SHORT NOTE

Pheomelanin-based colouration is correlated with indices of flying strategies in the Barn Owl

Motti Charter · Yossi Leshem · Ido Izhaki · Alexandre Roulin

Abstract Resource polymorphism refers to individuals from the same population foraging in alternative habitats or on alternative food. Food specialization can be associated with adaptations such as colour polymorphism, with pale and dark colours conferring differential camouflage in different habitats. Pale and dark-reddish pheomelanic Barn Owls (*Tyto alba*) forage on different prey species in closed and open habitats, respectively. We show here that darker-reddish owls have heavier stomach content when found dead, and their 5th secondary wing feather is more deeply anchored inside the integument. These correlations suggest that their feathers bend less when flying, and that darker-reddish Barn Owls are able sustain more intense flying than their paler conspecifics.

Keywords Colour polymorphism · Feather · Flying · Foraging · Melanin · Stomach content

Zusammenfassung

Phäomelanin-Färbung bei Schleiereulen korreliert mit Merkmalen der Flugstrategie

Ressourcen-Polymorphismus beschreibt Individuen der-selben Population, die ihre Nahrung in alternativen Habi-taten suchen oder sich von anderem Futter ernähren. Nahrungsspezialisierung kann einhergehen mit Anpassun-gen wie einem Farb-Polymorphismus, bei dem helle und dunkle Farben unterschiedliche Tarnung in unterschiedli-chen Habitaten gewähren. Helle und dunkel-rötliche phä-omelanische Schleiereulen (*Tyto alba*) bejagen jeweils andere Beutearten in geschlossenem beziehungsweise offenem Habitat. Hier zeigen wir, dass die dunkel-rötlichen Eulen einen schwereren Mageninhalt haben, und dass ihre fünfte Armschwinge tiefer im Integument verankert ist. Diese Korrelationen deuten darauf hin, dass ihre Federn sich im Flug weniger biegen, und dass dunklere rötliche Schleiereulen einen kräftigeren Flug aufrecht erhalten können, da ihre helleren Artgenossen mit schwerem Mageninhalt tot aufgefunden wurden.

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Introduction

Within populations, individuals can adopt alternative for-aging strategies, a phenomenon that allows the optimal exploitation of distinct ecological niches and hence reduces the level of competition (Skulason and Smith 1995). In order to specialize on alternative food sources, a number of morphological adaptations may be required, such as cryptic colouration (Bond 2007). In many animals, individuals of the same age and same sex display one of several colour

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variants that facilitate camouflage in different habitats (Roulin 2004a). If different morphs forage in different habitats and/or on different food sources, various adaptations beyond that of colouration may be required, such as a specific morphology.

The Barn Owl (*Tyto alba*) varies in the degree of heritable pheomelanin-based colouration from white to reddish and in the number and size of black feather spots. In both Switzerland and Israel, reddish owls forage more frequently on voles in open habitats, while lighter-coloured individuals forage on Muridae close to forests/mixed habitats (Roulin 2004b; Charter et al. 2012; Dreiss et al. 2012). This raises the hypothesis that colour polymorphism is associated with foraging and/or flying strategies. Accordingly, lighter-coloured Barn Owls have more feather barbs on the inner primary vane (Roulin et al. 2013), are heavier and shorter-tailed (Roulin 2006) and disperse shorter distances (Van den Brink et al. 2012; Roulin 2013). Flying methods may therefore differ between pale and dark Barn Owls; consequently, differently coloured owls may differ in how they adjust stomach content and how deeply the wing feathers are anchored in the "feather-bearing integument" to stabilize the feathers against external forces (Homberger and de Silva 2000). Indeed, Durant et al. (2013) showed that breeding males adjust their stomach content to the foraging effort by avoiding eating when they have to sustain intense foraging activities in order to feed their brood. Therefore, if one colour morph is better able to sustain intense flying activities, this morph could fly with a heavier stomach content than the other morph. Furthermore, their wing feathers should be more deeply anchored in the feather-bearing integument in order to prevent the feathers from bending too much while flying (Homberger and de Silva 2000). We examined these two predictions by measuring morphological features of Barn Owl carcasses collected along roads.

Methods

Stomach contents of dead Barn Owls were collected daily along highways in the Champagne and Lorraine regions of France between 1995 and 2008. The dead owls were collected mainly in winter and autumn. Carcasses were frozen at −20 °C and thawed 1 day before dissection. Sex was identified by gonad inspection (316 males and 364 females). A total of 475 individuals possessing a Bursa of Fabricius were assigned the age category "juvenile", and those without this organ were assigned to the categories "yearling" or "adult" depending on whether wing feathers were all of the same new generation ($n = 101$) or of different generations ($n = 104$), respectively. Body weight (mean ± SE: 291 ± 1.1 g; range 186–386 g) was measured

to the nearest g after removal of the stomach content, which was weighed and Box–Cox transformed to normalise data distribution. Wing and bill lengths were measured to the nearest mm (296 ± 0.3 mm; 273–315 mm) and 0.1 mm (19.2 ± 0.3 mm; 17.3–21.3 mm), respectively. Pheomelanin-based colouration was scored on the breast, belly, flank and underside of the wings by comparing reddish-brown colouration with eight colour chips ranging from VIII for white to I for dark-reddish. Spots were counted on the breast within a 60 × 40 mm frame, their diameter measured to the nearest 0.1 mm and a mean value computed (Roulin 2004c).

