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Article

Evolution of vocal performance and song complexity in island birds

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Oceanic islands share distinctive characteristics thought to underlie a set of parallel evolutionary trends across islands and taxonomic groups – including life-history traits, morphology and visual signals. To which extent acoustic signals also change in parallel on islands is less clear. Some important processes associated with insularity, such as founder effects and reduced sexual selection, could lead to a decrease in vocal performance and song complexity on islands. In a field-based study, we recorded 11 insular species and their closest mainland relatives. Out of the 11 species pairs, 6 live in the tropics (São Tomé/Mount Cameroon) and 5 in the temperate region (Madeira/southern France). For each species, we measured two proxies of vocal performance (song duration and syllable rate) and one proxy of song complexity (syllable diversity). This study did not recover a clear relationship between the island environment and song traits. If as expected, syllable rate was lower in island species than in their mainland counterparts, the two other proxies showed no clear island–mainland pattern of divergence. Several factors may explain the absence of reduction for song duration and syllable diversity. Among those, relaxation of interspecific competition on islands may have led to an increase in syllable diversity, or correlations between song variables may have constrained song evolution. More studies on island species are needed to draw a better picture of divergence patterns and go beyond the confounding ecological factors that could explain peculiar song characteristics in islands.

Keywords: acoustic communication, insularity, sexual selection, sexual signals, tropics, vocal performance

Introduction

The small area and isolation of oceanic islands make them amenable natural laboratories for the study of ecology and evolution (Whittaker et al. 2017). They share a set of ecological conditions driving convergent evolution in insular species across the world (Grant 1998), as documented for a wide range of traits including life-history traits



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(Adler and Levins 1994, Covas 2012, Novosolov et al. 2013), body size (dwarfism and gigantism of animals and plants: Lomolino 2005, Clegg and Owens 2002; but see Meiri et al. 2008), brain size (Sayol et al. 2018) and ecological niche expansion (Grant 1998, Blondel 2000, Scott et al. 2003, Eloy de Amorim et al. 2017). Such convergences across diverse traits under insular conditions are grouped under the name ‘insularity syndrome’ and could also include convergent evolution in communication signals (Figuerola and Green 2000, Baker 2006, Morinay et al. 2013, Doutrelant et al. 2016, Robert et al. 2021b).

In insular birds, the evolution of acoustic signals remains poorly understood. In particular, if some trends have been found for decreased song frequencies in islands compared to the mainland (Robert et al. 2021b), it remains poorly known if vocal performance and song complexity are affected by insularity. Even if this question has been investigated for a long while (Lack and Southern 1949), previous studies comparing bird songs on islands vs the mainland have not been conclusive. In 15 studies reviewed by Price (2008), only 8 showed a decrease in song complexity on islands. Similarly, Morinay and coworkers (2013) did not find a significant pattern of parallel complexity or vocal performance reduction in a study comparing online-libraries records of songs of 49 island passerines and their closest mainland relatives. However, in that study, songs were recorded in different habitats and recording conditions, and such uncontrolled variation may have masked insular-mainland differences. Large-scale studies controlling these variations are thus needed to test whether vocal performance and song complexity are different on islands compared to the mainland.

Vocal performance reflects the degree of challenge to the motor system, the respiratory system or other physiological processes involved in singing (Cardoso 2017). We chose syllable rate and song duration as two proxies of vocal performance. Trade-offs between song parameters (e.g. ‘vocal deviation’, Podos 2001) are used as a proxy of song performance by some authors (Cardoso 2017) but are not used here because their strength is thought to differ a lot between different families (Podos et al. 2004). Syllable rate is a classic indicator of vocal performance (Morinay et al. 2013, Hill and Pawley 2019, but see Kroodsma 2017 and associated replies: Cardoso 2017, Podos 2017, Vehrencamp et al. 2017, Cardoso and Atwell 2018). In the robin, *Erithacus rubecula*, Brémond (1968) showed for instance that conspecifics reacted less to song artificially modified with increased silence and thus reduced syllable rate. Song duration has been less used as a proxy for vocal performance, but long songs are expected to constitute a challenge for the respiratory system (Suthers and Zollinger 2008). It has been used for this purpose in a study comparing online-libraries records of songs of the island and mainland passerines (Morinay et al. 2013). Both acoustic components are probably involved in mate choice and male–male competition in many species (Gil and Gahr 2002, Catchpole and Slater 2008). In relation to performance, artificially increased syllable rates are preferred by females in canaries (*Serinus canaria*, a Fringillidae as the

