopelia turtur* (0.65%) and *Upupa epops* (0.45%) (Ristow *et al.*, 1983a; 1986; Wink *et al.*, 1993). On favourable mornings, falcons hunt more than they use and food caching in the territory is a regular event. More than 4% of prey items are cached, in the shade beside bushes, stones or rocks (Wink *et al.*, 1993). They are retrieved later in the day, usually by the female.

Migration is not a continuous process but depends on wind velocity and wind directions and food supply for the young is sufficient on days with winds from north or northwest between 10-30 km/h. During periods without wind, which can last as long as 10% of the nestling period, prey abundance is very low. During these intervals, nestlings lose weight and then, in case of clutches

with 3 young (the third young usually being the smallest), siblicide is a regular event (from 140 nests with 3 chicks, the 3rd young was killed in 17 instances = 12%) and the 3rd young is eaten by the survivors (Ristow *et al.*, 1983a; Wink *et al.*, 1993).

Food items (insects, birds) taken by Eleonora's Falcon appear to have low pesticide levels; a pesticide analysis of failed eggs in 1977 and 1990 revealed low levels of HCB, PCBs, DDE and dieldrin, indicating that this falcon is not yet directly endangered by organochlorine contamination (Clark & Peakall, 1977; Ristow *et al.*, 1980; Wink *et al.*, 1993)

Physiology

The body temperature T_b is $41.6 \pm 0.48^\circ\text{C}$ in males and $41.4 \pm 0.19^\circ\text{C}$ in females. Incubation temperatures (measured inside the egg) accounted for $38.6 \pm 1.24^\circ\text{C}$ (Wink *et al.*, 1980a). Ambient and especially soil temperatures during the day exceed $45\text{--}55^\circ\text{C}$, indicating that incubation rather serves to cool than to heat the eggs under these conditions. If nest sites are disturbed and eggs exposed to the open sun, lethal temperatures are obtained and can lead to egg losses. Even without disturbance, breeding success was significantly lower in open eyries (0.8–1.3 chick/nest) than in sheltered nests under rocks or in crevices (1.75 chick/nest) (Wink *et al.*, 1982a). Continuous brooding is essential during the first 5 days of hatching, since young falcons gain the capability for independent thermoregulation at an age of 6 days (Wink *et al.* 1980a). This finding would explain why female falcons brood their newly hatched young so firmly.

Eleonora's Falcons take regular dust and sun baths and, during rare occasions of rain, also rain baths (Ristow *et al.*, 1979b). In cases when open water is available, Eleonora's Falcons were seen bathing in open water (Walter 1979; A. Martin pers. comm.; P. Marriott in Ristow *et al.*, 1995).

Dispersal of young falcons

Non-breeding juvenile falcons in their 1st year form a small proportion of a colony (4.5%); most birds disperse during their first year and ringing recoveries of birds ringed near Crete were obtained from Spain to Turkey during the breeding season. After the second year nearly all recoveries or retraps during the breeding season were from the natal colony, indicating a high degree of natal philopatry (Ristow *et al.*, 1979a; Wink *et al.*, 1987a). Mean distance to the natal territory was 192 ± 153 m in males and 738 ± 1104 m in females, indicating that females tend to settle further away from their site of birth or even migrate to different colonies (Swatschek *et al.*, 1993). Because of the high philopatry genetic relatedness of birds from a single colony was higher between each other than between unrelated birds from other colonies (Swatschek *et al.*, 1993).

Survival

Adult survival estimates, based on analysis of colour-ringed birds, indicate an adult yearly survival of 87–89% and an immature survival until first breeding of 22% (Wink *et al.*, 1987a; Ristow *et al.*, 1991). The oldest Eleonora's Falcon retrapped was 16 years old; others 14 (2x), 13 (1x), 11 (5x), 10 (7x), 9 (6x), and 8 years (7x). We have calculated an age model of breeding Eleonora's Falcons and found that 50% of the breeding birds were older than 8.7 years (Ristow *et al.*, 1989; 1991).

Parasites

Eleonora's Falcons were found to be parasitized by a malaria parasite, *Leucocytozoon toddi*, and several ectoparasites, including hippoboscids flies (*Ornithophila gestroi*), Mallophaga (*Laemobotrior tinnunculi*, *Degeeriella rufa*) and ticks (*Haemaphysalis hoodi*). Ectoparasite infection increases during growths of the nestlings and reaches about 70–85% in adult falcons (Wink *et al.*, 1979).

