

Insularity and the evolution of melanism, sexual dichromatism and body size in the worldwide-distributed barn owl

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Abstract

Island biogeography has provided fundamental hypotheses in population genetics, ecology and evolutionary biology. Insular populations usually face different feeding conditions, predation pressure, intraspecific and interspecific competition than continental populations. This so-called island syndrome can promote the evolution of specific phenotypes like a small (or large) body size and a light (or dark) colouration as well as influence the evolution of sexual dimorphism. To examine whether insularity leads to phenotypic differentiation in a consistent way in a worldwide-distributed nonmigratory species, we compared body size, body shape and colouration between insular and continental barn owl (*Tyto alba*) populations by controlling indirectly for phylogeny. This species is suitable because it varies in pheomelanin-based colouration from reddish-brown to white, and it displays eumelanic black spots for which the number and size vary between individuals, populations and species. Females are on average darker pheomelanic and display more and larger eumelanic spots than males. Our results show that on islands barn owls exhibited smaller and fewer eumelanic spots and lighter pheomelanic colouration, and shorter wings than on continents. Sexual dimorphism in pheomelanin-based colouration was less pronounced on islands than continents (i.e. on islands males tended to be as pheomelanic as females), and on small islands owls were redder pheomelanic and smaller in size than owls living on larger islands. Sexual dimorphism in the size of eumelanic spots was more pronounced (i.e. females displayed much larger spots than males) in barn owls living on islands located further away from a continent. Our study indicates that insular conditions drive the evolution towards a lower degree of eumelanism, smaller body size and affects the evolution of sexual dichromatism in melanin-based colour traits. The effect of insularity was more pronounced on body size and shape than on melanic traits.

Introduction

Island biogeography led to the development of seminal hypotheses that have influenced evolutionary biology (MacArthur & Wilson, 1967; Carlquist, 1970; Lack, 1971; Grant, 1998; Whittaker, 1998). Insular populations usually experience weaker interspecific competition than continental populations because of reduced species diversity (Crowell, 1962; Grant, 1998). As a result,

insular populations have wider ecological niches than their mainland counterparts (Diamond, 1970; Keast, 1970), which can explain the evolution of a large or small body size on islands (Foster, 1964; Lomolino, 1985; Sch ule, 1993; Fitzpatrick, 1998; Clegg & Owens, 2002; Meiri, 2007), and thus facilitate niche expansion. The 'island rule', stating that large-bodied species evolve towards smaller sizes whereas small-bodied species evolve towards larger sizes, has been verified in mammals and birds. The importance of feeding ecology and intraspecific competition in the evolution of avian body size on islands has also been acknowledged (Clegg & Owens, 2002).

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Interestingly, conditions prevailing on islands exert selection not only on body size and the ability to expand ecological niches but also affect sexual selection processes. Continental animals display a larger number of colour patches than their insular counterparts (Grant, 1965; Fitzpatrick, 1998), and they produce songs that are more complex (Otte, 1989; Hamao & Ueda, 2000; Baker *et al.*, 2006). The degree of colourfulness and song complexity is usually thought to be the result of sexual selection (Andersson, 1994), and two forms of this process can explain phenotypic differentiation between continental and insular animals. First, sexual selection increases the risk of extinction (McLain, 1993; Doherty *et al.*, 2003; Morrow & Pitcher, 2003) because it is antagonistically related to natural selection by promoting traits that enhance mating success at the cost of survival. Furthermore, in polygamous species, a small proportion of males can secure a large fraction of the females, which increases the risk of population extinction because of reduced effective population size. Small populations such as those found on islands are particularly affected by this effect (Berger, 1990; Manne *et al.*, 1999). As a consequence, colourful and/or sexually dichromatic species may be less able to persist on islands after their invasion than drab and sexually monomorphic species. Accordingly, introduction success of sexually dichromatic birds on oceanic islands was weaker than of monomorphic birds, a relationship that was more pronounced on islands containing more species already introduced (McLain *et al.*, 1995, 1999; Sorci *et al.*, 1998; but see Donze *et al.*, 2004 for a counter-example with galliformes species). Second, ecological conditions prevailing on islands may lead to a reduction in the intensity of sexual selection because insular populations exhibit lower levels of genetic variation than continental populations because of genetic drift, founder effect and low rate of dispersal (Griffith, 2000). This hypothesis predicts that after the invasion of an island, species evolve towards a reduced degree of colouration and sexual dimorphism.

