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Article

Is black plumage an adaptation to high elevations in a cosmopolitan bird genus?

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Black plumage is expected to absorb and retain more heat and provide better protection against UV radiation compared with lighter plumages. Black plumage is common in species of the genera *Turdus* and *Platycichla* that inhabit highlands across different regions of the world. Considering this geographical recurrent pattern we tested the hypothesis that black plumage in these two genera has evolved as a co-adaptive response to inhabiting highlands, reconstructing ancestral character states for plumage and altitudinal distribution using maximum-likelihood methods, and a Pagel's multistate discrete method. For these analyses, we used a phylogeny based on mitochondrial and nuclear DNA regions that included 60 of the 66 recognized species in the genera *Turdus* and *Platycichla*. We found that black-plumage coloration evolved independently on eight occasions within these two genera, and species with black plumage occur more often at highlands. Our results support the hypothesis that black-plumage is adaptative in highlands; but, studies in other bird groups with black-plumage inhabiting at the same elevations will provide evidence for this adaptive hypothesis or if the evolution of black-plumage in other groups is explained by other evolutionary forces.

Keywords: black color, color evolution, comparative analysis, highland birds, Passeriformes, UV defense

Introduction

The climatic conditions prevailing at highlands (> 2500 m a.s.l.) impose several constraints to those species that colonize and inhabit high mountain habitats. At these elevations low temperatures, low atmospheric pressure and oxygen levels, and high solar radiation often function as barriers, limiting the number of species that adapt to these conditions (Körner 2007, Keller et al. 2013). A fair amount of studies have focused on breathing rates (Ramirez et al. 2007, Storz et al. 2010, Ivy and Scott 2015), body morphology (Price 1991, Landmann and Winding 1995, Bears et al. 2008), cold tolerance (Swanson and Liknes 2006, Swanson and Garland 2009), mass change (Bears et al. 2008) or change in plumage color (Friedman and Remeŝ 2017, Delhey 2018, Galván et al. 2018, Medina et al. 2018), to understand the adaptive response of birds to highland environments.

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The evolution of plumage coloration is the consequence of the combined effect of sexual and natural selection and the effect of each of these evolutionary forces varies among species and between sexes, since each of these forces may affect differently the individual reproduction in each species (Hill 1991, Bennett et al. 1994). For instance, species in which concealment is important, plumage coloration matches the surroundings, or the coloration of other species (Bortolotti 2006). This is the case of ptarmigans whose plumage change seasonally to match the background (Madge and McGowan 2002), or cuckoos whose plumage mimic that of hawk predators (Gluckman and Mundy 2013, Trnka and Grim 2013). In many other species, there are striking differences in plumage coloration between sexes, in which females are usually cryptic and males have bright and sometimes extravagant plumages as a result of sexual selection (e.g. Paradisaeidae, Pipridae, Cotingidae; Andersson 1994, Zahavi and Zahavi 1997, Bortolotti 2006, Dale et al. 2015). Despite that evolutionary causes of plumage coloration have received much attention (Darwin 1871, Wallace 1889, Huxley 1942, Mayr 1942, Cowless et al. 1967), the effect of high mountain environmental conditions on the evolution of plumage coloration has been overlooked (McNaught and Owens 2002, Galeotti et al. 2003, Badyaev and Young 2004).

In birds (e.g. Turdidae and Thraupidae), insects (e.g. flies and butterflies) and reptiles, there is a remarkable pattern wherein species that inhabit highlands have black or more melanized body coloration (Isler and Isler 1999, Clement and Hathway 2000, Ellers and Boggs 2002, 2004, Collar 2005, Pool and Aquadro 2007, Parkash et al. 2008, 2010, Wittkopp et al. 2011). Although this pattern has been reported multiple times, to our best knowledge the relationship between black coloration and highland occupancy in birds have not been studied using a comparative phylogenetic approach; although this method has been used to study the effect of other habitats in bird coloration (Delhey 2018, Galván et al. 2018).