COLONIAL BREEDING AND ITS CONSEQUENCES

Breeding colonially on isolated islands provides a number of advantages: nest sites are usually protected from predators, such as mammals, raptors & owls and snakes. This is also true for Eleonora's Falcon. Predators rarely occur on the breeding islands, exceptions are rats (which were introduced during historic times) and occasionally Peregrines *Falco peregrinus*, Lanner Falcons *Falco biarmicus*,

and Bonelli's Eagle *Hieraetus fasciatus* and probably Sparrowhawk *Accipiter nisus*, Eagle Owl *Bubo bubo*, and Raven *Corvus corax*. Because Eleonora's Falcons have a delayed breeding period which coincides with the onset of migration of palaeartic birds to Africa, also a number of migrating raptors (eagles, harriers, owls) pass the island and may prey on falcon nestlings.

In common with other falcon species, Eleonora's Falcon shows a defence reaction at its nest. Due to its colonial breeding a social defence reaction has evolved towards aerial intruders. If an aerial predator approaches the island closer than 0.5 km, an alarm call is given (which resembles the call of solitary falcon species in such situations) and a combined effort of the nearest falcons drives the intruder away through direct mobbing. In case of a terrestrial intruder or when a raptor lands within the territory of an individual pair, the neighbours respond to the alarm call, but stay outside the territory and circle above it. Individual nest defence is left to the pair concerned, which attack the intruder by a series of stoops. As the alarm call is usually not given when a pair has eggs, but readily when young are present, the colonial/social function of the alarm call has to be interpreted cautiously (Ristow *et al.*, 1982). In Table 1, we have listed the instances of social defence reactions towards raptors and ravens (other interactions with herons, gulls, shearwaters and other larger birds, which are sometimes mobbed by Eleonora's Falcons, were omitted from this tabulation, but see Ristow *et al.*, 1982) observed during 11 spring/summer and 20 autumn seasons of our field studies. As can be seen, only occasional defence responses occur from May to July, because most falcons are absent. From mid July onwards the sensitivity towards intruders increases (see data for *F. tinnunculus*) and from August onward all intruders are mobbed, except sometimes Peregrine and Kestrel that are resident on the island. Social mobbing appears effective because we found only 14 nestlings killed by predators as compared to 4350 successfully fledged young.

Sooty Falcons apparently show the same colonial defence behaviour, as Walter (1979b) describes two instances when 20 or several Sooty Falcons mobbed an Egyptian Vulture and a Pallid Harrier, respectively. An apparent difficulty of breeding colonially is the maintainance of a monogamous breeding system. In the period before and during egg-laying, sufficient food is not available in the direct neighbourhood of the breeding colony. As far as we know, both partners hunt individually 20-60 km away and meet in the territory for casual courtship. The synchrony of their prolonged presence in the breeding territory increases during July as well as the male's share in supporting its mate by courtship feeding. In the time of absence, any male which stays in the colony could try to intrude a foreign territory and try to copulate with the respective female. A high rate of extra-pair young (EPY) would be a logical expectation (Birkhead & Møller, 1992). We have analyzed 60 young falcons from 17 families by multilocus DNA fingerprinting and found for all families that the social mothers and fathers were also the genetical parents, i.e. EPY could not be detected (Swatschek *et al.*, 1993). This finding corresponds with other falcons in which EPY are rare (Oliphant *et al.*, 1993). So the question is, how do Eleonora's Falcons avoid EPYs? A week prior to the onset of laying a male will sometimes sit alone in the territory for several hours waiting to feed its mate, being away for hunting, thus mate guarding would be difficult. If the female is present, copulations take place quite often and we observed copulations every 30 min. Half a week before egg laying, the copulation frequency remains the same, but the pair spends more time together. On the day of egg laying, only a single copulation was seen in 5 hours. Because of the high copulation frequency we can expect sperm competition; i.e. even if there was an extra-pair copulation, the sperm of the extra-pair male would be diluted in such a way that its chance to fertilize an egg becomes very small. More field work needs to be done, to elucidate the actual rate of extra-pair and intra-pair copulations.

MOLECULAR PHYLOGENY OF ELEONORA'S FALCONS AND ALLIES

Using nucleotide sequences of the mitochondrial cytochrome b gene it is possible to reconstruct the evolutionary past of birds, including Accipitridae and Falconidae (Mindell, 1997; Seibold *et al.*, 1993; Wink 1995; Wink & Seibold, 1996; Wink *et al.*, 1996; Wink *et al.*, 1998). For the present analysis we have sequenced approx. 1100 nucleotides of the cytochrome b gene of several individuals

of *F. eleonora*, *F. concolor*, *F. subbuteo*, *F. vespertinus*, *F. amurensis*, *F. peregrinus*, *F. cherrug*, *F. biarmicus*, *F. rusticolus*, *F. chicquera*, *F. tinnunculus* and *F. punctatus* using an automatic sequencer (ALFexpress, Pharmacia). Aligned sequences were analysed with the phylogeny programme PAUP* (Swofford, 1998) and Maximum Parsimony (MP), Maximum Likelihood (ML), and Neighbour Joining (NJ) methods were used to reconstruct the underlying molecular phylogeny. For details of methodology see Avise (1994), Wink (1998), Wink *et al.*, (1996, 1998) and Leisler *et al.*, (1997).