Ecological conditions prevailing on islands and continents are often different, and this will affect the intensity of natural and sexual selection. Phenotypic comparison of insular and continental species or populations can bring useful information on the ecological factors driving the evolution of body size, body shape and colouration. Phenotypic traits can evolve only if genetically inherited from one generation to the next, and hence the study of the effect of insular conditions on phenotypic evolution should consider traits for which the expression is under strong genetic control. Melanin-based colouration is a good candidate trait because melanin pigments are endogenously produced and inter-individual variation in the degree of reddish-brownness (pheomelanin-based colouration) and in black to grey colourations (eumelanin-based colouration) is often strongly heritable (Roulin, 2004c) with evidence for a condition-dependent component in some species (Fargallo *et al.*, 2007).

Melanin-based colour traits are therefore particularly suited to study the effect of selective processes prevailing on islands and continents on phenotypic evolution because inter-individual differences in colouration is mostly because of genetic factors. As the production of melanic colourations is usually weakly sensitive to habitat quality, colour differences between insular and continental populations should be because of differential selection rather than environmentally induced variation in the physiological production of melanic pigments.

To investigate the effect of insular conditions on phenotypic evolution, we considered the cosmopolitan barn owl (*Tyto* sp.), a family comprising seven *Tyto* species and 33 *Tyto alba* subspecies. This bird is not migratory although individuals can move several hundred kilometres, an important feature as phenotypic differences between continental and insular birds is more pronounced in resident than migratory birds (Fitzpatrick, 1998). Both among and within barn owl populations, plumage varies continuously from white to reddish-brown pheomelanin and from immaculate to heavily marked with black eumelanin spots of varying size (Roulin *et al.*, 2001a). As shown in Switzerland, variation in plumage traits is strongly heritable and not or weakly sensitive to environmental factors (Roulin & Dijkstra, 2003). A recent animal model analysis applied to 2711 individuals showed that the variation in spot diameter is dominated by additive genetic variance ($h^2 = 0.82$ in males and 0.53 in females), the rearing environment has no detectable effect, whereas year of hatching explains 6% of the variance in males and 10% in females (Roulin *et al.*, in press). On the European continent, white and reddish individuals have a different diet (Roulin, 2004a), indicating that plumage colouration is associated with predator-prey interactions possibly through an effect of colouration on camouflage. Barn owls are monogamous but females that produce two annual broods frequently desert their offspring before completion of parental duties to remate with another partner (Roulin, 2002). At least in Switzerland, spot size is sexually selected, with females displaying larger spots having a selective advantage over smaller-spotted female conspecifics (Roulin *et al.*, in press). Males assess this trait to select a female and to adjust paternal investment (Roulin, 1999; Roulin & Altwegg, 2007).

Data were collected on barn owl skin museum specimens collected in Eurasia, America, Africa, and Oceania and on many islands located worldwide. We compared the degree of melanin-based colouration, sexual dichromatism, body size (i.e. bill length) and body shape (i.e. wing and tail length) of barn owls located on islands and on continents. As species that invade islands usually expand their ecological niche (Diamond, 1970; Keast, 1970), we predict barn owls to be differently sized, shaped and plumaged on islands compared to continents. As insular conditions may be more pronounced on small than large islands and on islands far than close to a

continent, we investigated whether the evolution of the same phenotypic traits is associated with island size and island–continent distance.

Materials and methods

Data collection

To obtain information on phenotypic traits in barn owls distributed worldwide, A. Roulin visited 45 museums in 1999, 2000 and 2007. From labels attached to 5021 skin specimens, we gathered information on taxonomic status and site of collection. Using a geographical atlas, we determined latitude, island surface as well as shortest distance to the nearest continent. We compared pheomelanin-based colouration of the breast and belly with eight colour chips ranging from one for dark reddish-brown to eight for white (Roulin, 1999). The mean colour score of the two body parts was denoted ‘plumage colouration’ and used in the statistical analyses. A 60 × 40 mm frame was placed on the same two body parts within which eumelanin spots were counted and their diameter measured to the nearest 0.1 mm. As for plumage colouration, mean number of spots and mean spot diameter were calculated over the two body parts. Assessment of plumage traits is reliable (Roulin, 1999, 2004b). As previously shown, skins kept in museums during decades did not fade (Roulin, 2003). Although variation in plumage traits within species/subspecies was substantial, individuals belonging to the same species/subspecies resemble each other (repeatability analysis for pheomelanin-based colouration: $r \pm SE = 0.306 \pm 0.029$, $F_{38,4548} = 41.01$, $P < 0.0001$; number of spots: 0.314 ± 0.030 , $F_{38,4426} = 40.96$, $P < 0.0001$; spot diameter: 0.494 ± 0.033 , $F_{38,4484} = 87.74$, $P < 0.0001$) (Lessells & Boag, 1987). Bill length was measured to the nearest 0.1 mm, and wing and tail length to the nearest 1 mm. We measured bill length because in the barn owl this trait is closely associated with overall body size (Roulin *et al.*, 2001b).

