

Original Article

Sociospatial structuration of alternative breeding strategies in a color polymorphic raptor

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It has been proposed that niche and behavioral processes may promote the coexistence of alternative color morphs in discrete areas. In this study, we tested the hypothesis that alternative melanin-based phenotypes perform differently when co-occurring in breeding areas. We assessed the influence of microhabitat and social drivers on both the resulting nest-site distribution and the variation in reproductive success of interacting phenotypes of the colonial, color polymorphic Eleonora's falcon (*Falco eleonora*). We combined measures of social, behavioral, and breeding performance, as well as environmental variables under a spatially explicit approach. We found that alternative morphs were segregated over suitable habitats by forming permanent same-color clusters. This pattern was mainly due to social dominance relationships; the pale morph, which was less dominant but more aggressive than the dark morph, settled close to pale conspecifics but far from dark ones. This segregation was also influenced by the settling of dark morph males in less dense areas and at higher altitudes than pale ones. Although the timing of reproduction did not differ between morphs, the dark morph attained higher reproductive output during the study years. The evidence suggests that pale and dark falcons adopt different breeding strategies, with pale morphs behaving highly colonially and dark morphs being more territorial, yet their relative advantages depend on the environmental conditions. We suggest that balancing selection may act on such competitive asymmetries, likely contributing to the evolutionary stability and long-term maintenance of color polymorphism in wild populations.

Key words: alternative breeding strategies, coloniality, genetic color polymorphism, neighbors, nest-sites, point pattern analyses, social environment, spatial distribution, territoriality.

INTRODUCTION

The selection of an optimal nest-site is a critical decision in the life cycle of birds that may strongly influence lifetime fitness (Jones 2001), yet such optima might differ among individuals with different phenotypes. Birds can use a variety of direct and indirect cues to make decisions concerning nest-site selection, such as physical habitat features at various spatial scales, as well as the presence of conspecifics and their activities, including breeding performance and behavioral interactions (e.g., Sergio and Penteriani 2005; Nocera et al. 2006). Variation in genetically determined coloration is of particular interest in this context because it may honestly advertise different aspects of individual quality (Roulin et al. 2000; Vroonen et al. 2013; Marie-Orleach et al. 2014). Indeed, discrete morphs often vary in many

phenotypic traits apart from coloration, such as behavior and physiology (see reviews in Roulin 2004; Ducrest et al. 2008).

In many bird species, males compete for access to mates and ecological resources. Because melanin-based coloration is often an important cue in intrasexual competitive and aggressive interactions (e.g., Lank et al. 1995; Boerner and Krüger 2009; Da Silva et al. 2013), it is likely that melanin ornaments are associated with social dominance and reproductive strategies and thus used as a criterion in mate choice (see review in Roulin 2004). Therefore, melanin-based coloration is also expected to play an important role in determining the selection of an optimal nest-site. This may be due to differential habitat selection or asymmetric competitive abilities between competing morphs, or both. For example, the white-throated sparrow (*Zonotrichia albicollis*) segregates spatially according to morph, with white males settling in high-density neighbor-rich areas and tan males settling in low-density neighborhoods (Formica et al. 2004). In the Gouldian finch (*Erythrura*

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gouldiae), males of the red morph, which are more aggressive than males of the other 2 morphs, are more likely to acquire access to limited nest cavities and higher quality nest-sites (Brazill-Boast et al. 2013).

Covariation between reproductive parameters and coloration has been frequently reported (Roulin 2004), often resulting in differences in the laying date and number of fledglings produced by each morph. From an evolutionary point of view, competing color morphs represent equally fit strategies; otherwise, selection should cause extinction of the morph with the lower fitness (Galeotti et al. 2003; Roulin 2009). Therefore, fitness advantages to a given morph are expected to be context-dependent. Accordingly, contrasting results among different studies indicate that, at the intraspecific level, the sign and magnitude of covariations between reproductive parameters and polymorphism can vary in both space and time (Roulin 2004). For instance, Brommer et al. (2005) found that light-colored tawny owls (*Strix aluco*) achieved a higher fitness than dark melanic owls in a local Finnish population, whereas the dark morph performed better throughout Finland, apparently as a consequence of climate warming (Karell et al. 2011). These fluctuations highlight the influence of changing environmental and social conditions on the relative success of alternative strategies over time.

The coexistence and long-term maintenance of genetic color polymorphism may be promoted if different phenotypes confer important selective advantages in different habitats (Dreiss et al. 2012; Arista et al. 2013; Castella et al. 2013) or, alternatively, if different morphs co-occur in the same habitat but perform differently in some way over time (Kassen 2002; Formica et al. 2004; Formica and Tuttle 2009). Under the first scenario, heterogeneous habitats can act as divergent selective force either directly on coloration or indirectly on genetically correlated physiological or behavioral traits. Broad scale geographic variation in coloration is assumed to represent local adaptation to specific environmental conditions and selective agents, which may be identified by relating environmental characteristics with the frequency of phenotypes (Mullen and Hoekstra 2008; Antoniazza et al. 2010; Dreiss et al. 2012). However, in general, morphs coexist along most of the species' range. At smaller scales, and in specific areas where environmental gradients are minimal or absent, morph-dependent habitat segregation may be diffused, and thus different selective forces and mechanisms of coexistence should be analyzed at finer scales.

Our aim here is to assess whether coloration is used as a signal by conspecifics to select nesting sites, adjust the level of defensive behavior and, ultimately, promote the co-occurrence, and apparent evolutionary stability, of alternative phenotypes in the breeding grounds of the color polymorphic Eleonora's falcon (*Falco eleonorae*). Individuals of both sexes display a genetically determined and heritable melanin-based color polymorphism with 2 discrete morphs derived from a recessive allele (pale) and a dominant allele (dark eumelanic) of the *MC1R* gene (Gangoso et al. 2011). Overall, the frequency of the dark morph is lower than that of the pale one (dark ca. 30% and pale ca. 70%), and both morphs co-occur at temporally and geographically stable frequencies in sympatric populations (Mayol 1977; Walter 1979; Ristow et al. 1998). Although Eleonora's falcons are colonial breeders, they actively defend a well-defined territory of variable size around the nest-site against competitors and intruders (Walter 1979). Nests are mainly located in small caves, crevices, and under bushes and boulders. Pair formation takes place in the nest-site chosen by the male falcon (Walter 1979). Such discrete polymorphisms and their influence on nest-site distribution in breeding grounds are ideal systems for addressing questions related to the selective pressures that generate and maintain the heritable component of phenotypic variation in nature.

In an Eleonora's falcon population from the Canary Islands, we tested the hypothesis that alternative phenotypes perform differently when co-occurring in breeding areas. Moreover, we tested different predictions, derived from 3 nonmutually exclusive mechanisms. By combining measures of social, behavioral, and breeding performance, as well as environmental variables under a spatially explicit approach, our goal was to identify the influence of microhabitat features and social drivers on the resulting nest-site distribution as well as on the variation in reproductive success of interacting phenotypes.