Table 1. Occurrence of social defence reactions against raptors, owls, or ravens in a colony of more than 200 pairs of Eleonora's Falcon

<i>Species</i>	<i>date</i>	<i>frequency</i>	<i>number of mobbing falcons</i>
<i>Aquila nipalensis</i>	7.9.1977	1x	80
<i>Aquila pomarina</i>	20.9.-2.10.	2x	10
<i>Aquila spec.</i>	22.9.83	1x	10
<i>Hieraaetus fasciatus</i>	12.-15.6.	2x	0
	2.8.-13.10.	26x	2-100
<i>Hieraaetus pennatus</i>	21.8.-28.9.	3x	3-10
<i>Milvus migrans</i>	20.8.-11.9.	6x	15-50
<i>Circaetus gallicus</i>	4.10.95	1x	20
<i>Circus aeruginosus</i>	26.5.-9.6.	4x	0
		1x	3
	2.9.-5.10.	26x	3-100
<i>Circus macrourus</i> (?)	12.9.80	1x	10
<i>Falco tinnunculus</i>	26.5.-7.7.	14x	0
		2x	1-2
	17.7.-2.10.	10x	0
		11x	2-20
<i>Falco biarmicus</i>	2.9.-8.10.	8x	8-70
<i>Falco peregrinus</i>	5.6.-7.7.	9x	0
		5x	1-5
	4.8.-7.10.	10x	0
		11x	2-50
<i>Accipiter nisus</i>	1.6.93	1x	0
	19.9.-2.10.	4x	10-100
<i>Buteo buteo</i>	10.-27.9.	3x	4-20
<i>Buteo rufinus</i>	5.-11.9.	2x	3-100
<i>Pernis apivorus</i>	26.5.-7.6.	7x	0
		1x	1
	7.9.-2.10.	9x	3-40
<i>Otus flammeus</i>	1.10.77	1x	150
<i>Corvus corax</i>	20.6.92	1x	0
	4.9.-11.10.	15x	4-70

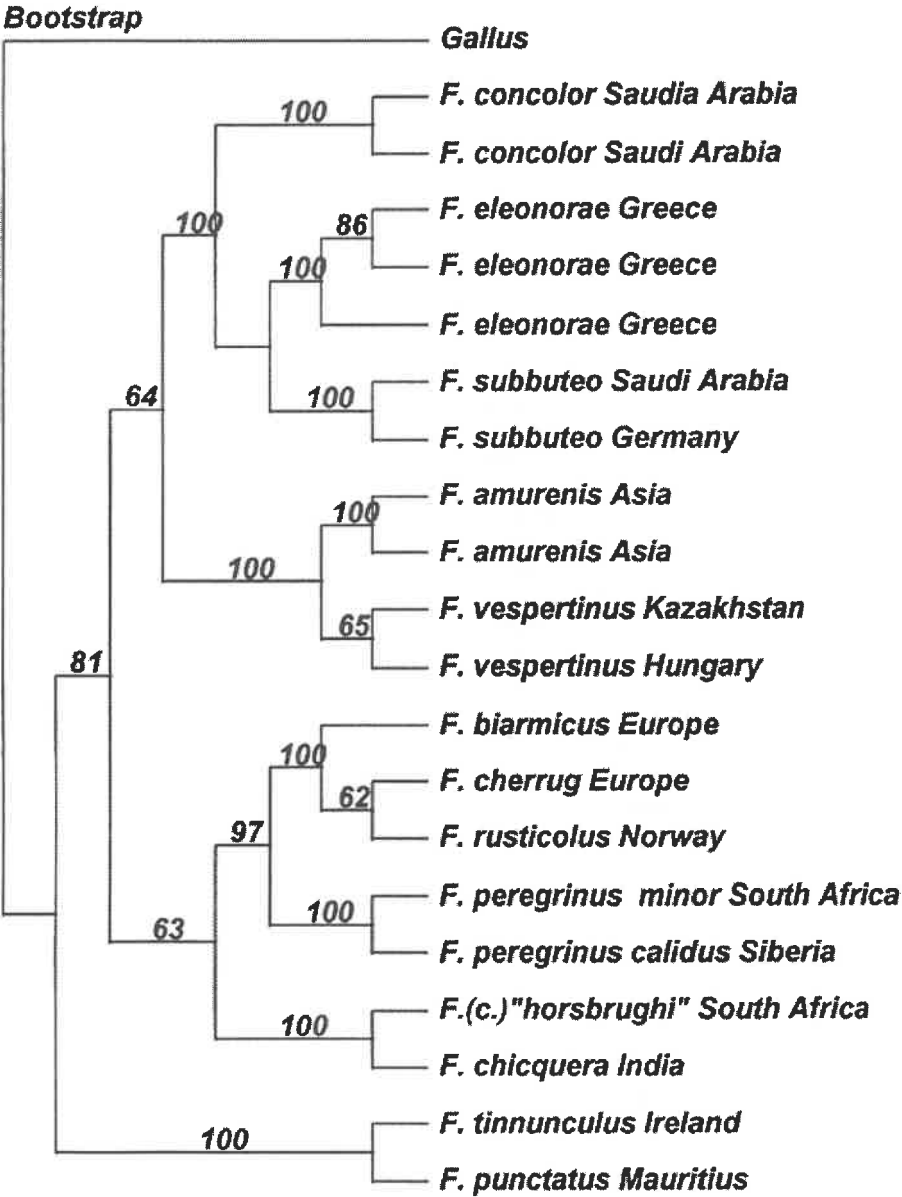
Tyto alba: 4 carcasses were found on the island, one of them might have been killed by the falcons