To compare phenotypic traits of barn owls located on continents and islands, we calculated mean values of individuals belonging to the same species or subspecies and found on the same continent. We applied the same procedure for individuals living on the same island. In case a species is distributed on several islands, we therefore obtained several values, one per island. Because the European barn owl comprises the two interbreeding subspecies *T. a. alba* and *T. a. guttata*, we pooled them. We did not consider the greater sooty owl (*T. tenebricosa*), because this species is not reddish-brown but black and it does not display black spots as in the other barn owls. For the analysis of mean phenotypic traits, we pooled data on females and males because plumage traits are strongly correlated between the sexes (Pearson correlation between mean colour values measured in females and males across 36 *Tyto* species:

$r = 0.92$, $P < 0.0001$; number of spots: $r = 0.96$, $P < 0.0001$; spot diameter: $r = 0.94$, $P < 0.0001$). Table 1 indicates barn owl species considered in the present study, their location and number of individuals measured.

Statistics

Our aim in this study is to examine whether insular and continental owls differ in plumage, size and shape because ecological conditions prevailing on islands are different from those on continents. However, owls on islands and continents can share similar phenotypes because of shared evolutionary history. To obtain results that are independent of phylogenetic relationships between barn owl species, we performed comparative analyses. Unfortunately, no complete phylogeny is yet available for the barn owl family, and for this reason, we employed an indirect comparative method that was found suitable in our previous analysis of the same dataset (Roulin *et al.*, 2009). We then used phylogenetic regression approach (Freckleton *et al.*, 2002) to take into account the phylogenetic correlation, approximated by the geographical distances (km) between the mean distributional range of each pair of barn owl species or populations located on continents or islands (see Roulin *et al.*, 2009 for details and justification for the use of this proxy). The distance matrix obtained is then used as the variance–covariance matrix in a generalized linear model (Freckleton *et al.*, 2002; McCulloch *et al.*, 2008), and maximum likelihood estimation of model parameters was performed. Several analyses were performed to obtain a model for each dependent variable measured. The approach followed to select explanatory variables within each model was to compare them using the weighted AIC criteria (Appendix S1), and the percentage of deviance explained by each factor is reported to rank factors within each model. This has the advantage to avoid the use of *P*-values, which could induce multiple testing. All analyses were performed using *R* scripts specifically made for this study and that are available upon request. Once the best model was identified for each response variable based on the observed response values, the phylogenetic residuals were taken to represent the results graphically and in tables.

We performed two sets of analyses on standardized data ([value–mean]/standard deviation). First, we tested whether barn owls located on islands are phenotypically different from those located on continents. We had a sample of 15 continental species and 34 insular species (totalling 65 data points, as a single species can occur on more than one island). Morphological traits (bill, wing and tail lengths), plumage traits (pheomelanin-based colouration, number and size of eumelanin spots) and sexual dichromatism in the same plumage traits were entered as dependent variables in separate analyses. In all analyses, we introduced absolute latitude and

Table 1 Barn owl species, location and number of individuals located on continents and islands. The symbol # is for 'number'.