- I) *Exploitation of alternative ecological niches*: morph-dependent exploitation of the same habitat may be related to diverse resources and the way in which they are utilized (e.g., Skulason and Smith 1995). In this case, we focused on the distribution of nest-sites. We expected that dark and pale morphs segregate and thus show different nest-site preferences/requirements by selecting different microhabitat features.
- II) *Morph-dependent competitiveness*: as in many cavity-nesting systems, the opportunity to breed and acquire a high quality nest-site will be closely related to aggressive and competitive abilities (e.g., Wiebe 2003; Aitken and Martin 2008). We tested this prediction through a decoy presentation experiment. If coloration has a major function in signaling defensive behavior, the dominant morph will show higher levels of aggressiveness, as the decoy with the same morph should elicit a stronger defensive response. Dominant status is often associated with high quality individuals, which are usually expected to initiate reproduction at an earlier date (Arcese and Smith 1985, Kokko 1999). Therefore, we expect that the subordinate morph will settle later and will achieve lower reproductive output as a consequence of frequent intraspecific confrontations (Boerner and Krüger 2009).
- III) *Heterogeneity in the social environment created by conspecific interactions*: beyond the context of sexual selection, individuals of the same sex may be attracted to conspecifics displaying the same color if, for instance, they present similar microhabitat requirements (convergent pattern) or experience less agonistic interactions from conspecific neighbors of the same color morph (optimal "social niche," Formica et al. 2004). We therefore predict that the spatial distribution of nest-sites will be (nonrandomly) segregated with respect to coloration.

MATERIALS AND METHODS

Field procedure

Our study was conducted between July and October in 2007–2011 on Alegranza Island (1050 ha, 289 m a.s.l.), the northernmost island of the Canary Archipelago, which is located 100-km west off the African coast (Figure 1a). The island has a volcanic origin and the climate is semiarid, being particularly dry in summer. Vegetation consists only of a sparse xerophytic shrubland. The Eleonora's falcon colony from Alegranza comprises approximately 120 breeding pairs, 45% of the total number of pairs breeding in the archipelago (Gangoso et al. 2011). We sampled all accessible nests, which represented the vast majority of the population of this island (c.a. 85%), in all study years. This species is well suited for testing our hypothesis because it feeds on nondefendable food (flying migratory birds) far from nesting areas (ranging from 0.5 to 400 km far off-shore, Gangoso L, unpublished data) and has no mammalian predators on these islands, which allows the study of nest-site distribution in the absence of foraging or interspecific predation constraints.

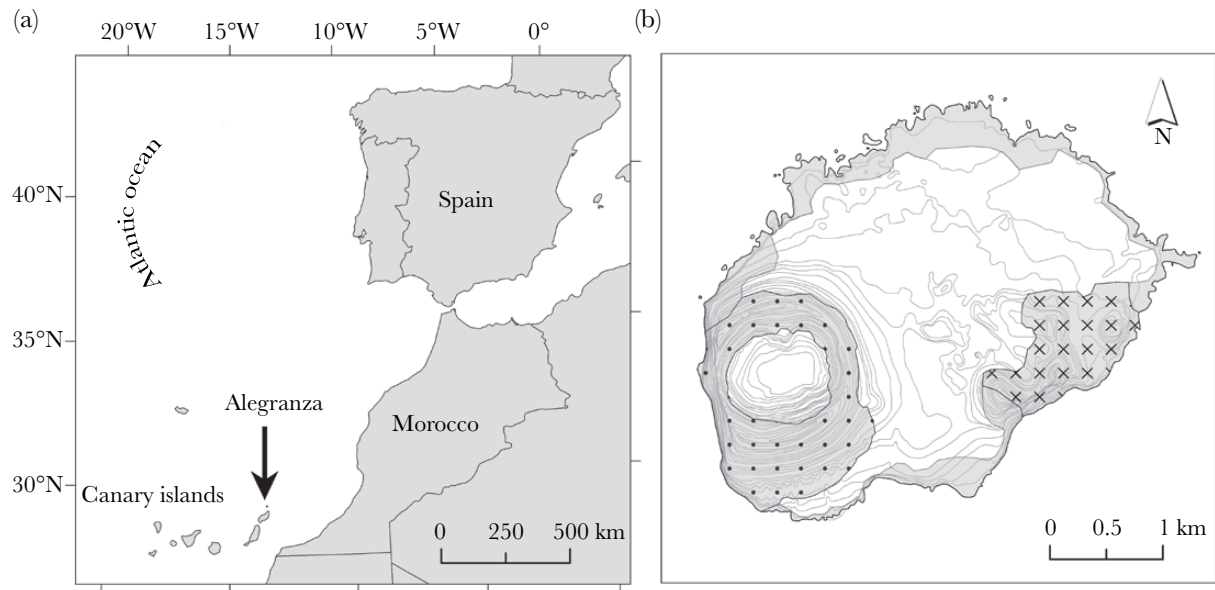


Figure 1

(a) Geographical location of the study area, Alegranza Island. (b) Homogeneous plots surrounding the location of Eleonora's falcon nests. Gray area shows the main plot used for PPA enclosing all nests. We subdivided the main plot into 2 internally homogeneous subplots, Caldera (dots) and Rapalobos (crosses), identifying the 2 main regions on the island where most nests are concentrated.

During the study period and for each Eleonora's falcon nest, we recorded the morph of both parents using a spotting scope. Breeding pairs may be composed of either the same or different color morphs without any evidence of assortative/disassortative pairing in relation to color morph (two-tailed Pearson test, all years: $\chi^2 = 1.48$, $df = 1$, $P = 0.28$, $N = 462$) and the same individual can be paired with mates of alternative color morphs over successive years (Gangoso L, Grande JM, unpublished data). Birds were sexed according to behavior and morphology (Walter 1979), which was later confirmed by molecular analyses (Gangoso et al. 2011). Nests were accessed on at least 2 occasions; first to quantify clutch size and record their geographic position (Garmin GPS-Map 62); and second, to quantify the final number of fledglings which were then measured (wing length) and ringed with aluminum and plastic rings. The age ± 1 day of fledglings was calculated using the wing length, according to Ristow and Wink (2004). Laying date was then calculated by subtracting 30 days (duration of the incubation period ± 2 days) from the hatching date of the oldest nestling within each nest.

Exploitation of alternative ecological niches

To compare the environmental characteristics adjacent to the nest-site between alternative color morphs, we used generalized linear models (GLMs). Because we were interested in assessing the repeatability of patterns between years, rather than controlling for the effect that year may have, GLMs were applied for each study year separately. By using partial regression analysis, we broke down the proportion of variation explained by spatial and environmental predictors into single-variation fractions plus their joint effect.

We derived spatial variables from principal coordinates of neighbor matrices (PCNM, Borcard and Legendre 2002), which represented the spatial structure of the data and allowed us to test and control for spatial autocorrelation. The PCNM approach is based on a principal coordinate analysis of a truncated geographical distance matrix among sampling locations. The method creates a set of PCNM eigenvectors, consisting of independent (and hence orthogonal) variables that codify spatial relationships at different

scales over the entire sampling area. The PCNM method was performed using the PCNM package (Legendre et al. 2013). Only the eigenvectors that model positive spatial correlation (Moran's I larger than expected value) were retained, because negative autocorrelation does not correspond to processes of interest in the present study. Eigenvectors are extracted according to a hierarchy that accounts for spatial patterns at progressively finer scales. Although precisely defining broad or fine scale is not straightforward, the PCNMs associated with higher eigenvalues usually represent variation at broader scales; whereas PCNMs derived from smaller eigenvalues represent variation at finer scales (Borcard and Legendre 2002; Borcard et al. 2011). Visual inspection of the PCNM values plotted over the respective sampled points (nests coordinates) in each year indicated variation at 3 different scales (Supplementary 1: Section 1 and Figure A1). Number of eigenvectors (ranging from 15 in 2010 to 21 in 2008) and patterns were similar among years. Consequently, we defined the first PCNM variables (PCNM-1 to PCNM-6) as producing variation at broader scales, the following variables (PCNM-7 to PCNM-10) as producing variation at medium scales, and the remaining variables (PCNM-11 to PCNM-21) as producing variation at finer scales. The produced PCNM vectors were then used as spatial explanatory variables in a logistic regression model with nest occupancy by a dark (1) or a pale (0) male falcon as the response variable. We performed an initial GLM with binomial error and a logit link function to select the most influential PCNM eigenvectors on the probability of nest occupancy by either dark or pale males. An automated model selection procedure based on the second order Akaike's Information Criterion (AICc) and using the genetic algorithm of the *glmulti* package (Calcagno and Mazancourt 2010) was performed to determine which eigenvectors produced the best-fitted model (Burnham and Anderson 2002).

