

## LETTER

## Worldwide patterns of bird colouration on islands

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### Abstract

Island environments share distinctive characteristics that offer unique opportunities to investigate parallel evolution. Previous research has produced evidence of an island syndrome for morphological traits, life-history strategies and ecological niches, but little is known about the response to insularity of other important traits such as animal signals. Here, we tested whether birds' plumage colouration is part of the island syndrome. We analysed with spectrophotometry the colouration of 116 species endemic to islands and their 116 closest mainland relatives. We found a pattern of reduced brightness and colour intensity for both sexes on islands. In addition, we found a decrease in the number of colour patches on islands that, in males, was associated with a decrease in the number of same-family sympatric species. These results demonstrate a worldwide pattern of parallel colour changes on islands and suggest that a relaxation of selection on species recognition may be one of the mechanisms involved.

### Keywords

Colouration, Goldsmith tetrahedral colour space, Insularity syndrome, Parallel evolution, Sexual selection, Species recognition.

*Ecology Letters* (2016)

### INTRODUCTION

Islands provide a unique natural design to study the role of determinism and contingency in evolution (Grant 1998; Losos & Ricklefs 2009). Their shared characteristics such as isolation, small area, mild climate and reduced species diversity are repeated in different geographic regions around the world, providing natural replicates to examine whether independent exposure to similar ecological conditions leads to parallel evolution, that is, repeated evolution of the same phenotype in independent populations (Bailey *et al.* 2015). Parallel patterns of evolution on islands are best documented in vertebrates. Insular populations tend to exhibit broader niches than their mainland counterparts (Grant 1998; Blondel 2000), a tendency for dwarfism or gigantism (the 'island rule'; e.g. Lomolino 2005; but see: Meiri *et al.* 2008) and changes in reproductive life histories, corresponding to reduced fecundity, slower developmental periods and higher survival (Adler & Levins 1994; Covas 2012; Novosolov *et al.* 2013). These parallel changes are often collectively referred to as 'the insularity syndrome'.

Despite the considerable interest generated by evolution in island populations (Losos & Ricklefs 2009; Warren *et al.* 2015), it remains unknown whether there is a consistent response to insularity of several other traits that are central to animal fitness and also expected to be influenced by insularity. This is the case of animal signals worldwide (but see Morinay *et al.* 2013 for bird song). This is unfortunate because signalling traits play a major role in fundamental evolutionary

processes such as species recognition or mate choice, and are therefore central to understanding evolution on islands.

For colour signals, increased polymorphism has been reported in some island populations of snails and lizards (e.g. Hayashi & Chiba 2004; Raia *et al.* 2010; Runemark *et al.* 2014), but no general interspecific pattern has emerged. In birds, it is often thought that insular taxa evolve dull colouration and are less sexually dichromatic, but supporting evidence is actually very limited. This idea is based on a few studies that investigated variation on a small number of islands, species or families (Grant 1965; Figuerola & Green 2000; Roulin & Salamin 2010; Fabre *et al.* 2012). The only large-scale study available was conducted on Western Palearctic insular subspecies (Fitzpatrick 1998) and found partial support for the idea of decreased colouration on islands. However, a major limitation of all these studies is that they were based on a subjective human description of colouration, that is, qualitative description of plumage brightness from textbooks and scoring published illustrations. Conversely, there are some spectacularly colourful insular avian communities, such as the Hawaiian honeycreepers or birds of paradise, and hence, as summarised by Grant (2001, p90), 'there are more questions about plumage evolution on islands than answers'.

Two components of signalling traits may be affected by insularity: intensity and complexity. Signal intensity is thought to arise from the interaction between social, sexual and natural selection (Hill & McGraw 2006). On islands, a decrease in signal intensity is expected due to a decrease in the intensity

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of sexual selection and/or a change in life-history trade-offs (increased parental care or longevity leading to decreased investment in costly signals: Figuerola & Green 2000; Botero & Rubenstein 2012). Sexual selection is expected to be less intense on islands due to the lower indirect fitness benefits of mate choice and associated decrease in extra-pair paternity (Hamilton & Zuk 1982; Griffith 2000), which may arise from both lower parasite pressure (e.g. Ishtiaq *et al.* 2012) and reduced genetic diversity (Frankham 1997). However, predation is also reduced on islands (Beauchamp 2004), which could relax selection for camouflage and promote elaboration and diversification of signals (Runemark *et al.* 2014). In addition, a decrease in territoriality and aggression towards conspecifics may occur as a response to increased density and/or food availability on islands (Stamps & Buechner 1985). This could promote sociality and favour social signals such as badges of status (Tibbetts & Safran 2009). It is thus difficult to predict if the intensity of colour signals will respond to insularity in a consistent way, and if so in which direction.

Signal complexity, on the contrary, is expected to be lower on islands due to the limited number of closely related sympatric species (Grant 1965; Figuerola & Green 2000). According to the 'species recognition hypothesis', signals play an important role in encoding species identity (Sætre *et al.* 1997) and signal divergence should be more important in sympatric pairs of closely related species than in allopatric ones (e.g. Seddon 2005; Martin *et al.* 2010; but see McKnaught & Owens 2003). In relatively simple communities, simple specific signals may be expected if those signals are more efficient for coding species identity (Maynard-Smith 1991), whereas in species-rich communities, the need to signal species identity may require an increased signal complexity. Supporting these predictions, the most complex pheromones and songs are found in species from the most speciose families in moths (Byers 2006) and birds (Seddon *et al.* 2008). In addition, the number of sympatric sister species affected bird song complexity (Morinay *et al.* 2013), as well as dewlap pattern (Ord & Martins 2006; Vanhooydonck *et al.* 2009; Morinay *et al.* 2013) and display complexity in lizards (Ord & Martins 2006). In birds, the effect of sympatric species diversity on colour complexity has only been recently investigated at the community level and needs to be clarified (Martin *et al.* 2015).