Species	Location	Continents # specimens	Islands		Total # specimens
			# Islands	# Specimens	
<i>Tyto alba affinis</i>	Sub-Saharan Africa	508	1	3	511
<i>T. a. alba/guttata</i>	Europe	1829	6	364	2193
<i>T. a. bargei</i>	Curaçao	0	1	17	17
<i>T. a. contempta</i>	Columbia to Venezuela	81	0	0	81
<i>T. a. crassirostris</i>	Papua New Guinea, Solomon, Tanga group	0	3	10	10
<i>T. a. delicatula</i>	Australia	78	0	0	78
<i>T. a. deroepstorffi</i>	Andaman	0	1	2	2
<i>T. a. detorta</i>	Cape Verde	0	1	22	22
<i>T. a. erlangeri</i>	Middle east, Egypt,	88	2	14	102
<i>T. a. ernesti</i>	Corsica, Sardinia	0	2	87	87
<i>T. a. everetti</i>	Savu island (Timor)	0	1	17	17
<i>T. a. furcata</i>	Cuba, Jamaica	0	2	52	52
<i>T. a. glaucops</i>	St Domingo in West Indies	0	1	15	15
<i>T. a. gracillirostris</i>	Canary islands	0	1	19	19
<i>T. a. guatemalae</i>	Panama to Amazon	34	0	0	34
<i>T. a. hellmayri</i>	Guianas to Amazon, Trinidad	34	1	3	37
<i>T. a. hypermetra</i>	Grande Comore, Mayotte, Madagascar	0	2	68	68
<i>T. a. insularis</i>	Grenada, Dominica, St-Vincent in West Indies	0	3	20	20
<i>T. a. interposita</i>	Vanuatu	0	1	17	17
<i>T. a. javanica</i>	South Asia, Lesser Sunda, Java, Sulawesi, Singapore, Sunda	46	3	83	129
<i>T. a. lulu</i>	Fiji island, Easter, Loyalty, New Caledonia, Niue, Rotuma, Samoa, Solomon, Tonga, Vanuatu	0	10	145	145
<i>T. a. meeki</i>	New Guinea	0	1	19	19
<i>T. a. nigrescens</i>	Dominica in West Indies	0	1	5	5
<i>T. a. pratincola</i>	North and Central America, Bermuda	200	1	6	206
<i>T. a. punctatissima</i>	Galapagos	0	1	11	11
<i>T. a. schmitzi</i>	Madeira	0	1	38	38
<i>T. a. soumagnei</i>	Madagascar	0	1	1	1
<i>T. a. stertens</i>	Region around India, Ceylon	94	1	8	102
<i>T. a. subandean</i>	Columbia, Ecuador	11	0	0	11
<i>T. a. sumbaensis</i>	Molucca, Savu, Sumba	0	3	12	12
<i>T. a. thomensis</i>	Sao Tomé	0	1	18	18
<i>T. a. tuidara</i>	South America, Falkland	146	1	1	147
<i>T. aurantia</i>	New Britain in the Bismarck Archipelago	0	1	14	14
<i>T. capensis</i>	Equatorial to South Africa	128	0	0	128
<i>T. castanops</i>	Tasmania	0	1	36	36
<i>T. inexpectata</i>	Sulawesi	0	1	10	10
<i>T. longimembris</i>	Australia, South Asia, Sulawesi, Fiji, New Caledonia, New Guinea, Philippine, Taiwan	38	5	49	87
<i>T. novaehollandiae</i>	Australia, Admiralt, Papua New Guinea	25	2	7	32
<i>T. rosenbergii</i>	Sulawesi	0	1	53	53
Sum		3340	65	1246	4586

hemisphere because plumage traits vary with distance to the equator in a nonrandom way (Roulin *et al.*, 2009). When testing whether insular and continental populations differ in plumage traits, we incorporated bill length as a covariate because *Tyto* species displaying larger black spots have a longer bill (Roulin *et al.*, 2009). Second, we tested whether barn owl plumage traits and morphology are associated with island size and island–continent distance. We calculated mean trait values for each barn owl species found on each single island (34 barn owls species totalling 65 data points). Again, sexual dichro-

matism, plumage and morphological traits were entered as dependent variables in separate analyses. We introduced \log_{10} -transformed island surface (mean \pm SD = 101 565 \pm 211 565 km², range = 44 and 786 000 km²), \log_{10} -transformed shortest distance to continent (891 \pm 994 km, range = 3 and 4300 km) and absolute latitude as covariates. Because the aim of the article is to compare phenotypes of owls occurring on islands and continents, we considered the island–continent distance rather than the shortest distance between an island and another land which could be an island instead of a

continent. In analyses on plumage traits, we also incorporated bill length as an extra covariate.