As a second step, we performed a similar GLM to select the most influential environmental predictors on the probability of nest occupancy by either dark or pale males. We obtained 10 predictor variables describing the landscape structure of each nest-site. Variables were chosen according to species distribution models of

this particular falcon in the Mediterranean (Kassara et al. 2011) and to particular features of our study area, such as the distance to the unique fresh water pond of the island, visibility from each nest, and minutes of shadow covering each nest, as no vegetation or human structures are present on Alegranza Island (Table 1). Relief variables were derived from a digital elevation model with a spatial resolution of 0.5 m (www.ign.es). Environmental variables were calculated in ArcGis 10.1 (ESRI, Redlands, CA) using bilinear interpolation between the cell of nest location and adjacent cells. Due to the spatial resolution of the digital elevation model used, the spatial extent covers an area of 2.25 m² centered in the nest point. The roughness index was calculated following Sappington et al. (2007) with a moving-window routine over a 3 × 3 cell neighborhood centered on each cell. Multicollinearity was assessed by calculating generalized variance inflation factors (gVIFs). Those variables showing VIF values > 10 were removed before performing the GLMs.

Finally, we regressed the same response variable with all previously selected explanatory variables (PCNMs and environmental variables) as well as the *x* and *y* coordinates of each nest-site. Geographic coordinates were included because PCNMs do not test the linear relationship between these coordinates and the response variable. We did not include other polynomial terms in the model because potential spatial relationships are addressed in detail using point pattern analysis (PPA) (see below). Likewise, although we considered the distance to neighbor nests as a social-related variable in these general analyses, we performed specific point pattern analyses to investigate the effect of social relationships. Again, multicollinearity was checked and explanatory variables were selected based on the minimum AICc.

Table 1
Environmental variables used to describe the landscape structure of Eleonora's falcon nest-sites

Variable (units)	Description
Altitude (m)	
Aspect (degrees)	Orientation of the nest
Profile curve	Curvature (second derivative of the slope) alongside the slope direction
Slope (degrees)	
Roughness index (0–1)	Vector Ruggedness Measure proposed by Sappington et al. (2007) measures the variation in 3-dimensional orientation of grid cells within a neighborhood. This method effectively captures variability in slope and aspect into a single measure. Ruggedness values in the output raster can range from 0 (no terrain variation) to 1 (complete terrain variation)
Dist. to coast line (m)	
Dist. to water pond (m)	
Dist. to nearest nest (m)	Distance to nearest nest taking altitude into account
Viewshed (ha)	Visibility of island terrain and ocean waters from each nest (up to 5 km around the coast line)
Shadow (min)	Number of minutes of shadow covering each nest. Hillshade models identify each cell that will be in the shadow of another cell at a particular time of day. As no vegetation or human structures are present on Alegranza Island, only topography was incorporated to these models. Shadow time was obtained for accumulative time calculated every 10 min on July 21st (mean laying date) in 2009. Photoperiod was nearly identical for all years.

Morph-specific competitiveness (dominance relationships)

In 2008 and 2009, we performed a decoy presentation experiment during the incubation stage. We studied the defensive response of Eleonora's falcons toward an intruder (decoy) in a total of 33 nests (16 nests in 2008 and 17 in 2009) that were selected based on the criteria that clutches were laid on a similar date (± 2 days). In 18 nests, both adults were of pale morph while only in 1 nest both adults were of dark morph. In the remaining 14 nests, at least 1 adult was dark (8 nests with a dark male and 6 nests with a dark female). These proportions (both pale: 55%, both dark: 3%, and 1 pale/1 dark: 42%) resemble the actual proportion of morph type pairings found in the study population across years (63.71%, 2.53%, and 33.76%, $N = 474$). In raptors, territory intrusion and defense are predominantly carried out by males (Wiklund and Andersson 1980; Boerner and Krüger 2009). Therefore, we used 2 decoys simulating a dark and a pale perched male Eleonora's falcon (Supplementary 1: Section 2 and Figure A2) that were presented alternately within a 2-day interval and in a random order, totalling 66 trials.

We placed the decoy within 5 m of the nest when both pair members were present. To reduce disturbance in the colony, decoys were placed within a 1-min interval. The birds' behavior was recorded continuously during 15 min, after a 5-min acclimation period. The defensive behavior can be displayed in many different ways and with different intensity, ranging from faint approaches (e.g., overfly) and alarm calls to more aggressive interactions that include a closer approach and even a physical contact by using the bird's talons. For the purpose of this analysis, we considered only direct attacks, defined as the number of occasions a falcon approached the decoy to less than 20 cm or entered into physical contact with the decoy. We observed the nests from a distance ranging from 100 to 200 m, registering the defensive behavior (number of attacks) and, when possible, the sex of the attacker. All the trials were performed avoiding the hot midday periods.

We tested morph-specific effects on the defensive behavior of falcons by means of generalized linear mixed models (GLMMs) with Poisson error and log link function, where the number of attacks to the decoy was the dependent variable. In a preliminary analysis, we found that the order of presentation of the decoys had no effect on the defensive behavior of Eleonora's falcons ($F_{1,63} = 0.17$, $P = 0.68$), so we did not include this variable in posterior analyses. We included the color morph of the decoy, the color morph of both breeding adults of the nest tested, and the interaction of these with the color morph of the decoy as explanatory variables. Year was included as a random factor. In all GLMMs, we used AICc as a criterion for model selection and used model averaging to summarize results (Grueber et al. 2011). For the model averaging procedure, we generated a global model containing all the predictors. We standardized input variables before model analysis. This allows the standardization of binary variables (i.e., color morphs) as dummy variables to a common scale. We then derived a set of submodels (including the null model) from the global model by using the dredge function implemented in the *MuMIn* package (Barton 2013). To delineate a "top model set" from the set of submodels, we selected those models with a difference of $\Delta AICc < 2$. We used the natural average method to weight the estimate and error for each variable (Burnham and Anderson 2002). If more than 1 model is selected in the top model set, final model averaging combines parameter estimates derived from the top model set. As a measure of goodness-of-fit for mixed-effects models, we calculated the

variance explained (conditional R^2 , see Nakagawa and Schielzeth 2013) for each of the selected top models.

Covariation between coloration and breeding output

We tested adult morph effects on productivity (number of fledglings raised, $N = 451$ nests in the 2007–2011 period) and on laying date ($N = 363$ nests) using GLMMs with Gaussian error distribution and identity link function. In the model of productivity, we included the morph of both pair members, their interaction, and the morph of the male and female closest neighbors as explanatory variables. In the model of laying date, the morph of both pair members and their interaction were included as explanatory variables. Year was included as a random factor in all models. Again, we used AICc as a criterion for model selection and model averaging to summarize results of models with similar AICc's (<2) to the best model.

