Clinal variation in morph frequency in Swainson's hawk across North America: no support for Gloger's ecogeographical rule

4 authors:

Arjun Amar
Percy FitzPatrick Institute of African Ornithology
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Chevonne Reynolds
University of the Witwatersrand
57 PUBLICATIONS   **1,054** CITATIONS

Julia van Velden
Stellenbosch University
16 PUBLICATIONS   **231** CITATIONS

Christopher Briggs
State University of New York College of Environmental Science and Forestry
29 PUBLICATIONS   **141** CITATIONS

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Clinal variation in morph frequency in Swainson's hawk across North America: no support for Gloger's ecogeographical rule

ARJUN AMAR[1]*, CHEVONNE REYNOLDS[1,2], JULIA VAN VELDEN[1] and CHRISTOPHER W. BRIGGS[3]

[1]*Fitzpatrick Institute of African Ornithology, DST-NRF Centre of Excellence, University of Cape Town, Rondebosch, 7701, South Africa*

[2]*Animal, Plant and Environmental Sciences, University of the Witwatersrand, Braamfontein 2001, South Africa*

[3]*Department of Biology, Hamilton College, Clinton, NY 13323, USA*

In polymorphic species of birds, clinal variation in plumage coloration is frequently observed. These clines often follow Gloger's ecogeographical rule, which predicts that greater numbers of dark morphs will breed in wetter areas. More recent research on polymorphic raptors has suggested this pattern might be due to a cryptic advantage of dark morph hawks foraging in conditions with lower solar radiation during their breeding season. We explore this question for Swainson's hawk (*Buteo swainsoni*) using the MORPHIC internet application, which sources photographs from the internet and helps to build spatial datasets of visible phenotypes. Using these data, we test for clinal variation in the proportion of dark morph Swainson's hawks and examine which environmental variables are associated with the morph distribution in the breeding range of this species. We found good evidence for a long- suspected latitudinal cline, with the highest proportion of dark morphs occurring within the west of the breeding range of the species, and a decreasing frequency toward the east of the range. The distribution of these morphs was most closely associated with rainfall and temperature. However, in contrast to Gloger's rule, we found that dark morphs were more common in drier and cooler areas of their breeding range, conforming to the thermal melanism hypothesis. Similarly, we found no evidence that dark morphs were associated with areas of lower solar radiation. Taking this evidence together, polymorphism in Swainson's hawks may be affected largely by the energetic needs of individuals on their breeding grounds rather than their non-breeding grounds.

ADDITIONAL KEYWORDS: Bogarts rule – *Buteo swainsoni* – Gloger's ecogeographical rule – large scale – MORPHIC – NDVI – plumage polymorphism – precipitation – temperature – raptor.

INTRODUCTION

Polymorphism occurs when individuals of the same species within a population display two or more distinct morphs or forms. Approximately 3.5% of the world's bird species are colour-polymorphic (Galeotti *et al.*, 2003). Adaptation to local conditions should be reflected in relative changes of morph frequency as local habitat or climate condition select against inappropriate phenotypes, resulting in clines across large spatial scales (Antoniazza *et al.*, 2010; Amar *et al.*, 2014). For many bird species, morph frequencies have been correlated with rainfall (Roulin *et al.*, 2009; Amar *et al.*, 2014; Sordahl, 2014), with darker morphs occurring more frequently in areas with greater rainfall. The idea that darker birds are more common in areas with greater rainfall links to Gloger's ecogeographical rule (Rensch 1929), first observed over 100 years ago (Gloger, 1833), which proposes that darker birds occur more frequently in wetter or more humid areas.

Polymorphism is particularly common in Accipitridae, with 22% of species being polymorphic (Galeotti & Rubolini, 2003; Galeotti *et al.*, 2003).

*Corresponding author. E-mail: arjun.amar@uct.ac.za.

Galeotti & Rubolini (2003) proposed that these polymorphisms may be maintained by disruptive selection for species occupying diverse niches, allowing adaptation to local conditions. Galeotti *et al.* (2003) suggested that variation in detectability of the different morphs at different light levels was the most likely explanation for the evolution and maintenance of colour polymorphism in birds. More recently, Tate *et al.* (2016) found that light levels were a better predictor than rainfall levels for the spatial structuring of black sparrowhawk (*Accipiter melanoleucus* Smith 1830) morphs across a broad geographical area (> 1500 km). That study also provided evidence on the probable mechanism for this pattern, with dark morphs having greater hunting success in duller light levels as compared with light morphs, which foraged more successfully in brighter light conditions. However, there have been no other studies testing if spatial patterns of morphs are associated with solar radiation for any other polymorphic raptors.

For species with large ranges, quantifying the presence or nature of a cline is hampered by the requirement to collect field data for many specimens across extensive geographical areas. Therefore, despite clinal variation being fairly common, occurring in around about 20% of polymorphic species (Galeotti *et al.*, 2003), it has only been empirically explored in a handful of species, such as black sparrowhawk (Amar *et al.*, 2014, Tate *et al.*, 2016), barn owl (*Tyto alba* Scopoli 1769; Antoniazza *et al.*, 2014) and bananaquit (*Coereba flaveola* Vieillot 1809; Wunderle 1981, MacColl & Stevenson 2003).

Recently, methods that make use of internet-sourced photographs have helped to overcome previous data acquisition limitations and allow for continental-scale data collection with relative ease and high accuracy (Leighton *et al.*, 2016). Leighton *et al.* (2016) showed that Google Images could be used in an unbiased way to replicate data collected from more intensive sampling methods such as field surveys or from extensively sourced museum specimens. The same study also showed that for one species of polymorphic raptor, similar patterns of clinal variation were detected using either the Google Images approach or visual observation of birds across the range of the cline.

Swainson's hawk (*Buteo swainsoni* Bonaparte 1838) is a migratory *Buteo* species that breeds across western North America and Mexico (Bechard *et al.*, 2010). Most populations arrive on their breeding grounds in April and leave around August, depending on the latitude (Kochert *et al.*, 2011). Most individuals over-winter in Mexico, and South America, primarily in the pampas of Argentina (see Fig. 2).

The species is polymorphic, and can be separated into one of three morphs (light, variable-light or dark) (Briggs *et al.*, 2010) (Fig. 1), in a similar manner to

other polymorphic *Buteo* species (Chakarov *et al.*, 2008). However, the species probably shows a more or less continuous gradient of polymorphism, as has now been suggested for buzzards (Kappers *et al.*, 2017). Swainson's hawks are suspected to show clinal variation in their morph frequency from west to east across their breeding range in North America, with increasing frequencies of darker morphs in the west (Wheeler *et al.*, 2003). However, no empirical data to support this supposition for this species have been published, nor do we understand the environmental factors that may drive the spatial structuring of morphs in the population.