The aim of this study is to test whether a general trend exists in the evolution of colour intensity or complexity in insular bird species. This can only be achieved by analysing a large number of unrelated taxa from distinct geographic areas (Blondel 2000). In addition, such a test requires that colour is measured objectively and analysed using models of bird (and not human) colour vision. All previous studies on insular bird colouration have relied on human-based assessment of colouration, which makes results potentially biased because birds and humans perceive colours differently. Birds have four types of photoreceptors (three in humans) including one sensitive to ultraviolet radiation and, in addition, in the human-visible domain, birds and humans perform best at different wavelengths for discriminating among subtle colour variations (Håstad & Ödeen 2008).

We used spectrophotometry and a physiological model of avian colour space (Goldsmith 1990; Stoddard & Prum 2008)

to compare the colouration of endemic island species to their mainland counterparts in a large number of continental and insular bird species. Signal intensity was estimated by measuring brightness and colour intensity, measured as the occupied volume of colours within the colour space, where a colour space is a graphical representation intended to describe how visual stimuli appear to animals (Renoult *et al.* 2015). Signal complexity was estimated by counting the number of colour patches. Measurements were made on both sexes to estimate changes in dichromatism and to take into account that colour evolution can be independent in males and females (e.g. Price & Eaton 2014). In addition, we examined whether the number of closely related sympatric species could explain part of the changes in signal complexity. We expected signal complexity to be positively associated to the number of closely related sympatric species both on islands and the mainland. In addition, we explicitly tested whether the lower number of sympatric species on islands could explain part of the changes in signal complexity and dichromatism by testing the interactions among sex, insularity and the number of sympatric species.

## METHODS

### Data set

Plumage colouration was measured from skins held in the British and American Natural History museums. We measured a total of 232 species (116 endemic insular species and their closest 116 mainland relatives breeding at similar latitude). These species were distributed over 46 islands or archipelagos (Fig. 1) and belonged to 13 orders and 66 families (see Appendix S1 for information on island size and Table S1 for the species list).

### Colour measurements

#### Spectrometry

All measures were taken by the same person (CD). Colours were measured with an Ocean Optics USB 4000 spectrometer, a PX2 Xenon light source (covering 300–700 nm), and a 200- $\mu$ m probe mounted with a back rubber cap and held at a fixed distance of 2 mm from the plumage surface. The reflec-

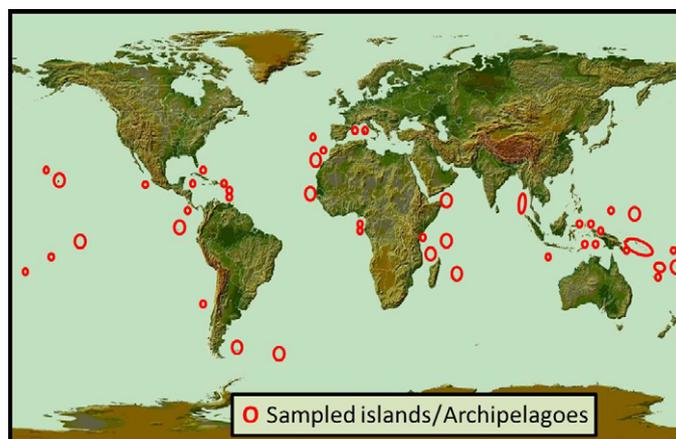


Figure 1 Archipelagos/islands where bird colourations have been measured.

tance of a white standard was measured between each individual. We measured three males and three females except in a few instances where  $< 6$  specimens were available. We measured colouration in at least six body regions (head, mantle, wing, chest, belly and tail measured in all but four species). In addition, we measured all visually distinct patches (up to 20) for those species where more patches were visible. Each patch was measured once and male and female average reflectances were computed for each patch of each species. Methods used to identify additional colour patches and to select the specimens measured are explained in Appendix S2.

#### *Visual models of avian vision to compute signal intensity*

We used the R package *pavo* (Maia *et al.* 2013) to model avian colour vision. Mean brightness for the whole body plumage colouration was estimated as the number of photons caught by double cones, the photoreceptors specialised in achromatic vision in birds (Osorio & Vorobyev 2005). Colour intensity here corresponds to the colour volume which was modelled using the Goldsmith's tetrahedron (Goldsmith 1990; Stoddard & Prum 2008), a model of colour space in which the distance between two colour stimuli is related to the perceived chromatic similarity. For each sex within species, we plotted the mean reflectance spectrum of each patch within the tetrahedron. We then computed the colour volume of the minimum convex polygon that contains all colour patches in the space of each sex within each species (Stoddard & Prum 2008). Colour volume indicates how perceptually distinct the various patches appear to birds, large volumes describing species with an overall high colour intensity in whichever visual environment (Renoult *et al.* 2015). Average disparity among patch hues, which measures colour diversity independently of saturation, and the mean distance between all colour pairs were also computed (Stoddard & Prum 2008). However, these measures were highly correlated to colour volume (all  $R > 0.81$ ) and were not analysed further.

Brightness was calculated for 226 of the 232 species initially selected. The data set includes the colour measurements of 4448 patches. To estimate colour volumes, we removed 57 black patches because the Goldsmith's model attributes random chromatic values to very dark spectra (Stoddard & Prum 2008). A patch was treated as black if the photon catch of all cones did not exceed 2% of the photon catch corresponding to a 100% reflecting white surface. In addition, we excluded species with  $< 4$  colour patches because a colour volume could not be calculated for such species (two insular and two continental species for females, and one of each for males). Colour volumes were hence computed for 223 species (223 for males, 221 for females). We analysed colouration assuming all species have either UVS or VS vision (Appendix S2). Results are presented with the UVS system only as analysing data with the VS system yielded identical conclusions.