It is well known that coloration of some bird species correlates with some climatic conditions (e.g. precipitation or temperature; Delhey et al. 2019, Romano et al. 2019). For example, in deserts populations of some bird species have lighter plumage coloration compared with populations inhabiting more humid environments (Gloger's rule; Gloger 1833, Serventy 1971, Delhey 2018); though many species inhabiting deserts have black-plumages (Ward et al. 2002). The lighter plumage presumably reduces heat transfer (Mayr 1963), but several hypotheses have been proposed to explain the adaptation of black-plumage to desertic environments (Serventy 1971; see Ward et al. 2002 for a review): resistance to abrasion, protection against feather-degradation by bacteria, protection against UV radiation, reduction of skin heat stress, reduction of metabolic costs by allowing birds activity at dawn and dusk when temperatures decrease drastically, social signaling and night camouflage (Zink and Remsen 1986, Ward et al. 2002, Burtt and Ichida 2004, Goldstein et al. 2004, Lodei 2013).

In cold highland environments, many bird species have also black plumage contradicting the Gloger's Rule that expect more species with dark plumage in warmer regions (Serventy 1971, Ward et al. 2002), but agreeing with the Bogert's rule (Bogert 1949, Clusella Trullas et al. 2007, Gaston et al. 2008), which proposes that darker color improves thermoregulation efficacy in cold conditions. The energetic cost of thermoregulation increases in birds as the difference between body temperature and ambient temperature increases (Calder and King 1974, Keller et al. 2013, Stager et al. 2015), and its effect is expected to be more severe at high elevations. Two conditions reduce the thermoregulation cost in birds: 1) hypothermia and torpor in which birds by lowering their body temperature reduce their thermal gradient, and 2) the use of an external heat source (e.g. solar radiation), which reduces the metabolic cost of maintaining the body temperature constant, particularly when ambient temperature is very low. Birds with dark coloration presumably absorb and retain more heat, and protect themselves more effectively against UV radiation than those birds with lighter plumages (Heppner 1970, Walsberg 1983, Bittner et al. 2002, Goldstein et al. 2004, Bortolotti 2006). Considering the higher cost of maintaining body temperature constant and the negative effect of UV radiation in highland environments, we hypothesize that dark plumage should evolve more frequently in highlands than at lower elevations.

In this study, our main objective is to reconstruct the evolution of plumage color and altitudinal distribution in two sister genera *Turdus* and *Platycichla* to test the hypothesis that black-plumage has evolved as an adaptation to inhabit highlands. We mapped the evolution of black-plumage evolution onto the phylogeny of the genus *Turdus* (Voelker et al. 2007) and examined whether evolutionary changes in black coloration are associated with occupancy of highland environments. We predicted that if black-plumage is an adaptation to inhabit cold highlands as Bogerts' Rule predict, thrushes with black-plumage evolved from lowlands species with lighter plumages. But, if black-plumage is not an adaptation to inhabit cold highlands, thrush species with black-plumage are expected to have evolved from a lowland species with black-plumage.

Material and methods

Scoring plumage and altitude distribution

We obtained the information on thrush species plumage from descriptions of species and illustrations (Clement and Hathway 2000, Collar 2005). We classified species' plumage into three categories: black, brown and grey. We assigned birds to a particular category if the plumage of a particular color (e.g. black) covers > 50% of the body, including the dorsal parts (dorsum of birds is more exposed to solar radiation and coloration on it is expected to have little influence of sexual selection, since in thrushes vocalizations play the main role for mating; Vargas-Castro et al. 2012, 2015). In species in which females have lighter plumage than males (Clement and Hathway 2000, Collar 2005), we used only the male coloration in our analysis. The altitudinal distribution of each species was obtained from Clement and Hathway (2000) and Collar (2005) and references therein, and from unpublished records of the authors. The distribution of the species included in Collar (2005) could be updated with recent eBird data and is possible to visually compare both distributions visiting each thrush species web page in Handbook of the birds of the world alive at <www.hbw.com>. The altitudinal distribution is reported as a range in these references, but for the analyses of the species included in this study, we used the lower, the upper and the midpoint of each species distribution. We used lower and upper distribution limits to test whether extreme altitudinal distributions influence the plumage color. However, we chose the mid distribution point as the best indicator for each-species altitudinal distribution, because abundance tends to peak around the center of the altitudinal distribution for many bird species (Clement and Hathway 2000).

