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Research article

No support for solar radiation as a major evolutionary driver of malar stripes in falcons

Michelle Vrettos[1], **Chevonne Reynolds**[2] **and Arjun Amar**[1]

[1]Fitzpatrick Institute of African Ornithology, University of Cape Town, Cape Town, South Africa
[2]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

Correspondence: Arjun Amar (arjun.amar@uct.ac.za)

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The malar stripes of falcons (*Falco* spp.) are often hypothesised to function by reducing the amount of solar glare reflected into the falcon's eyes while hunting, thereby aiding foraging efficiency in bright conditions. This 'solar glare hypothesis' is supported by intraspecific trends in peregrine falcons *Falco peregrinus*, in which populations inhabiting regions of higher average annual solar radiation exhibit larger and darker malar stripes on average. Here, we extend the methodological approach previously used in peregrine falcons to examine both intra- and interspecific relationships between solar radiation and malar stripe morphology across all extant falcon species, thereby providing a more robust test of the hypothesis that falcon malar stripes evolved as an adaptation against negative visual effects of solar glare. We obtained web-sourced photographs of all extant falcon species, taken across each species' geographic range, and related mean breeding season solar radiation at each photograph location to the size and darkness of the birds' malar stripes, simultaneously testing for intraspecific and interspecific relationships between malar stripe characteristics and solar radiation, and including phylogeny and relevant ecological traits as covariates. We found no consistent interspecific relationship between solar radiation and malar stripe characteristics Likewise, in 38 out of 39 species, malar stripe characteristics were not positively intraspecifically related to solar radiation, with only peregrine falcons showing trends towards larger and darker malar stripes in brighter regions. Falcon malar stripes are thus unlikely to represent an adaptation against visual effects of solar glare, and their adaptive significance is more likely to be explained by crypsis or social signalling, if indeed they do represent an adaptive trait. Malar stripes may have become co-opted for solar glare reduction in peregrine falcons due to the species' specialisation for high-speed aerial hunting, although the intraspecific patterns observed may alternately be explained by phylogeography.

Keywords: avian colouration, dark eye markings, facial plumage, falcon, malar stripe, solar glare

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Introduction

Animal colouration represents the outcome of various interacting evolutionary pressures (Burtt 1981, 1986, Romano et al. 2019). In the case of dark eye or under-eye markings, one such pressure may be the efficacy of dark pigment in absorbing excess sunlight or solar glare, and therefore reducing obstructive effects of sun glare on vision (Ficken et al. 1971, Yosef et al. 2012, Vrettos et al. 2021). Solar glare disrupts vision by flooding the retina with diffuse light, impairing contrast detection and object resolution (DeBroff and Pahk 2003). Dark pigments around or below the eyes may absorb this excess light, thereby aiding the animal in distinguishing and targeting objects in bright conditions, a crucial ability for diurnal predators hunting moving prey (DeBroff and Pahk 2003, Yosef et al. 2012, Vrettos et al. 2021).

Evidence suggests that such a role for dark eye markings may be widespread among animal taxa. Dark eye patches and facial masks are most commonly found in species associated with bright environments (Ficken et al. 1971, Ortolani 1999), while Burtt (1986) found that the eye-lines and upper mandibles of wood-warbler (Parulidae) species inhabiting bright environments are darker than predicted from the colouration of other body surfaces outside the visual field (Burtt 1986). Experimental lightening of the upper mandible in willow warblers *Empidonax trailii* and the facial mask in masked shrikes *Lanius nubicus* have also been found to reduce the birds' foraging efficiency in sunlight and induce a preference for foraging in more shaded locations (Burtt 1984, Yosef et al. 2012).

Mechanistic studies have likewise quantified the effects of dark eye markings on susceptibility to glare. Lebow (2020) found that larger dark facial patches were associated with a reduced amount of irradiance reflected into the eyes of avian museum specimens under laboratory conditions (Lebow 2020). Similarly, DeBroff and Pahk (2003) found that application of commercially available 'eye black' grease (commonly used by athletes) to human subjects significantly improved the subjects' visual performance in bright conditions (DeBroff and Pahk 2003).

A characteristic feature of the falcons (genus *Falco*) is the presence of paired dark malar stripes below the eyes, which are unique among raptors (Vrettos et al. 2021). These stripes vary substantially both within and between species, with some species exhibiting wide, solidly coloured malar stripes, varying in colour from pale grey to black, which provide the falcon with a 'hooded' appearance (e.g. the peregrine falcon *Falco peregrinus*), whereas other species exhibit thin, pale stripes consisting of only a few, scattered grey, black, or brown feathers (e.g. the saker falcon *Falco cherrug*) (Ferguson-Lees and Christie 2001). Falcon malar stripes are commonly hypothesised to function by reducing negative effects of solar glare or harsh sunlight on the falcon's vision, thereby aiding visual targeting of prey in bright conditions (the 'solar glare hypothesis' Vrettos et al. 2021). Bortolotti (2006) argued that falcon malar stripes are unlikely to serve such an anti-glare function, since some falcon species that inhabit bright desert environments (e.g. the saker falcon) have small or pale malar stripes, or even lack them entirely, whereas others inhabiting dark forest environments (e.g. orange-breasted *F. deiroleucus* and bat falcons *F. rufigularis*) have solid black heads (Bortolotti 2006). However, Vrettos et al. (2021) suggested that ecological differences between species may affect the strength of selection on glare-reducing traits. For example, orange-breasted and bat falcons specialise in hunting agile, airborne prey, and therefore presumably experience stronger selection on traits that aid visual tracking of moving targets than do saker falcons, ground-hunting generalists that feed more frequently on mammals (Vrettos et al. 2021). Phylogenetic structuring may likewise account for some differences in malar stripe characteristics between different falcon species, meaning that both phylogeny and ecology should be considered when testing the solar glare hypothesis interspecifically (Vrettos et al. 2021).

Vrettos et al. (2021) found support for the solar glare hypothesis in peregrine falcons using analysis of web-sourced 'citizen science' photographs taken across the species' range. Intraspecific variation in malar stripe characteristics in this species was consistent with the predictions of the hypothesis, with populations inhabiting regions of higher average annual solar radiation exhibiting wider and darker malar stripes, and overall darker or more hooded heads (Vrettos et al. 2021). While this evidence was correlative and did not demonstrate a causal link between solar radiation and malar stripe characteristics, the findings were suggestive of malar stripes functioning as an adaptation for solar glare reduction in falcons (Vrettos et al. 2021).

Here, we extended the approach of Vrettos et al. (2021) to all extant *Falco* species, to determine whether the same trend of larger and darker malar stripes in populations inhabiting regions of higher solar radiation would be observed intraspecifically within other falcon species, as well as interspecifically. We predicted that the trends found previously in peregrine falcons would be replicated across most species, and that there would be a positive association between a species' average malar stripe size and darkness and its average solar radiation environment. Following Vrettos et al. (2021)'s argument that ecological differences between species may affect the selective importance of glare-reducing facial markings, we also tested relationships between malar stripe characteristics and body mass, hand-wing index, prey preference, and habitat openness across species, and investigated whether adjusting for these factors affected observed relationships with solar radiation. We predicted that small, agile falcons, species specialised for hunting aerial (bird) prey, and species associated with open environments would show stronger intraspecific effects of solar radiation on malar stripe characteristics, as well as larger and darker malar stripes on average.