#### *Number of patches as an estimate of signal complexity*

Following Fitzpatrick (1998), the number of colour patches was used as a proxy of colour signal complexity. A patch is a plumage area characterised by a homogeneous colour and shape of spectrogram that are qualitatively different from those of the adjacent patches (Appendix S2).

Number of colour patches was assessed on the 232 species by the same observer (CD) directly on museum skins. To exclude an unintentional bias that could have affected estimates of patch counts, three other observers conducted independent counts of the number of patches from colour photographs of the specimens measured by CD in the museums (Appendix S2). The number of patches had a correlation of 0.58 and 0.30 to colour volume and brightness, respectively.

#### **Ecological and geographical variables**

##### *Number of sympatric species in the same family*

Following previous studies (Figuerola & Green 2000; Vanhooydonck *et al.* 2009; Morinay *et al.* 2013), we counted the number of sympatric species of the same family to test the species recognition hypothesis. Species were considered as sympatric if their breeding distribution overlaps, as assessed from the distribution maps of Del Hoyo *et al.* (1992–2011) and from other bibliographic sources listed in Appendix S3. Extinct species were included when known. We computed the total number of same-family sympatric species for 112 continental and 115 island species of the 116 pairs of species measured.

##### *Geography*

We analysed the effect of latitude as the mean absolute value of the locations where the specimens were collected (Fig. 1; the species' distributions varied between 54° S and 47° N). In addition, we tested the effect of island size and distance to the continent (data obtained from the UNEP website; Appendix S4). However, as these variables had no significant effects, models including them are given in Appendix S4 only.

#### **Statistical analyses**

We tested for an effect of insularity on bird colouration by comparing colouration of island and mainland species within pairs of closely related species (Griffith 2000; Beauchamp 2004; Covas 2012; Morinay *et al.* 2013). Analyses were conducted using linear mixed models with the package nlme in R (R Development Core Team, 2011). To account for phylogenetic dependency and for the paired structure of the analyses, we included in all models a random term consisting of 'species' (because we had averaged male and female values for each species) nested within 'pair' nested within 'family' nested within 'order'.

We also tested for an effect of archipelago (by including a random term) and for spatial autocorrelation using Moran's I autocorrelation coefficient (function Moran.I in package APE). These effects were not significant (all  $P$  values  $> 0.28$  for the Moran's I and  $P > 0.18$  for archipelago) and thus were not included in subsequent analyses.

We first analysed the whole data set to investigate whether the three indexes of colouration, colour volume and brightness (colour intensity), and number of patches (colour complexity) differed between island and mainland species. Volume was log transformed to achieve normality. The explanatory variables were 'insularity' (Yes/No), 'sex' and 'latitude'. We also included the two-way interactions between these three variables.

Second, we investigated the association between colour complexity and the number of closely related sympatric species. If this variable partly explains the insularity effect, we would expect it to remove or decrease the effect of insularity on colour complexity in our statistical model. Hence, we repeated the same general models as above adding the 'number of sympatric species' and the two-way interactions between 'insularity', 'sex', 'latitude' and 'number of sympatric species'. We did not expect any effect of number of closely related species on signal intensity (brightness and colour volume) and there were indeed no association between these variables (results not shown).

The final models were obtained by sequentially eliminating explanatory variables showing  $P$  values  $> 0.05$  using a backwards stepwise approach. The minimal models provided the  $P$  values of significant terms, whereas  $P$  values for non-significant terms were obtained by reintroducing each non-significant variable into the minimal model. Because we ran the same statistical models on more than one estimate of colouration, effectively testing the insularity effect several times, we also present ' $P_c$ ' values, which correspond to significant  $P$  values corrected for false recovery rates (Benjamini & Hochberg 1995; Pike 2011).

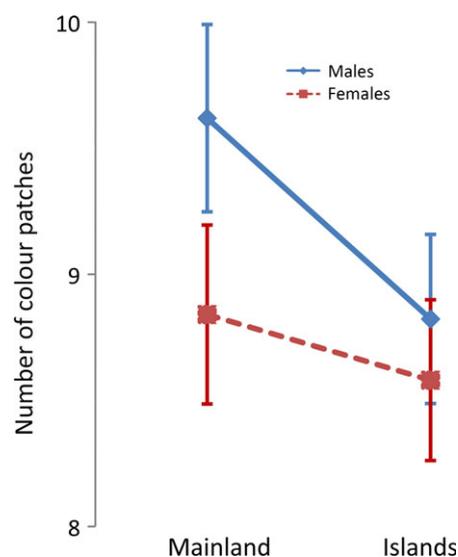
## RESULTS

In spite of considerable variation between species in response to insularity (Appendix S5, Fig. S2–7), our results revealed a global pattern of decreased colouration on islands. The plumage of island birds had significantly lower values of brightness and colour volume than the plumage of their mainland counterparts ( $F_{1,112} = 5.2$ ,  $P = 0.023$ ,  $P_c = 0.027$  and estimate =  $-0.01$  and  $F_{1,109} = 7.9$ ,  $P = 0.006$ ,  $P_c = 0.018$  and estimate =  $-0.33$ , respectively, Fig. 2). There was no significant interaction between sex and insularity, suggesting similar levels of dichromatism between island and mainland species for brightness and colour volume ( $P = 0.15$  and  $P = 0.67$ , respectively). There was a global effect of sex on colour volume, showing that overall (i.e. combining islands and

