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Temporal variation in the sex ratio of a colonial raptor: the case of Eleonora's falcon (*Falco eleonorae*)

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Abstract

Eleonora's falcon (*Falco eleonorae*) is a long-distance migratory bird of prey, which winters in Madagascar and breeds in the Mediterranean Sea. Even though there are several studies regarding the behaviour of the species, little is known about their sex ratios. In birds, offspring sex ratios can greatly vary from parity (1:1 sex ratio) and the observed biases are generally considered to be species-specific adaptive strategies. The aim of this study was to assess the sex ratio of Eleonora's falcon offspring and to associate any observed variations in the sex ratios with specific ecological and biological factors. Additionally, the sexual size dimorphism of offspring was investigated. The results showed a slightly male-biased overall sex ratio that varied temporally, being female-biased early in the breeding season, as well as early within a brood. The sex ratio also varied with nest orientation and brood size. Female chicks were shown to be 11% heavier than males. The results suggest an adaptive sex ratio bias scheme that is being regulated by different sex allocation strategies depending on the parental quality, the abundance of food and the quality of the habitat. However, continued detailed research is necessary to safely interpret the adaptive significance of the observed bias in sex ratio, and to reject the likelihood of artefacts.

Introduction

Eleonora's falcon (*Falco eleonorae*) is a medium-sized bird of prey which exhibits reversed sexual size dimorphism (Figure 1). It is a long-distance migratory bird, that breeds in the Mediterranean and winters in Madagascar. It breeds in colonies, in remote and steep islets where it lays 1 to 3 eggs (Ristow and Wink, 2000). It has a unique foraging behaviour, feeding on insects during the pre-laying period and shifting its diet to small migratory passerines after the eggs are laid. The global population is estimated to be 29,200-29,600, with almost 90% breeding in Greece.

One of the least studied fields in the research of Eleonora's falcon is sex ratios. In natural populations the proportions of females and males can greatly vary, often resulting in sex ratios that deviate from parity (1:1 ratio). A variety of studies in birds showed that the variations in the offspring sex ratios can be associated with specific factors (i.e. hatching rank, season, food, parental quality) that affect the allocation of the sexes within a population (Navara, 2018). In Eleonora's falcon, a previous study regarding sex ratios in a small colony in north Crete, identified a slight bias towards male offspring, as well as a bias towards females early in the breeding season (Ristow and Wink, 2004).

In this study, the aim was to investigate **the offspring sex ratio** and its **temporal variation**. Additionally, the sex ratio was **associated with** specific **ecological** and **biological** factors and the **sexual weight dimorphism** of offspring was investigated.

Figure 1. Eleonora's falcon female individual.

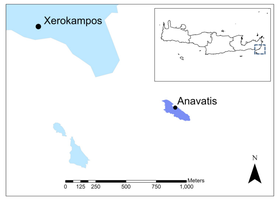

Figure 2. Study area in southeastern Crete, Greece.

Materials & Methods

The study was conducted in a small islet in southeastern Crete, which is part of the Natura 2000 network and has a surface of just 1.4 ha (Figure 2). The colony hosts approximately 100-140 individuals (40-50 pairs) per year. The data was collected during **12 consecutive years**, between 2009 and 2020 and during each year 3 visits on the field were conducted.

The sex was identified with **molecular sexing techniques**. DNA was extracted from blood and feathers and all DNA samples were amplified with PCR for the CHD1 gene. Females would give 2 bands on an agarose gel, while males one.

The sex ratio was calculated as the **proportion of males**. Specific parameters such as **hatching order (rank) and season, age, brood size, nest type and orientation**, as well as **sector** were examined for their potential effect on the sex ratio. For this reason, **generalized linear mixed models (GLMMs)** were constructed where the sex (1-0) was the response variable, the aforementioned parameters were the fixed variables, whereas year was the random variable.

Results

The results showed a slight male bias in the sex ratio (0.51; annually: 0.52 ± 0.08), although it was not found to be statistically significant. However, in years when the number of offspring suddenly increased and during the year with the lowest number of offspring, the sex ratio was female-biased (Figure 3).

The GLMM results showed that sex was best explained by orientation, rank, age and brood size (Table 1). Specifically, the earlier within the breeding season an individual was hatched, the probability of being female increased. Similarly, within a brood, chicks that were hatched first tent to be females, while the third-hatched chicks were males. Additionally, early in the season female 3-chick broods were more frequent. More females were also hatched in nests with an eastern and south-southwestern orientation.

Regarding the sexual weight dimorphism in Eleonora's falcon chicks, females were found to be 11% heavier than males. This difference in body mass between female and male chicks did not vary with rank, season or brood size.

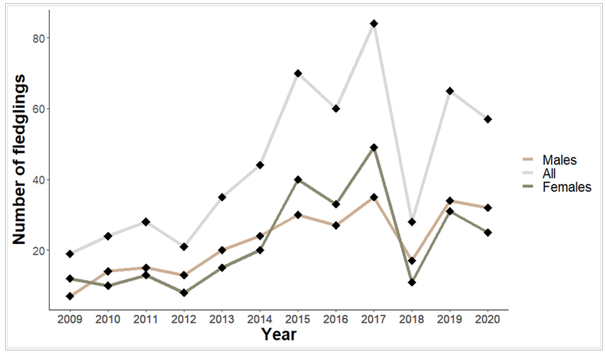

Figure 3. Fluctuations in the number of Eleonora's falcon offspring over years

Table 1. Results of the GLMM model with the best combination of predictors for offspring sex.

Variables	Estimates	Standard Error	Z – value	P
Intercept	2.632	0.8	3.291	<.01 ***
Orientation	0.002	0.001	2.410	0.015 *
Rank	0.569	0.162	3.514	<.01 ***
Age	-0.103	0.028	-3.679	<.01 ***
Brood size	-0.501	0.186	-2.706	0.006**
	Variance	Standard Deviation		
Year	0.015	0.124		
AIC	611.3			

Discussion

The observed male bias is in accordance with a previous research in Eleonora's falcon, as well as with the general theory that the sex ratio should be biased towards the less expensive sex, when daughters and sons are not equally costly to rear (Fisher, 1930).

The temporal variation of the sex ratio, both with season and rank, can be explained by the parental condition hypothesis (Trivers & Willard, 1973). Consequently, experienced parents that are in good condition and are able to pass on their genes to their offspring would invest in the most expensive sex, hence females, when conditions are benign early in the breeding season or early within a brood. Similarly, experienced and older parents would select the most suitable nests or the nests with the best orientation and would invest more in females that represent the costlier sex in Eleonora's falcon. Early in the season or within a brood the food is more abundant, whereas the nests with eastern and south-southwestern orientation are located in the sector of the islet that consists of more sheltered, under shade nests or isolated nests in higher elevation.

Since Eleonora's falcon is a species that is expected to be highly vulnerable in the case of a moderate climatic scenario (Dimalexis *et al.,* 2019) and there is currently little research going on in relation to the sex ratio patterns of its breeding colonies, it is proposed that more studies should be designed towards this direction and attempt to assess offspring sex ratio in a variety of highly accessible colonies across Greece and preferably on a multiyear basis.

Conclusions

In the current study, the sex ratio of Eleonora's falcon varied both **temporally** and **spatially**, and consistency in the results across years was observed. Although, there are some restrictions in the interpretation of such results, it is concluded that the quality of the habitat, the abundance of food, as well as the quality of the parents are probably the most significant drivers of sex allocation in this metapopulation. Therefore, it is indicated that the costlier parental investment towards females might lead to different sex allocation strategies for the parents to ensure the production of the most sensitive sex when conditions are benign.

References

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