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SHORT NOTE

Ring recoveries of dead birds confirm that darker pheomelanic Barn Owls disperse longer distances

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Abstract Variation in melanin coloration is widespread and often associated with other phenotypic traits. A recent study showed that darker-reddish pheomelanic Barn Owls (*Tyto alba*) move longer distances between birth and breeding sites. Because this study considered only individuals recovered within a limited study area, it remains unclear whether the association between melanism and dispersal applies to a larger geographic scale. I analysed an independent dataset of birds ringed in the same study area but recovered dead along roads within and outside this area. As expected, dark pheomelanic owls dispersed further than lighter reddish conspecifics at a larger spatial scale.

Keywords Melanin-based coloration · Color polymorphism · Dispersal · Barn Owl

Zusammenfassung

Totfunde beringter Vögel bestätigen, dass dunklere, pheomelanistische Schleiereulen weiter abwandern.

Variationen in der Melaninfärbung sind weit verbreitet und oft mit anderen Merkmalen verknüpft. Kürzlich zeigte eine Studie, dass dunkler rot gefärbte Schleiereulen (*Tyto alba*), eine Färbung hervorgerufen durch Pheomelanin, längere Distanzen zwischen dem Ort an dem sie aufgezogen wurden und dem Brutplatz zurücklegen. Da diese Studie nur Individuen innerhalb eines bestimmten Versuchsgebiets berücksichtigen konnte, blieb es unklar, ob die Verknüpfung zwischen Melanismus und Abwanderung auch für größere geographische Maßstäbe gilt. Deshalb wurde ein unabhängiger Datensatz von Vögeln analysiert, die im gleichen Gebiet beringt worden waren, aber innerhalb und außerhalb diesen Gebiets entlang von Straßen tot wieder gefunden wurden. Wie erwartet, wanderten dunklere, pheomelanistische Eulen auch in diesem größeren Maßstab weiter ab als ihre helleren Artgenossen.

Introduction

Melanin-based coloration plays important roles in (1) predator–prey interactions by conferring camouflage (Hoekstra et al. 2005), (2) social interactions with darker melanic individuals being usually dominant over lighter-coloured conspecifics (Senar and Camerino 1998), (3) mate choice (Houtman and Falls 1994) and (4) thermoregulation (Walsberg 1983; Clusella-Trullas et al. 2007). Recent studies have shown that heritable melanin-based colour traits can be associated with a number of life-history, morphological, physiological and behavioural traits (Roulin 2004). Melanin-based colour traits are due to the deposition of one of two pigments, the black eumelanin and/or the reddish-brown pheomelanin. As demonstrated by chemical analyses, reddish-brown coloration as found in the Barn Swallow (*Hirundo rustica*) (McGraw et al. 2005), Tawny Owl (*Strix aluco*) (Gasparini et al. 2009) and Barn Owl (*Tyto alba*) (Roulin et al. 2008) is due to the deposition of large amounts of pheomelanin pigments.

A recent study in Swiss Barn Owls also showed that darker-reddish pheomelanic individuals move longer distances between birth site and the site where they breed for

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the first time (van den Brink et al. 2012). Even if the relationship between dispersal behaviour and coloration was robust, the study was performed in a restricted area (25 × 15 km), raising the question of whether it applies to a much larger geographic scale. If darker-reddish Barn Owls disperse longer distances beyond Switzerland, and particularly in the southern direction (e.g. Bairlein 1985), the European cline variation in the degree of reddishness (owls are darker-reddish in northern compared to southern Europe; Antoniazza et al. 2010) may gradually disappear unless darker-reddish Barn Owls are strongly counter-selected in southern Europe.

Here, I used an independent dataset of birds recovered dead by the general public to test whether the distance travelled between the sites of ringing and of death is higher in darker- rather than lighter-reddish Barn Owls. Thus, compared to the previous study by van den Brink et al. (2012), the area where birds were retrieved was much larger and the recovery cause different (found dead along roads vs. capture of breeding individuals).

Methods

The study was carried out in western Switzerland (46°49′N, 06°56′E) between 1988 and 2012 where owls breed in nest-boxes. From 1994 to 2012, I measured coloration in 1,572 and 1,649 nestling males and females, and in 448 and 593 breeding males and females, respectively. The degree of reddishness on the breast, belly, flank and underside of wings was compared with eight colour chips ranging from −1 for darker-reddish to −8 for white. A mean value over the four values was calculated and used in the statistical analyses.

From 1994 to 2012, the Swiss Ornithological Institute at Sempach recorded 167 individuals of known coloration that were recovered dead along roads. This sample consisted of 65 female and 66 males ringed as nestlings and 23 females and 13 males ringed as adults. Birds were recovered dead either in their first year of life (30 female and 33 male yearlings) or at a later age (58 female and 46 male adults). Fourteen birds were recovered in spring, 55 in summer, 44 in autumn and 54 in winter. Most birds were recovered dead in Switzerland ($n = 159$) and 8 in France. Distance travelled between the sites of ringing and death was known to the nearest km. This distance was log+1 transformed to obtain a normal distribution. Number of days between the moment when birds were ringed and recovered dead (median is 220 days, range 2–4,012) was also log+1 transformed. The latter measure was not associated with plumage coloration (linear mixed model with year of recovery as random variable, coloration: $F_{1,155.2} = 0.89$, $P = 0.35$; age at the time of recovery (yearling vs. adult): $F_{1,149.6} = 95.25$, $P < 0.0001$; sex: $F_{1,149.7} = 0.12$, $P = 0.73$; all interactions were non-significant, P values >0.56). Two-tailed statistical analyses were performed with the software JMP 8.0 and P values <0.05 were considered significant.