Sexual dimorphism in pheomelanin-based colouration, number of eumelanic spots and spot diameter was obtained by dividing mean male trait value by mean female trait value. High values for sexual dimorphism indicate that males are much lighter coloured than females but display a similar number of spots of a similar size. Using this index of sexual dichromatism, we carried out similar analyses as explained previously except that we added mean trait value of males and females as an independent variable. This is necessary because indices of sexual dichromatism are correlated with mean trait values (pheomelanin-based colouration: $r = -0.52$, $n = 61$, $P < 0.0001$; number of eumelanic spots: $r = 0.57$, $n = 61$, $P < 0.0001$; spot diameter: $r = 0.59$, $n = 61$, $P < 0.0001$). This indicates that the degree of sexual dimorphism in melanin-based traits is higher in dark than pale melanic barn owl species.

Results

Island–continent comparison

Compared to barn owls located on continents, those on islands displayed smaller and fewer eumelanic spots and lighter pheomelanic colouration. However, the island factor explained only a small fraction of the deviance (4.9, 4.3 and 3.8%, respectively; Table 2). Sexual dimorphism in pheomelanin-based colouration was less pronounced on islands than continents, in the northern than southern hemisphere, and in temperate zones than near the equator. With respect to size of black spots and their number, sexual dimorphism was more pronounced in the temperate zones than near the equator but did not differ between the northern and southern hemispheres and between continents and islands. Owls had shorter wings and tail on islands than continents, whereas bill length did not differ between insular and continental owls and was mainly explained by absolute latitude (20.1% of deviance, owls had longer bill near the equator than in temperate zones; Table 2) and hemisphere with owls located on the northern hemisphere having a longer bill than owls on the southern hemisphere. Globally, with respect to plumage traits, latitude explained a larger fraction of the deviance than insularity and hemisphere. All statistical analyses are reported in Table 2 and illustrated in Fig. 1.

Island size and island–continent distance

Owls located on large islands displayed smaller eumelanic spots (but the percentage of the deviance is only 1.1), were lighter pheomelanic and had longer wings, tail and bill than owls found on smaller islands (Table 3). Island–continent distance was only associated with pheomelanic colouration and bill length, with owls

Table 2 Models testing whether barn owls located on continents are phenotypically different from barn owls living on islands. Only the best models, selected based on weighted AIC scores, are presented. Initial models are given in the electronic appendix and comprised the independent variables ‘absolute latitude’, hemisphere (northern vs. southern), whether owls live on continents or islands, and bill length. For morphological traits (i.e. wing, tail and bill lengths), we did not include the dependent variable bill length. Dependent variables are indicated in italics. The table gives coefficient estimates (\pm SD) and percentage of deviance explained by each factor.

	Estimates	Deviance explained (%)
Mean spot diameter		
Absolute latitude	-0.005 ± 0.001	30.4
Bill length	0.002 ± 0.001	5.6
Island–continent comparison	-0.089 ± 0.038	4.9
Mean number of spots		
Absolute latitude	-0.003 ± 0.001	13.1
Bill length	-0.001 ± 0.001	12.1
Island–continent comparison	-0.031 ± 0.019	4.3
Hemisphere	-0.035 ± 0.020	3.8
Pheomelanin-based colour		
Absolute latitude	0.022 ± 0.006	10.8
Hemisphere	0.405 ± 0.166	8.1
Island–continent comparison	0.270 ± 0.172	3.8
Sexual dimorphism in mean spot diameter		
Mean spot diameter	0.302 ± 0.085	31.3
Absolute latitude	-0.059 ± 0.039	2.7
Sexual dimorphism in mean number of spots		
Mean number of spots	0.126 ± 0.030	20.8
Absolute latitude	-0.044 ± 0.028	13.0
Sexual dimorphism in pheomelanin-based colour		
Island–continent comparison	-3.236 ± 1.465	7.4
Absolute latitude	-0.132 ± 0.052	3.0
Hemisphere	-3.675 ± 1.416	9.5
Wing length		
Island–continent comparison	-0.027 ± 0.010	11.5
Tail length		
Island–continent comparison	-0.056 ± 0.03	5.1
Hemisphere	0.041 ± 0.026	4.1
Bill length		
Absolute latitude	-0.001 ± 0.001	20.1
Hemisphere	0.029 ± 0.012	7.2

located on islands further away from the continent being paler reddish and having longer bill (Table 3). Sexual dimorphism in plumage traits was not correlated with island size but sexual dimorphism in the size of black spots increased with the island–continent distance. Sexual dimorphism in pheomelanin-based colouration and number of spots was less pronounced in large than small species. Compared to owls located in temperate zones, those near the equator displayed more and larger black spots and a darker reddish plumage and had a longer bill and slightly shorter wings. Sexual dimorphism in pheomelanin-based colouration was more pronounced near the equator than in the temperate zones, while the