We performed an additional study on carcasses collected along roads in Israel during 2010 ($n = 6$), 2011 (19), 2012 (44) and 2013 (51). In November 2013, we thawed the carcasses and examined wing feathers (5th primary and 5th secondary), respectively positioned at the mid-point of the ulna and humerus, where the size of the feather-bearing integument is maximal. We inserted the top of a ruler distally to the feather being measured until it touched the skin (which corresponds to the feather-bearing integument); the distance between the skin and the top of the feather represents the part of the feather not anchored inside the integument. We then extracted the feather to measure its full length. The difference between these two distances indicates the length of the section of feather anchored inside the integument (Homberger and de Silva 2000). Sex, age and plumage traits were assessed as noted above for the French owls. Statistical analyses were performed with the software JMP 8.0. Tests are two-tailed and P values <0.05 are considered significant. When removing non-significant continuous variables from the models, the change in the number of degrees of freedom can be larger than 1 because not all morphological traits could be measured in all individuals.

Results

Stomach content

Of the Barn Owls examined, 201 (30 %) had an empty stomach while those of 479 individuals contained pellets or prey remains (mean ± SE mass of stomach content: 16.9 ± 0.5 g; range 0.5–50 g). Individuals with either empty or full stomachs did not differ with respect to wing length, bill length, age, sex, pheomelanin-based colouration and number and size of black spots (logistic regression, all P values > 0.17).

When considering only individuals with food or pellets in the stomach, redder owls showed a heavier stomach content (ANCOVA: $F_{1,475} = 6.50$, $P = 0.01$; Fig. 1; this variable was already significant before removing non-significant variables), males had heavier content compared to females
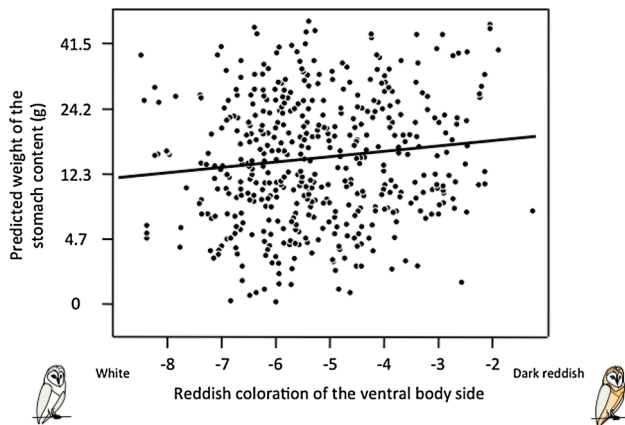
Fig. 1 Weight of stomach content in relation to pheomelanin-based reddish colouration in Barn Owl (*Tyto alba*) carcasses collected in France. Predicted values are from linear mixed model presented in "Results"

$(F_{1,475} = 7.79, P = 0.005; 23.8 \pm 0.7$ vs. 20.9 ± 0.7 g), and heavier birds had heavier stomach content $(F_{1,475} = 40.72, P < 0.0001)$. The following variables were not significant and hence were removed from the final model: number of spots $(F_{1,449} = 0.005, P = 0.94)$, age $(F_{2,451} = 0.37, P = 0.69)$, spot diameter $(F_{1,453} = 0.45, P = 0.50)$, bill length $(F_{1,460} = 2.30, P = 0.13)$ and wing length $(F_{1,471} = 2.21, P = 0.14)$. Adding year and season of collection as two random variables (explaining 0 and 2.8 % of the variation) in linear mixed models did not modify our conclusions. In the sample of birds with either empty or full stomachs, body mass was not related to the three plumage traits alone nor in interaction with sex (ANCOVAs, P values >0.15).

Length of the feather section anchored inside the feather-bearing integument

Mean length of the 5th primary feather anchored inside the integument was 2.09 ± 0.02 mm (range 1.4 and 2.6 mm) and of the 5th secondary feather was 1.69 ± 0.01 mm (range 1.4 and 2.1 mm). This section of the feather anchored in the integument was significantly associated with pheomelanin-based reddish colouration, depending on whether the considered feather was a primary or secondary (linear mixed model with individual identity as random variable explaining 25.5 % of the between individual variation, primary/secondary: $F_{1,159.7} = 22.19, P < 0.0001$; coloration: $F_{1,105} = 0.03, P = 0.86$; interaction: $F_{1,101.1} = 11.39, P = 0.001$). In this model, we controlled for length of feather external to the integument $(F_{1,156.7} = 5.18, P = 0.024$; shorter feathers are more deeply anchored), and sex $(F_{1,102.7} = 0.38, P = 0.54)$. Because age was not significant $(F_{2,111.2} = 0.13, P = 0.88)$, and we did not know the age of three individuals, we removed
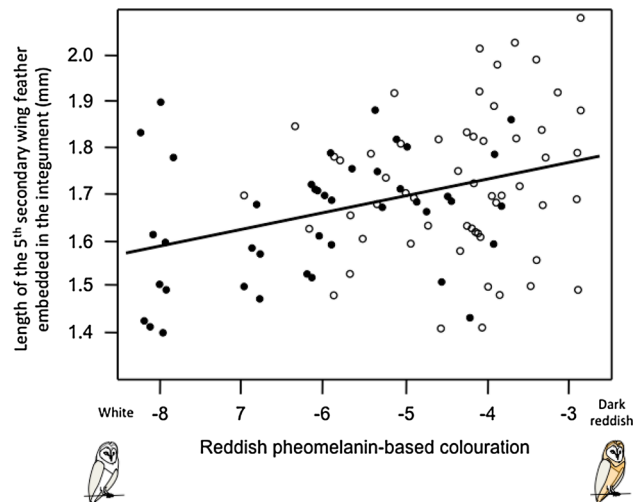