In this study, we use the internet application MORPHIC (Leighton *et al.*, 2016) to collate image data on the morph distribution of Swainson's hawks across their North American breeding range, to empirically test for a longitudinal cline and to explore the association between morph distribution and several environmental variables. Specifically, we test two hypotheses. First, we test whether the distribution of morphs fits Gloger's ecogeographical rule (Rensch 1929), which proposes that dark morphs are more prevalent in breeding areas with higher rainfall, which may be driven by a variety of mechanisms (e.g. improved resistance to higher parasite levels typically found in wetter environments) (Zink & Remsen, 1986; Burtt & Ichida, 2004; Lei *et al.*, 2014). Second, we test for the light-level hypothesis (Galeotti *et al.*, 2003; Tate *et al.*, 2016; Tate & Amar, 2017), which proposes that morphs are adapted to variable light conditions, due to background matching and crypsis from prey. If this was true for this species, we would predict that dark morph Swainson's hawks would be more prevalent in areas with lower solar radiation during the breeding season. These two hypotheses are somewhat interrelated, with the light-level hypothesis being proposed as a potential mechanism to explain Gloger's ecogeographical rule (Tate *et al.*, 2016).

METHODS

SWAINSON'S HAWK MORPH DATA

We used the internet application MORPHIC (Leighton *et al.*, 2016) to compile photographs of Swainson's hawks throughout their North American breeding range. We conducted region- (USA: State; Canada: Province) specific searches as recommended by Leighton *et al.* (2016). Thus, for each region we included the species common name, the species scientific name and the specific region.

Each photo returned was classified as usable by the researcher if it provided location at the scale required (minimum of State or Province, but more typically given to the nearest town, or national park)
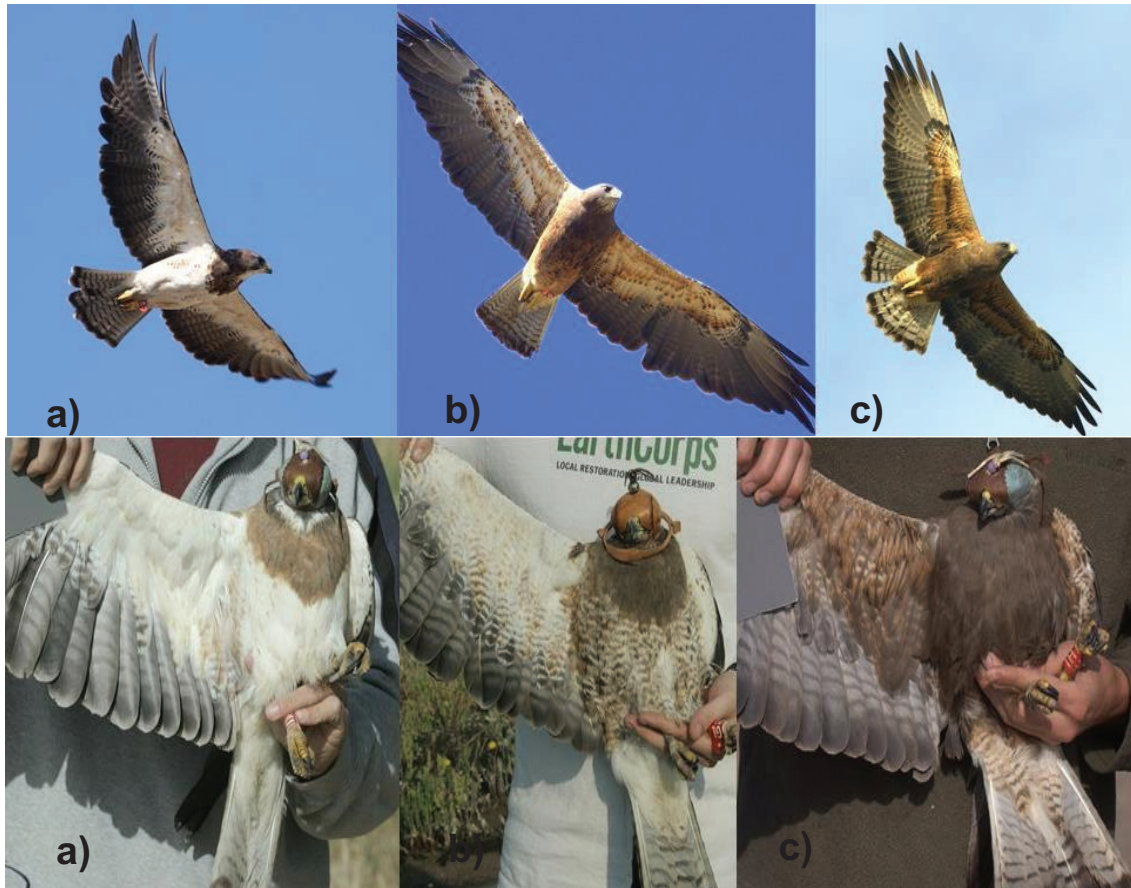
Figure 1. Examples of Swainson's hawk morphs, classified into three morph types: A, light; B, variable-light; C, dark. For analysis, we grouped light and variable-light into a single non-dark class. All photos by Chris Briggs.

and showed a Swainson's hawk with the morph clearly visible. Birds were categorized into one of three morphs: light, variable-light or dark, using the same methods and criteria as Briggs *et al*. (2010). We did not attempt to separate birds with rufous plumage, and these birds were classified as dark morphs (Clark & Wheeler, 2001).

Locational information was sought from the webpage associated with the image. If no location was stated, the image was reverse image searched, using either TinEye Reverse Image Search (https://tineye.com) or Google Search by Image (https://images.google.com) to find the original webpage and photographer. If the original webpage did not give a location, the original photographer's email address was found where possible, and the location was obtained through correspondence.

All data points falling outside a 500-km buffer of the species' known breeding distribution were discarded as these may represent errors in location assignment by photographers or represent vagrant birds. Similarly, photographs from outside the breeding

period for a region were excluded as these may be birds transiting through an area at either the end or the beginning of each breeding season and may not reflect environmental conditions experienced during breeding.