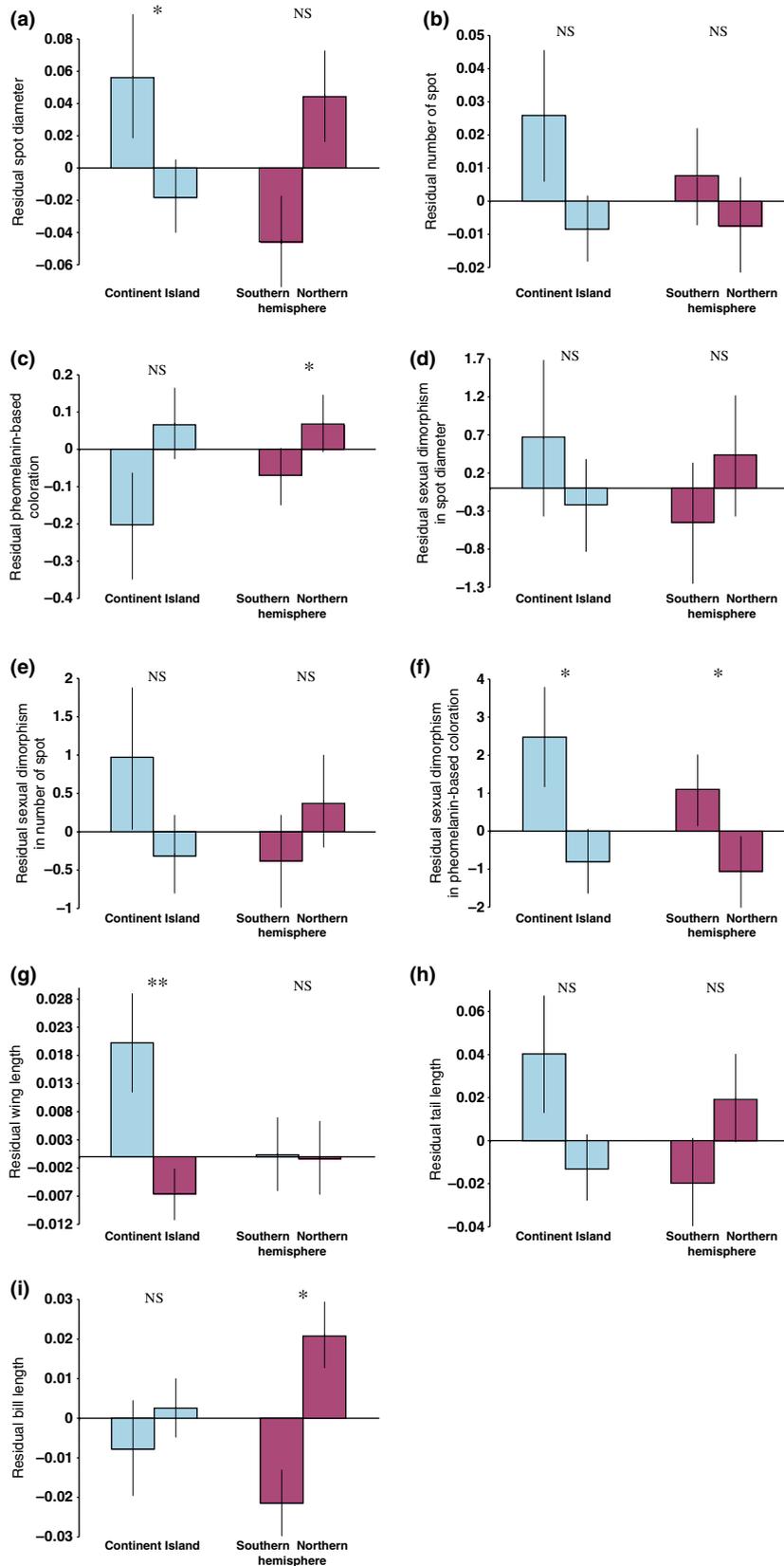


Fig. 1 Phylogenetic standardized residual mean phenotypic values of barn owls occurring on continents and islands, and on the southern and northern hemispheres. Residuals were extracted from the models found in Table 2. Note that residuals are only used for displaying the results but not during the regression analyses. Means are quoted \pm SE. * and ** indicate that barn owls located on continents display a phenotypic trait to a different extent (respectively at $P < 0.05$ and $P < 0.01$) than owls living on islands (similarly for owls located on the southern and northern hemispheres). NS indicates a lack of significant effect.