Material and methods

Photograph selection

We obtained photographs of adult falcons (maximum of 1000 per species) from two online citizen science

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databases, the Macaulay Library (https://www.macaulaylibrary.org) and GBIF (https://www.gbif.org). We obtained photographs for a total of 39 species, treating the Barbary falcon *Falco* (*peregrinus*) *pelegrinoides/babylonicus* as a distinct species due to its unresolved taxonomic position (Ferguson-Lees and Christie 2001, Fuchs et al. 2015, McClure et al. 2020). Photographs were filtered to include only those taken within the resident and/or breeding range of the species (using species distribution maps provided by BirdLife International 2020) and, for species in which migratory and resident populations overlap geographically, taken within the breeding months, when wintering migrants were unlikely to be present. For species with fewer than 100 usable photographs available from this standard search, we sourced additional photographs from Flickr (https://www.flickr.com), Oiseaux (https://www.oiseaux.net), BirdGuides (https://www.birdguides.com), the African and Oriental Bird Club Image Databases (https://africanbirdclub.org/afbid, https://www.macaulaylibrary.org/oriental-bird-images/), and private photographers via email correspondence (Acknowledgements). See the Supporting information for full details of the photograph selection and filtering process.

Malar stripe scoring

Following Vrettos et al. (2021), we quantified three malar stripe characters: 1) length, 2) width, and 3) darkness (Fig. 1). A single observer (MV) visually scored each character on an eleven-point scale (based on the ten-point visual scales used by Vrettos et al. (2021), with a zero score added to account for birds without definable malar stripes) (Fig. 2). Photographs were scored in random order, with the observer unaware of their location and species during the scoring process. Following Vrettos et al. (2021), the angle, position, and degree of plumage distortion of the bird's head in each photograph were also scored according to a set of visual scales (Supporting information), so that these could be included in statistical models as fixed covariates to account for any potential effects of visual distortion on the malar stripe scores (Vrettos et al. 2021). Detailed definitions of all variables and the scoring system used are provided in the Supporting information.

Solar radiation data

For each photograph GPS location, we extracted 30-year (1991–2020) average monthly downward surface shortwave radiation (hereafter solar radiation) (W m^{-2}) from the TerraClimate dataset (Abatzoglou et al. 2018) using Google Earth Engine (Gorelick et al. 2017). For photographs that lacked embedded coordinates, the coordinates of the general area were instead sourced from Google Maps based on the written description of the photograph's location. For each datapoint, the monthly values for the six-month period encompassing the species' or population's breeding season (March–August for boreal summer breeders, and September-February for austral summer breeders) were then averaged to produce a single solar radiation value for each datapoint, representing the 30-year average of solar radiation conditions experienced during the relevant species' breeding season at that GPS location. For full details regarding how these breeding seasons were defined, see the Supporting information.

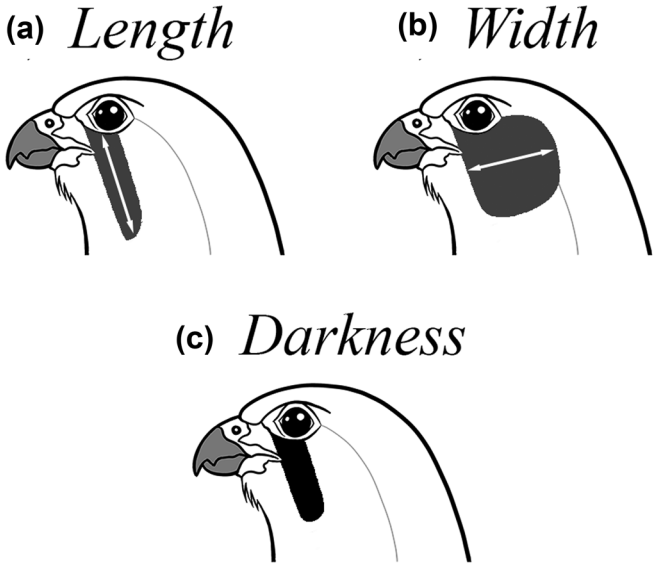

Figure 1. Illustration of the three malar stripe variables quantified in this study, namely (a) malar stripe length, (b) malar stripe width, and (c) malar stripe darkness. Scoring variables and categories were adapted from those used by Vrettos et al. (2021).

Species trait data

For each species, we collected data on four biometric and ecological traits: body mass (g), hand-wing index (HWI), prey preference, and habitat openness. We sourced body mass estimates and HWI values from AVONET (Tobias et al. 2022). We independently calculated body mass estimates for the peregrine and barbary falcons, based on values provided in Ferguson-Lees and Christie (2001) and Dunning (2008), since these two taxa are not differentiated in AVONET. To model prey preference, we assigned all species a score of 1–4 representing the proportion of birds in their diet, based on diet descriptions provided in Ferguson-Lees and Christie (2001), with higher scores representing a higher degree of specialisation on bird prey (Supporting information). We likewise derived a 'habitat openness' term for each species by converting habitat descriptions provided in BirdLife International (2020) and Ferguson-Lees and Christie (2001) into scores of 1–5, with higher scores representing more open (less forested) habitats (Supporting information). For the rock kestrel *Falco rupicolus*, which the literature largely treated as conspecific with the common kestrel *F. tinnunculus*, we instead assigned scores for prey preference and habitat openness based on the species' description in 'Roberts birds of southern Africa' (Hockey et al. 2005).

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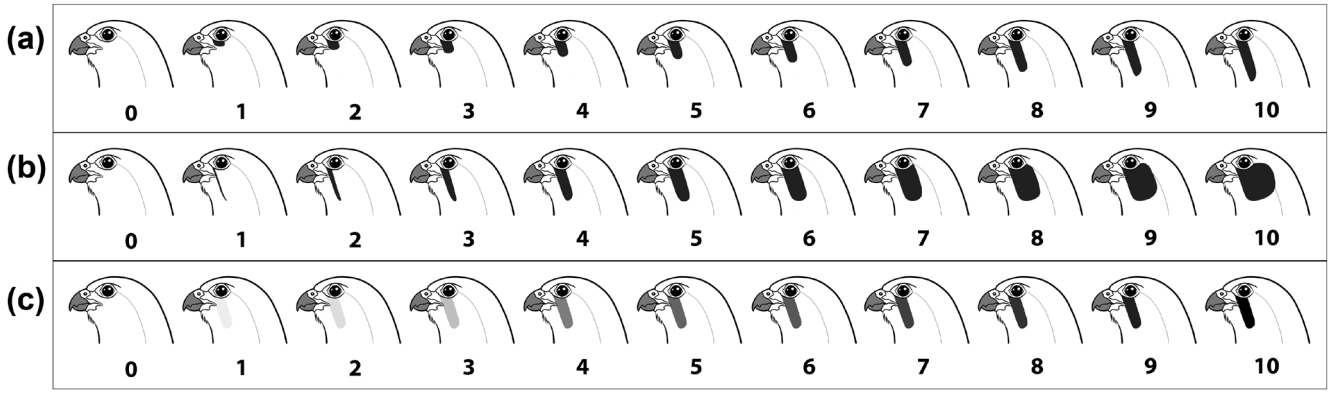

Figure 2. Eleven-point visual scales used to quantify variation in (a) malar stripe length, (b) malar stripe width, and (c) malar stripe darkness in web-sourced photographs of falcons. Scoring variables and categories were adapted from those used by Vrettos et al. (2021).