Ancestral state reconstruction and comparative analysis

We used the molecular phylogeny of thrushes published by Voelker et al. (2007) which includes 60 of the 66 recognized species in the genera *Turdus* and *Platycichla*, and several subspecies and individuals per species and subspecies (Voelker et al. 2007, Melo et al. 2010). This phylogeny is based on mitochondrial (cytochrome b and ND2) and nuclear DNA regions (RAG1, beta fibrinogen intron 5, aconitase 1 intron 10 and myoglobin intron 2). We eliminated from the ancestral state reconstruction and comparative analysis all subspecies that have the same plumage color. Additionally, we eliminated individuals of the same species and subspecies that were in the same clade, so that we ended with a tree that included 65 taxa (Fig. 1). In the case of *T. olivaceus* the relationship between subspecies and their taxonomic status is unclear (Voelker et al. 2007, Melo et al. 2010); and for that reason we used in our analysis those subspecies with different plumage pattern included in different clades.

We reconstructed ancestral character states for plumage using the maximum-likelihood method in Mesquite ver. 3.02 (Maddison and Maddison 2015). We used Markov k-state one parameter model for the maximum-likelihood analysis, which assumes an equal rate of change of characters, as in previous studies of discrete ancestral state character reconstructions (Schluter et al. 1997, Price et al. 2009, Odom et al. 2013). To reconstruct the altitudinal distribution of the species we used the square-change parsimony method in Mesquite ver. 3.02 weighted by branch length. This method assumes that large evolutionary changes, in this case altitudinal distribution, occur more likely in longer branches; but, this method minimizes the evolutionary changes by dividing the the sum of squared changes between the branch lengths (Nunn 2011). Additionally, this method provides values equivalent to the maximum likelihood estimate under Brownian motion (Schluter et al. 1997, Maddison and Maddison 2000, Nunn 2011).

We tested if black-plumage coloration in thrushes occurs more often in species that inhabit high elevations using a phylogenetic regression with a mixture of discrete (non-black = 0, and black plumage = 1; dependent variable) and continuous characters (lower, upper and midpoint altitudinal distribution values; independent variable). We used the function 'compar.gee' of the library 'ape' in R, with a binomial family to run a logistic regression analysis corrected by the phylogenetic relationship between species.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mm4qb48> (Sandoval and Barrantes 2019).

Results

Fourteen *Turdus* species have black-plumage based on our classification method. The reconstruction of the coloration of thrushes using maximum likelihood indicated that black coloration evolved from a brown ancestor at the basal node (rate = 0.18; –log likelihood = 69.55; Fig. 1a), and black-plumage evolved independently on eight occasions. In four cases the black-plumage evolved as basal in a clade, and within these clades, seven species maintained the black-plumage, but five species lost the black-plumage and evolved to another plumage (Fig. 1). In the other four occasions (once at the north of Europe, once in south of Africa and twice in South America) black-plumage evolved from a black/gray ancestor (Fig. 1). Squared-change parsimony reconstruction of the altitudinal origin of all thrushes indicated that the genus evolved from an ancestor inhabiting approximately 1413 m a.s.l. (SE = 387 m, confidence intervals: 639–2186 m a.s.l.; Fig. 1). From the 11 species with midpoint elevation higher than 2000 m a.s.l., six species (*T. kessleri*, *T. rufitorques*, *T. nigrescens*, *T. infuscatus*, *T. plebejus* and *T. merula*) evolved between 920 and 1536 m a.s.l. (Fig. 1). The other five species (*T. serranus*, *T. chiguanco*, *T. fuscator*, *T. olivaceus smithi* and *T. olivaceus abyssinicus*) evolved above 2000 m a.s.l. (Fig. 1).

Black plumage was correlated with altitudinal distribution in thrushes (Fig. 2). The black plumage was associated with higher elevations, in the lower (slope estimate ± SE = 0.0016 ± 0.0005, $t = 3.26$, $df = 26.94$, $p = 0.003$), upper (slope estimate ± SE = 0.0012 ± 0.0003, $t = 3.67$, $df = 26.94$, $p = 0.001$) and midpoint of the altitudinal distribution of thrush species (slope estimate ± SE = 0.0022 ± 0.0005, $t = 4.15$, $df = 26.94$, $p < 0.001$).