All three methods used for tree building (MP, ML and NJ) produce identical trees, as shown in Figures 1 and 2, indicating that the reconstructed phylogeny can be regarded as a solid base for further discussions and interpretations.

Figure 1. Molecular phylogeny of Eleonora's Falcons and allies.

A. The NJ bootstrap cladogram represents the results of 1000 replications (distance algorithm logdet); origins of birds is indicated after each taxon name

Neighbour Joining



B. Branch lengths in the Maximum Likelihood tree are proportional to evolutionary distances; MLE settings: Assumed nucleotide frequencies: A=0.298, C=0.341, G=0.121, T=0.238; all sites were assumed to evolve at same rate; transition/transversion ratio was set to 2; score of the best tree found= 4609

Maximum Likelihood

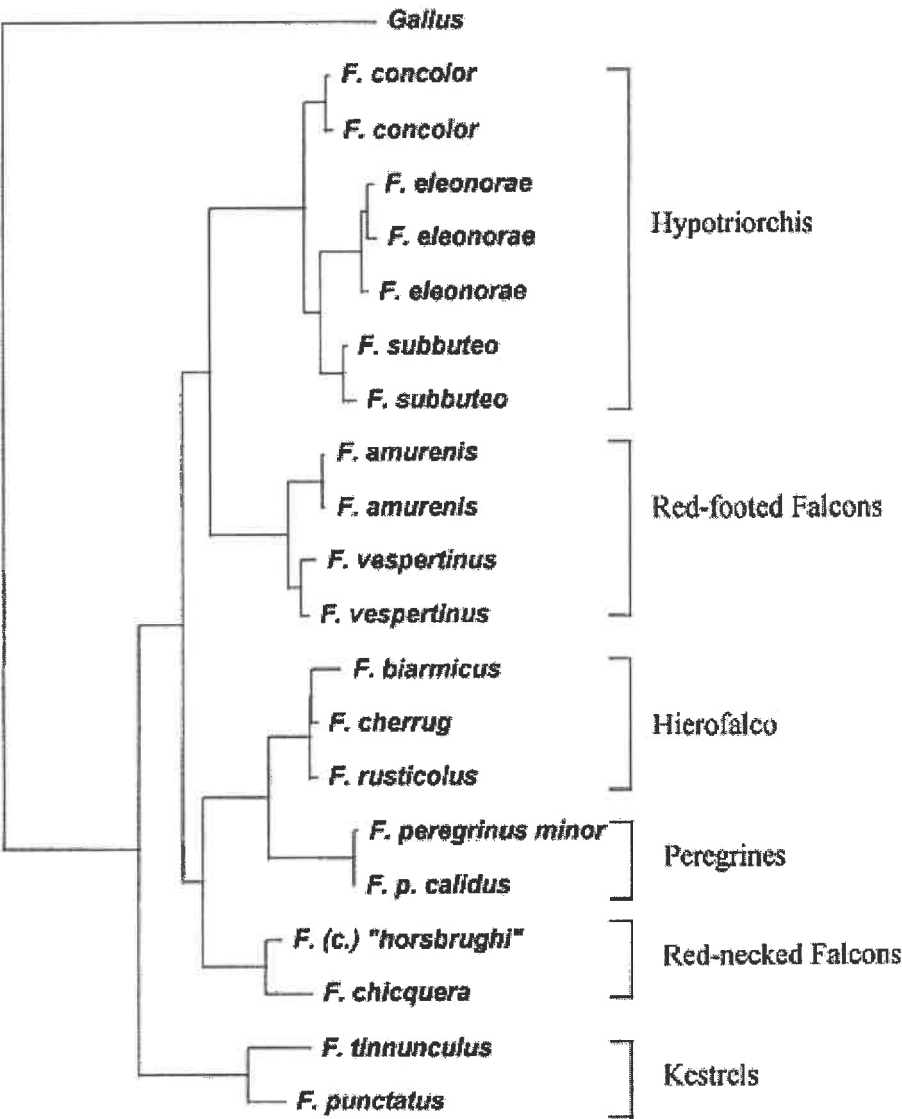


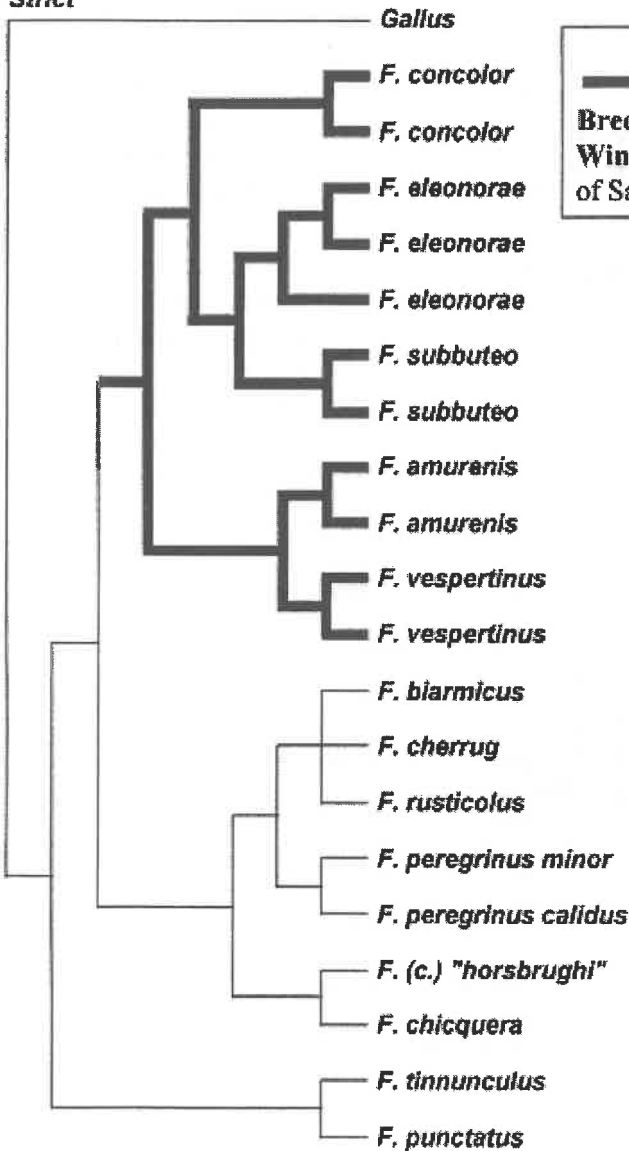
Figure 2. Correlation between phylogeny and ecological/behavioural traits of Eleonora's Falcons and allies

Base is a Maximum parsimony tree (length 570 steps; CI=0.767; RI=0.834; HI=0.233) (heuristic search, unweighted characters)