ENVIRONMENTAL VARIABLES

Selection of dates and geographical zones

Swainson's hawks are known to breed at slightly different times of the year based on latitude. We therefore divided the breeding range into three similarly sized bands (Fig. 2) based on known breeding dates for the species at different latitudes. Environmental data were then extracted to match these dates within these specific bands so that the environmental variables represented the breeding conditions in those areas. The Southern band was from the 26th to 37th parallel, and the breeding time frame from 10 April to 1 July (Bednarz, 1988). The Central band was from the 37th to 46th parallel, with corresponding breeding dates of 20 April to 7 August
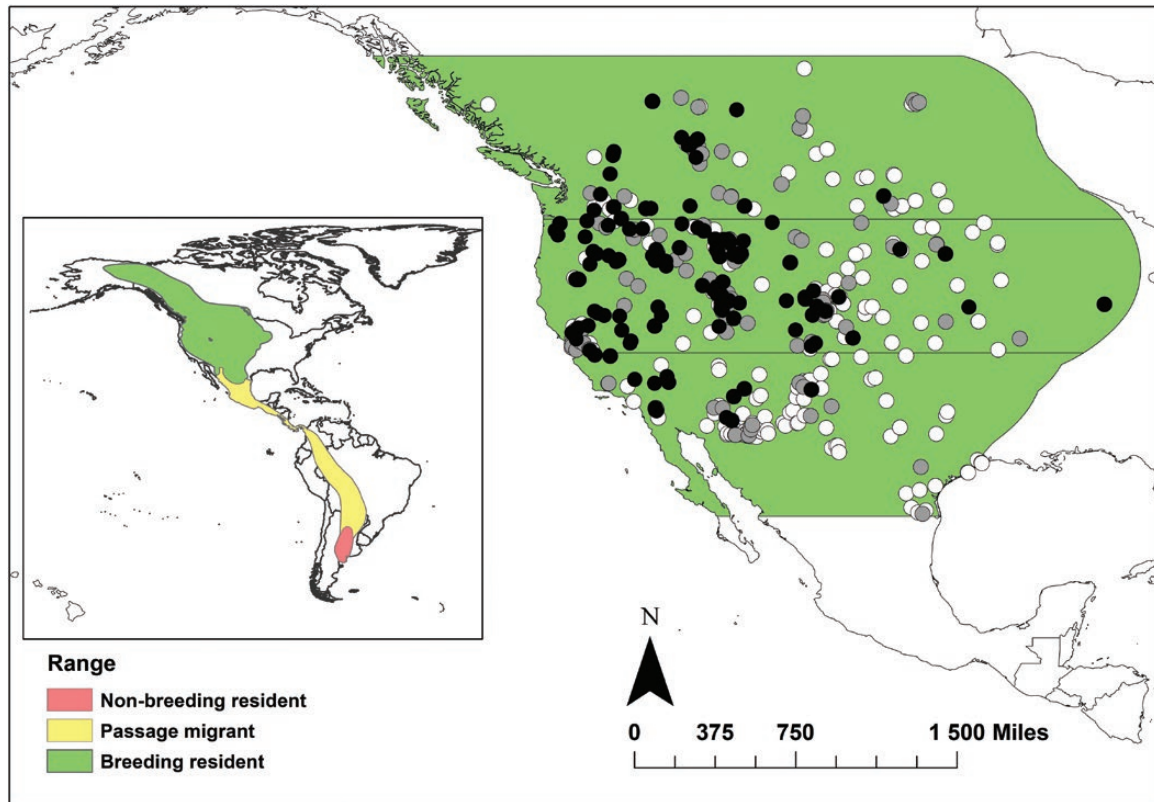
Figure 2. Map showing the morph distribution of the data retrieved from Google Images. The green band of the larger map represents the known North American breeding range of Swainson's hawk with a 500-km buffer. This band is further divided into semi-equal sub-bands, i.e. a North, Central and South band for which environmental data matching known dates of Swainson's hawk breeding were extracted. Morphs are represented in grey scale, i.e black = dark, grey = variable-light and white = light. Inset shows the full range of Swainson's hawk across North and South America. Green, breeding range; yellow, passage migrant; red, non-breeding range.

Table 1. Information on the environmental variables used to explore factors associated with the distribution of Swainson's hawk morphs. Abbreviations are the names used in the model selection output. Data on the environmental variables were collected separately for the different time periods associated with the different latitudinal bands

Variable	Abbreviation	Units	Min.	Max.	Mean ± SD
Max. Temperature	MaxTemp	°C	8	36	23 ± 5
Precipitation	Rain	mm	3	726	189 ± 120
Solar Radiation	Solar	W/m²	300	582	454 ± 52
NDVI	NDVI	unitless	−0.40	0.57	0.27 ± 0.09
Tree Cover	Trees	%	0	54	9 ± 13

(Olendorff, 1973; Dunkle, 1977; Cottrell, 1981; Estep, 1989; Woodbridge, 1991). Finally, the Northern band ranges from the 46th to the 57th parallel, and breeding dates were set to the date of the first image and ending on 15 August (Fitzner, 1980). No images were recorded north of the 57th parallel.

We used the open source platform Google Earth Engine (Gorelick *et al.*, 2017) to access and extract the environmental co-variates (Table 1). Data on the average minimum and maximum daily temperatures (°C), precipitation (mm) and solar radiation (W/m²) across each geographical band were sourced from the Daymet V3 Daily Surface Weather and Climatological Summaries (Thornton *et al.*, 2017), which provide gridded estimates of daily weather parameters for North America at a spatial resolution of 1 × 1 km. Tree

canopy cover for each band was extracted from the GLCF: Landsat Tree Cover Continuous Fields dataset (Sexton *et al*., 2013), at a resolution of 30 × 30 m. Finally, Normalized Difference Vegetation Index (NDVI) data were extracted at a resolution of 250 × 250 m from the MODIS Terra daily NDVI product (Didan, 2015). For climate and NDVI data we calculated the 12-year average for each band (2005–2016), which represented 95% of the period when all the Swainson's hawk photos used in this study were taken. To generate co-variates to test for environmental correlates with morph distribution we extracted the average of each co-variate for each georeferenced image within a 20-km buffer. This buffer size was used to provide an overview of environmental conditions of the area from where photos were sourced. We used functions from the *raster* package in R statistical software to extract these environmental data (Hijmans *et al*., 2017).