Statistical analysis

We investigated relationships between malar stripe characteristics, mean breeding season solar radiation, and species traits using Bayesian generalised linear mixed models (GLMMs), constructed using R-INLA (Rue et al. 2009, Lindgren and Rue 2015). This approach uses the integrated nested laplace approximation (INLA) method to estimate posterior distributions of model parameters, including random effects such as spatial autocorrelation (Rue et al. 2009, Dinnage et al. 2020). To enable simultaneous modelling of both spatial and phylogenetic effects, we used the 'spatio-phylogenetic' method developed by Dinnage et al. (2020), with phylogenetic information supplied in the form of a multi-locus consensus tree derived from Fuchs et al. (2015), and the spatial effect modelled using the stochastic partial differential equation (SPDE) approach, using a triangulated spatial mesh constructed from the latitude and longitude coordinates of each photograph location (Lindgren and Rue 2015, Dinnage et al. 2020). Full details of the statistical approach and construction of the statistical models are provided in the Supporting information.

To model intraspecific and interspecific effects, we used a contextual effects or 'within-between' approach (van de Pol and Wright 2009, Dinnage et al. 2018), in which the solar radiation predictor term was decomposed into a within-species term, calculated by subtracting the mean solar radiation value for each species from the individual values, and a between-species term, representing the mean solar radiation value for each species. For each malar stripe (response) variable, we thus constructed three sets of models: 1) a simple model, containing only the within-species and between-species solar radiation terms and the visual distortion scores as fixed predictors; 2) additive models, containing the two solar radiation terms and distortion scores along with each of the trait variables; and 3) interactive models, which included interaction terms between each solar radiation term and each trait variable. To account for potential collinearity between the trait variables, we assessed these separately, such that each additive and interactive model contained only one trait variable. All models included both phylogenetic and spatial random effects, along with a random slope and intercept term for each species, allowing intraspecific relationships between malar stripe variables and solar radiation to be calculated independently for each species. Males and females of species that exhibited sexual dichromatism in facial plumage (the Amur falcon *Falco amurensis*, common kestrel *Falco tinnunculus*, lesser kestrel *Falco naumanni*, and red-footed falcon *Falco vespertinus*) were coded as different 'species', allowing the model to estimate separate random slope and intercept terms for each sex and thus preventing sex differences from obscuring relationships with solar radiation. We standardised all response and fixed effect variables prior to model fitting to enable direct comparison between effect sizes, and log-transformed the body mass estimates to increase their normality and reduce outlier effects. Since the trait variables all consisted of single values for each species, and intraspecific relationships between malar stripe characteristics and solar radiation were thus not expected to vary between models, only the random slopes from the simple (solar radiation only) models were interpreted. The magnitudes of the phylogenetic and spatial effects were measured according to their standard deviations, representing the predicted deviation from the average response for each observation based on its phylogenetic or spatial position (Dinnage et al. 2020).

To corroborate the results of the INLA models, and to enable direct comparison with the results of Vrettos et al. (2021), we then extracted only those species that exhibited substantial relationships between malar stripe characteristics and solar radiation (95% credible intervals for the random slope estimates did not or only marginally overlapped zero, where we defined a 'marginal' overlap as an overlap with zero < 0.1), and re-assessed these relationships using generalised least squares (GLS) models, constructed using the R package 'nlme' (Pinhiero et al. 2022). We compared the results of these models to the INLA random slope estimates for these species. Full details and results of these models are provided in the Supporting information.

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Results

Data description

We extracted information from 10 606 photographs, depicting 10 906 individual birds of 39 species (Fig. 1, Supporting information). Per-species sample sizes ranged from 1000 photographs for the American kestrel *Falco sparverius* to only 11 for the Taita falcon *F. fasciinucha*, for an average of ~ 272 photographs per species (Supporting information). The range of average six-monthly solar radiation values represented by these photographs spanned from 1126.43 to 3191.61 W m^{-2}, with the highest average solar radiation experienced by the grey falcon, *F. hypoleucos* (2966.44 W m^{-2}) and the lowest by the gyrfalcon, *F. rusticolus* (1537.10 W m^{-2}) (Fig. 3, Supporting information). Malar stripe scores across species spanned the full range of available values (0–10), with the widest and darkest malar stripes found in the orange-breasted and bat falcons (with modal scores of 10 for both variables), and the smallest and palest malar stripes found in the Dickinson's *F. dickinsoni* and grey kestrels *F. ardosiaceus*, with modal scores of 0 for all three variables (Supporting information).

Malar stripe characteristics and solar radiation

We found no support for positive relationships between solar radiation and malar stripe characteristics between species, with two of the three malar stripe variables (length and darkness) unrelated to solar radiation (Table 1, Fig. 4), while the interspecific relationship between solar radiation and malar stripe width was negative (i.e. narrower malar stripes in species inhabiting regions of higher solar radiation) (Table 1, Fig. 4). Likewise, we found no overall positive effect of solar radiation on malar stripe variation within species, with length and width showing no relationship to solar radiation (Table 1, Fig. 4), while malar stripe darkness was negatively related to solar radiation, suggesting an average intraspecific trend towards paler malar stripes in regions of higher solar radiation (Table 1, Fig. 4). These relationships were largely unaffected by addition of the trait variables or interaction terms to the models, with the exception that the negative interspecific relationship between solar radiation and malar stripe width disappeared after addition of habitat openness to the model, although including an interaction term between the between-species solar radiation term and habitat openness recovered the relationship (Table 1, Fig. 4).

Effects of species traits

We found very little evidence for additive effects of species ecological traits on malar stripe characteristics, with the only relationship observed being a negative one between malar stripe width and habitat openness (i.e. narrower malar stripes in species inhabiting more open environments), although this was only observed when an interaction term between the between-species solar radiation predictor and habitat openness was also included in the model (Fig. 4, Supporting information). However, there was moderate evidence for interactions between the trait variables and solar radiation. For malar stripe length, there was a positive interaction between body mass and the between-species solar radiation parameter, indicating that the interspecific relationship between solar radiation and malar stripe length was more positive between larger species (Fig. 4, Supporting information). For width, there was a positive interaction between the between-species solar radiation parameter and habitat openness, indicating that the negative effect of solar radiation on malar stripe width was less pronounced between species inhabiting more open habitats, and likewise that the negative interspecific effect of habitat openness on malar stripe width was weaker in regions of higher solar radiation (Fig. 4, Supporting information). For darkness, there was a marginally negative interaction between body mass and the within-species solar radiation parameter, suggesting that intraspecific trends towards paler malar stripes in regions of higher solar radiation were stronger in smaller species (Fig. 4, Supporting information).