Results

Distance travelled by Barn Owls between the sites where I ringed them and where they were reported dead along roads varied between 0 and 451 km (median 10 km). In a linear mixed model with year of ringing as random variable, the distance travelled was longer in darker- than lighter-reddish birds ($F_{1,161.7} = 8.49$, $P = 0.0041$; Fig. 1), while controlling for the age when found dead (i.e. yearlings vs. adults) ($F_{1,161.8} = 11.34$, $P = 0.0009$, nestlings moved longer distances than adults) and the log-transformed duration between the moment when birds were ringed and recovered dead ($F_{1,154.1} = 18.67$, $P < 0.0001$). In a preliminary model, sex was not significant ($F_{1,160.5} = 0.008$, $P = 0.93$) and hence removed from the final model (keeping sex in the model did not modify the results). Including the season when birds were found dead did not modify the conclusion. A more complex model containing all two- and three-way interactions showed that none of them were significant. Models where I replaced the random variable "year of recovery" by the "year of ringing" were qualitatively similar; replacing the age at ringing by the age when found dead also gave similar results (not shown). Finally, removing any random variables and using a multiple regression analysis gave similar results. In a

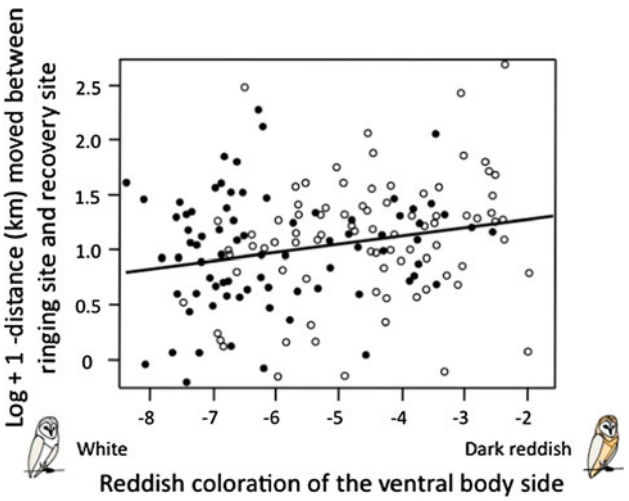

Fig. 1 Relationship between reddish pheomelanin-based coloration and distance moved between the sites of ringing and of recovery in Swiss Barn Owls (*Tyto alba*). Leverages of the model presented in the results are given. All individuals were found dead along roads. *Closed circles* males, *open circles* females

simple Pearson's correlation, darker-reddish birds still appeared to move longer distances ($r = -0.18$, $n = 167$, $P = 0.02$). This demonstrates that the association between distance travelled and reddish coloration is robust.

The absence of sex effects on dispersal distances is surprising, and hence I performed further analyses without considering plumage coloration. Among 131 birds ringed as nestlings, it appeared, as expected, that females moved longer distances than males (median 16 vs. 10.5 km; linear mixed model with year as random variable, sex: $F_{1,120.8} = 4.34$, $P = 0.039$; duration between the moment when birds were ringed and recovered dead: $F_{1,127.2} = 6.48$, $P = 0.012$). Among 36 birds ringed as adults, dispersal distances were not associated with sex (similar model, sex: $F_{1,32.12} = 0.008$, $P = 0.93$; duration: $F_{1,32.92} = 4.11$, $P = 0.05$).

Discussion

To date, the only way to obtain data on dispersal behaviour that is not constrained by the size of a study area is to analyse ring recoveries. The Barn Owl is one of the few bird species for which we can obtain a large number of recoveries from ringed birds. In Germany, for example, about 13 % of all ringed birds are reported dead by the general public (Bairlein 1994). Using a dataset of 167 birds for which sex and coloration were known, as well as the distance travelled between the sites where they were ringed and found dead along roads, confirmed that darker-reddish pheomelanic Barn Owls disperse longer distances.

As in the previous study by van den Brink et al. (2012) on natal dispersal, I again found that dispersal distances were associated with coloration independently of sex. Pheomelanin-based coloration is sexually dimorphic with females displaying on average a darker-reddish coloration than males, implying that, whatever their sex, female-like reddish Barn Owls moved longer distances than male-like pale birds. Sex-specific hormones associated with coloration may regulate dispersal behaviour or, alternatively, darker-reddish owls may be poorly adapted to the study area, forcing them to move. Although we indeed detected that darker- and lighter-reddish Barn Owls are adapted to different habitats, we did not, however, find evidence that darker-reddish birds performed less well than lighter-reddish conspecifics (Dreiss et al. 2012).

The association between dispersal distances and reddish coloration has a number of important evolutionary implications assuming that this association is not restricted to the Swiss population. In Europe, there is a pronounced cline in coloration, with birds being darker-reddish in northern Europe and paler-reddish in southern Europe, a variation that appears to be maintained by natural selection (Antoniazza et al. 2010). Because birds from northern populations move preferentially to the south (e.g. Kneis 1981; Bairlein 1985; Sarossy 2000; Wuntke and Ludwig 2000; Hillers 2011), and since they may travel longer distances than lighter-coloured birds born in southern Europe, the cline may not be evolutionarily stable. Indeed, introgression of genes of darker-reddish birds into the south may be more pronounced than the introgression of genes of lighter-reddish birds into the north. Population genetics studies are called for to answer this question, but also studies on whether darker-reddish birds are strongly counter-selected in southern Europe, which would help maintain the cline.

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