STATISTICAL ANALYSIS

For ease of analysis, we re-scored the morphs as either dark (1) or not dark (0) in a similar approach to that taken by Round (1987), in his examination of black bear morphs across a similar geographical area. This binary morph measure was the response variable and was modelled using a Binomial General Linear Model (GLM), fitted using the R statistical software (R Core Team, 2017). We first explored whether there was any evidence for a cline. To do this we fitted latitude, longitude and the interaction between these two terms as explanatory variables in a GLM. To ascertain the significance of each term, we examined whether the 95% confidence intervals of the estimate's coefficients overlapped zero. We then explored which environmental variables were important in explaining the variation in the distribution of dark morphs across their breeding range. We first checked for collinearity between our environmental variables, none of which was highly correlated with each other, with the exception of maximum and minimum temperature; we therefore excluded minimum temperature from further analysis. All environmental variables were scaled and centred for our analyses. For this analysis, we used a model selection approach and built a full model including all five environment variables without interactions (maximum daily temperature, precipitation, solar radiation, NDVI and tree cover). We then used the 'Dredge' function from the package *MuMIn* (Bartón, 2018) to explore the best model. If models were within four AIC$_c$ (corrected Akaike information criterion) units of the top model, we used model averaging applied to all plausible models to estimate the coefficients of each environmental term and their 95% confidence intervals.

We checked for any spatial autocorrelation in the model residuals of the final model by calculating Moran's I with functions from the *ape* package in R (Paradis *et al*., 2018). Moran's I was not significant and so no further steps were taken to adjust for spatial autocorrelation in the analysis.

RESULTS

DATA ON SWAINSON'S HAWKS FROM GOOGLE IMAGES

In total, our search within MORPHIC produced 5444 images, from which we obtained 1085 images of Swainson's hawk where we could identify the age (juvenile/sub-adult or adult), morph and location. These consisted of 219 juveniles/sub-adults and 866 adults. The juveniles and sub-adults were excluded from the analysis, giving a final usable image rate of 16%.

From the 866 adults, 21.4% were dark morphs (N = 185), 25.9% were variable-light morphs (N = 225) and 52.7% were light morphs (N = 456). Useable images were found throughout the breeding range of the species (Fig. 2). More images were found in the USA (N = 726) than in Canada (N = 140). The three USA states with the most images were Colorado (N = 101), California (N = 82) and Utah (N = 79).

EVIDENCE FOR CLINAL VARIATION

We found strong evidence for a longitudinal cline in the proportion of dark morph Swainson's hawks in the population (β ± SE = −0.31 ± 0.11; 95% confidence interval, CI [−5.26, −0.10]), with more dark morphs in the west and decreasing dark morph occurrence in the east (Fig. 3). No such cline was apparent by latitude (β ± SE = 0.50 ± 0.30; 95% CI [−6.05, 1.08]), nor was there an interaction between longitude and latitude (β ± SE = −0.01 ± 0.00; 95% CI [−4.72, 0.01]).

ASSOCIATION BETWEEN MORPHS AND ENVIRONMENTAL VARIABLES

We explored the association between dark morph occurrence and five environmental covariates (Table 1). Our final model selection revealed eight plausible models (ΔAIC$_c$ < 4) (Table 2). Among these models there was considerably more support for two of the five variables included in our models, with maximum temperature and average rainfall featuring in all eight plausible models (relative importance = 1). Using model averaging, these same two variables were the only variables whose confidence intervals did not overlap zero (Table 3). The analysis revealed a negative relationship with both maximum temperature (Fig. 4A) and rainfall (Fig. 4B), and thus dark morphs were
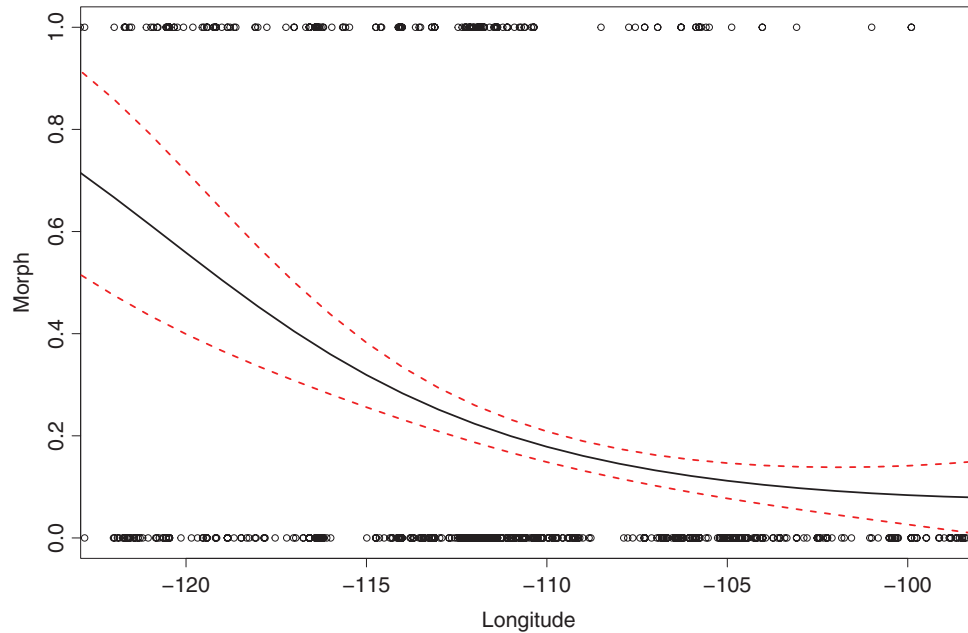
Figure 3. Plot showing clinal variation, with an increasing frequency of dark morph Swainson's hawks in the west. Red dotted line reflects 95% confidence interval. 1 = dark morphs, 0 = non-dark morphs.

Table 2. The eight plausible models (ΔAICc < 4) explaining the probability of a Swainson's hawk being a dark morph, generated from the General Linear Model analysing the binary probability of being a dark morph (1) or a non-dark morph (0)

Terms	d.f.	ΔAICc	Weight
MaxTemp+NDVI+Rain	4	0.00	0.28
MaxTemp+Rain	3	1.14	0.16
MaxTemp+NDVI+Rain+Solar	5	1.25	0.15
MaxTemp+Rain+Solar	4	1.79	0.11
MaxTemp+NDVI+Rain+Trees	5	1.87	0.11
MaxTemp+Rain+Trees	4	2.52	0.08
MaxTemp+NDVI+Rain+Solar+Trees	6	3.06	0.06
MaxTemp +Rain+Solar+Trees	5	3.11	0.06

associated with cooler and drier areas. There was some limited support for NDVI being associated with dark morphs (relative importance = 0.59); this variable had a positive association, indicating that there were more dark morphs in areas with higher primary productivity. However, the confidence intervals of NDVI overlapped zero (Table 3). There was very little evidence to support the idea that the distribution of dark morphs was associated with levels of solar radiation; this term featured in four of the eight plausible models (Table 2) (relative importance score = 0.38). The slope of the relationship was negative, indicating fewer dark morphs in areas with greater solar radiation, but the confidence intervals of this variable overlapped zero (Table 3).