chaffinch, *Fringilla coelebs*, we study in the present paper) (Drăgănoiu et al. 2002), and simulated intrusions (playback experiments) increase syllable rates in chiffchaffs *Phylloscopus collybita* (Linhart et al. 2013).

Song complexity may be linked to mate quality (Nowicki et al. 1998, Nowicki and Searcy 2004, Mennill et al. 2006, Byers and Kroodsma 2009). For instance, playback experiments in whitethroat *Sylvia communis* (a close relative of *Sylvia atricapilla*) and chaffinch showed that conspecifics gave stronger responses to longer songs with more elements (respectively: Balsby and Dabelsteen 2001, Leitão et al. 2006). Also, house wren *Troglodytes aedon* males sing less complex songs with lower syllable rates at lower latitudes (Kaluthota et al. 2016), generally associated with weaker sexual selection presumably due to lower seasonality or greater food availability (Read and Weary 1992, Martin et al. 2010, Weir and Wheatcroft 2011, Najar and Benedict 2019). There are several song complexity metrics; here we used the within-song syllable diversity following Morinay et al. (2013), who used it also in the island–mainland song comparisons.

On islands, vocal performance and song complexity may diverge for several reasons in a predictable or unpredictable way. Changes could be unpredictable due to drift (Parker et al. 2012, Potvin and Clegg 2014) or follow convergent evolutionary directions (island syndrome: Morinay et al. 2013) either due to founder effects, linked to the colonisation process, or due to adaptation to the peculiar ecological conditions of islands. In oscine passerines, the song has to be learned (Catchpole and Slater 2008), and founder events have been shown to disturb the learning process (Lachlan et al. 2014). On islands, the acoustic space is less saturated due to the reduced species diversity, which is expected to reduce the need for species recognition (Robert et al. 2019). Finally, competition for mating is also expected to be weaker (Griffith 2000). Overall, this means that some components of the vocal repertoire could be lost at the time of island colonisation because of the reduced and random sampling associated with founder events and that selective pressures on song evolution (species recognition and sexual selection) could be weaker on islands. Thus, vocal performance and song complexity are both expected to decrease in insular populations.

Here, we tested these predictions by conducting controlled recordings (in similar habitats, during the breeding period, with consistent recording apparatus and with equivalent sampling efforts) of the songs of 11 insular species (5 from a temperate island and 6 from a tropical island). We investigated how these 11 species differ from those of their closest mainland relatives. Morphology imposes evolutionary constraints on the song (Gil and Gahr 2002), and, as such, island–mainland differences in body mass (Clegg and Owens 2002, Lomolino 2005; but see Meiri et al. 2008) could lead to peculiar song features in island populations (Potvin 2013). Thus, we also controlled for differences in body mass between insular and continental species in our statistical analyses. The song of some of these focal species is already known as differing in terms of frequency ranges (Robert et al. 2021b). Yet, insular characteristics of the other features of their songs

have not been studied. We measured vocal performance (song duration and syllable delivery rate) and song complexity (syllable diversity) and predicted lower values on islands compared to the mainland, especially for vocal performance.