Heterogeneity in the social niche: spatial patterns and conspecific interactions

We used PPA (Wiegand et al. 2007) to describe the spatial distribution of Eleonora's falcon nests (n range: 82–111 during the study years) and to search for fine-scale processes underlying these patterns. Structured spatial patterns may arise from spatially structured habitat features (first-order effects) or from biological processes such as competition or conspecific attraction (second-order effects) promoting active spacing or clustering (Wiegand et al. 2007). To deal with spatial heterogeneity (Pélissier and Goreaud 2001), we created an homogeneous plot within the island surface that included all nests, and subsequently, we divided this main plot into 2 internally homogeneous subplots, identifying the 2 main regions on the island where most nests are concentrated (Caldera and Rapalobos) (Figure 1b). Finally, we measured territory size as the distance to the nearest neighbor. We used this proxy because in this species, the main benefit of maintain a breeding territory within the colony is to reduce the threat of intraspecific interference, kleptoparasitism, and predation (Walter 1979).

We implemented specific point-process models and calculated summary statistics (pair-correlation function $g(r)$) for the observed pattern for univariate and bivariate models (Wiegand and Moloney 2004) (see Supplementary 1: Section 3 for details on the procedure). The $g(r)$ statistic is equal to one under complete spatial randomness (CSR), whereas values above one indicate clustering and values below one indicate negative association (i.e., repulsion) (Melles et al. 2009). The patterns arising from multiple (199) simulations of the point-process were used to estimate 95%-confidence envelopes for the values of the summary statistic under a given point-process model (i.e., the 5th lowest and highest values). Departures from the point-process model highlighting that significant patterns occur if the observed summary statistic lies outside (above or below) the simulation envelopes (Wiegand and Moloney 2004). We performed 4 different analyses for every study year separately (see Supplementary 1: Section 3 for details).

Analysis 1

Univariate PPA (general patterns of nest distribution). We used a first-order univariate $g(r)$ test as a preliminary step to assess whether the spatial distribution of nests differed significantly from the null hypothesis of CSR. It defines a situation where a point is equally likely to occur at any location within the study plot, regardless of the location of other points. The mathematical model underlying CSR is a homogeneous spatial Poisson point process. Departures

from a Poisson process are interpreted as indication of aggregated or repulsive patterns (Diggle 2003).

Analysis 2

Three-dimensional PPA (dealing with altitude). We applied the 3-dimensional version of the standard g -statistic to the Caldera and Rapalobos subplots to analyze patterns derived also from altitude. The null hypothesis was again a uniform Poisson process representing CSR model.

Analysis 3

Space–time aggregation of nests. We analyzed space–time interactions in patterns of nest distribution by counting the number of pairs of events that are close in both space and time. We used egg laying date as a surrogate of the time of nest occupancy. To test the hypothesis of a stationary point process in both space and time, and because irregular space windows cannot be implemented in this procedure, we used $g(s,t)$ in its inhomogeneous version for testing patterns in the whole island. Analyses were performed for each male morph separately.

Analysis 4

Bivariate PPA (conspecific attraction of same colored individuals). We investigated second-order effects on spatial distribution of nests as a consequence of behavioral interactions. Univariate forms of $g(r)$ for a single-point pattern can be extended to bivariate analyses in order to test the relationships between 2 point patterns (Lotwick and Silverman 1982). The analysis was thus implemented in a bivariate marked point pattern framework, referred in our case to dark and pale morphs. It estimates, for instance, the mean density of dark morphs (subscript 1) at distance r of pale morphs (subscript 2) (g_{12}). We used “random labelling” as the null model, which assumes that the probability of 1 event (nest occupancy) is equal for all points, i.e., it does not depend on the color morph of neighbors. During the randomization procedure, nest points for 1 color morph (always the second subscript) are shuffled between nests locations of the other morph (always the first-reference subscript) and vice versa. We also tested for departures from the null model by assessing the significance of pairwise differences between g functions. Thus, $g_{12}(r) - g_{11}(r)$ reveals whether there is any relationship between nests of differently colored individuals (g_{12}), and also whether there is an additional pattern between the nests of falcons with the same color (in this example, dark g_{11}), independently from the location of the nests occupied by the alternative color morph. Analyses of morph relationships were performed only for the main plot, rather than for the subplots, and for each sex separately due to the small sample size. All analyses were run in R software v3.0.2 (R Core Development Team 2013).

RESULTS

Morph frequencies

In our study population, there was no significant variation in morph frequencies among years in both adults (males: $\chi^2 = 2.05$, $df = 4$, $P = 0.73$, $N = 467$; females: $\chi^2 = 2.52$, $df = 4$, $P = 0.64$, $N = 466$) and nestlings ($\chi^2 = 7.51$, $df = 4$, $P = 0.11$, $N = 708$) (Supplementary 2: Figure A2).

Exploitation of alternative ecological niches

The environmental component, in general, accounted for a low proportion of variation in nest occupancy by the different morphs,

whereas the spatial structure accounted for a higher proportion across all years except 2011 (Table 2). The proportion of deviance explained by the joint effect of environmental and spatial data was negligible (negative values) for all years except 2011. Of all the environmental predictors considered in the final models, only altitude was significantly different between nests occupied by different morphs across all years except 2007 (Table 2), with dark falcons selecting higher locations (all-years mean \pm SE = 160.74 ± 8.82 a.s.l.) than pale ones (all-years mean \pm SE = 75.68 ± 3.91 a.s.l.). Depending on the year, other environmental variables were also significant, indicating that in addition to altitude, other environmental features determining the distribution of nesting sites by different morphs are not consistent (Table 2). Overall, the influence of the spatial pattern resulted primarily from fine-scale variation and to a lesser extent from broad-medium-scale variation (Table 2), suggesting the influence of local factors (patterns within subplots) on nesting site distribution, rather than general patterns related to the location of major breeding clusters. The deviance explained by the final models including all variables was low (<35 %, see Table 2). Therefore, the remaining unexplained variation can result from either unmeasured environmental variables or, more likely, from biotic fine-scale processes that cause differences in the distribution of nesting sites by the different morphs (e.g., social interactions). These processes were assessed in detail using PPAs (see below).

Morph-specific competitiveness: dominance relationships and breeding output

In those trials, where the sex of the attacker was known, males attacked more often than females (32 vs. 13 attacks in 2008, and 33 vs. 9 in 2009). Overall, pale males attacked the decoy (regardless of its color morph) more often than dark males (pale male mean \pm SE = 5.75 ± 2.58 attacks; dark male mean \pm SE = 1.61 ± 0.54 attacks). The mean number of attacks \pm SE that the dark decoy received was 2 ± 0.96 from dark males and 6.33 ± 3.63 from pale males, whereas the pale decoy received 1.22 ± 0.55 from dark males and 5.17 ± 3.73 from pale males. The variance explained

(conditional R^2) by the 2 top models retained in the averaged model of defensive response to the decoy was 0.87 in both cases. Relative importance of the explanatory variables was as follows: the morph of the male (1), the morph of the female (1), and the morph of the decoy (0.7). None of the confidence intervals for the parameter estimates included zero (Table 3), indicating that all these predictors significantly influenced defensive behavior (see Supplementary 2: Table S1 for details). The probability of attacking the decoy was higher for pale males and females than for dark morphs, and the dark decoy received more attacks than the pale decoy.