DISCUSSION

We found that Swainson's hawks show a very clear cline in their morph distribution, with an increasing proportion of dark morphs moving from the east to the west within their breeding range. This cline matches other reports (e.g. Wheeler *et al.*, 2003) that were based on approximate proportions of the different morphs throughout their range, rather than on empirical data, and matches anecdotal accounts from ornithologists (W. S. Clark, pers. comm.). The longitudinal cline in Swainson's hawks observed in this study also matches evidence for the few other species that have been studied so far in North America. For example, Roulin & Randin (2015) explored variation in the

Table 3. Conditional model average parameter estimates for all variables featuring in our plausible models (ΔAICc < 4), together with the relative importance score for each variable. The variables in bold are those whose 95% confidence intervals did not overlap zero

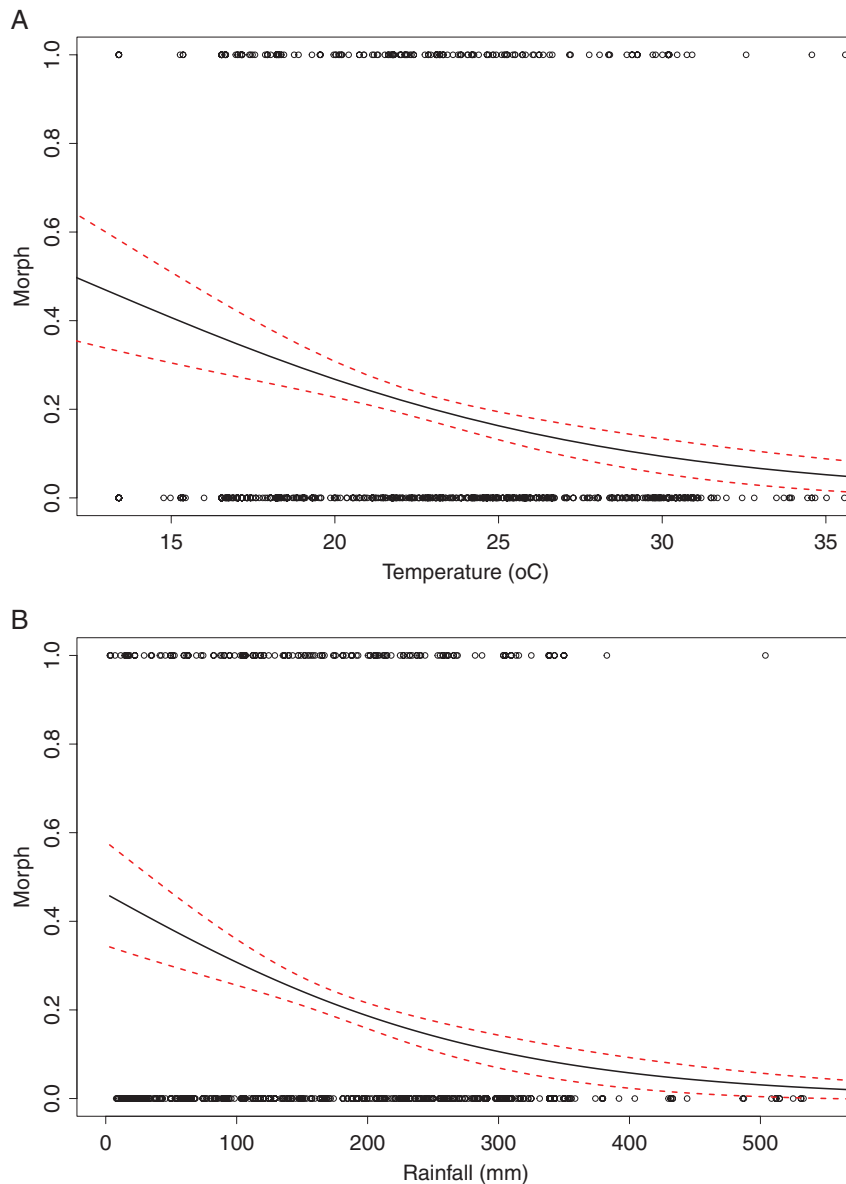| Variable	Variable estimate	Lower 95% CI	Upper 95% CI	Variable importance
Intercept	−1.40	−1.58	−1.22	1
MaxTemp	**−0.63**	**−0.90**	**−0.35**	**1**
Rain	**−0.79**	**−1.11**	**−0.48**	**1**
NDVI	0.09	−0.03	0.33	0.59
Solar	−0.04	−0.33	0.10	0.38
Trees	0.02	−0.15	0.27	0.31

Figure 4. Relationship between the probability of a Swainson's hawk being a dark morph and (A) temperature and (B) rainfall. These were the only two variables that featured in our plausible models whose confidence intervals did not overlap zero.

colour patterns of the barn owl across North America. Examining the cline in coloration within the same area of study, they also found a decrease in the reddish pheomelanin coloration in this species between 120° and 100°W.

Within their breeding range, the distribution of dark morph Swainson's hawks was most closely associated with rainfall and temperature. However, the direction of these relationships did not match predictions based on Gloger's ecogeographical rule (Rensch, 1929). This rule predicts that darker birds occur more frequently in wetter or more humid areas, perhaps because of increased invertebrate, bacterial or fungal feather parasites (Burtt & Jann, 1999; Kose & Møller, 1999). In contrast to Gloger's rule we found that dark morphs occurred more frequently in drier areas within the breeding range. Drier climates may increase feather wear from particulate matter, and increased melanin may increase feather resistance to mechanical abrasion in drier and dustier regions. For example, both Bosner (1995) and Burtt (1986) showed that melanization in feathers increased mechanical strength. In fact, drier areas such as deserts have previously been associated with darker plumages (Ward *et al*. 2002), for example as seen in grey gulls (*Larus modestus* Tschudi 1843) (Walsberg *et al*., 1978).