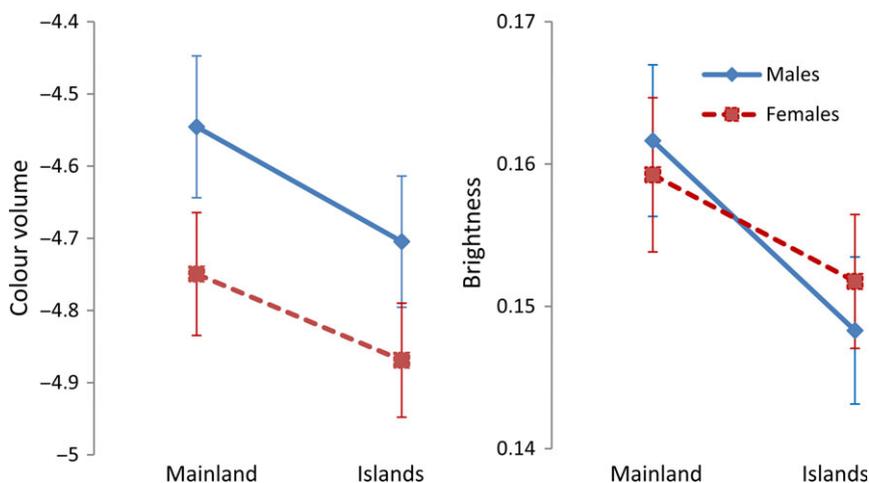
mainland species) males have a larger colour volume than females;  $F_{1,224} = 21.4$ ,  $P < 0.001$ ,  $P_c < 0.001$  and estimate =  $0.42$ , Fig. 2), but not higher values of brightness ( $F_{1,224} = 0.01$  and  $P = 0.90$ , Fig. 2). Latitude had no significant effect on brightness ( $F_{1,111} = 1.8$ ,  $P = 0.076$ , estimate =  $0.0005$  and  $P_c = 0.11$ ) or colour volume, either alone or in association with insularity ( $P > 0.70$ ).

The number of colour patches was lower on islands than on mainland, with a significant interaction between 'insularity' and 'sex' showing a stronger effect for males (Fig 3, 'insularity\*sex'  $F_{1,230} = 4.7$ ,  $P = 0.032$ ,  $P_c = 0.09$  and estimate =  $-0.51$ ; estimate =  $-0.80$  for males and estimate =  $-0.28$  for females). The number of patches did not co-vary positively with latitude after correction for multiple testing ( $F_{1,114} = 5.3$ ,  $P = 0.023$ ,  $P_c = 0.07$  and estimate =  $0.04$ ).

When we included the number of same-family sympatric species in the analyses, the variation in the number of patches



**Figure 3** The number of colour patches is lower on islands than mainland. Red and dashed line: females, blue and plain line: males. Raw data.



**Figure 2** Colour volume and brightness of male and female plumage are generally lower on islands than mainland. Red and dashed line: females, blue and plain line: males. Raw data.

was significantly affected by the interaction between this factor and sex. The number of patches in males, but not females, was positively related to the number of same-family species living in sympatry (Table 1, Fig. 4). In this model, the interaction between sex and insularity was no longer significant ( $P = 0.91$ ), which was expected if the number of closely related sympatric species explains most of the changes in colour complexity observed on islands for males. However, the main effect 'insularity' remained significant, confirming an overall decrease in number of patches on islands even after controlling for the number of same-family sympatric species (Table 1).

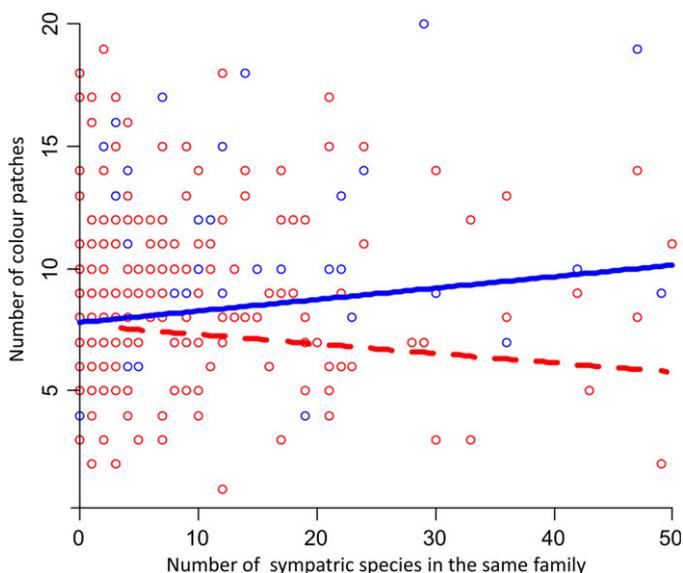
## DISCUSSION

Our study provides the first evidence of a global trend for reduced signal intensity and complexity of avian plumage on islands. Reduced signal intensity (colour volume and brightness) was found for both sexes, whereas the reduction in colour complexity (lower number of patches) was stronger for males than females. Signal complexity in males was positively

**Table 1** Effect of the number of sympatric species on the number of coloured plumage patches ( $N = 232$  species).

Number of patches	Estimate	ddl	$F$	$P$ value
Insularity	-0.72	109	4.45	<b>0.037</b>
Latitude	0.04	109	3.97	<b>0.049</b>
Sex	0.11	225	0.59	0.44
Number of sympatric species	-0.038	109	3.45	0.06
Sex $\times$ Number of sympatric species	0.05	225	16.58	<b>0.0001</b>

Bold values correspond to significant effect.



**Figure 4** The number of patches of males – but not females – increase with the number of same-family sympatric species. Red and dashed line: females, blue and plain line: males. The regression lines are the ones estimated by the model that takes into account the random family effects and the effect of latitude.

related to the number of closely related sympatric species. Our results therefore show that predictable, parallel, patterns of evolution occur for signalling traits on islands and that insular populations have generally less elaborate signals than mainland populations. In addition, these results suggest that species recognition is a key factor explaining the decrease in male signal complexity on islands and, more generally, shaping the complexity of colour signals.