Breeding output was higher in those nests with a dark male, irrespective of the color morph of the female, over time (dark male mean \pm SE = 1.81 ± 0.11 fledglings; pale male mean \pm SE = 1.54 ± 0.05 fledglings, $N = 462$, mixed model Anova with year as a random factor: $F_{1,455,1} = 6.13$, $P = 0.01$; see Supplementary 2: Table S2). The averaged model of breeding output retained only 2 top models, for which conditional R^2 was 0.25 in both cases. Relative importance of the predictors was as follows: the morph of the male (1), the morph of the female (1), the morph of the female neighbor (1), and the morph of the nearest male neighbor (0.56). The color morph of the male had the highest averaged coefficient and it was the only variable that clearly affected productivity (i.e., the only variable for which confidence intervals for the parameter estimates did not include zero, see Table 3). The probability of raising more fledglings was higher in those nests with a dark male (see Supplementary 2: Table S1 for details). Laying date did not differ between alternative color morphs. Conditional R^2 of all models with laying date as the dependent variable was nearly zero and all confidence intervals included zero as well (Table 3).

Spatial patterns and conspecific relationships

The distance to the nearest neighbor was larger for dark males than for pale males (GLMM with male morph as the explanatory variable and year as a random factor, $F_{1,466} = 4.49$, $P = 0.03$, $N = 470$). The distance to the nearest neighbor also depended on the color morph of both the male of the target nest and the nearest male

Table 2

Results of the final GLMs including all previously selected environmental and spatial (PCNM variables denoted as PCNM-2 to PCNM-17; B indicated broad-scale patterns, whereas M indicates medium-scale patterns and F indicates fine-scale patterns) explanatory variables to select the most influential ones on the probability of dark males nest occupancy

	2007 (111)	2008 (101)	2009 (97)	2010 (83)	2011 (82)
% of explained deviance					
Environmental	13.36	12.11	15.24	12.12	11.81
Spatial	18.87	25.85	21.02	23.10	5.76
Joint effect environmental + spatial	-8.59	-4.44	-8.23	-10.92	1.66
Final model	23.63	33.53	28.03	24.29	19.23
Explanatory variables					
PCNM-2 B			*		
PCNM-8 M	**				
PCNM-11 F	*			*	*
PCNM-13 F		**			
PCNM-15 F				*	
PCNM-16 F	*	**			
PCNM-17 F		*			
Altitude		*	*	**	*
Slope			*		*
Profile_curve	*				
Viewshed	*	*			
Near neighbor distance				**	

Sample sizes (nests) are shown in brackets beside the years. Only significant (“**” 0.01, “*” 0.05) variables retained in the final models are shown. The deviance explained by each partial regression analysis, their joint effect and the deviance explained by the final GLMs is also shown for each study year.

neighbor (a similar GLMM considering also the color morph of the nearest male morph and its interaction with the color morph of the target male; male morph * male neighbor morph: $F_{1,353.2} = 3.60$, $P = 0.05$), with larger distances between dark to pale and pale to dark males than between dark to dark and pale to pale males (e.g., pale to dark vs. pale to pale: $F_{1,458.5} = 6.58$, $P = 0.01$).

First-order univariate tests showed significant nest clustering when considering the entire island (main plot) and the Rapalobos subplot (Figure 2a and c, respectively). In both sites, a strong pattern of clustering becomes evident at distances up to 200 m, whereas the $g(r)$ statistic indicated that nests were randomly distributed at scales over 200 m. The $g(r)$ also indicated that the local neighborhood density was 2-fold higher in Rapalobos than on the entire island. Conversely, the $g(r)$ test revealed no departure from CSR at all distance classes in the Caldera subplot (Figure 2b). In addition, pale male density was lower in Caldera than in Rapalobos. These patterns were consistent across all study years (Supplementary 2: Figure A3), although the aggregation pattern was higher in 2007.

Due to the high slope of the Caldera and Rapalobos subplots (Figure 3a and b), we applied a 3-dimensional version of the g -statistic to these subplots separately. This analysis revealed patterns of aggregation in the Caldera subplot (Figure 3c), which could not be observed in the former univariate PPA. When considering

altitude, clustering patterns in Caldera emerged at distances ranging from 100 to 200 m, but with a lower intensity than that found in Rapalobos (Figure 3d). The 3-dimensional PPA showed that local neighborhood density in Rapalobos was more than 20 times higher than expected by a random distribution. Aggregation patterns were densest at distances up to 300 m (Figure 3d) and less dense between 400 and 600 m, likely reflecting the orography of this area—which comprises 2 closely located hills (Rapadura and Lobos) separated by a narrow valley. Similar patterns were found across all years (Supplementary 2: Figure A4).

The space–time PPA revealed different patterns of nest occupation by alternative color morphs (Figure 4). Only dark males showed spatiotemporal clustering, which took place at small spatial distances (<100 m) and within the whole temporal range allowed by the test (10 days) (Figure 4a). In contrast, occupancy of nests by pale males took place more regularly across the space and time ranges considered (Figure 4b). The pattern of spatiotemporal aggregation at small spatial distances of dark males was consistent across years, although the location of peaks along the temporal scale varied slightly over time (Supplementary 2: Figure A5).

Although significant patterns of aggregation among nests of pale males (g_{22}) were found in 2007, nests of same-colored individuals, both males and females, generally did not show departures from

Table 3
Summary statistics of the averaged models of dominance relationships (aggressiveness) and breeding output (productivity and laying date)

Explanatory variables	Models											
	Aggressiveness				Productivity				Laying date			
	2.5%	97.5%	Estimate	SE	2.5%	97.5%	Estimate	SE	2.5%	97.5%	Estimate	SE
Decoy morph	-0.46	-0.00	-0.16	0.14								
Male morph	0.96	1.74	1.35	0.19	-0.48	-0.04	-0.26	0.11	-0.79	2.69	0.56	0.82
Female morph	1.58	3.23	2.41	0.41	-0.35	0.12	-0.11	0.12	-2.45	1.3	-0.29	0.74
Nearest male neighbor morph					-0.28	0.16	-0.03	0.11				
Nearest female neighbor morph					-0.33	0.14	-0.09	0.12				

Confidence intervals (2.50% and 97.50%) and full model averaged coefficients (with shrinkage) ± SE for the variables retained in final models are shown.