Phylogenetic and spatial effects

Phylogeny was the most reliable predictor of malar stripe characteristics across species, with the phylogenetic term explaining a greater amount of the variation in malar stripe characteristics than did most of the fixed effects (Table 1, Fig. 4, Supporting information). Spatial effects had a statistically significant but small effect on malar stripe characteristics (Table 1, Fig. 4, Supporting information). The magnitudes of the phylogenetic and spatial effects were largely consistent between models, and largely unaltered by the addition of trait variables or interaction terms (Fig. 4, Supporting information). However, in the model for malar stripe width that included an interaction term between habitat openness and the between-species solar radiation parameter, the estimated phylogenetic effect was much lower than that in the simple model due to the strong explanatory power of the interaction term (Fig. 4, Supporting information).

Malar stripe characteristics and solar radiation – individual species

Most species showed no intraspecific relationship between malar stripe characteristics and solar radiation (Table 2), with relationships observed in only six of the 39 species. In the gyrfalcon, Eleonora's falcon *Falco eleonorae*, and Madagascar kestrel *F. newtoni*, the relationships were negative, with the gyrfalcon exhibiting negative relationships for all three malar stripe variables (i.e. shorter, narrower, and paler malar stripes in regions of higher solar radiation), while in the Eleonora's falcon negative relationships were observed for length and darkness only, and in the Madagascar kestrel for darkness only (Table 2). In contrast, the peregrine falcon, Dickinson's kestrel *Falco dickinsoni*, and rock kestrel showed positive relationships between solar radiation and malar stripe

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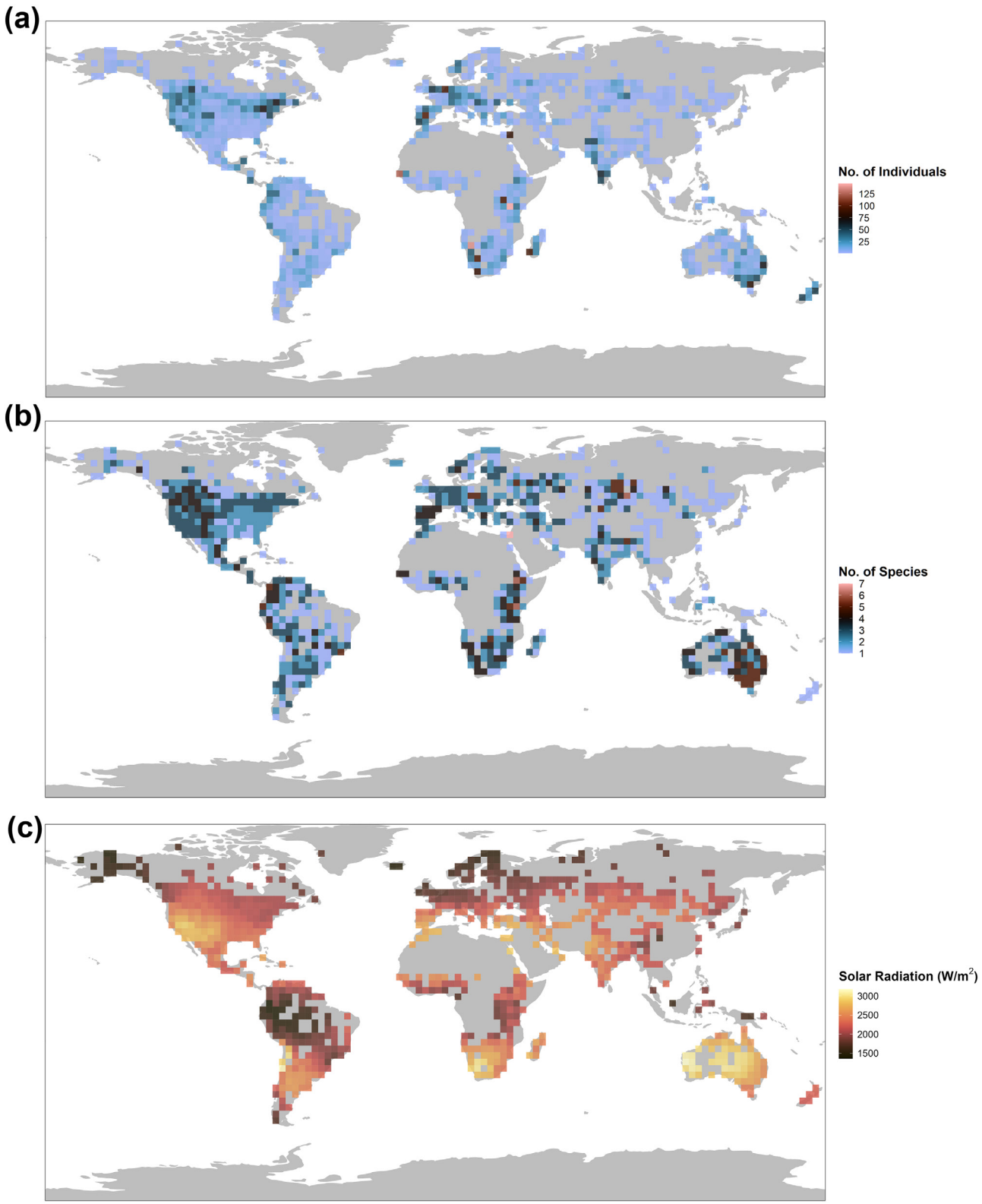

Figure 3. Geographical distribution of photographic observations used in this study, represented in terms of (a) density of individual birds per 3 × 3 degree longitude/latitude grid square, and (b) density of species, along with (c) the average solar radiation value (W m^{-2}) of observations per 3 × 3 degree latitude/longitude grid square. Per-observation solar radiation values represent the mean monthly solar radiation experienced during the breeding season for each photographed bird (averaged over six months). Maps constructed using the R package 'ggplot2' (Wickham 2016).

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Table 1. Marginal posterior means, standard deviations, and 95% credible intervals of the solar radiation parameters in the simple, additive, and interactive INLA models for each malar stripe variable, along with the standard deviations of the phylogenetic and spatial random effects in the simple models, showing only the most relevant results. Solar radiation parameters represent the mean monthly solar radiation experienced during the breeding season (averaged over six months), decomposed into a within-species and a between-species term. Fixed effects which demonstrated a substantial effect on the response (95% credible intervals do not or only marginally overlap zero) are bolded.