### Reduced signal intensity in islands birds

Two hypotheses could explain the lower colour intensity observed in islands birds: life-history trade-offs and reduced intersexual selection. Regarding the former, island birds are known to invest more in parental care and offspring quality than their mainland counterparts (Covas 2012). Trade-offs between parental care and sexually secondary traits (Figuerola & Green 2000) or between longevity and mate attraction (Botero & Rubenstein 2012) could thus explain the reduced signal expression of islands bird. Although the paucity of data on parental care and survival available in the literature prevented us from testing this hypothesis with our database, a preliminary analysis supported this mechanism. Based on the 18 pairs of species from our database, for which data were available, we found that males (but not females) from species with a longer duration of parental care have lower colour volume (Appendix S6, Fig. S8).

The alternative hypothesis considers that reduced colour intensity on islands is the consequence of reduced intersexual selection. At least three phenomena may lead to less stringent mate choice on islands and thus lead to a less variable mating success and reduced sexual selection: (1) less overall genetic diversity within island populations; (2) reduced parasite pressure and (3) long-term pair bonds.

First, island populations are thought to have lower levels of genetic diversity than mainland ones as a result of a combination of stochastic processes like founder effects, bottlenecks and lower population size (Frankham 1997). The indirect benefits of mate choice (i.e. the benefits of passing 'good genes' onto offspring, such as genes associated with enhanced condition or attractiveness) are predicted to decrease when males are very similar in their genetic makeup (Petrie *et al.* 1998). Under this hypothesis, there may be less stringent mate choice to obtain indirect fitness benefits on islands. Accordingly, levels of extra-pair paternity (EPP), which can be viewed as a strategy to pass 'good genes' onto offspring, were found to be lower on islands (Griffith 2000). However, variation in the success of EPP is expected to affect male but not female colouration (Møller & Birkhead 1994) and hence would lead to lower levels of dichromatism on islands, a pattern which we did not observe here in general for colour intensity. Second, less stringent mate choice may also arise from lower parasite pressure on islands. One of the central hypotheses for the evolution of elaborate secondary sexual characters is that these traits evolve to signal parasite resistance, and where parasite pressure is strong, individuals should evolve more elaborate secondary sexual traits (Hamilton & Zuk 1982). Given that islands are thought to hold impoverished parasites communities (e.g. Ishtiaq *et al.* 2012), the decrease in insular bird

colouration might to some extent reflect the lower parasite pressure on islands, an hypothesis already put forward in Hamilton & Zuk's (1982) seminal paper. Third, reduced sexual selection on islands could stem from longer duration of pair bonds. If on islands, as elsewhere (Botero & Rubenstein 2012), increased longevity is associated with lower divorce rate and longer pair bonds; this should result in lower lifelong variance in mating success and hence lower sexual selection (Figuerola & Green 2000).

Signals are also affected by competition for mates, territory or food and, thus, by intrasexual selection and/or social selection. On islands, reduced aggression towards conspecifics is expected due to higher densities, which leads to higher costs of aggression or territoriality as encounters with conspecifics are very frequent (Stamps & Buechner 1985). Accordingly, Morinay *et al.* (2013) found that island birds were less likely to produce broadband aggressive song elements (rattles and buzzes) than mainland ones. However, song is a longer range signal than colour and is more clearly involved in territorial interactions. Colours often encode dominance in group interactions, or aggressiveness in closer encounters with conspecifics (Hill & McGraw 2006). Hence, high population densities, as found on islands, could favour the appearance and increased intensity of colour signals used to communicate at short distance. In birds, dominance interactions in flocks are often mediated by 'badges of status' that are usually black (Tibbetts & Safran 2009). It is therefore possible that the reduced plumage brightness on island results from an increased occurrence of melanic black patches due to increased sociality. For example, Uy & Vargas-Castro (2015) found an increase in frequency of melanic individuals on small islands in the Chestnut-bellied monarch (*Monarcha castaneiventris*). However, in our data set the number of large black patches (head, mantle, wing, tail, breast and belly) was similar between island and mainland species. In addition, we found no difference between island and mainland species in relation to whether at least one of the sexes was all black (Appendix S7). Hence, in our data set the decrease in brightness is not due to an increase in blackness, but to a more continuous change in colouration towards duller tones. This can be due to an increase in melanin content, but also to an increase in carotenoid content or to a change towards darker structural colours (e.g. thicker keratin cortex in feathers reducing incoherent scattering of light waves). Clearly, the functional and evolutionary causes of the reduced brightness on islands will need further investigation.

#### **Males and females exhibit similar trends for reduced signal intensity on islands**

The decrease in plumage colour intensity observed here on islands did not significantly differ between the sexes (neither for colour volume nor for brightness). Hence, insularity is not globally associated with changes in dichromatism *per se*. This result is in line with previous studies based on subjective estimates of dichromatism in Tres Marias islands birds (Grant 1965) and in the Anseriformes (Figuerola & Green 2000). However, these authors found complex results: no change in

dichromatism, but a sexual difference in brightness on islands. The similar dichromatism we documented on islands and mainland contrasts with the common assumption that island species are less dimorphic when dimorphism refers to body size (Raia *et al.* 2010). Colouration and body size may therefore be under different selection regimes.

Mating system is supposed to have a strong influence on sexual dichromatism, with monogamous birds tending to be less dichromatic (Price & Eaton 2014). Species that colonise and persist on islands are mainly monogamous (Sorci *et al.* 1998; Covas 2012) and in our sample more than 84% of species with known mating system were also socially monogamous (mainland: 27 species of 29; islands: 14 of 16). This high level of monogamy together with other factors, like increased population densities and biparental care (see above), could thus help explain the similar level of dichromatism observed on islands and mainland areas.