Methods

Study site and species pairs

Our study was based on the comparison of vocal performance and song complexity proxies of insular and continental related species pairs. We focused on two pairs of insular and continental acoustic communities. The tropical pair comprised São Tomé Island, hereafter referred to as ‘tropical island’, and Mount Cameroon, hereafter referred to as ‘tropical mainland’. The temperate pair comprised Madeira Island, hereafter referred to as ‘temperate island’, and southern France, hereafter referred to as ‘temperate mainland’. São Tomé and Madeira are located 250 km and 657 km away from the mainland, respectively. We worked on comparable mature or primary forests (mature laurel and evergreen oak forests in the temperate zone and primary rainforests in the tropics) with similar propagation properties (Robert et al. 2019). For each community (tropical island, tropical mainland, temperate island and temperate mainland), we worked on three sites (separated by at least 3 km, Supporting information).

On the islands, we recorded the common vocalising species. We then recorded their closest vocalising relative on the mainland (see Supporting information for an example of each typical song). In the tropics, AR, TL, MM and CD recorded the vocalisations of the following six pairs of species: one non-oscine, the African emerald cuckoo (*Chrysococcyx cupreus insularum* versus *Chrysococcyx c. cupreus*), and five oscines – a pair of orioles (São Tomé oriole *Oriolus crassirostris* vs western black-headed oriole *Oriolus brachyrynchus*), a pair of paradise-flycatchers (São Tomé paradise-flycatcher *Terpsiphone atrochalybeia* vs red-bellied paradise-flycatcher *Terpsiphone rufiventer*), a pair of prinias (São Tomé prinia *Prinia mollerii* versus green longtail *Urolais epichlorus*), a pair of speiropes (black-capped speirops *Zosterops lugubris* vs Mount Cameroon speirops *Zosterops melanocephalus*) and a pair of sunbirds (Newton’s sunbird *Anabathmis newtonii* vs northern double-collared sunbird *Cinnyris reichenowi*). In the temperate region, AR and CD recorded the vocalisations of five pairs of oscines species: a pair of European robins (*Erithacus rubecula* in Madeira and southern France), a pair of Eurasian blackbirds (*Turdus merula cabrerai* and *Turdus m. merula*), a pair of Eurasian blackcaps (*Sylvia atricapilla heineken* and *Sylvia a. atricapilla*), a pair of firecrests (Madeira firecrest *Regulus madeirensis* and common firecrest *Regulus ignicapilla*) and a pair of common chaffinches (*Fringilla coelebs madeirensis* and *Fringilla c. coelebs*). These pairs were chosen based on molecular phylogenies or on taxonomy as a proxy for relatedness (Covas 2012, Morinay et al. 2013, Doutrelant et al. 2016). Although the sunbird pair is made up of two species currently placed in two distinct genera,

ongoing molecular analyses have recovered them as sister species (Rauri Bowie, Martim Melo and Luis Valente, unpubl.). If several continental species were good candidates (it was the case for 2 out of the 11 pairs: the prinia species and the paradise-flycatcher species), we matched the pairs by habitat (species inhabiting the same habitat were selected). All 11 insular taxa have been described as, at least, differentiated subspecies from mainland populations, except for the robin which was formerly described as an endemic subspecies of Macaronesia (Hounscome 1993) but is now included in the nominate subspecies (Clements 2000, Garcia-del-Rey 2011, Billerman et al. 2020). Except for the cuckoo pair, all tropical pairs are made of well-differentiated species, whereas in the temperate region all pairs represent conspecific populations or a very recent speciation event in the case of the firecrests (whose insular population was treated as conspecific with the mainland species until recently, Päckert et al. 2001). Hence tropical pairs represent older divergence events (although still considered recent as they occurred in the Plio-Pleistocene border, ca 2–3 mya: Melo 2007) than those of the temperate pairs.

Morphological data

We obtained the body mass for each of the 22 focal taxa. We found body mass data in the literature for tropical mainland and all temperate taxa (*Regulus madeirensis*: Billerman et al. 2020; Madeiran robin and blackbird: Hounscome 1993; Madeiran chaffinch: Grant 1979; Madeiran blackcap: Dietzen et al. 2008). For São Tomé island taxa, body mass data were collected on the field by MM (available on SAFRING database, Univ. of Cape Town). When only ranges were reported or when masses were reported separately for males and females, we assumed the midpoint median was the mean of the two values. Body mass did not differ significantly between the island and mainland species (pairwise comparisons using Wilcoxon rank-sum test, $p > 0.35$).