An additional proposed mechanism for Gloger's ecogeographical rule is that dark morphs may be more cryptic in rainier and therefore duller light conditions. This light-level hypothesis as proposed by Galeotti *et al*. (2003) has recently received some empirical support from Tate *et al*. (2016), who found that dark morphs of black sparrowhawks were more common in areas with lower solar radiation, and that solar radiation was a better predictor for morph distribution than rainfall levels. In contrast to that study, we found very little support for such a pattern in Swainson's hawk. Although solar radiation did feature in three of the plausible models, and the relationship was negative (as predicted), these models had low evidence ratios, and the confidence intervals of the variable substantially overlapped zero. Thus, unlike Tate *et al*. (2016) we found little evidence to suggest that the spatial structuring of the morphs in this species fits with either Gloger's rule or that predicted by the light-level hypothesis.

In contrast to our two proposed hypotheses, there was evidence to support Bogert's rule, or the thermal melanism hypothesis (Bogert, 1949). Dark morph Swainson's hawks occurred more frequently in cooler areas. As predicted by the thermal melanism hypothesis, there may be an increased energetic demand imposed by the cooler climate in the western portion of the range. While Bogert's rule is more frequently associated with ectotherms (Clusella-Trullas *et al*., 2007, 2008), increased evidence has also

associated it with endotherms (e.g. Hetem *et al*., 2009; Delhey, 2018) and is a key hypothesis proposed for the common occurrence of dark plumage of desert birds (Ward *et al*. 2002).

Within the Swainson's hawk range, cooler areas in the west may have increased temperature swings, leading to a need to deal with a large range of temperatures. Increased heat absorption of darker plumage may have thermal benefits, reducing the need to increase metabolism (but see Marder, 1973), resulting in higher energetic demands for lighter individuals in cooler environments (Heppner, 1970; Clusella-Trullas *et al*., 2007; Galván *et al*., 2018). Evidence from both Australia (Delhey, 2018) and the Iberian peninsula (Galván *et al*., 2018) show bird species generally have increasingly darker plumage in cooler areas. Roulin & Randin (2015) studied barn owl morphs within a similar region to our study and found an increase in plumage melanism (pheomelanin-based coloration and spot size) in areas with lower ambient temperature. For eastern screech owls (*Megascops asio*), darker birds (i.e. grey morphs) may have a selective advantage in colder areas, because they have been found to have lower metabolic rates at lower temperatures (Mosher & Henny, 1976) and may use less food (Dexter, 1996). Similarly, dark seabirds have lower basal metabolic rates compared to light-coloured birds (Ellis, 1984). Taken together, darker plumages may confer thermoregulatory advantages and save darker individuals energy during cold periods without incurring energetic costs during warm periods, assuming consistently low wind speeds (Walsberg *et al*., 1978).

Our results suggest that a difference in thermal reflectivity may influence the ability of Swainson's hawks to handle colder environments, which may explain why darker morphs are more common in cooler areas, although it is unclear at what life stage(s) this may be most valuable. For example, Dreiss *et al*. (2016) found differences in huddling and oxygen consumption of barn owl nestlings, with darker individuals consuming more oxygen and having lower body temperatures. This result runs counter to the expectation from our study, but differences in habitat, nesting habits and phylogeny may explain these differences and highlight the need to understand the complete life cycle of a species to determine selective pressures at each stage.

Differences within the wintering habitat are unlikely to play a major role in the cline we observed, because there is no known migratory connectivity (i.e. individuals across North America intermix in their wintering range; Sarasola *et al*., 2008). Therefore, environmental conditions observed across North America are the more likely

drivers of the observed cline. This idea is bolstered by similar clines reported in other North American *Buteo* species, such as red-tailed hawks (*Buteo jamaicencsis* Gmelin 1788; Wheeler 2003) and possibly broad-winged hawks (*Buteo platypterus* Vieillot 1823; Alderfer, 2006), whose migratory patterns and wintering areas contrast strongly with those of Swainson's hawks. Similarly, there is no observed genetic population structure across the Swainson's hawk range (Hull *et al.*, 2007) that might explain the observed cline due to historical wintering population allopatry and subsequent contact, for example as seen in snow geese (*Chen caerulescens*; Cooke *et al.*, 1988).

In conjunction with the large-scale patterns we observed, microclimatic differences or differences in foraging locations (Preston, 1980; Dreiss *et al.*, 2012) may play a role alongside temperature and rainfall in maintaining the polymorphism in this species. Individual preferences for these microclimatic differences could even play a role in low natal dispersal (Briggs *et al.*, 2012) and high nest-site fidelity (Fitzner, 1978; Woodbridge *et al.*, 1995). More work should focus on these differences to better understand if our climatic variables are the drivers or if other factors such as parasites (Burtt & Ichida, 2004; Lei *et al.*, 2014), prey (Roulin, 2004; Charter *et al.*, 2012), vegetation (Tate & Amar, 2017; Delhey, 2018), thermal ecology (Mosher & Henny, 1976; Dreiss *et al.*, 2016) or pleiotropic interactions (Ducrest *et al.*, 2008; Roulin & Ducrest, 2011) may drive the observed cline.

AUTHOR CONTRIBUTIONS

A.A. and C.B. conceived the idea for this research. J.V. and C.R. collected the data. A.A. and C.R. analysed the data. A.A., C.B and C.R. wrote and edited the paper.

ETHICS STATEMENT

No ethical approval was required for this study.

DATA STATEMENT

All data were sourced from open access platforms and are thus readily available. All images were accessed using MORPHIC (www.morphs.io) and all environmental data were extracted from the available dataset in Google Earth Engine (https://earthengine.google.com/).

REFERENCES

Alderfer J. 2006. *National geographic complete birds of North America*. Washington, DC: National Geographic.

Amar A, **Koeslag A**, **Malan G**, **Brown M**, **Wreford E. 2014.** Clinal variation in the morph ratio of Black Sparrowhawks *Accipiter melanoleucus* in South Africa and its correlation with environmental variables. *Ibis* **156:** 627–638.

Antoniazza S, **Burri R**, **Fumagalli L**, **Goudet J**, **Roulin A. 2010.** Local adaptation maintains clinal variation in melanin-based coloration of European Barn Owls (*Tyto alba*). *Evolution* **64:** 1944–1954.

Antoniazza S, **Kanitz R**, **Neuenschwander S**, **Burri R**, **Gaigher A**, **Roulin A**, **Goudet J. 2014.** Natural selection in a postglacial range expansion: the case of the colour cline in the European barn owl. *Molecular Ecology* **23:** 5508–5523.