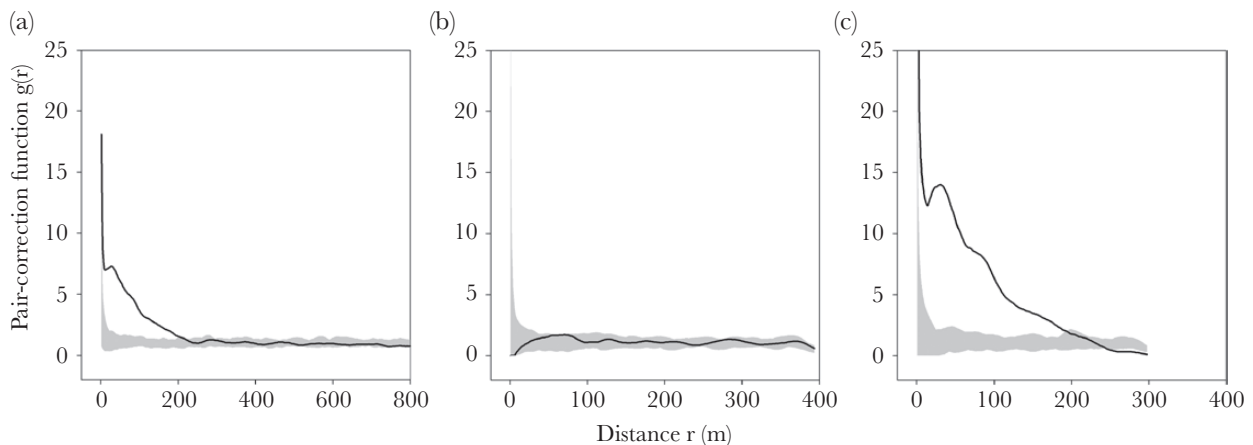


Figure 2
 (a) Results of univariate point pattern analyses (i.e., the study of the spatial arrangements of points in space) of nest distribution in 2007 for the main plot ($N = 70$ nests), (b) Caldera subplot ($N = 61$ nests), and (c) Rapalobos subplot ($N = 50$). The pair-correlation function $g(r)$, defined as the expected density of nests within a given ring radius of an arbitrary point (nest), divided by the mean density of the pattern, provides a measure of spatial ordering. The $g(r)$ estimated from the data and related to the scale (r) is contrasted with simulation envelopes (gray area) derived from 199 simulations of the null model of CSR within the study area. Patterns are considered aggregated if the $g(r)$ statistic lies above the simulation envelopes. Results corresponding to 2008–2011 are presented in Supplementary 2: Figure A3.

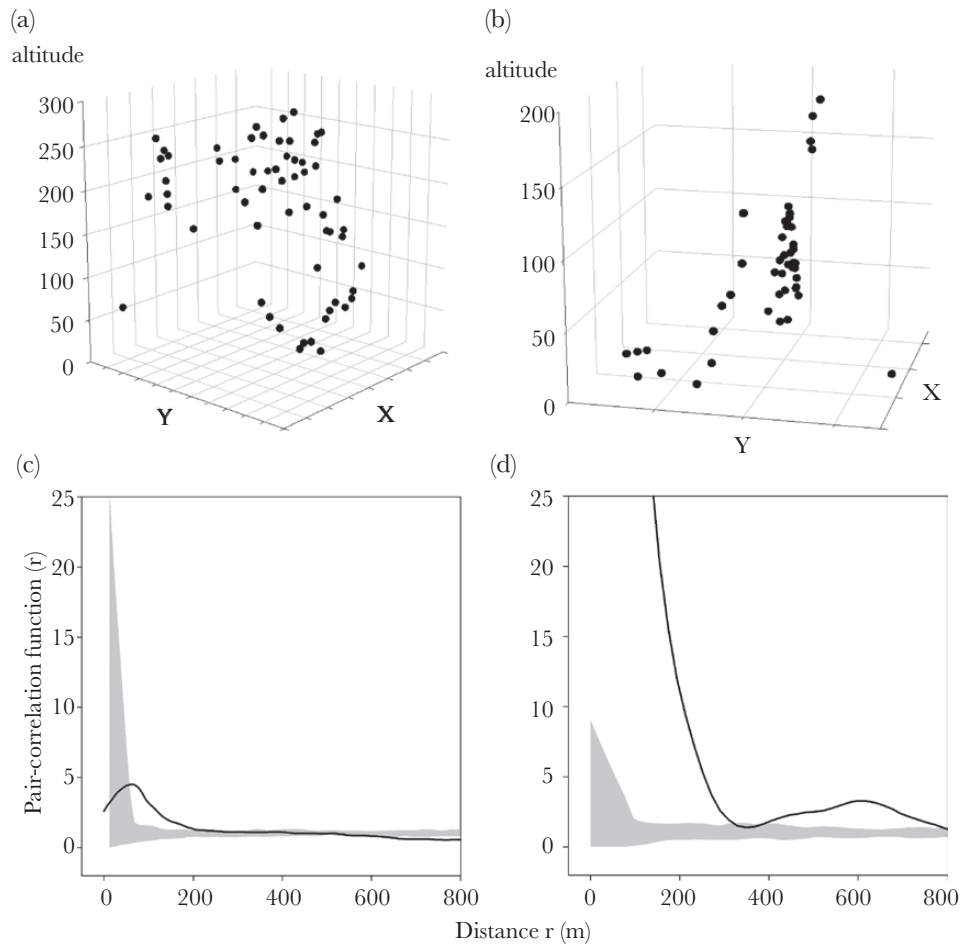


Figure 3

(a) Three-dimensional distribution of nests in the Caldera subplot and (b) Rapalobos subplot. Sample sizes are identical to those of Figure 2(c) and (d) Results of the 3-dimensional point pattern analyses from 2007. Three-dimensional version of the standard g -statistic (black lines) contrasted with simulation envelopes (gray area) derived from 199 simulations of the null model of CSR within the study area. Results corresponding to 2008–2011 are presented in Supplementary 2: Figure A4.

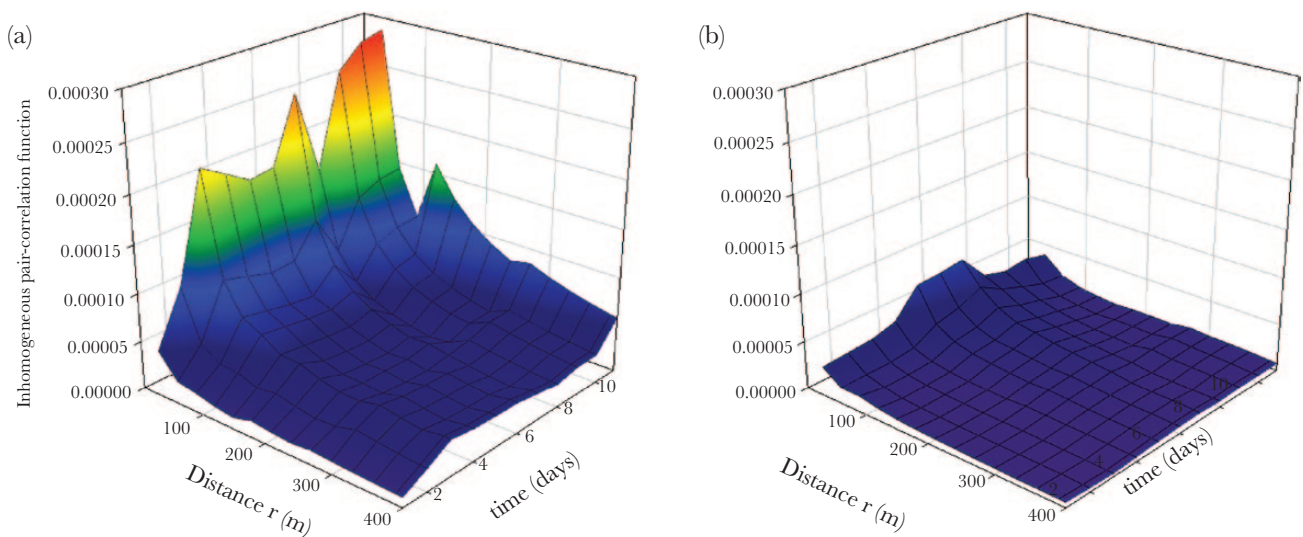


Figure 4

Graphical representation of the estimated space–time inhomogeneous pair correlation function $g(s,t)$ obtained for nests with (a) a dark male and (b) a pale male falcon from the main plot in 2007 ($N = 70$). Values above 0 indicate spatiotemporal clustering. Results corresponding to 2008–2011 are presented in Supplementary 2: Figure A5.

random expectations over time (Supplementary 2: Figure A6). However, results of the bivariate PPA revealed a pattern of negative association (i.e., repulsion) between nests of alternative color morphs. This negative association was more pronounced in the case of pale males repulsing dark ones ($g_{12}-g_{21}$, Figure 5b) than in dark males repulsing pale ones ($g_{12}-g_{11}$), given that the latter only occurred in 2007 (Figure 5a). In all study years, a significant repulsion of dark males by pale males was observed at distances below 200 m (Figure 5b and Supplementary 2: Figure A7). On the other hand, pale females showed slight negative associations to dark females (Figure 5d) at distances that varied from 100 to 200 m in all years except 2010 (Supplementary 2: Figure A7). Like males, dark females showed no departures from the null model in most years, with only small signs of repulsion in 2007 (Figure 5c) and of aggregation in 2010 (Supplementary 2: Figure A7).