Variable	Variable type	Mean	SD	0.025	0.975
Length					
Phylogenetic effect (SD)	Random	0.462	0.827	0.350	0.634
Spatial effect (SD)	Random	0.056	0.013	0.033	0.084
Solar radiation (Within species)	Fixed	−0.032	0.038	−0.108	0.042
Solar radiation (Between species)	Fixed	−0.043	0.071	−0.184	0.097
+ Body mass		−0.033	0.076	−0.183	0.117
+ HWI		−0.035	0.072	−0.179	0.108
+ Prey preference		−0.039	0.074	−0.185	0.107
+ Habitat openness		−0.039	0.073	−0.183	0.105
+ Interaction with body mass		−0.101	0.084	−0.266	0.064
+ Interaction with HWI		−0.004	0.081	−0.164	0.154
+ Interaction with prey preference		−0.017	0.076	−0.168	0.133
+ Interaction with habitat openness		−0.047	0.074	−0.192	0.098
Width					
Phylogenetic effect (SD)	Random	0.537	0.976	0.410	0.729
Spatial effect (SD)	Random	0.241	0.038	0.175	0.239
Solar radiation (Within species)	Fixed	−0.028	0.035	−0.097	0.041
Solar radiation (Between species)	**Fixed**	**−0.177**	**0.074**	**−0.323**	**−0.033**
+ Body mass		**−0.206**	**0.081**	**−0.366**	**−0.046**
+ HWI		**−0.173**	**0.075**	**−0.322**	**−0.026**
+ Prey preference		**−0.171**	**0.075**	**−0.319**	**−0.024**
+ Habitat openness		−0.140	0.076	−0.291	0.010
+ Interaction with body mass		**−0.233**	**0.089**	**−0.409**	**−0.057**
+ Interaction with HWI		**−0.159**	**0.082**	**−0.321**	**0.000**
+ Interaction with prey preference		**−0.162**	**0.083**	**−0.325**	**0.000**
+ Interaction with habitat openness		**−0.183**	**0.071**	**−0.323**	**−0.043**
Darkness					
Phylogenetic effect (SD)	Random	0.533	1.029	0.421	0.714
Spatial effect (SD)	Random	0.224	0.027	0.176	0.283
Solar radiation (Within species)	**Fixed**	**−0.084**	**0.042**	**−0.168**	**−0.002**
Solar radiation (Between species)	Fixed	−0.100	0.071	−0.241	0.040
+ Body mass		−0.131	0.079	−0.287	0.025
+ HWI		−0.108	0.074	−0.253	0.036
+ Prey preference		−0.095	0.073	−0.239	0.047
+ Habitat openness		−0.069	0.076	−0.220	0.081
+ Interaction with body mass		**−0.175**	**0.087**	**−0.347**	**−0.005**
+ Interaction with HWI		−0.096	0.081	−0.258	0.062
+ Interaction with prey preference		−0.107	0.080	−0.265	0.050
+ Interaction with habitat openness		−0.085	0.076	−0.237	0.065

characteristics, with positive relationships observed in the peregrine falcon for all three malar stripe variables (although this relationship was only marginal for darkness (Table 2)), in the Dickinson's kestrel for length and darkness only, and in the rock kestrel for darkness only (Table 2). However, only the relationships found for the peregrine falcon, gyrfalcon, and Madagascar kestrel were replicated in the GLS analysis (Supporting information).

Discussion

The solar glare hypothesis predicts that populations inhabiting regions of higher solar radiation should exhibit larger and darker malar stripes, owing to stronger selection on these traits to counteract negative visual effects of solar glare or bright sunlight (Vrettos et al. 2021). In contrast to these predictions, we found that falcons exhibit an overall interspecific trend towards narrower malar stripes in species inhabiting regions of higher solar radiation, and a general intraspecific trend towards paler malar stripes in individuals or populations inhabiting regions of higher solar radiation. Our results thus contradict the solar glare hypothesis and suggest that solar radiation is not a major evolutionary driver of malar stripe characteristics in falcons. Vrettos et al. (2021) argued that positive associations between solar radiation and malar stripe characteristics in peregrine falcons were suggestive of malar stripes having evolved as adaptations against negative visual effects of solar glare in falcons (Vrettos et al. 2021). While our study replicated this previous study's positive relationships

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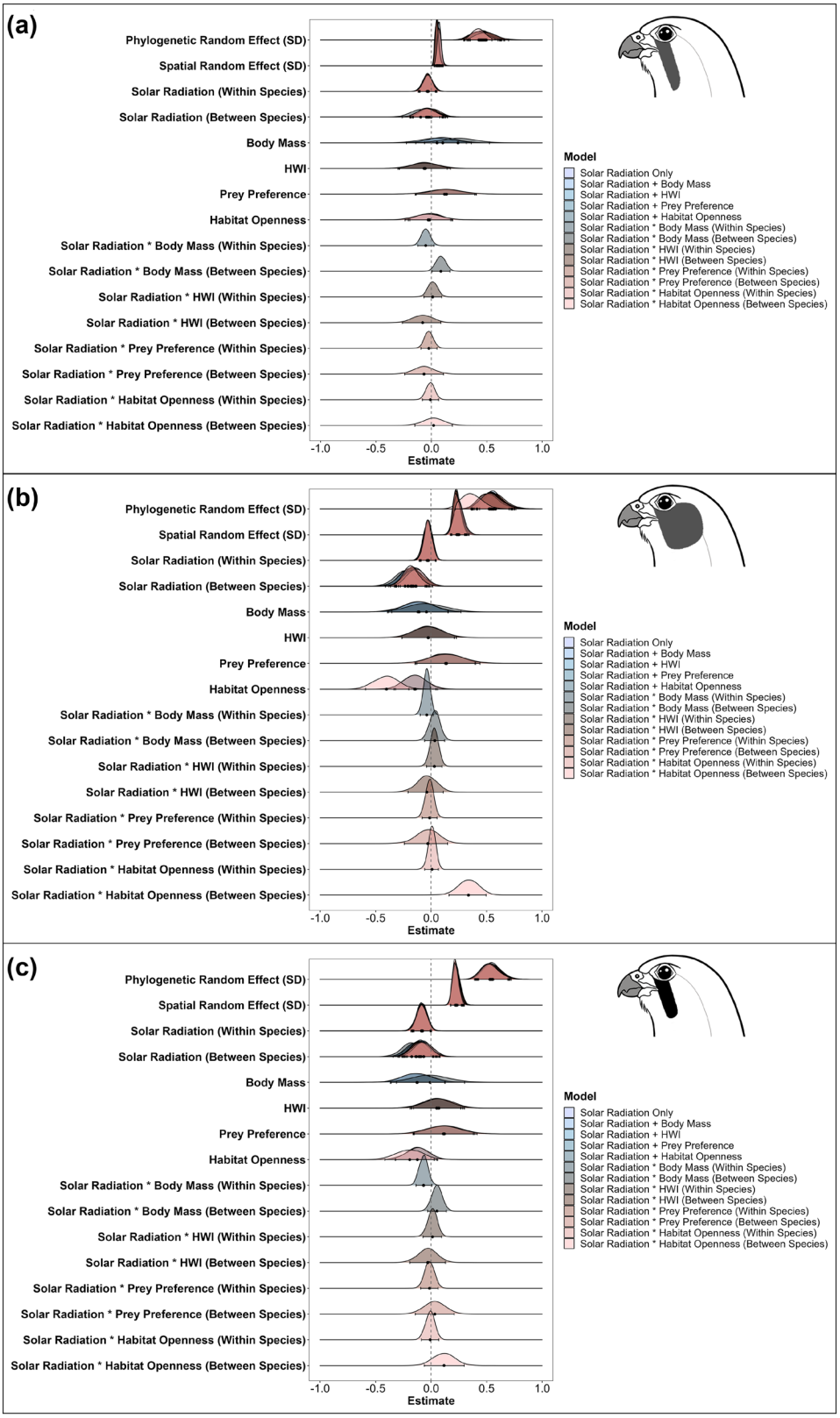

Figure 4. Marginal posterior probability distributions of the fixed effects and standard deviations of the phylogenetic and spatial random effects in the INLA models for (a) malar stripe length, (b) malar stripe width, and (c) malar stripe darkness, colour coded according to model specification. Since all fixed effect variables were standardised prior to model fitting, these coefficients are comparable to one another. Plots created using the R package 'phyr' (Li et al. 2020).