Bartón K. 2018. *MuMIn: multi-modal inference. Model selection and model averaging based on information criteria (AICc and alike)*. R Package version 1.42.1. https://cran.r-project.org/web/packages/MuMIn/

Bechard MJ, **Houston CS**, **Sarasola JH**, **England AS. 2010.** Swainson's Hawk (*Buteo swainsoni*), version 2.0. In: Poole AF, ed. *The Birds of North America.* Ithaca: Cornell Lab of Ornithology.

Bednarz JC. 1988. A comparative study of the breeding ecology of Harris' and Swainson's Hawks in southeastern New Mexico. *The Condor* **90:** 311–323.

Bogert CM. 1949. Thermoregulation in reptiles, a factor in evolution. *Evolution* **3:** 195–211.

Bosner R. 1995. Melanin and abrasion resistance of feathers. *The Condor* **97:** 590–591.

Briggs CW, **Collopy MW**, **Woodbridge B. 2012.** Correlates and fitness consequences of natal dispersal in Swainson's Hawks. *The Condor* **114:** 764–770.

Briggs CW, **Woodbridge B**, **Collopy MW. 2010.** Temporal morph invariance of Swainson's Hawks. *Journal of Raptor Research* **44:** 70–73.

Burtt EH. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monographs* **38:** 1–126.

Burtt EH, **Ichida JM. 2004.** Gloger's rule, feather-degrading bacteria and color variation among Song Sparrows. *The Condor* **106:** 681–686.

Burtt EH, **Jann MI. 1999.** Occurrence of feather-degrading Bacilli in the plumage of birds. *The Auk* **116:** 364–372.

Chakarov N, **Boerner M**, **Krüger O. 2008.** Fitness in Common Buzzards at the cross-point of opposite melanin–parasite interactions. *Functional Ecology* **22:** 1062–1069.

Charter M, **Peleg ORI**, **Leshem Y**, **Roulin A. 2012.** Similar patterns of local Barn Owl adaptation in the Middle East and Europe with respect to melanic coloration. *Biological Journal of the Linnean Society* **106:** 447–454.

Clark WS, **Wheeler BK. 2001.** *A field guide to hawks of North America revised*. Boston: Houghton Mifflin.

Clusella-Trullas S, **Terblanche JS**, **Blackburn TM**, **Chown SL. 2008.** Testing the thermal melanism hypothesis: a macrophysiological approach. *Functional Ecology* **22:** 232–238.

Clusella-Trullas S, **van Wyk JH**, **Spotila JR. 2007.** Thermal melanism in ectotherms. *Journal of Thermal Biology* **32:** 235–245.

Cooke F, **Parkin DT**, **Rockwell RF. 1988.** Evidence of former allopatry of the two color phases of lesser snow geese (*Chen caerulescens caerulescens*). *The Auk* **105:** 467–479.

Cottrell MJ. 1981. *Resource partitioning and reproductive success of three species of hawks (Buteo spp.) in an Oregon prairie*. Unpublished MSc Thesis, Oregon State University.

Delhey K. 2018. Darker where cold and wet: Australian birds follow their own version of Gloger's rule. *Ecography* **41:** 673–683.

Dexter M. 1996. *Plumage dichromatism and thermal ecology of the Eastern Screech owl* (Otus asio). Unpublished MSc Thesis, Wake Forest University.

Didan K. 2015. *MOD13Q1MODIS/Terra vegetation indices 16-day L3 global 250 m SIN Grid V006*. Sioux Falls: NASA EOSDIS Land Processes DAAC.

Dreiss AN, **Antoniazza S**, **Burri R**, **Fumagalli L**, **Sonnay C**, **Frey C**, **Goudet J**, **Roulin A. 2012.** Local adaptation and matching habitat choice in female Barn Owls with respect to melanic coloration. *Journal of Evolutionary Biology* **25:** 103–114.

Dreiss AN, **Séchaud R**, **Béziers P**, **Villain N**, **Genoud M**, **Almasi B**, **Jenni L**, **Roulin A. 2016.** Social huddling and physiological thermoregulation are related to melanism in the nocturnal Barn Owl. *Oecologia* **180:** 371–381.

Ducrest A-L, **Keller L**, **Roulin A. 2008.** Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution* **23:** 502–510.

Dunkle SW. 1977. Swainson's Hawks on the Laramie Plains, Wyoming. *The Auk* **94:** 65–71.

Ellis HI. 1984. Energetics of free-ranging seabirds. In: Whittow GC, Rahn H, eds. *Seabird Energetics*. Boston, MA: Springer US. 203–234.

Estep JA. 1989. *Biology, movements, and habitat relationships of the Swainson's Hawk in the Central Valley of California, 1986–87*. 52. Sacramento: California Department of Fish and Game.

Fitzner RE. 1978. *Behavioral ecology of the Swainson's Hawk* (Buteo swainsoni*) in Southeastern Washington*. Unpublished PhD Thesis, Washington State University.

Fitzner RE. 1980. In: Energy USDo, ed. *Behavioral ecology of the Swainson's Hawk* (Buteo swainsoni) *in Washington*. Richland: Pacific Northwest Laboratory.

Galeotti P, **Rubolini D. 2003.** The niche variation hypothesis and the evolution of colour polymorphism in birds: a comparative study of owls, nightjars and raptors. *Biological Journal of the Linnean Society* **82:** 237–248.

Galeotti P, **Rubolini D**, **Dunn PO**, **Fasola M. 2003.** Colour polymorphism in birds: causes and functions. *Journal of Evolutionary Biology* **16:** 635–646.

Galván I, **Rodríguez-Martínez S**, **Carrascal LM. 2018.** Dark pigmentation limits thermal niche position in birds. *Functional Ecology* **32:** 1531–1540.

Gloger CL. 1833. *Das Abändern der Vögel durch Einfluss des Klimas*. Breslau: A. Schulz.

Gorelick N, **Hancher M**, **Dixon M**, **Ilyuschenko S**, **Thau D**, **Moore R. 2017.** Google Earth Engine: planetary-scale geospatial analysis software for everyone. *Remote Sensing of Environment* **202:** 18–27.

Heppner F. 1970. The metabolic significance of differential absorption of radiant energy by black and white birds. *The Condor* **72:** 50–59.

Hetem RS, **de Witt BA**, **Fick LG**, **Fuller A**, **Kerley GIH**, **Meyer LCR**, **Mitchell D**, **Maloney SK. 2009.** Body temperature, thermoregulatory behaviour and pelt characteristics of three colour morphs of springbok (*Antidorcas marsupialis*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* **152:** 379–388.