Fig. 2 Length of the 5th secondary wing feather embedded in the feather-bearing integument in relation to pheomelanin-based reddish colouration in Barn Owl (*Tyto alba*) carcasses collected in Israel. Predicted values from the model presented in "Results" are given. *Closed circles* males, *open circles* females

this variable. The significant interaction between colouration and which feather was measured (primary/secondary) is explained by the 5th secondary feather being more deeply anchored in the integument in darker-reddish individuals (ANCOVA: $F_{1,102} = 4.87, P = 0.03$; feather length outside the integument: $F_{1,102} = 3.86, P = 0.052$; sex: $F_{1,102} = 0.33, P = 0.57$; interaction sex $\times$ colour: $F_{1,102} = 5.42, P = 0.022$; Fig. 2), which was not the case for the 5th primary (all P values > 0.16). Because sex was strongly related to colouration (Student's t test: $t_{111} = 7.22, P < 0.0001$), it reduced the ability to detect a relationship between colouration and how deeply feathers are anchored in the feather-bearing integument. After removing sex from the model, we found a stronger relationship between the length of the 5th primary feather anchored in the integument and colouration (Pearson's correlation: $r = 0.32, n = 111, P = 0.0006$, Fig. 2; 5th primary: $r = -0.11, n = 108, P = 0.25$). Number of spots and spot diameter were also correlated with the extent to which feathers were anchored for the 5th primary $(r = -0.09, n = 108, P = 0.34; r = -0.04, n = 108, P = 0.71)$ and for the 5th secondary feather $(r = 0.36, n = 111, P < 0.0001; r = 0.27, n = 118, P = 0.004)$, which is not surprising since these plumage traits are correlated (Pearson's correlation, number $\times$ size of spots: $r = 0.74, n = 119, P < 0.0001$; number of spots $\times$ colour: $r = 0.54, n = 119, P < 0.0001$; spot size $\times$ colour: $r = 0.52, n = 119, P < 0.0001$).

Discussion

The present study adds new findings to the hypothesis that, in the Barn Owl, pheomelanin-based colouration covaries

with traits associated with flying activities (see "Introduction"). We show that, in Barn Owls found dead on roads, the darker individuals had heavier stomach content than the lighter-coloured ones and their secondary wing feathers were more deeply anchored in the feather-bearing integument. Redder birds showed heavier stomach content because either (1) they eat more than their lighter-coloured conspecifics (Dreiss et al. 2010), or (2) redder birds (but not lighter-coloured ones) fly at lower heights above the ground after having consumed food items and are thus at a greater risk of being hit by a car, or (3) redder birds eat and fly afterwards at a time when the risk of being hit by a car is particularly high, or (4) lighter-coloured owls fly less often than reddish individuals when their stomach is full. The latter interpretation is consistent with the finding that wing feathers are more deeply anchored in the feather-bearing integument in darker-reddish birds in order to sustain intense flying activity when the stomach is full. Because a full stomach will increase the cost of flying (Durant et al. 2013), and because feathers more deeply anchored inside the feather-bearing integument will stabilize the feathers against external forces (Homberger and de Silva 2000), we suggest that darker-reddish Barn Owls can sustain more intense flying activities and hence fly more often than paler owls when their stomach is full.

Our observations have a number of life-history implications. First, the finding that feathers are more deeply anchored in the feather-bearing integument in reddish Barn Owls is consistent with their higher dispersal tendency (Van den Brink et al. 2012; Roulin 2013). Second, in some years, darker-reddish males feed their brood at a higher rate (Roulin et al. 2001), which may require feathers to be more deeply anchored in the feather-bearing integument. In line with the hypothesis that darker-reddish individuals sustain more intense flying is the observation that they have a heavier heart (Roulin et al. 2001). To conclude, dark- and light-coloured Barn Owls have developed different life-history strategies that may require a battery of specific adaptations, including colour-specific regulation of stomach content and feather structure. All these colour-related morphological and behavioural adaptations may partly explain why, within populations, dark and pale Barn Owls exploit different parts of the environment (Charter et al. 2012; Dreiss et al. 2012), and why on the world scale Barn Owls vary in colouration across regions (Roulin et al. 2009; Antoniazza et al. 2010).

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