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Table 2. Means, standard deviations and 95% credible intervals for the marginal posterior probability distributions of the INLA random slope estimates for the relationships between malar stripe characteristics and mean breeding season solar radiation in each species. Variables and species in which one or more substantial relationships were found (95% credible intervals do not or only marginally overlap zero) are bolded.

	Random slope estimate											
	Length				Width				Darkness			
Species	Mean	SD	0.025	0.975	Mean	SD	0.025	0.975	Mean	SD	0.025	0.975
Red–footed falcon												
Male	0.187	0.134	−0.075	0.453	−0.052	0.102	−0.254	0.148	0.063	0.132	−0.196	0.323
Female	0.036	0.140	−0.239	0.312	−0.027	0.107	−0.237	0.182	−0.018	0.137	−0.288	0.250
Dickinson's kestrel	**0.179**	**0.079**	**0.023**	**0.335**	0.098	0.063	−0.026	0.222	**0.228**	**0.083**	**0.067**	**0.391**
Laggar falcon	0.150	0.095	−0.037	0.338	0.123	0.076	−0.026	0.273	0.036	0.100	−0.159	0.231
Peregrine falcon	**0.087**	**0.041**	**0.007**	**0.169**	**0.073**	**0.036**	**0.002**	**0.144**	**0.086**	**0.045**	**−0.002**	**0.174**
Black falcon	0.077	0.081	−0.083	0.236	0.010	0.064	−0.115	0.135	0.053	0.082	−0.108	0.215
Red–necked falcon	0.067	0.051	−0.032	0.167	0.016	0.043	−0.069	0.100	0.051	0.055	−0.056	0.158
African hobby	0.052	0.109	−0.162	0.266	0.011	0.082	−0.150	0.173	0.100	0.107	−0.108	0.311
Rock kestrel	0.045	0.062	−0.077	0.168	0.060	0.051	−0.040	0.160	**0.153**	**0.065**	**0.026**	**0.281**
Aplomado falcon	0.043	0.043	−0.042	0.129	−0.005	0.039	−0.082	0.071	0.076	0.048	−0.018	0.171
Australian kestrel	0.041	0.059	−0.075	0.158	−0.011	0.051	−0.111	0.090	0.048	0.065	−0.079	0.176
Seychelles kestrel	0.036	0.213	−0.380	0.459	0.010	0.192	−0.369	0.389	0.014	0.231	−0.441	0.471
Common kestrel												
Male	0.028	0.043	−0.055	0.112	0.042	0.037	−0.031	0.116	0.037	0.046	−0.054	0.129
Female	0.061	0.045	−0.027	0.149	0.050	0.038	−0.026	0.126	0.044	0.048	−0.050	0.138
Lesser kestrel												
Male	0.027	0.061	−0.092	0.147	0.047	0.049	−0.049	0.144	−0.039	0.063	−0.163	0.085
Female	0.135	0.077	−0.016	0.287	0.071	0.059	−0.045	0.187	−0.028	0.077	−0.178	0.122
Orange-breasted falcon	0.024	0.047	−0.069	0.117	0.006	0.043	−0.077	0.090	0.049	0.054	−0.056	0.155
Merlin	0.022	0.045	−0.066	0.111	−0.024	0.040	−0.102	0.055	−0.037	0.050	−0.135	0.061
Bat falcon	0.021	0.044	−0.067	0.109	−0.043	0.040	−0.122	0.037	0.073	0.051	−0.026	0.173
Greater kestrel	0.014	0.049	−0.081	0.110	0.067	0.042	−0.015	0.150	0.064	0.053	−0.040	0.169
Spotted kestrel	0.014	0.132	−0.246	0.273	−0.060	0.105	−0.266	0.146	−0.000	0.135	−0.265	0.264
Taita falcon	0.013	0.168	−0.317	0.343	−0.012	0.135	−0.277	0.253	−0.053	0.170	−0.388	0.279
Mauritius kestrel	0.011	0.213	−0.408	0.431	0.008	0.193	−0.373	0.389	−0.009	0.232	−0.469	0.449
Oriental hobby	0.002	0.126	−0.246	0.251	0.114	0.105	−0.092	0.321	0.099	0.133	−0.162	0.362
Saker falcon	0.001	0.141	−0.276	0.277	0.007	0.110	−0.210	0.224	0.080	0.141	−0.200	0.358
Lanner falcon	0.000	0.047	−0.093	0.093	0.027	0.041	−0.053	0.108	0.075	0.052	−0.026	0.177
Australian hobby	−0.006	0.065	−0.133	0.121	0.055	0.054	−0.050	0.161	0.056	0.069	−0.079	0.191
Barbary falcon	−0.007	0.133	−0.269	0.253	0.010	0.102	−0.190	0.209	0.044	0.131	−0.212	0.301
Grey falcon	−0.008	0.177	−0.348	0.347	−0.003	0.144	−0.287	0.281	−0.006	0.181	−0.362	0.350
Eurasian hobby	−0.009	0.049	−0.105	0.087	0.028	0.041	−0.052	0.110	0.069	0.052	−0.032	0.172
Fox kestrel	−0.010	0.112	−0.230	0.209	−0.027	0.084	−0.192	0.139	0.047	0.109	−0.167	0.261
Amur falcon												
Male	−0.023	0.174	−0.368	0.319	−0.038	0.144	−0.322	0.245	−0.034	0.180	−0.390	0.319
Female	−0.093	0.187	−0.465	0.271	0.161	0.161	−0.149	0.484	0.018	0.199	−0.369	0.406
American kestrel	−0.031	0.042	−0.115	0.053	−0.022	0.037	−0.095	0.057	0.040	0.046	−0.051	0.132
Banded kestrel	−0.033	0.184	−0.397	0.328	−0.168	0.157	−0.482	0.135	−0.146	0.194	−0.535	0.230
Brown falcon	−0.037	0.055	−0.146	0.071	−0.026	0.048	−0.121	0.069	0.014	0.061	−0.105	0.135
New Zealand falcon (Kārearea)	−0.038	0.104	−0.244	0.167	−0.018	0.092	−0.200	0.163	−0.006	0.119	−0.240	0.228
Prairie falcon	−0.053	0.064	−0.177	0.072	−0.011	0.051	−0.111	0.090	−0.046	0.065	−0.174	0.083
Sooty Falcon	−0.067	0.184	−0.431	0.292	0.028	0.157	−0.279	0.337	−0.019	0.194	−0.402	0.363
Grey kestrel	−0.094	0.054	−0.200	0.011	−0.034	0.046	−0.125	0.056	−0.044	0.059	−0.160	0.071
Madagascar kestrel	−0.096	0.087	−0.268	0.075	−0.044	0.072	−0.186	0.098	**−0.218**	**0.095**	**−0.406**	**−0.032**
Eleonora's falcon	**−0.328**	**0.115**	**−0.556**	**−0.105**	−0.084	0.088	−0.257	0.088	**−0.329**	**0.116**	**−0.559**	**−0.102**
Gyrfalcon	**−0.445**	**0.116**	**−0.675**	**−0.221**	**−0.415**	**0.010**	**−0.613**	**−0.221**	**−0.685**	**0.134**	**−0.951**	**−0.426**

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found for peregrine falcons, these trends were not reflected in any other species, or interspecifically across falcon species, suggesting that malar stripe variation in most falcon species is primarily driven by other factors (Vrettos et al. 2021).