A. Distribution

Maximum Parsimony

Strict



Distribution

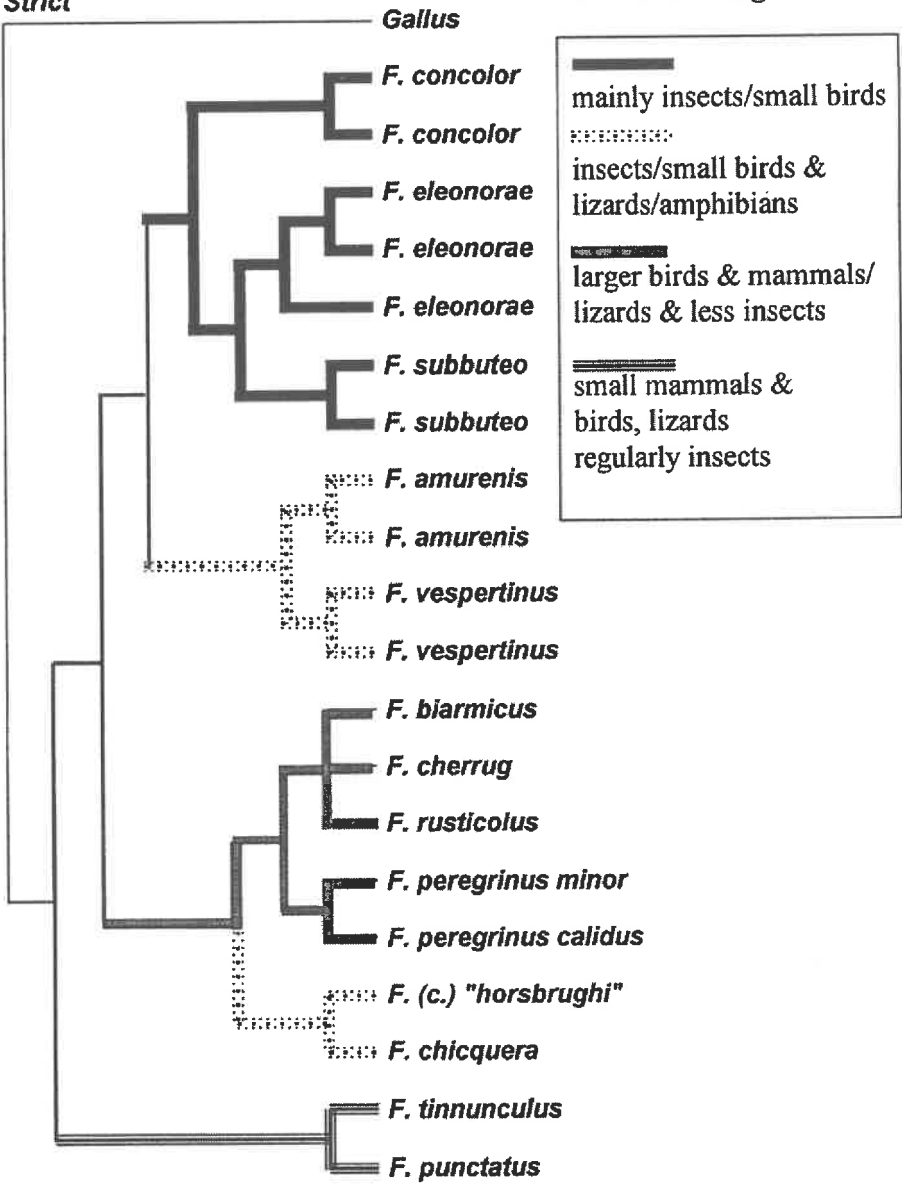
—
Breeding: Europe/Asia
Wintering: Africa south
of Sahara/Madagascar