DISCUSSION

In this study, we tested the hypothesis that alternative phenotypes show different performances when co-occurring in breeding areas. We found that social dominance relationships, and to a lesser extent morph-specific ecological requirements, influence the spatial distribution of falcon nests. As predicted under the mechanisms of exploitation of alternative ecological niches and heterogeneity in

the social environment, the spatial distribution of Eleonora’s falcon nests was not random with regard to color morph. Instead, alternative morphs were segregated over suitable habitats by forming same-color clusters or permanent neighborhoods (the same patterns observed across years). This pattern of segregation of breeding territories within the same population was already reported in other bird species, such as the common guillemot *Uria aalge* (Birkhead et al. 1980), and the color polymorphic white-throated sparrow *Zonotrichia albicollis* (Formica et al. 2004; Formica and Tuttle 2009). In all these studies, the authors concluded that segregation was due to social rather than ecological reasons, which suggests that behavior may be a widespread, yet rarely addressed, mechanism shaping spatial distribution of competing morphs at small geographical scales. In agreement with this, evidence of morph-specific habitat selection in our study population was weak. Nests of pale and dark male falcons did not differ for most of the environmental variables considered. Only altitude differed between morphs, with dark male falcons occupying higher locations.

Melanin-based coloration is known to play an important role in thermoregulation (Roulin 2004) because melanin can affect efficiency of solar absorption. Dark morphs present a lower reflectance and higher temperature excess when irradiated than pale morphs (Roulin 2004). It might be possible that dark individuals gain benefit in terms of thermoregulation at high altitudes, which

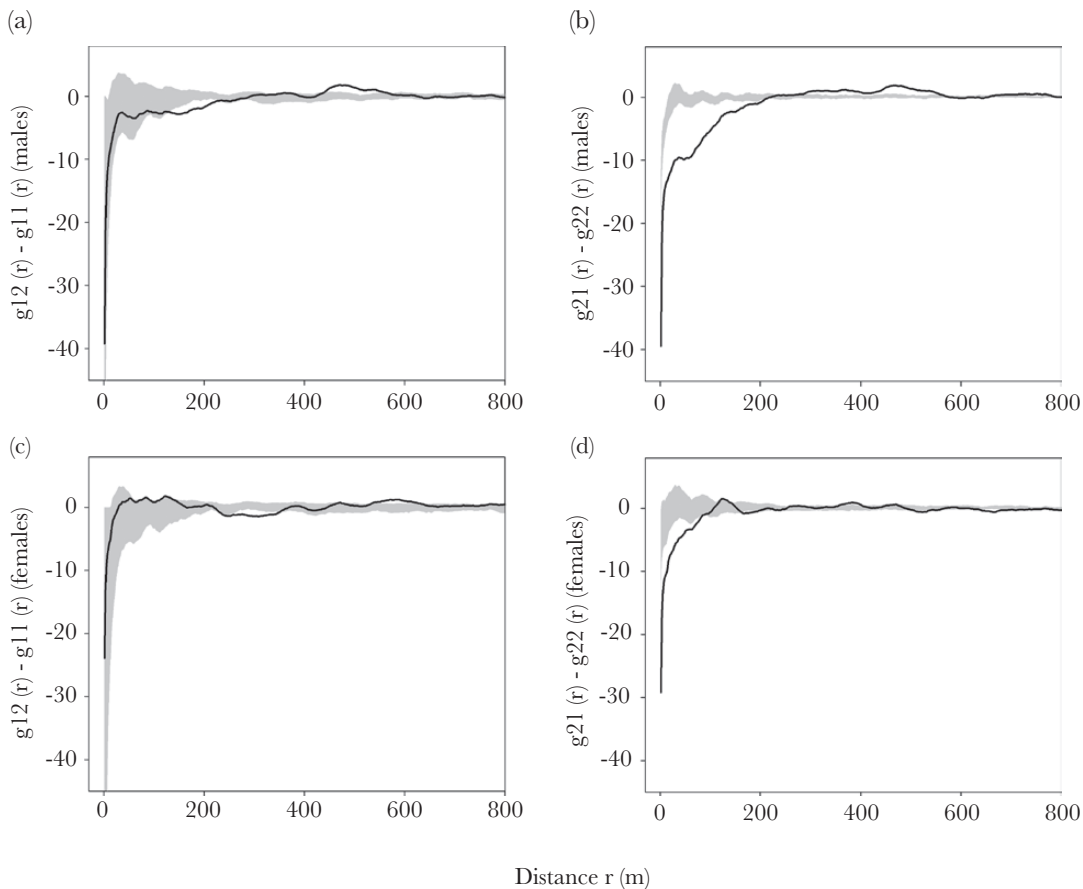


Figure 5 (a) and (b) Results of bivariate point pattern analyses of males ($N = 70$) and (c) and (d) females ($N = 70$) highlighting patterns between 2 point patterns (the 2 morph types) (g_{12} or g_{21}), additionally to the same-color morph distribution pattern (g_{11} or g_{22}) in 2007. Code 1 indicates the dark morph, whereas code 2 denotes the pale morph. In the bivariate case, only neighbors of the opposite pattern are counted within a ring of an arbitrary point. The observed test statistic is represented with a black line, whereas gray areas enclose simulation envelopes from 5th lowest to highest values of the test statistic taken from 199 simulations of the null model of random labelling. Values above the envelopes represent clustering, whereas values below the envelopes represent repulsion. Results corresponding to 2008–2011 are presented in Supplementary 2: Figure A7.

are predictably cooler than low altitudes (Körner 2007). We cannot discard this possibility, but if it were the case, one would also expect that dark individuals select more shady nests. However, this variable did not differ between nests occupied by pale and dark falcons. In this species, the main function of maintaining a territory within the colony is the nest defense against conspecific competitors and predators, because food resources are external to the breeding colony. Walter (1979) found that Eleonora's falcons having comparatively higher and larger territories were dominant, that is, rarely attacked or intimidated by a neighbor. Regardless of potential advantages for a particular color morph, higher positions may confer competitive advantages by providing, for instance, a better lookout from perches, which might facilitate the detection of intruders, the delivery of prey to a female in the air, and defensive behaviors (e.g., nose dive).