The interspecific relationships we found between solar radiation and malar stripe characteristics were largely unaffected when adjusting for body mass, HWI, prey preference, or habitat openness. These results contradict Vrettos et al. (2021)'s suggestion that ecological differences between species may explain interspecific differences in malar stripe characteristics (Vrettos et al. 2021). Body mass, HWI, and prey preference were all unrelated to malar stripe characteristics, while the relationship between malar stripe width and habitat openness was opposite to that predicted by the solar glare hypothesis, with wider malar stripes occurring in species inhabiting shaded forest environments. However, we found some evidence that body mass and habitat openness affect the relationship between solar radiation and malar stripe characteristics. The interactions between solar radiation and body mass were opposite to those predicted under the solar glare hypothesis, with smaller species exhibiting stronger intraspecific trends towards paler malar stripes in regions of higher solar radiation, and weaker or less positive effects of solar radiation on malar stripe length interspecifically. This provides further evidence against the solar glare hypothesis as a general explanation for the evolution of falcon malar stripes, and suggest that malar stripes did not evolve as an adaptation to aid visual targeting of agile, aerial prey (Vrettos et al. 2021).

The direction of the interaction between solar radiation and habitat openness, however, was consistent with the predictions of the solar glare hypothesis, with species inhabiting more open habitats experiencing more positive (less negative) relationships between solar radiation and malar stripe width, and vice versa for species inhabiting regions of higher solar radiation. This could suggest a trade-off between the opposing selective pressures of solar glare reduction and habitat crypsis, with the former selecting for darker malar plumage in brighter environments, and the latter for lighter overall plumage (Galeotti et al. 2003, Amar et al. 2013, Tate et al. 2016). However, the fact that we did not observe any other interspecific trends consistent with predictions, and that most species showed no intraspecific trends in malar stripe characteristics with increasing solar radiation, perhaps suggests that any such tradeoff is relatively weak, if existent.

We found intraspecific relationships between solar radiation and malar stripe characteristics for only six of the 39 species: the peregrine falcon, gyrfalcon, Eleonora's falcon, Dickinson's kestrel, rock kestrel, and Madagascar kestrel. Of these, only three (the peregrine falcon, Dickinson's kestrel, and rock kestrel) showed relationships consistent with the predictions of the solar glare hypothesis, and only those for the peregrine falcon were replicated in GLS analysis. Indeed, since the Dickinson's kestrel typically lacks clearly definable malar stripes (Ferguson-Lees and Christie 2001), it is likely that the trends observed for this species were spurious and driven by the small number (33 out of 111) of birds with non-zero scores. Similarly, the negative relationships observed for the Eleonora's falcon were not reliably replicated in the GLS models and appeared to be driven by the presence of dark-morph birds (39 out of 121), 10 of which received zero scores (Supporting information). More robust negative trends were observed for the gyrfalcon and Madagascar kestrel, with the gyrfalcon demonstrating strong negative relationships between solar radiation and all three malar stripe variables (i.e. thinner, shorter, and paler malar stripes in regions of higher solar radiation), while the Madagascar kestrel demonstrated such a trend for malar stripe darkness only. These relationships are inconsistent with the predictions of the solar glare hypothesis, and are more consistent with malar plumage playing a role in crypsis (Galeotti et al. 2003, Amar et al. 2013, Tate et al. 2016). However, the fact that both species were represented by small sample sizes (177 individual birds for the Madagascar kestrel, and only 90 for the gyrfalcon) suggests that the biological significance of these trends should be treated with caution.

Our findings and those of Vrettos et al. (2021) suggest that peregrine falcons are unique among falcons in exhibiting larger and darker malar stripes in regions of higher solar radiation, with these trends holding both for mean annual solar radiation and mean monthly solar radiation during the breeding season (Vrettos et al. 2021). The peregrine falcon is notable for its unusual speed, reportedly being able to reach diving speeds up to 100 km faster than those recorded for other bird-eating falcon species such as the gyrfalcon (Tucker et al. 1998, Ferguson-Lees and Christie 2001). Peregrine falcons also have the fastest vision of any raptor studied, with a flicker fusion frequency ~ 20 Hz higher than that recorded for the saker falcon, potentially a result of the peregrine's high degree of specialisation for aerial hunting of agile bird prey (Potier et al. 2020). Peregrine falcons may thus plausibly experience exceptionally strong selection for traits that aid visual detection and targeting of prey due to their uniquely specialised ecology. The positive relationships we found between malar stripe characteristics and solar radiation in peregrine falcons may thus possibly be explained by malar stripes in peregrines representing an exaptation for solar glare reduction (i.e. having become evolutionarily co-opted to serve a function different to the context in which the trait originally evolved Gould and Vrba 1982), despite malar stripes not serving this role in falcons generally. However, the relationships observed between malar stripe characteristics and solar radiation environment in both the present study and Vrettos et al. (2021) were fairly weak, and solar radiation explained only a small amount of the variation in malar stripe characteristics. Thus, the relationships observed may instead have arisen as a result of phylogeography or intraspecific phylogenetic structuring (e.g. subspecies or populations inhabiting similar latitudes or experiencing similar solar radiation environments exhibiting phenotypic similarity to each other due to recent common ancestry or gene flow (White et al. 2013, Bell et al. 2014, Talbot et al. 2017, Wink 2018, Johnson et al. 2023). Future studies may attempt to account for this intraspecific population structuring by incorporating

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one or a combination of the published subspecies-level phylogenies for this species (White et al. 2013, Wink 2018, Johnson et al. 2023). However, accounting for phylogenetic structure below the species level, and thus distinguishing between the adaptive and neutral hypotheses for geographic variation in malar stripe characteristics in peregrine falcons, is beyond the scope of the present study.