Recordings

We made recordings of each of the study species by using Fostex FR2 recorders [Fostex, Tokyo] coupled with unidirectional microphones Sennheiser ME66/K6 [Sennheiser, Hanover] (flat frequency response between 20 Hz and 20 kHz). The signal was sampled at 44.1 kHz with a 16 bits digitisation, and files were saved in .wav format. Data were collected during the breeding season in 2016 and 2017 (temperate mainland: Apr 2017; temperate island: Mar 2017; tropical mainland: Nov 2016; tropical island: Sept 2016). Each recording was selected from different locations: in each of the four communities, recordings were obtained in three distinct sites; within each site, recordings were obtained at least 200 m apart to ensure they came from different individuals. We recorded the typical vocalisations usually recognised as ‘song’ by the ornithologist community based on our own experience and on xeno-canto (<www.xeno-canto.org/>) and Macaulay (Cornell Lab of Ornithology, <www.

macaulaylibrary.org/>) online-libraries. We restricted the analyses to the highest quality files, and, on average, we measured 7.04 (\pm 3.02) songs per individual, 10.27 (\pm 2.19) individuals per species and 72.32 (\pm 29.46) songs per species (1591 songs analysed in total; sample sizes are presented in the Supporting information). These recordings were obtained at less than 30 m (mostly between 5 and 20 m) from the focal bird.

Using Avisoft software [Avisoft Bioacoustics, Berlin], we computed spectrograms and oscillograms with fast Fourier transforms (FFT 1024 points; Frame 50%; Hamming window; Overlap 75%). We determined song duration using cursor placement on oscillograms. On oscillograms and spectrograms, we visually identified the number of different syllables (short repeated units as defined by Catchpole and Slater 2008) within each song as a measure of syllable diversity. We divided the number of syllables per song by the song duration to obtain syllable rate (Supporting information). Duration and syllable diversity were significantly and positively correlated ($r=0.45$, $p < 0.001$, Supporting information). Syllable rate was significantly but moderately correlated to both syllable diversity ($r=0.13$, $p < 0.001$) and duration ($r=-0.058$, $p < 0.05$).

To assess whether we had recorded enough individuals to characterise species song characteristics in an accurate way, we computed accumulation curves of the means of song duration and maximum sampled syllable rate (Supporting information). This was not done for syllable diversity as this would require labelling all syllables from all songs to see whether adding a new song would add to an existing accumulated syllable diversity, which was technically unfeasible with our means.

Statistical analyses

All three dependent variables (song duration, syllable rate and syllable diversity) were log-transformed to ensure their normality (based on graphical assessment of residuals). We used linear mixed-effects models (LMM) using the *R* package nlme to explore patterns of variation. For each of the three response variables, we ran a model testing insularity (island/mainland), latitude (tropical/temperate), the interaction between latitude and insularity, body mass and altitude as fixed effects. We included bird mass (from HBW, Billerman et al. 2020) as a proxy for syrinx mass, long recognised as influencing the timing of sound production (Brackenbury 1978, Gaunt 1987). Syrinx mass primarily determines the minimum frequency that a bird can achieve (Ryan and Brenowitz 1985, Potvin 2013), but it may also affect other variables such as syllable rate as a result of trade-offs between rate and frequency bandwidth (Podos 1996, 1997). We included altitude because of its negative correlation with temperature and species number, which has been found to influence song properties such as frequency (Morton 1975, Kirschel et al. 2009). Finally, we included 'species' nested in 'pair' nested in 'family' as a random factor to account for the phylogenetic structure of the data (Griffith 2000, Beauchamp 2004, Covas 2012, Morinay et al. 2013, Doutrelant et al. 2016). We weighted the analyses by

sample size, i.e. by the number of recordings per individual. We selected the best model by minimising the Akaike information criterion (AIC: Akaike 1987) and considered that models differing by less than 2 AIC units were equivalent.