The territory size of dark male falcons was larger than that of pale falcons. In this context, the fact that dark males occupy better locations suggests that they have the opportunity to choose. This implies that they should settle before pale ones or that they are more aggressive. However, the timing of nest occupancy did not differ between alternative morphs, although there was a general, yet not significant, tendency of earlier settlement by dark males across all years. Nevertheless, dark males showed patterns of spatio-temporal clustering at small scales, whereas pale males widely filled the suitable habitat over the established time frame. Johnson and Burnham (2013) found that white male Gyrfalcons *Falco rusticolus* fathered significantly earlier clutches than gray males, whereas no significant association was found between female color and laying date. Further, Dreiss and Roulin (2010) found that not only color morph is associated with laying date but also the between-year change in coloration in barn owls (*Tyto alba*). Thus, females that acquire larger eumelanic spots over time bred earlier and laid larger eggs, whereas adults of both sexes produced larger clutches and broods when they became less reddish pheomelanic.

Interestingly, the apparent dominance of the dark morph with regard to the choice of better nest-sites was not associated with aggressiveness. Several studies have shown differential defensive behavior between alternative color morphs in a number of related species, such as the common buzzard *Buteo buteo* (Boerner and Krüger 2009), marsh harrier *Circus aeruginosus* (Sternalski and Bretagnolle 2010), barn owl *Tyto alba* (van den Brink and Dolivo et al. 2012), European kestrel *Falco tinnunculus* (van den Brink and Henry et al. 2012), and tawny owl *Strix aluco* (Da Silva et al. 2013). Our decoy presentation experiment demonstrated that the dark morph was less aggressive than the pale one, as the latter was the subject of most aggressive interactions that were further increased when a pale male and female were present. In contrast, Boerner and Krüger (2009) found a stronger defensive behavior from light-colored common buzzard males toward an interspecific predator, whereas the reverse pattern was found in females, and no differences in aggressiveness against intraspecific competitors. Likewise, Tuttle (2003) found that male and female pale white-throated sparrows were more aggressive than tan conspecifics, whilst behavioral responses to intrusions did not differ between morphs. In an experimental study with barn owls, van den Brink and Dolivo et al. (2012) found that those nestlings displaying smaller black eumelanic spots were bolder, more aggressive and agitated while handled than large-spotted nestlings. These authors suggested that the shy behavior of the more eumelanic barn owls seems to pursue the avoidance of a direct confrontation or even a fight, which could also be the case in our study species.

The frequency of agonistic interactions is expected to be related to the local conspecific density (Mougeot et al. 2003). In this regard, individual decisions (where to settle) can modify the social landscape to achieve the optimal social niche (Formica and Tuttle 2009). Dark males were concentrated in a less dense area and thus had larger territories. In contrast, pale males were preferentially located in areas where local neighborhood density was intensified. Moreover, each male morph settled close to males of the same color and far from different ones. One of our most important findings is precisely this negative association (repulsion) between alternative phenotypes, which was more intense in the case of pale males reacting to dark males. Interestingly, and despite this segregation, mate pairing is not assortative in this species. A hypothesis that may explain this pattern of segregation is the possibility of a contagious distribution resulting from extreme philopatry. A nest with at least 1 dark adult may produce dark juveniles over time, which can later recruit close to their natal nests and ultimately form same color neighborhoods. However, long-term data on leg ring recoveries appear to contradict this hypothesis. The distance of recruitment from the natal nest was very similar between morphs (pale $N = 34$, mean \pm SE = 1408 ± 185.73 m vs. dark $N = 9$, mean \pm SE = 1558.44 ± 438.35 m) and was shorter in males (mean \pm SE = 1163.24 ± 257.96 m) than in females (mean \pm SE = 1703.18 ± 281.55 m), although the difference was not significant ($F_{1,40} = 2.87$, $P = 0.09$). These distances do not suggest that young falcons recruit at sufficiently short distances from their natal nest to form clusters, but rather disperse all over the island surface.

Fitness consequences

For genetic polymorphisms to be evolutionarily stable, the alternative forms must gain equal fitness benefits over evolutionary time (Smith 1982). A likely mechanism would be local adaptation, with morphs behaving differently in different environments. We found that dark males produced more fledglings than pale males, irrespective of the proximity of different male and female morphs. It is important to note that breeding output in this population strongly depends on external abiotic factors, that is, the influx of migratory bird prey depends primarily on seasonal trade winds (Gangoso et al. 2013). In addition, during prolonged periods of food scarcity, intraspecific predation becomes one of the most important factors affecting breeding output. Our data on ring recoveries indicate that intraspecific predation was much more frequent in dense areas (18 cases in Rapalobos and 3 in Caldera), where the opportunity of predation is higher (Lima 2009), and that predation events always occurred between nearby nests, most of them (95.24 %) in the nests of pale-pale pairs.

Taken together, the evidence suggests that pale and dark falcons adopt different breeding strategies, with pale morphs behaving highly colonially and dark morphs being more territorial, although their relative advantages depend on the environmental conditions. Moreover, alternative phenotypes may be unevenly affected by different habitat features and the fitness consequences ensuing (e.g., Krüger 2002). The territorial strategy seems to have clear advantages: by living in more isolated neighborhoods, dark males avoid high rates of agonistic interactions and also intraspecific kleptoparasitism and predation, which are ultimately translated into higher breeding output. In addition, the higher contact rate between individuals in dense colonies is also likely to increase the probability of parasites and pathogens transmission (Côté and Poulin 1995; Brown and Brown 2004). Gangoso et al. (2011, 2015) found that innate immunity of nestling Eleonora's falcons was morph-specific,

with dark males exhibiting lower immune responses than pale ones. This suggests that the noncolonial strategy of dark falcons may be advantageous in terms of pathogen-related fitness costs. The alternative, highly colonial strategy of pale falcons could be particularly advantageous under conditions of high food availability and in those areas where the abundance of predators becomes an important selective agent, due to the social defensive behavior of the species. Moreover, the higher immune capacity of pale falcons would be beneficial under conditions of high population densities. Therefore, color polymorphism can be maintained within this population because of temporal fluctuations in selective regimes (food availability, pathogens, competitors, and predators) favoring 1 or the other strategy.

The finding of higher breeding output achieved by dark falcons might suggest that the dark phenotype will gradually spread through the population. However, dark individuals not only produce dark offspring. The Mendelian inheritance of this trait, coupled with the fact that most dark individuals are heterozygous for the *MC1R* allelic variant (Gangoso et al. 2011), leads to that dark–dark and dark–pale (or pale–dark) pairs have pale chicks with a probability of 25% and 50%, respectively. In addition, morph frequencies in this study population are in Hardy–Weinberg equilibrium (Gangoso et al. 2015) and the probability of recruitment relative to morph frequencies in each cohort did not differ between alternative phenotypes (2007 cohort: $\chi^2 = 0.14$, $df = 1$, $P = 0.71$, $N = 152$; 2009 cohort: $\chi^2 = 0.98$, $df = 1$, $P = 0.32$, $N = 164$; 2010 cohort: $\chi^2 = 0.77$, $df = 1$, $P = 0.38$, $N = 173$). Nonetheless, it is important to note that this is a long-distance migratory species and thus, the relative advantages of each particular strategy may be counterbalanced by other factors when migrating to and overwintering in Madagascar. The observation of directional selection favoring the dark morph during the breeding season may be thus a transient situation that can mirror temporal perturbation around an evolutionary equilibrium (e.g., Emaresi et al. 2014). We suggest that balancing selection may act on such competitive asymmetries and different breeding strategies over time, likely precluding 1 morph overcoming the other morph and thus contributing to the evolutionary stability and long-term maintenance of color polymorphism in wild populations.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>

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