Discussion

The black-plumage in the genus *Turdus* is more common in highland species, and its evolution correlates with the

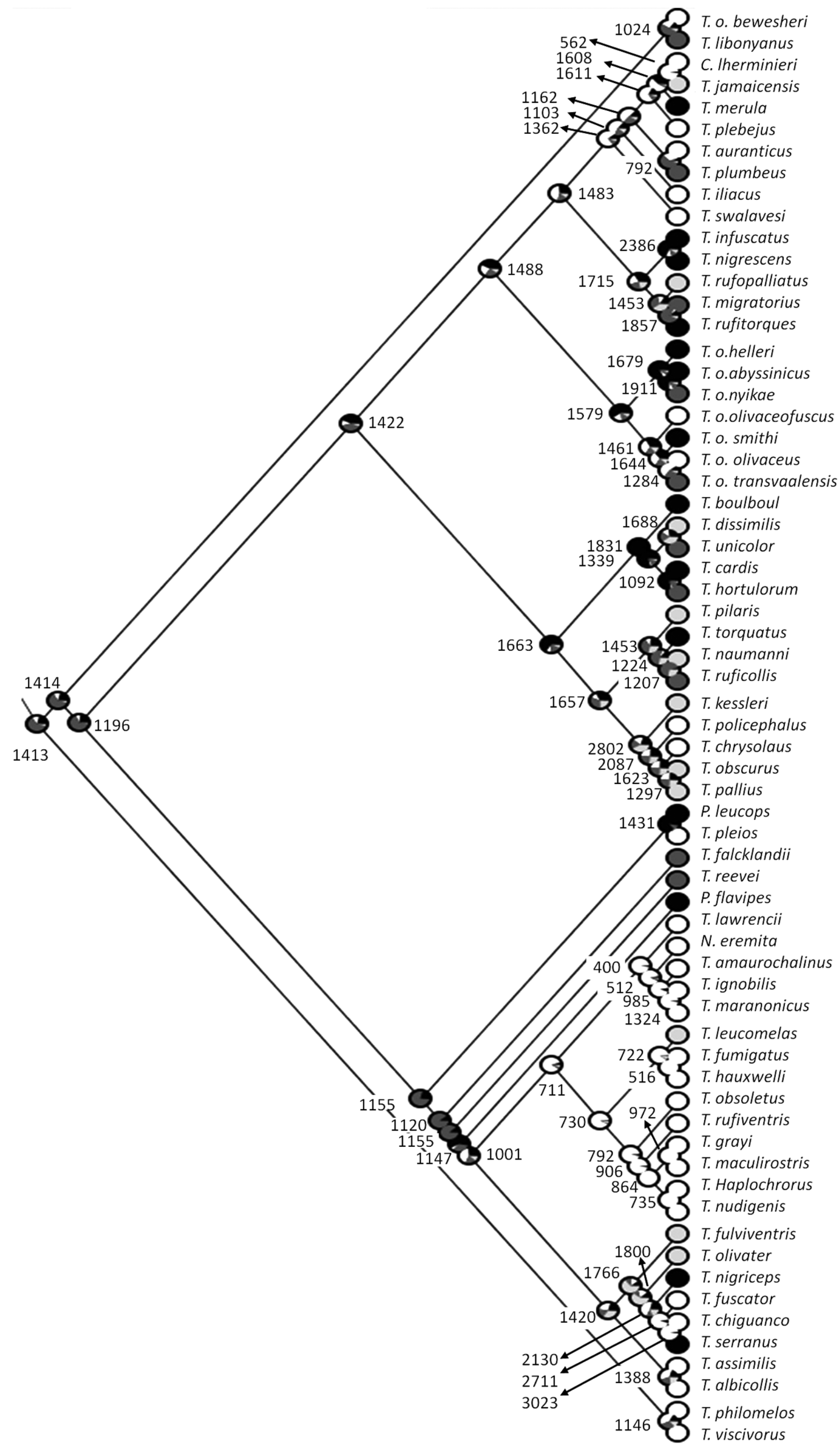

Figure 1. Maximum-likelihood reconstruction using a Markov k-state one parameter model with equal characters change rate for black-plumage color. Black circles: black-plumage color. White circles: brown plumage color. Dark grey circles: grey plumage color; light grey circles: multiple plumage color. Proportional likelihood of ancestral states characters are indicated by the color distribution inside the circles. Number inside of the figure represent the altitudinal distribution in meters (rounded to the closed number) of the ancestors of actual species according to the altitudinal reconstruction.