We were also interested in assessing which particular species could be driving potential song differences between islands and the mainland. For this, we compared song duration, syllable rate and song complexity for each of the 11 island–mainland species pairs, by conducting t-tests. All statistical analyses were conducted in R v.3.05.1 (<www.r-project.org>).

In order to investigate how phylogenetic relationships among species could influence our results, we also analysed the same variables (song duration, syllable rate and syllable diversity) using a Bayesian phylogenetic mixed model (BPM) approach (Supporting information).

Results

All three song variables were affected by the interaction between latitude and insularity in different ways (Table 1).

Syllable rate

As predicted, the syllable rate was lower on islands (Table 1, Fig. 2). The syllable rate was not affected by altitude, but it was significantly influenced by body mass, with lighter species singing faster (Table 1). When we looked at each species independently, four tropical pairs (cuckoo, oriole, speirops and sunbird) out of six showed lower syllable rates on the island, thereby driving the insularity \times latitude effect (the paradise-flycatcher and the prinia showing higher syllable rate on the island). Three temperate pairs (robin, firecrest and chaffinch) out of five showed lower syllable rate on the island (the blackcap showing higher syllable rate and the blackbird showing no change, Fig. 1). Accumulation curves of the mean of maximum sampled syllable rate (Supporting information) showed that a plateau was reached for 9 out of 11 pairs, except for the paradise-flycatcher and the blackcap, for which increasing the sampling effort would have increased their already higher syllable rate on the island, which would have been conservative for our results.

Song duration

Contrary to our expectation, song duration was longer in the tropical island than in the tropical mainland, and it did not differ between the temperate island and the mainland (latitude by insularity interaction Table 1, Fig. 2). It was not affected by altitude, but it was significantly influenced by body mass, with heavier species producing longer songs (Table 1). When looking at each species independently, we found that four tropical pairs (cuckoo, oriole, paradise-flycatcher and sunbird) out of six showed longer songs on the island, thereby driving the island \times latitude effect (the speirops showed a significantly lower song duration, and the prinia did not show any significant variation). The absence of difference in song

Table 1. Variation of metrics of song performance and complexity proxies in island and mainland birds. Results of the best linear-mixed models for the two vocal performance variables: song duration, and syllable rate and one measure of song complexity – syllable diversity. Variables were considered on a logarithmic scale. Variables with a significant effect in bold.

Song metrics	Independent variables	T	df	Estimate	p-value
Syllable rate (logged)	Intercept	8.76		1.61	
	Altitude	–	–	–	–
	Mass	–3.42	1571	–0.29	< 0.001
	Insularity (Island)	–4.85	1571	–0.10	< 0.001
	Latitude (Tropics)	–0.64	8	–0.16	0.54
	Insularity × latitude (Island × tropics)	–1.58	1571	–0.05	0.11
Song duration (logged)	Intercept	1.99		0.86	
	Altitude	–1.72	1570	–0.06	0.09
	Mass	2.94	1570	0.50	< 0.01
	Insularity (Island)	0.88	1570	0.04	0.38
	Latitude (Tropics)	–0.58	8	–0.33	0.58
	Insularity × latitude (Island × tropics)	3.91	1570	0.26	< 0.001
Syllable diversity (logged)	Intercept	4.43		1.74	
	Altitude	–4.89	1571	–0.14	< 0.001
	Mass	–	–	–	–
	Insularity (Island)	–4.37	1571	–0.12	< 0.001
	Latitude (Tropics)	–0.88	8	–0.44	0.41
	Insularity × latitude (Island × tropics)	7.12	1571	0.40	< 0.001

duration between the island and mainland in the temperate area is due to the fact that only two pairs (firecrest, chaffinch) out of five showed longer songs on the island (the blackbird and the blackcap showed shorter songs, and the robin did not show any change, Fig. 2). Accumulation curves of the mean of song duration maxima (Supporting information) showed that all species were sufficiently sampled, except the insular speirops and blackbird. Since both species presented shorter

songs on islands, increasing sampling effort could have shown no variation between the island and mainland or could have reinforced the insularity effect.