Hijmans R, **van Etten J**, **Cheng J**, **Mattiuzzi M**, **Sumner M**, **Greenberg J**, **Lamigueiro O**, **Bevan A**, **Racine E**, **Shortridge A**, **Ghosh A. 2017.** *Raster V2.6–7*. https://www.rspatial.org/.

Hull JM, **Anderson R**, **Bradbury M**, **Estep JA**, **Ernest HB. 2007.** Population structure and genetic diversity in Swainson's Hawks (*Buteo swainsoni*): implications for conservation. *Conservation Genetics* **9:** 305–316.

Kappers EF, **Chakarov N**, **Krüger O**, **Mueller AK**, **Valcu M**, **Kempenaers B**, **Both C. 2017.** Classification and temporal stability of plumage variation in common buzzards. *Ardea* **105:** 125–136.

Kochert MN, **Fuller MR**, **Schueck LS**, **Bond L**, **Bechard MJ**, **Woodbridge B**, **Holroyd G**, **Martell M**, **Banasch U. 2011.** Migration patterns, use of stopover areas, and austral summer movements of Swainson's Hawks. *The Condor* **113:** 89–106.

Kose M, **Møller AP. 1999.** Sexual selection, feather breakage and parasites: the importance of white spots in the tail of the barn swallow (*Hirundo rustica*). *Behavioral Ecology and Sociobiology* **45:** 430–436.

Lei B, **Amar A**, **Koeslag A**, **Gous TA**, **Tate GJ. 2014.** Differential haemoparasite intensity between Black Sparrowhawk (*Accipiter melanoleucus*) morphs suggests an adaptive function for polymorphism. *PLoS One* **8:** e81607.

Leighton GRM, **Hugo PS**, **Roulin A**, **Amar A. 2016.** Just Google it: assessing the use of Google Images to describe geographical variation in visible traits of organisms. *Methods in Ecology and Evolution* **7:** 1060–1070.

MacColl ADC, **Stevenson IR. 2003.** Stasis in the morph ratio cline in the Bananaquit on Grenada, West Indies. *The Condor* **105:** 821–825.

Marder J. 1973. Body temperature regulation in the brown-necked raven (*Corvus corax ruficollis*)—II. Thermal changes in the plumage of ravens exposed to solar radiation. *Comparative Biochemistry and Physiology Part A: Physiology* **45:** 431–440.

Mosher JA, **Henny CJ. 1976.** Thermal adaptiveness of plumage color in Screech Owls. *The Auk* **93:** 614–619.

Olendorff R. 1973. *The ecology of the nesting birds of prey of northeastern Colorado.* Fort Collins: Natural Resources Ecology Laboratory, Colorado State University.

Paradis E, **Schliep K**, **Schwartz R. 2018.** ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **1:** 3.

Preston C. 1980. Differential perch site selection by color morphs of the red-tailed hawk (*Buteo jamaicensis*). *Auk* **97:** 782–789.

R Core Team. **2017.** *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rensch B. 1929. *Das Prinzip geographischerRassenkreise und das Problem der Artbildung.* Berlin: Gebrüder Bornträger.

Roulin A. 2004. Covariation between plumage colour polymorphism and diet in the Barn Owl *Tyto alba*. *Ibis* **146:** 509–517.

Roulin A, **Ducrest A-L. 2011.** Association between melanism, physiology and behaviour: a role for the melanocortin system. *European Journal of Pharmacology* **660:** 226–233.

Roulin A, **Randin C. 2015.** Gloger's rule in North American Barn Owls. *The Auk* **132:** 321–332.

Roulin A, **Wink M**, **Salamin N. 2009.** Selection on a eumelanic ornament is stronger in the tropics than in temperate zones in the worldwide-distributed barn Owl. *Journal of Evolutionary Biology* **22:** 345–354.

Sarasola JH, **Negro JJ**, **Hobson KA**, **Bortolotti GR**, **Bildstein KL. 2008.** Can a 'wintering area effect' explain population status of Swainson's Hawks? A stable isotope approach. *Diversity and Distributions* **14:** 686–691.

Sexton J, **Song X-P**, **Feng M**, **Noojipady P**, **Anand A**, **Huang C**, **Kim D-H**, **Collins K**, **Channan S**, **DiMiceli S**, **Townshend J. 2013.** Global, 30-m resolution continuous fields of tree cover: landsat-based rescaling of MODIS Vegetation Continuous Fields with lidar-based estimates of error. *International Journal of Digital Earth* **6:** 427–448.

Sordahl TA. 2014. Distribution of color-morphs of the Eastern Screech-Owl in Iowa. *The Wilson Journal of Ornithology* **126:** 321–332.

Tate GJ, **Amar A. 2017.** Morph specific foraging behavior by a polymorphic raptor under variable light conditions. *Scientific Reports* **7:** 9161.

Tate GJ, **Bishop JM**, **Amar A. 2016.** Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morphs in a polymorphic bird. *Ecology Letters* **19:** 679–686.

Thornton P, **Thornton M**, **Mayer B**, **Wei Y**, **Devarakonda R**, **Vose R**, **Cook R. 2017.** *Daymet: daily surface weather data on a 1-km grid for North America, version 3.* Oak Ridge: Oak Ridge National Labratory Distributed Active Archive Center.

Walsberg GE, **Campbell GS**, **King JR. 1978.** Animal coat color and radiative heat gain: a re-evaluation. *Journal of Comparative Physiology* **126:** 211–222.

Ward JM, **Blount JD**, **Ruxton GD**, **Houston DC. 2002.** The adaptive significance of dark plumage for birds in desert environments. *Ardea* **90:** 311–323.

Wheeler BK, **Economidy JM**, **White CM. 2003.** *Raptors of Western North America: the Wheeler guides.* Princeton: Princeton University Press.

Woodbridge B. 1991. *Habitat selection by nesting Swainson's Hawks: a hierarchical approach*. Unpublished MSc Thesis, Oregon State University.

Woodbridge B, **Finley KK**, **Bloom P. 1995.** Reproductive performance, age strucutre and natal dispersal of Swainson's Hawks in the Butte Valley, California. *Journal of Raptor Research* **29:** 187–192.

Wunderle JM. 1981. An analysis of a morph ratio cline in the Bananaquit (*Coereba flaveola*) on Grenada, West Indies. *Evolution* **35:** 333–344.

Zink R, **Remsen J. 1986.** Evolutionary processes and patterns of geographic variation in birds. *Current Ornithology* **4:** 1–69.