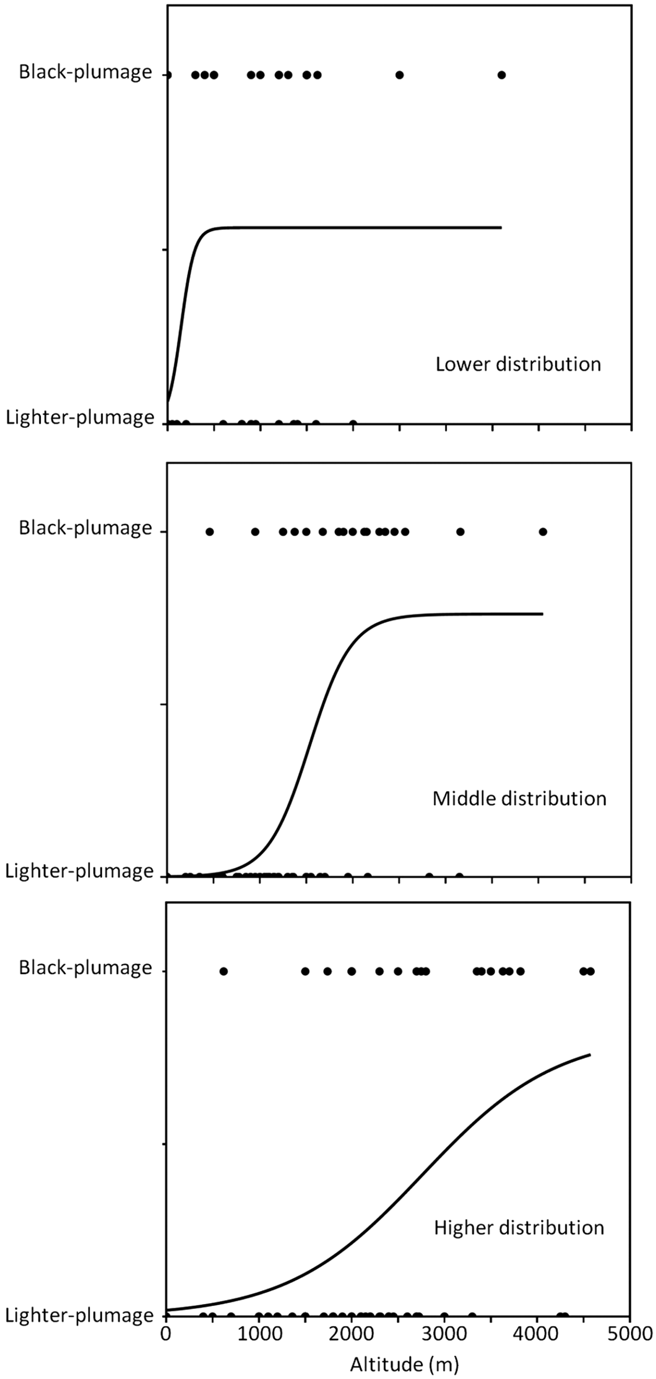

Figure 2. Logistic regression of the relationship between the altitudinal distribution using the lower, higher and middle distribution per thrush species (each dot) and the occurrence of black-plumage.