Syllable diversity

As expected, syllable diversity was lower on the temperate island than on the temperate mainland, but in contrast, it was

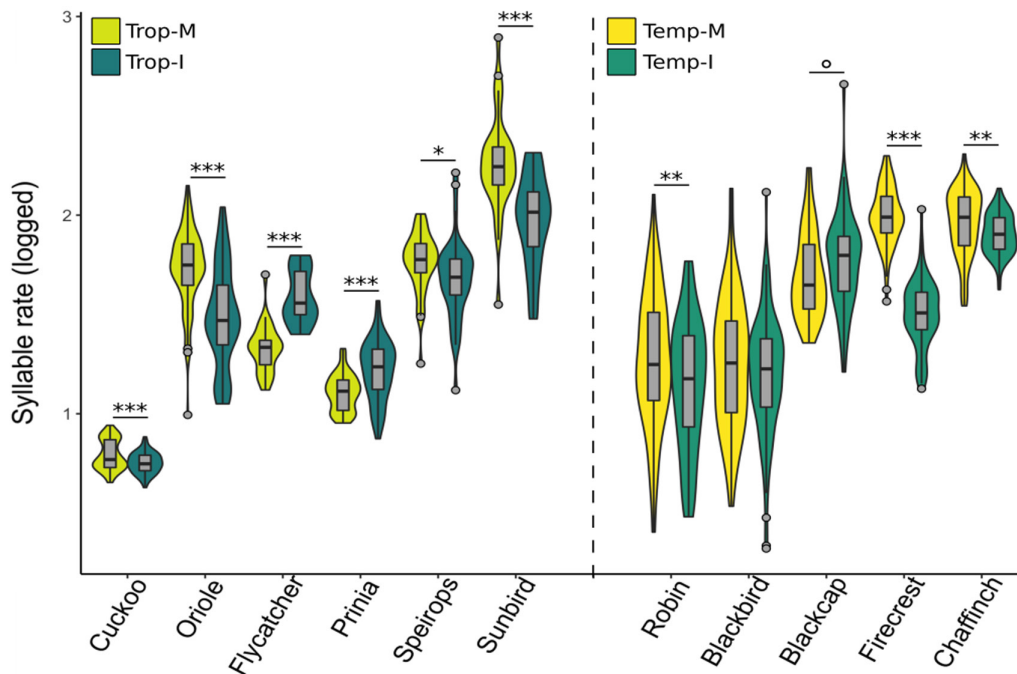


Figure 1. Syllable rate (log) for 11 focal bird species, from tropical (Trop, left) and temperate (Temp, right) zones and respective mainland (M) and islands (I). Symbols associated with p-values for paired t-tests: no symbol: non-significant, ° < 0.1, * < 0.05, ** < 0.01, *** < 0.001. Shape of the violin plot show the probability density of the data at different values and boxplot indicate quartiles of the distribution.