Table 3 Models testing the relationships between phenotypic traits, island size and the shortest distance between island and the closest continent. Only the best models, selected based on weighted AIC scores, are presented. Initial models are given in the electronic appendix and comprised the independent variables 'absolute latitude', island superficiality (\log_{10} -transformed), island–continent distance (\log_{10} -transformed), and bill length. Dependent variables are indicated in italics. The table gives coefficient estimates (\pm SD) and percentages of deviance explained by each factor.

	Estimates	Deviance explained (%)
Mean spot diameter		
Absolute latitude	-0.006 ± 0.001	41.4
Bill length	0.003 ± 0.001	6.7
Island size	-0.039 ± 0.018	1.1
Mean number of spots		
Absolute latitude	-0.002 ± 0.001	13.9
Bill length	-0.001 ± 0.001	8.6
Pheomelanin-based colour		
Absolute latitude	0.019 ± 0.005	14.7
Island size	0.137 ± 0.068	4.9
Island–continent distance	0.202 ± 0.110	5.0
Sexual dimorphism in mean spot diameter		
Absolute latitude	-0.073 ± 0.043	21.1
Mean spot diameter	0.292 ± 0.087	15.7
Island–continent distance	-1.831 ± 0.780	8.8
Sexual dimorphism in mean number of spots		
Mean number of spots	0.124 ± 0.027	33.5
Bill length	0.037 ± 0.017	2.4
Sexual dimorphism in pheomelanin-based colour		
Bill length	-0.113 ± 0.038	17.4
Absolute latitude	-0.169 ± 0.059	5.1
Wing length		
Island size	0.015 ± 0.004	20.6
Absolute latitude	0.001 ± 0.001	1.4
Tail length		
Island size	0.040 ± 0.012	16.7
Bill length		
Absolute latitude	-0.001 ± 0.001	24.9
Island size	0.020 ± 0.005	17.3
Island–continent distance	0.016 ± 0.008	4.2

opposite pattern was found for sexual dimorphism in spot diameter. All results are given in Table 3.

Discussion

The results show that insularity is affecting melanin-based colour traits, sexual dichromatism and body shape in barn owl species. Owls displayed smaller eumelanic spots (Fig. 1a) and had shorter wings on islands than continents (Fig. 1f). There was also a relatively strong positive correlation between island size and body size and shape (Table 3). The difference between islands and continents was also present for sexual dimorphism in pheomelanin-based colouration, for which the difference in colouration between males and females was reduced on islands compared to continents (Fig. 1f). On small

islands, owls were also redder pheomelanic than owls living on larger islands (Table 3). Finally, sexual dimorphism in the size of eumelanic spots was more pronounced in owls located on remote islands than on islands located closer to a continent (Table 3). The following discussion is presenting the potential reasons explaining the effects of insularity on the evolution of body size/shape and melanin-based traits in barn owls.

Evolution of body size and shape on islands

Limited food supplies, reduced level of competition and predation on islands favour small-bodied individuals (Wassersug *et al.*, 1979; Lawlor, 1982), flightlessness and lower basal metabolic rates compared to their continental relatives (Diamond, 1981; McNab, 1994). These properties are more pronounced on smaller islands. Accordingly, barn owls were shorter-winged on islands than continents, and they were smaller (with respect to wing, tail and bill length) on tiny than large islands. The evolution towards reduced flying capacities was independent of body size, because bill length did not differ between insular and continental species. Because insular populations are often characterized by high population densities because of impoverished natural enemies and by better tolerance of conspecifics (Stamps & Beuchner, 1985), barn owls living on small islands may have smaller territories. It appears that on islands birds have lower needs to fly and given that this activity is costly, selection may favour a reduction in flying activities, promoting the evolution of shorter wings on islands compared to continents. The evolution towards shorter wings may further limit dispersal ability of barn owls living on islands, particularly on small ones. This may disrupt the equilibrium between selection, genetic drift and gene flow, thereby leading to rapid differentiation on small islands and ultimately speciation (e.g. Jordan & Snell, 2008). As a consequence, phenotypic variability may be reduced on islands compared to continents, on small than large islands, and on islands located far than close to mainland. It will be interesting to test these predictions in barn owls with a specific focus on whether these effects differ between body size, body shape and melanin-based traits.