#### **Decrease in male signal complexity on islands and the role of species interactions**

Contrary to what we found for plumage intensity (brightness and colour volume), our analyses suggested that the decrease in the number of coloured plumage patches (a proxy of signal complexity) is stronger for male than female island birds. This concurs with previous studies that found indication of a reduction in the number of patches in insular male birds at the intraspecific level (Fitzpatrick 1998) and in paradise flycatchers (Fabre *et al.* 2012). Although the number of colour patches could be linked to other functions, such as camouflage or mate choice, our result suggests that the number of colour patches responds, at least in part, to interspecific interactions and species recognition. First, we found that males of species that co-occur with a higher number of same-family species have a higher number of patches, both on islands and mainland regions. Second, island birds, which live with fewer same-family species than their mainland relatives (average and range: 2.5 and 0–21 on islands vs. 14 and 0–50 on mainland), have fewer patches overall. Finally, the significant effect of the interaction between sex and insularity on the number of colour patches became non-significant when the interaction between sex and the number of same-family sympatric species was added to the model, as expected if the number of sympatric species partly explains the number of patches. Thus, overall, these results agree with the recent results obtained by Martin *et al.* (2010, 2015) suggesting an important role of interspecific interactions on colour pattern evolution at community level.

Both interspecific territorial aggression (Seehausen & Schluter 2004) and selection against hybridisation (Pfennig & Pfennig 2009) can explain why interspecific interactions affect the evolution of signals that allow rapid and unambiguous species identification. As the costs of mating with the wrong species can be higher for females (that bear the cost of egg production) than for males, our observation that male signal complexity is more affected by the number of sympatric species than female signal complexity can further suggest that selection against hybridisation is an important determinant of plumage colour evolution.

### Not all species show decreased colouration on islands

Even though we found a clear and significant general trend for reduction in intensity and complexity of colour signals on islands, the values of the estimates of some models are low and the  $P$  values lie between 0.02 and 0.03, documenting an important amount of variation among (and within) bird orders and families in their response to insularity. In fact, some insular species have brighter or more complex colouration than their mainland relatives (Appendix S5, Figs. S2–7). For instance, plumage brightness increased on islands in the Strigiformes (four pairs). In addition, in the Passeriformes (77 pairs) and Psittaciformes (7 pairs) there was important variation among species in the response of colour volume to insularity, especially in females of several species that presented augmentation on islands. This variation can be partly due to the fact that with broad-scale analyses such as the one conducted here, we do not know the background and luminosity where the birds are actually displaying and this may change the apparent intensity of signals. However, large volumes describe species with an overall high colour intensity in whichever visual environment and so our main results should not be significantly affected by this potential problem.

The documented variation in the responses to insularity offers a wealth of interesting possibilities to conduct in-depth tests of the possible effect of the different factors that may drive the evolution of colouration. In addition to the factors discussed above, other selective pressures and stochastic factors may influence colouration in opposite directions. Predation is supposed to directly affect the conspicuousness (Hill & McGraw 2006) and/or variability of signals (Hayashi & Chiba 2004; Runemark *et al.* 2014). Islands usually have fewer predators (Beauchamp 2004) and the effect of predation is likely to vary across islands depending on the type of predators present, their density and diversity. In addition, predators are more likely to be absent in small islands, which may therefore show increased colouration (reversed insularity syndrome *sensu* Raia *et al.* 2010). In support for this prediction, birds originating from smaller islands and archipelagos (where predators are expected to be less abundant) tended to present more variable colour volume in our data set than birds originating from larger islands and archipelagos (Appendix S4, Fig S1). Random factors such as drift and founder effects could also explain part of the variation in changes observed on small islands and reduce patterns of parallel evolution. In addition, indirect selection and pleiotropy may contribute to some of the observed changes and explain reversed patterns in species where colours have no signalling function (Grant 1965; Raia *et al.* 2010; Roulin & Salamin 2010). For instance, the melanocortin system, which regulates the production of melanin pigments, also influences aggressiveness, stress and immunity (Ducrest *et al.* 2008). As a consequence of reduced stress (Muller *et al.* 2007) or immune response (Matson 2006) on islands, the melanocortin system could indirectly lead to reduced melanin-based colouration and thus increased brightness in some species. This hypothesis was suggested for insular barn owls (Roulin & Salamin 2010) and lizards (Raia *et al.* 2010) and could apply here to the Strigiformes or some Accipitriformes, which contrast with the general pattern found in having increased brightness on islands (Fig. S8).

### CONCLUSION

Over 50 years after Mayr's (1963) seminal work on evolution on islands, numerous questions on the validity and mechanisms behind the patterns of evolution on islands remain (Warren *et al.* 2015). This study represents a step towards answering some of these open questions by revealing a general trend for reduced plumage colouration in island birds worldwide. These changes may arise from the relaxation of several selective pressures related to sexual selection and species recognition, the latter being supported by the results obtained here. In addition, shifts in life-history strategies, predator pressure and other yet unidentified factors are likely to be at play, and the importance of all these factors remains to be tested by experiments and finer scale studies. For example, different body parts (dorsum, head and chest) were shown to respond differently to predation and social and sexual selection (Gomez & Théry 2007) and the responses of these different body parts to insularity should be investigated. Finally, as many of the insular species studied here have unknown life-history traits, any tests of hypotheses will require extensive additional fieldwork.

More generally, this study contributes to the debate around the predictability or contingency of evolution in the wild (Losos & Ricklefs 2009; Bailey *et al.* 2015), simultaneously providing evidence of similar outcomes in spite of different origins, and also variation in response to the island environment. On islands, there would thus be a general tendency for animals to predictably evolve towards a slower pace of life (Adler & Levins 1994; Covas 2012; Novosolov *et al.* 2013) and reduced colouration, these changes being different facets of the island syndrome.