B. Food and feeding

Maximum Parsimony

Strict

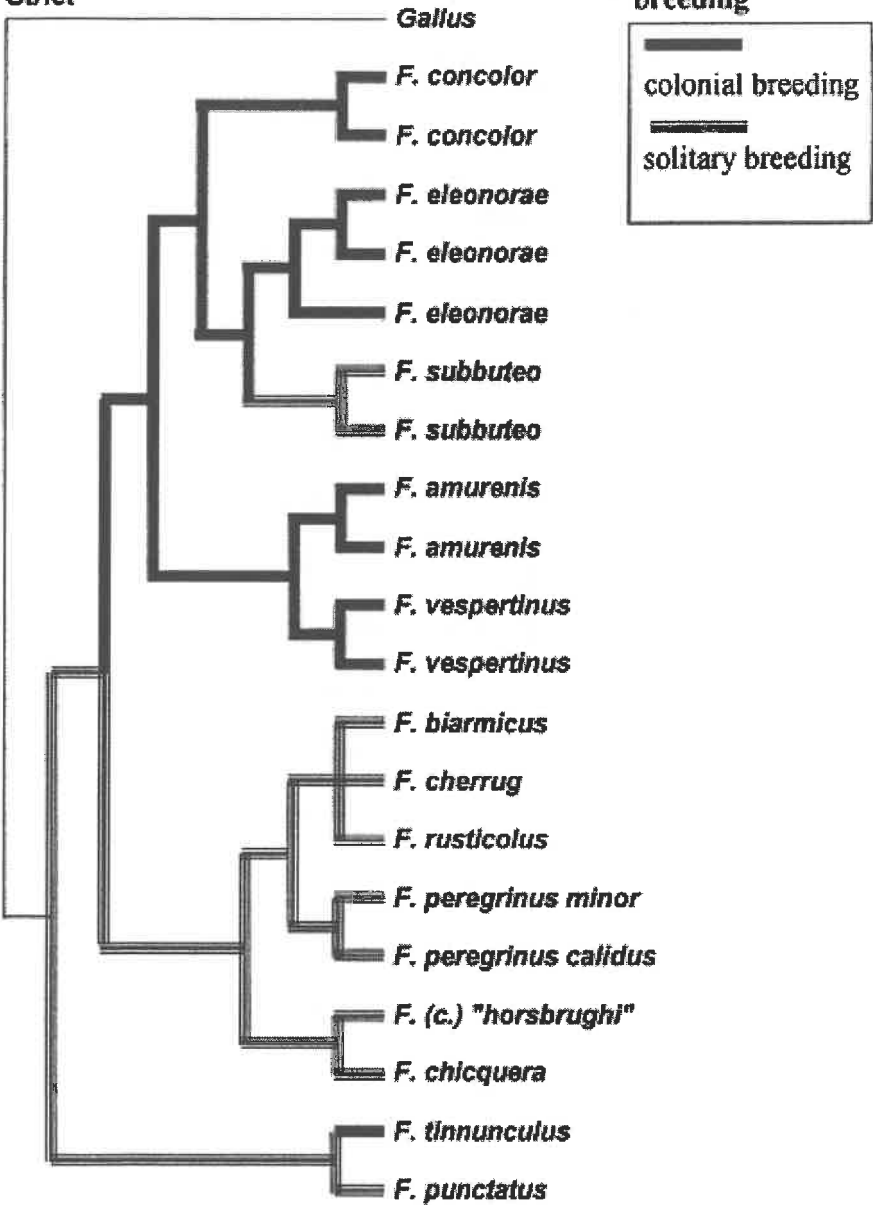
Food & Feeding



C. Occurrence of colonial breeding

Maximum Parsimony
Strict

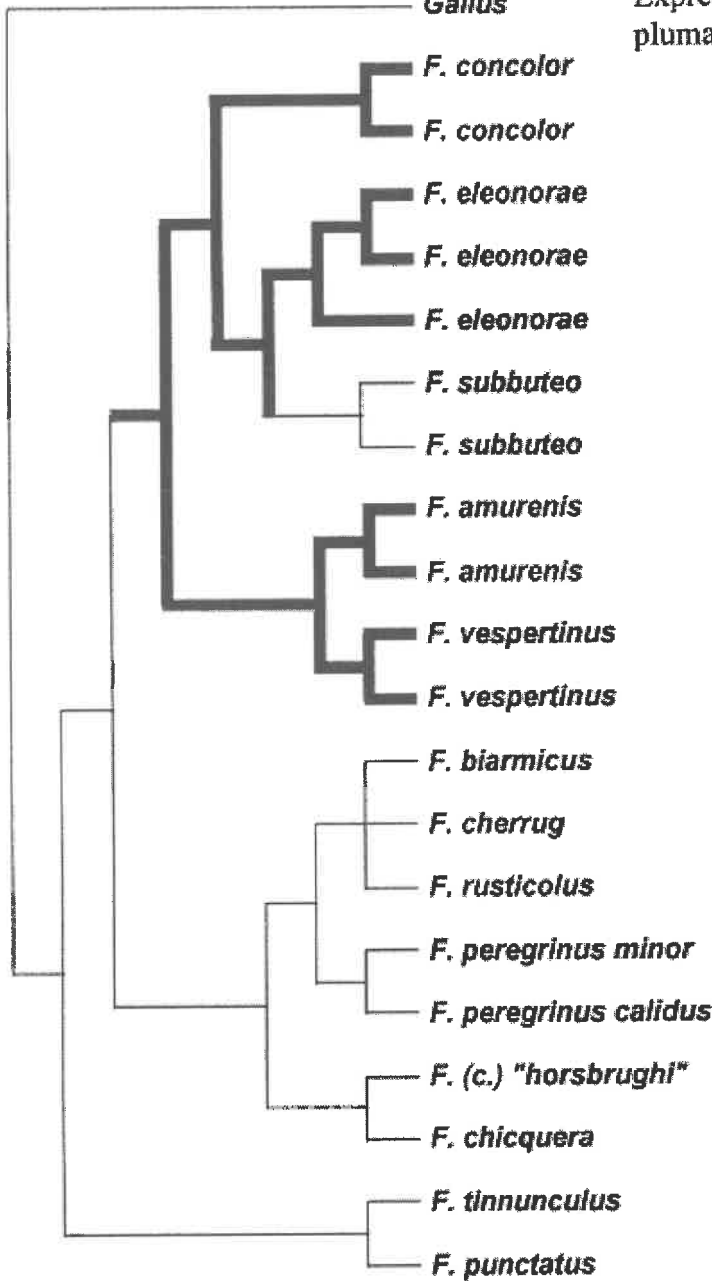
Colonial/solitary
breeding



D. Occurrence of dark plumage or dark morph

Maximum Parsimony

Strict



Expression of dark plumage or morph

According to these analyses, *F. eleonora*, *F. concolor*, and *F. subbuteo* form a closely related monophyletic group which has been recognized as the "Hobby" group or Hypotriorchis, confirming earlier results (Seibold *et al.*, 1993; Wink & Seibold, 1996; Wink *et al.*, 1998). Distances between these taxa range between 2.2 and 3.2% nucleotide substitutions. Assuming a crude calibration of a molecular clock for mitochondrial genes (Shields & Wilson, 1979, Tarr & Fleischer, 1993) which equates 2% nucleotide substitutions with 1 million years of divergence, the three falcon species must have evolved about 1 to 1.5 million years ago.

Also *F. vespertinus* and *F. amurensis* form a closely related pair of sibling species (sequence divergence 2% = 1 million years) which cluster as a sister clade to the Hobby-group (distance 7.2-8.1%; = 3.6-4 million years). According to these data, both clades share common ancestry and appear to be monophyletic (Fig. 1, 2).