The negative relationships we found between malar stripe characteristics and solar radiation, and between malar stripe width and habitat openness, are consistent with the 'light level-detectability' hypothesis for raptor plumage colouration (Galeotti et al. 2003, Tate et al. 2016). This hypothesis predicts that darker-coloured individuals should experience selective benefits in low light conditions due to their ability to camouflage against dark skies, and likewise for lighter-coloured individuals in bright conditions (Amar et al. 2013, Tate et al. 2016). However, background-matching is unlikely to explain the evolutionary significance of falcon malar stripes specifically, since malar stripes are restricted to a small area of the body and are thus presumably of minor importance in camouflage compared to other ventral plumage that is more conspicuous to prey (Vrettos et al. 2021). Thus, the relationships observed may simply be a result of larger or darker malar stripes tending to occur in species with overall darker or more strongly marked plumage and vice versa, and therefore being selected along with other plumage traits to which they are genetically linked. If falcon malar stripes do represent an adaptive trait, their adaptive significance is thus more likely to be explained by a more specific form of crypsis, such as serving to disguise the falcon's eye and thereby reducing detectability by prey (as eyes or faces are the among the most easily recognised visual targets for prey animals) (Barlow 1972, Gavish and Gavish 1981). Alternately, falcon malar stripes may serve in visual communication or signalling, for example as aposematic devices (e.g. by enhancing the visual appearance of the eye and bill and thus enabling the bird to look larger or more threatening Negro et al. 2007), or as visual markers of individual identity or status (Dale 2006). Malar stripe size and darkness may also serve as signals of mate quality, in keeping with the quality-signalling roles demonstrated for other melanin-based plumage in kestrels (Wiehn 1997, Vergara and Fargallo 2011, López-Idiáquez et al. 2016), and for contrasting facial markings in other bird species (Ferns and Hinsley 2004, Galván and Sanz 2007).

This study exhibits a number of methodological limitations which may impact the reliability of its results. For example, while both this study and Vrettos et al. (2021) use direct downward shortwave radiation as a proxy for the intensity of solar glare or the likelihood of experiencing harsh, vision-affecting sunlight, the frequency and intensity of glare are affected by factors other than the intensity of solar radiation, such as the angle of the sun (which is affected by altitude and latitude) and the presence of reflective surfaces (Chawda and Shinde 2022). The use of solar radiation as a proxy for glare, and the fact that we were unable to model or account for these additional factors at the spatial scale required for this study, thus mean that our methodology may not adequately account for the frequency or intensity of solar glare experienced by falcons or the strength of selection for putatively glare-reducing traits, as direct downward shortwave radiation may be a poor or inappropriate means with which to model this selective pressure. Likewise, our study relied on subjective visual measurements of malar stripe characteristics from photographs, rather than using more quantitative measurements (e.g. the use of spectrophotometry to analyse malar stripe darkness) under controlled conditions or those in which the size and darkness of the malar stripe could be measured objectively (e.g. using live birds or museum specimens). The use of 'citizen science' photographs presents methodological challenges to studies of animal phenotypic variation since photographs vary in quality and are vulnerable to sources of uncontrolled variation such as differences in camera specifications, shutter speeds, lighting conditions, and exposure (Laitly et al. 2021). However, colour data from 'citizen science' photographs have been found to correlate substantially with those derived from spectrometry measurements (Laitly et al. 2021), while subjective measurements of plumage characteristics based on visual scales have also been used successfully to model plumage variation in other raptor species (Briggs et al. 2010, Dreiss and Roulin 2010, Amar et al. 2019, Romano et al. 2019). Vrettos et al. (2021) likewise found that malar stripe measurements based on subjective visual scoring correlated significantly with quantitative measurements obtained using image processing software (Vrettos et al. 2021), whereas a previous study found only minor or non-significant differences between subjective scores of plumage characteristics from multiple independent observers, suggesting that a single observer is sufficient to produce reproducible results (Amar et al. 2013). Another methodological challenge to our study was that some falcon species have solidly coloured facial plumage, without clearly defined malar stripes. We repeated our analysis on a subset of the data with these birds removed (Supporting information for details) to determine whether their inclusion affected our results. Most of the trends we observed were not meaningfully altered in this reduced analysis (Supporting information), suggesting that our results were largely robust to these concerns.

Due to the number and complexity of our models, our analysis concerned only the effects of solar radiation on falcon malar stripe characteristics, without considering those of other climatic variables. While Vrettos et al. (2021) found only moderate effects of climatic variables other than solar radiation, such as temperature and rainfall, on malar stripe characteristics in peregrine falcons, evidence from other bird taxa indicates that geographical trends in plumage characteristics are strongly affected by these factors (Delhey 2018, Delhey 2019, Romano et al. 2019). Indeed, the trends we observed (wider and/or darker malar stripes in falcons inhabiting dimmer and/or more forested regions) appear consistent with Gloger's ecogeographic rule, which states that darker-coloured individuals should occur in regions of higher rainfall (Delhey 2018, Delhey 2019, Romano et al. 2019), as both low light conditions and high vegetation cover are

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characteristic of high-rainfall environments. While background-matching has been proposed as a mechanism behind Gloger's rule, physiological mechanisms (dark plumage colouration conferring increased protection from ectoparasite damage in wetter regions where parasites are likely to be more numerous, or being pleiotropically linked to immune advantages which confer a similar benefit) have also been suggested (Burtt and Ichida 2004, Romano et al. 2019). The trends we observed also potentially indicate trends consistent with Bogert's rule, which predicts that darker individuals should occur in colder regions, due to thermal benefits conferred by the heat-absorbing properties of dark pigments (Amar et al. 2019, Romano et al. 2019). Thus, the observed negative relationships with solar radiation may possibly be explained by underlying relationships with other, covarying climatic factors, while relationships between overall plumage colouration (with which malar stripe characteristics covary) and climatic conditions could also potentially obscure positive relationships between malar stripe characteristics and solar radiation. Thus, assessing the effect of solar radiation in conjunction with those of rainfall and temperature, in addition to assessing the correlation between malar stripe characteristics and overall body plumage, may provide more comprehensive insight into their relative effects on malar plumage.

In conclusion, our results suggest that solar radiation is not a primary selective driver of malar stripe characteristics in falcons, and that the solar glare hypothesis is unlikely to explain the function and evolutionary significance of falcon malar stripes. However, malar stripe size and darkness are (weakly) positively associated with solar radiation in peregrine falcons, potentially indicative of malar stripes having been co-opted for solar glare reduction in this species, although the observed intraspecific patterns may alternately be explained by phylogeography or population structuring. In other falcon species, malar stripes may potentially serve as cryptic devices or function in visual signalling, although testing such hypotheses is beyond the scope of the present analysis. Our results are also purely correlative, and do not demonstrate any functional role for falcon malar stripes. Future studies of this nature should thus incorporate functional or experimental analyses, as well as evolutionary analyses (e.g. ancestral character state reconstruction) to determine when malar stripes originally evolved in falcons, and the habitat and ecology of the ancestral falcon species in which they originated. Such analyses would enhance understanding of the evolutionary significance of falcon malar stripes and thus provide valuable insight into the function of this characteristic plumage feature.

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Author contributions

Michelle Vrettos: Data curation (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Chevonne Reynolds**: Conceptualization (supporting); Methodology (equal); Project administration (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Arjun Amar**: Conceptualization (lead); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Supervision (equal); Writing – original draft (supporting); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.gxd2547wq (Vrettos et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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