### ACKNOWLEDGEMENTS

We thank Paul Sweet and Robert Prys-Jones from the American and British Natural History Museum for their kind support and Doris Gomez, Olivier Gimenez, Julien Claude, Gonçalo Cardoso and Martim Melo for discussions and advice. Emeline Mourcq helped building the database and Nathalie Grnac, Romain Guerreiro, Andrea Baquero and Thibaut Powolny helped with data collection at the museums. Adrian Skerrett gave useful information on Seychelles birds. M. Melo, S. Anderson and R. Bowie gave us access to unpublished phylogenetic data. We are thankful for the insightful comments of three anonymous reviewers that greatly helped to improve this study. This work was funded by the 'Agence Nationale de la Recherche' (ANR 09-JCJC-0050-0) and the Languedoc Roussillon Region (fund 'chercheur(se) d'avenir 2011) to CD, the European Program Synthesis to RC and CD and a Collection Study Grant from the AMNH to RC. RC was funded by a Marie Curie Fellowship, programmes 'Ciência 2008' and IF (01411/2014/CP1256/CT0007; Portuguese Science and Technology Foundation FCT) and Project 'Biodiversity, Ecology and Global Change' (co-financed by North Portugal Regional Operational Programme 2007/2013 ON.2 – O Novo Norte and NSRF-ERDF). This research is a joint research programme conducted under the International Associated Lab CNRS-CIBIO.

## AUTHORSHIP

CD, RC and PAC designed the study. RC collated the database. CD measured the plumage colouration and wrote the first draft of the manuscript. CD, RC, PAC, AG and MP defined the statistical design. MP collected the biogeographical data and ran the statistical analyses. JR ran the animal vision modelling. All authors contributed to revisions of the manuscript.

## REFERENCES

- Adler, G.H. & Levins, R. (1994). The Island syndrome in rodent populations. *Q. Rev. Biol.*, 69, 473–490.
- Bailey, S.F., Rodrigue, N. & Kassen, R. (2015). The effect of selection environment on the probability of parallel evolution. *Mol. Biol. Evol.*, 32, 1436–1448.
- Beauchamp, G. (2004). Reduced flocking by birds on islands with relaxed predation. *Proc. R. Soc. Lond. B*, 271, 1039–1042.
- Benjamini, Y. & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. B*, 1, 289–300.
- Blondel, J. (2000). Evolution and ecology of birds on islands: trends and prospects. *Vie Et Milieu-Life And Environment*, 50, 205–220.
- Botero, C.A. & Rubenstein, D.R. (2012). Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *PLoS ONE*, 7, e32311.
- Byers, J.A. (2006). Pheromone component patterns of moth evolution revealed by computer analysis of the Pherolist. *J. Anim. Ecol.*, 75, 399–407.
- Covas, R. (2012). Evolution of reproductive life histories in island birds worldwide. *Proc. R. Soc. Lond. B*, 279, 1531–1537.
- Del Hoyo, J., Elliot, A. & Christie, D.A. (1992–2011). *Handbooks of the birds of the world*. Lynx Editions, Barcelona.
- Ducrest, A.-L., Keller, L. & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol. Evol.*, 23, 502–510.
- Fabre, P.-H., Irestedt, M., Fjeldså, J., Bristol, R., Groombridge, J.J., Irlam, M. et al. (2012). Dynamic colonization exchanges between continents and islands drive diversification in paradise-flycatchers (Terpsiphone, Monarchidae). *J. Biogeogr.*, 39, 1900–1918.
- Figuerola, J. & Green, A.J. (2000). The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Funct. Ecol.*, 14, 701–710.
- Fitzpatrick, S. (1998). Intraspecific variation in wing length and male plumage coloration with migratory behaviour in continental and island populations. *J. Avian Biol.*, 29, 248–256.
- Frankham, R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity*, 78, 311–327.
- Goldsmith, T.H. (1990). Optimization, constraint, and history in the evolution of eyes. *Q. Rev. Biol.*, 65, 281–322.
- Gomez, D. & Théry, M. (2007). Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a neotropical rainforest bird community. *Am. Nat.*, 169(S1), S42–S61.
- Grant, P.R. (1965). Plumage and the Evolution of Birds on Islands. *Syst. Zool.*, 14, 47–52.
- Grant, P.R. (1998). *Evolution on Islands*. Oxford University Press, New York.
- Grant, P.R. (2001). Reconstructing the evolution of birds on islands: 100 years of research. *Oikos*, 92, 385–403.
- Griffith, S.C. (2000). High fidelity on islands: a comparative study of extrapair paternity in passerine birds. *Behav. Ecol.*, 11, 265–273.
- Hamilton, W.D. & Zuk, M. (1982). Heritable true fitness and bright birds: a role for parasites? *Science*, 218, 384–386.
- Håstad, O. & Ödeen, A. (2008). Different ranking of avian colors predicted by modeling of retinal function in humans and birds. *Am. Nat.*, 171, 831–838.
- Hayashi, M. & Chiba, S. (2004). Enhanced colour polymorphisms in island populations of the land snail *Euhadra peliomphala*. *Biol. J. Linn. Soc.*, 81, 417–425.
- Hill, G.E. & McGraw, K.J. (2006). *Bird Coloration. Function and Evolution*. Harvard University Press, Cambridge, MA.
- Ishtiaq, F., Beadell, J.S., Warren, B. & Fleischer, R.C. (2012). Diversity and distribution of avian haematozoan parasites in the Western Indian Ocean region: a molecular survey. *Parasitology*, 139, 221–231.
- Losos, J.B. & Ricklefs, R.E. (2009). Adaptation and diversification on islands. *Nature*, 457, 830–836.
- Maia, R., Eliason, C.M., Bitton, P.P., Doucet, S.M. & Shawkey, M.D. (2013). pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.*, 4, 906–913.
- Martin, P.R., Montgomerie, R. & Loughheed, S.C. (2010). Rapid sympatry explains greater color pattern divergence in high latitude birds. *Evolution*, 64, 336–347.
- Martin, P.R., Montgomerie, R. & Loughheed, S.C. (2015). Color patterns of closely related bird species are more divergent at intermediate levels of breeding-range sympatry. *Am. Nat.*, 185, 443–451.
- Matson, K.D. (2006). Are there differences in immune function between continental and insular birds? *Proc. R. Soc. Lond. B*, 273, 2267–2274.
- Mayr, E. (1963). *Animal species and evolution*. Belknap Press of Harvard University Press Cambridge, Massachusetts.
- Meiri, S., Cooper, N. & Purvis, A. (2008). The island rule: made to be broken? *Proceedings of the Royal Society B-Biological Sciences*, 275, 141–148.
- McKnaught, M.K. & Owens, I.P.F. (2003). Interspecific variation in plumage coloration among birds: species recognition or light environment? *J. Evol. Biol.*, 15, 505–514.
- Møller, A.P. & Birkhead, T.R. (1994). The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution*, 48, 1089–1100.
- Morinay, J., Cardoso, G.C., Doutrelant, C. & Covas, R. (2013). The evolution of birdsong on islands. *Ecol. Evol.*, 3, 5127–5140.
- Muller, C., Jenni-Eiermann, S., Blondel, J., Perret, P., Caro, S.P., Lambrechts, M.M. et al. (2007). Circulating corticosterone levels in breeding blue tits *Parus caeruleus* differ between island and mainland populations and between habitats. *Gen. Comp. Endocrinol.*, 154, 128–136.
- Novosolov, M., Raia, P. & Meiri, S. (2013). The island syndrome in lizards. *lobal Ecol. Biogeogr.*, 22, 184–191.
- Ord, T.J. & Martins, E.P. (2006). Tracing the origins of signal diversity in anole lizards: phylogenetic approaches to inferring the evolution of complex behaviour. *Anim. Behav.*, 71, 1411–1429.
- Osorio, D. & Vorobyev, M. (2005). Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proc. R. Soc. Lond. B*, 272, 1745–1752.
- Petrie, M., Doums, C. & Moller, A.P. (1998). The degree of extra-pair paternity increases with genetic variability. *Proc. Natl Acad. Sci. USA*, 95, 9390–9395.
- Pfennig, K.S. & Pfennig, D.W. (2009). Character displacement: ecological and reproductive responses to a common evolutionary problem. *Q. Rev. Biol.*, 84, 253.
- Pike, N. (2011). Using false discovery rates for multiple comparisons in ecology and evolution. *Methods Ecol. Evol.*, 2, 278–282.
- Price, J.J. & Eaton, M.D. (2014). Reconstruction the evolution of sexual dichromatism: current color diversity does not reflect past rates of male and female change. *Evolution*, 68–7, 2026–2037.
- R Development Core Team (2011). *R: A language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Raia, P., Guarino, F.M., Turano, M., Polese, G., Ripa, D., Carotenuto, F. et al. (2010). The blue lizard spandrel and the island syndrome. *BMC Evol. Biol.*, 10, 289.
- Renoult, J.P., Kelber, A. & Schaefer, H.M. (2015). Colour spaces in ecology and evolutionary biology. *Biol. Reviews*, DOI: 10.1111/brv.12230, in press.
- Roulin, A. & Salamin, N. (2010). Insularity and the evolution of melanism, sexual dichromatism and body size in the worldwide-distributed barn owl. *J. Evol. Biol.*, 23, 925–934.