occupancy of highlands. Black-plumage evolved independently multiple times from different ancestors within the genus and most of these events occurred at middle elevation. The multiple times that black-plumage thrushes colonized highlands support the adaptive response to the climatic conditions such as low temperatures and high levels of UV radiations, prevailing at high elevation (Walsberg 1983, Goldstein et al. 2004, Bortolotti 2006). In cold habitats black-plumage could favor thermoregulation by increasing absorption of solar radiation (Bittner et al. 2002), reducing the energy cost of maintaining the body temperature constant especially when the ambient temperature is very low. The melanin pigment in black feathers could also function as a UV radiation screen (Bechtel 1978), which increases rapidly with elevation (Bechtel 1978). This pigment absorbs more effectively the UV radiation than other pigments (Bergman 1982, Brenner and Hearing 2008). These two functions of black-plumage are not mutually exclusive and likely both have influenced the recurrent evolution of black plumage in highland thrushes than at other elevations. However, direct evidence comparing the thermoregulation effect and UV radiation absorption in close-related species with black-plumage and other color-plumage in highlands is needed to quantitatively test the function of black-plumage coloration. In most species of highland thrushes, males are black, while females are light black (Clement and Hathway 2000, Collar 2005). This sexual dichromatism could be the effect of females selecting darker males (sexual selection), or that males are more exposed to radiation during acoustic displays (sexual selection/natural selection). Displaying males of several bird species tend to be in more open areas because they use exposed perches to vocalize and transmit better and farther their acoustic signals (Krams 2001, Mathevon et al. 2005, Sandoval et al. 2015).

The most probable elevation for the origin of thrush species was between 1000 and 2000 m a.s.l., since the ancestral species for all analyzed species (after the altitudinal reconstruction) showed an ancestral middle distribution of 1413 m a.s.l. From this elevation different thrush species colonized lowlands and highlands on several occasions, according to the actual distribution of the species tha inhabit below and above the original ancestral distribution. Especifically for highland species, we found five colonization events in America, one in Europe and two in Africa. For example, *T. plebejus* an American highland species (2162 m a.s.l. in the middle species distribution point) evolved from an ancestor with a middle elevation distribution (ca 1611 m a.s.l.). Also, *T. olivaceus smithi* an African highland species (2450 m a.s.l. in the middle species distribution point) evolved from an African ancestor with a middle elevation distribution (ca 1643 m a.s.l.). These events of colonization were likely associated with the uplift of mountains in those continents or increasing warmer weather after the last glaciations. Both of these factors have been presumably important for highland colonization in other bird species (Cook 1974, Weir 2006, Barrantes 2009). However, to associate the origin of these species directly with geological and climatic events would require a different approach that incorporates the time scale and the study of geological events in each continent, which is beyond the scope of this investigation.

The latitudinal distribution of the thrush species could be a confounding factor for our results (Clement and Hathway 2000, Collar 2005), because low ambient temperature is presumably an important factor in the evolution of black plumage in thrushes, and at higher latitudes the temperature is lower than at equatorial latitudes at the same altitude (Freeman 2017). It is then expected that if black-plumage coloration is the result of adaptation to low temperatures, species with high latitudinal distributions would have black-plumage coloration independently of the altitude. However, this appears to be not the case, since from the six European and Eurasian thrush species occupying northern latitudes only two have black-plumage (Clement and Hathway 2000, Collar 2005, Supplementary material Appendix 1). Additionally, several of the thrush species occupying northern latitudes have complete (all individuals from a species migrate to non-reproductive areas without geographical overlap in both distributions) or partial (all individuals from one species migrate to non-reproductive areas, but reproductive and non-reproductive areas overlap geographically) latitudinal migrations (Clement and Hathway 2000, Collar 2005). Thereby, during the winter when ambient temperature lowers at higher latitudes, individuals are wintering in warmer areas; thus, these species have not had the pressure to evolve black-plumage coloration to cope with cold temperatures as seems to be the case for tropical highland species that inhabit cold environments year-round (Clement and Hathway 2000, Collar 2005).

In conclusion, we found that black-plumage coloration evolved independently on eight occasions in the genus *Turdus* and species with black-plumage occurred more often at highlands. Highland *Turdus* species evolved from a middle elevation ancestor and from there eight independent lineages colonized the highlands. However, not in all species that colonized the highlands evolved the black-plumage coloration.

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Author contributions – Both conceived the idea of the study and wrote the manuscript. The first author performed the analyses.

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Supplementary material (available online as Appendix jav-02041 at <www.avianbiology.org/appendix/jav-02041>). Appendix 1.