Evolution of melanin-based colour traits and sexual dimorphism on islands

Four different mechanisms can account for colour differentiation between insular and continental populations, namely random genetic processes, natural selection, sexual selection and indirect selection (i.e. selection acting on traits that are genetically correlated to colouration). With respect to the first mechanism, random genetic drift is unlikely to explain plumage differentiation because insular and continental barn owls would not differ in a systematic way as observed in this study, as genetic drift is a stochastic process.

In many animals, predator–prey relationships influence the evolution of melanin-based colouration with a specific role of colouration in camouflage (e.g. Götmark, 1987; Rohwer, 1990; Brodie, 1992; Bretagnolle, 1993; Nachman *et al.*, 2003; Galeotti & Rubolini, 2004; Roulin & Wink, 2004). Thus, conditions prevailing on islands may necessitate different levels of camouflage than on continents promoting colour differentiation. However, predator–prey relationships are unlikely to account for the evolution of smaller eumelanic spots on islands than continents. Indeed, in Switzerland, the degree of pheomelanin- but not eumelanin-based colouration was associated with diet (Roulin, 2004a), a result that is not surprising given that eumelanic spots occupy only a small proportion of the plumage (up to 15%), whereas pheomelanic pigments can be deposited on all feathers of the ventral body side. For the same reason, eumelanic spots may not have a thermoregulatory function. Therefore, to date, we do not have clear evidence that natural selection is responsible for the evolution of insular barn owls towards smaller eumelanic spots than continental owls. This issue should be further studied.

Is the evolution towards a lighter eumelanic plumage on islands the result of sexual selection? Animals that colonize islands face new ecological conditions for which they are not necessarily adapted. In those circumstances, natural selection may be particularly intense and thus counteract sexual selection and hence the evolution of sexual dichromatism. Detailed studies in a Swiss population showed that males mate preferentially with heavily spotted females and also invest more effort in reproduction when mated with females displaying larger black spots (Roulin, 1999; Roulin & Altwegg, 2007). If sexual selection accounted for the reduction in spot size on islands, we should have found an effect of insularity on sexual dimorphism in spot size, which was not the case.

The last mechanism states that insular conditions exert indirect selection on phenotypic traits that are genetically correlated with melanin-based colouration, an argument already proposed by Grant (1965). Colour traits are frequently associated with physiological processes, behaviour and morphology in many vertebrates (Jawor & Breitwisch, 2003; Roulin, 2004c; Ducrest *et al.*, 2008), associations that may stem from pleiotropic effects of genes regulating melanogenesis. For instance, the melanocortin system regulates not only the production of melanin pigments but also sexual behaviour, aggressiveness, exocrine gland activity, the hypothalamic-pituitary-adrenal axis (HPA) stress response, immune function and energy homeostasis (Ducrest *et al.*, 2008). If insular conditions exert selection on these traits as shown in a number of studies (Stamps & Beuchner, 1985; Perret & Blondel, 1993; Greenberg & Mettke-Hofmann, 2001; McNab, 2002; Müller *et al.*, 2007), melanin-based colouration may evolve towards different values compared to continental populations even if plumage traits are selectively neutral. A role for indirect selection on the

evolution of colouration on islands is plausible. Given the association between melanin-based colouration and the ability to resist various stressful factors (Almasi *et al.*, 2008; Ducrest *et al.*, 2008; Kittilsen *et al.*, 2009), island colonizers displaying small eumelanic spots were potentially better able to exploit the new ecological conditions met on islands than individuals exhibiting larger spots.

In conclusion, indirect selection is the most likely mechanism to explain the evolution of smaller eumelanic spots in insular barn owls. This pleads for a more thorough consideration of indirect selection in the evolution of phenotypic traits.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details of model selection for each analysis.

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