- Runemark, A., Brydegaard, M. & Svensson, E.I. (2014). Does relaxed predation drive phenotypic divergence among insular populations? *J. Evol. Biol.*, *27*, 1676–1690.
- Sætre, G.-P., Moum, T., Bures, S., Král, M., Adamjan, M. & Moreno, J. (1997). A sexually selected character displacement in flycatchers reinforces premating isolation. *Nature*, *387*, 589–592.
- Seddon, N. (2005). Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution*, *59*, 200–215.
- Seddon, N., Merrill, R.M. & Tobias, J.A. (2008). Sexually selected traits predict patterns of species richness in a diverse clade of suboscine birds. *Am. Nat.*, *171*, 620–631.
- Seehausen, O. & Schluter, D. (2004). Male–male competition and nuptial–colour displacement as a diversifying force in Lake Victoria cichlid fishes. *Proc. R.Soc. Lond. B*, *271*, 1345–1353.
- Sorci, G., Moller Anders, P. & Clobert, J. (1998). Plumage dichromatism of birds predicts introduction success in New Zealand. *J. Anim. Ecol.*, *67*, 263–269.
- Stamps, J.A. & Buechner, M. (1985). The territorial defense hypothesis and the ecology of insular vertebrates. *Q. Rev. Biol.*, *60*, 155–181.
- Stoddard, M.C. & Prum, R.O. (2008). Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *Am. Nat.*, *171*, 755–776.
- Tibbetts, E. & Safran, R. (2009). Co-evolution of plumage characteristics and winter sociality in New and Old World sparrows. *J. Evol. Biol.*, *22*, 2376–2386.
- Uy, J.A.C. & Vargas-Castro, L.E. (2015). Island size predicts the frequency of melanic birds in the color-polymorphic flycatcher *Monarcha castaneiventris* of the Solomon Islands. *Auk*, *132*, 787–794.
- Vanhooydonck, B., Herrel, A., Meyers, J. & Irschick, D. (2009). What determines dewlap diversity in *Anolis* lizards? An among-island comparison. *J. Evol. Biol.*, *22*, 293–305.
- Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilée, R., Condamine, F.L., Gravel, D. *et al.* (2015). Islands as model systems in ecology and evolution: prospects fifty years after MacArthur–Wilson. *Ecol. Lett.*, *18*, 200–217.

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Editor, Greg Grether

Manuscript received 14 December 2015

First decision made 8 January 2016

Manuscript accepted 27 January 2016