Kestrels diverge at the base of the falcon tree, leading to the Hypotriorchis-complex on one hand and the Peregrine/Hierofalco complex on the other hand; these relationships are discussed by Wink & Sauer-Gürth (1999) in this volume.

Because *F. concolor*, *F. subbuteo*, *F. eleonora*, *F. vespertinus* and *F. amurensis* share common ancestry we have a chance to analyse whether common traits can also be discovered in their biology and ecology. Data on *F. concolor*, *F. subbuteo*, *F. vespertinus*, and *F. amurensis* were taken from Glutz *et al.*, (1989), Cramp (1980), and Frumkin (1988, 1993, 1994), Frumkin & Clark (1988), Gaucher *et al.*, (1988, 1994, 1995), and Walter (1990).

In Figures 2 A-D the molecular phylogeny is used as a frame-work to analyse behavioural, ecological and morphological traits seen in these falcons and to ask which of these traits reflect common ancestry and sequential or parallel evolution.

In Figure 2 A, branches leading to taxa which have their breeding grounds in the Mediterranean, Europe or Asia, but migrate to South Africa or Madagascar, are printed in bold. *F. concolor*, *F. subbuteo*, *F. eleonora*, *F. vespertinus*, and *F. amurensis* share these properties as opposed to the other falcons which are either resident or make local movements only. This result indicates that the ancestor to the *F. concolor*/*F. subbuteo*/*F. eleonora*/*F. vespertinus*/*F. amurensis* -assemblage, which could have evolved 4-5 million years ago, must have been a falcon which wintered or lived in Africa south of the Sahara and started to migrate north for exploiting food sources or directly for breeding.

If the feeding ecology is classified in four categories 1. mainly insects and small birds, 2. some insects, small birds, lizards, and amphibians, 3. larger birds & mammals, lizards but less insects, and 4. small mammals & birds, lizards and also insects, Figure 2 B is obtained. The Hypotriorchis clade share properties of category 1; i.e. prey which is only hunted while in the air, whereas *F. amurensis* and *F. vespertinus* are in category 2, which adds lizards and amphibians to the diet; i.e. prey is also taken from the ground. The larger falcons of the Peregrine/Hierofalco group are in category 3, whereas kestrels are in group 4. Food and feeding habits are obviously similar in closely related monophyletic groups, but show adaptive traits, as can be seen in Red-necked Falcons *F. chicquera*, which share category 2 with *F. amurensis*, but are not directly related to them.

In Figure 2 C we have analyzed whether falcons breed solitarily or colonially. Again we find that colonial breeding appears as a shared character in *F. concolor*, *F. eleonora*, *F. vespertinus*, and *F. amurensis*, with the exception of *F. subbuteo* which usually breeds solitarily. Also the degree of coloniality differs between these taxa, with *F. eleonora* as the most colonial species and colony sizes of up to 300 breeding pairs. Colonial breeding is also known for some *F. tinnunculus* populations (and for *F. naumanni*, which has not been incorporated in this analysis but clusters as a true kestrel) but not for any of the other falcons (in this analysis). We can draw the evolutionary scenario that already the ancestor of *F. concolor*, *F. subbuteo*, *F. eleonora*, *F. vespertinus*, and *F. amurensis* had evolved the colonial breeding habit, but that *F. subbuteo* has lost this trait.

In Figure 2 D we have marked those falcons which either have dark plumage (*F. concolor*) or in which dark plumage or morphs occur. Again we see a common heritage in *F. concolor*, *F. eleonora*, *F. vespertinus* and *F. amurensis* with the exception of *F. subbuteo*, in which only light coloured falcons are known. If various plumage morphs are interpreted as a signal to conspecifics, it is hardly

a coincidence that *F. subbuteo* as the least colonial species in the group has lost the polymorphic trait. In *F. vespertinus* and *F. amurensis*, we see both a dark and a light colour morph, which depends on gender, males are dark (with reddish "trousers") whereas females show the typical light colour type. In *F. eleonora* we have a light and dark morph (see above), which is independent of gender. If we accept the phylogenetic relationships shown in Figures 1-2, we can draw the following evolutionary scenario. The ancestor of the *F. concolor*, *F. subbuteo*, *F. eleonora*, *F. vespertinus*, and *F. amurensis* complex must have been a polymorphic falcon, possibly the result of a hybridisation between a dark and a light falcon. In its descendants the light and dark plumage reappears, either depending on sex (*vespertinus/amurensis*) or independently of gender (*eleonora*) or in only a single light (*subbuteo*) or dark (*concolor*) form. It is worthwhile mentioning that fledglings of *F. concolor*, *F. vespertinus*, and *F. amurensis*, and normal *F. eleonora* resemble light plumage falcons and develop their dark plumage when one year old.

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