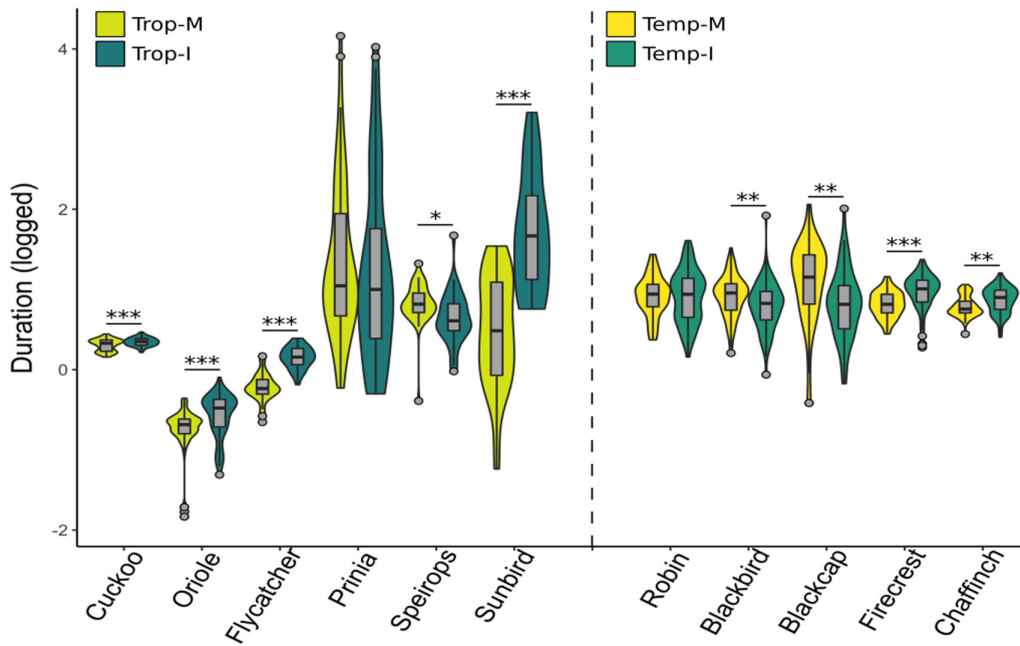


Figure 2. Duration (log) of the song of 11 focal bird species, from the tropical (Trop, left) and temperate (Temp, right) zones and respective mainland (M) and islands (I). Symbols associated with p-values for paired t-tests: no symbol: non-significant, ° < 0.1, * < 0.05, ** < 0.01, *** < 0.001. Shape of the violin plot show the probability density of the data at different values and boxplot indicate quartiles of the distribution.

higher on the tropical island than on the tropical mainland. Syllable diversity was not affected by body mass, but it was significantly negatively correlated to altitude (Table 1). The general increase we found in the tropical island was driven by three species pairs (paradise-flycatcher, prinia and sunbird) out of six (the speirops showed lower values and the cuckoo and oriole did not show any variation). The lower syllable diversity found in the temperate island was driven by three species pairs (blackbird, blackcap and chaffinch) out of five (the firecrest showed a significant increase and the Robin did not change, Fig. 3).

Effects of phylogenetic relationships

Results of the Bayesian phylogenetic mixed model are presented in Supporting information. Broadly, results of BPMM were equivalent to the LMM ones in terms of the fixed-effect structure of the final models. In particular, BPMM found a positive effect of insularity on syllable rate which was lower on islands. As in LMM, syllable rate was significantly affected by mass, with lighter species producing faster songs. Contrasting with LMM, altitude had a significant and positive (although very weak) effect on syllable rate. Song duration was not affected by altitude, but it was significantly influenced by body mass, with lighter species producing longer songs. Results of BPMM indicated a significant effect of interaction between ‘insularity’ and ‘latitude’ on song duration: song duration was higher in the tropical island than in the tropical mainland, but it did not differ between the temperate island and mainland. Overall, effects of the interaction ‘latitude × insularity’ were

weaker in the BPMMs than in LMMs. This indicates that phylogenetic relationships explain a part of the significant link between our three variables and the interaction ‘latitude × insularity’. The temperate pairs represent more recent colonisation and divergence events than the tropical pairs (except for the cuckoo pair) which probably enhanced the effect of latitude. As in LMM, BPMM indicated that syllable diversity changed with latitude and insularity (significant latitude by insularity interaction). It was lower on the temperate island than on the temperate mainland, but it was higher on the tropical island than on the tropical mainland. As in LMM, syllable diversity was not affected by body mass, but it was significantly positively (not negatively) correlated to altitude.

Discussion

A clear relationship between the island environment and song did not emerge from this study. The only supported pattern was a decrease in syllable rate both in the tropical and temperate islands. However, on islands, song duration was not lower (it even increased on the tropical island), and although syllable diversity was lower in the temperate island, this pattern did not hold in the tropics.

Syllable rate in island species

The most consistent result across latitudes was the lower syllable rates shown by insular species in comparison to their mainland counterparts. As mentioned in the introduction, the syllable rate is probably the song feature for which sexual selection towards exaggeration has been better

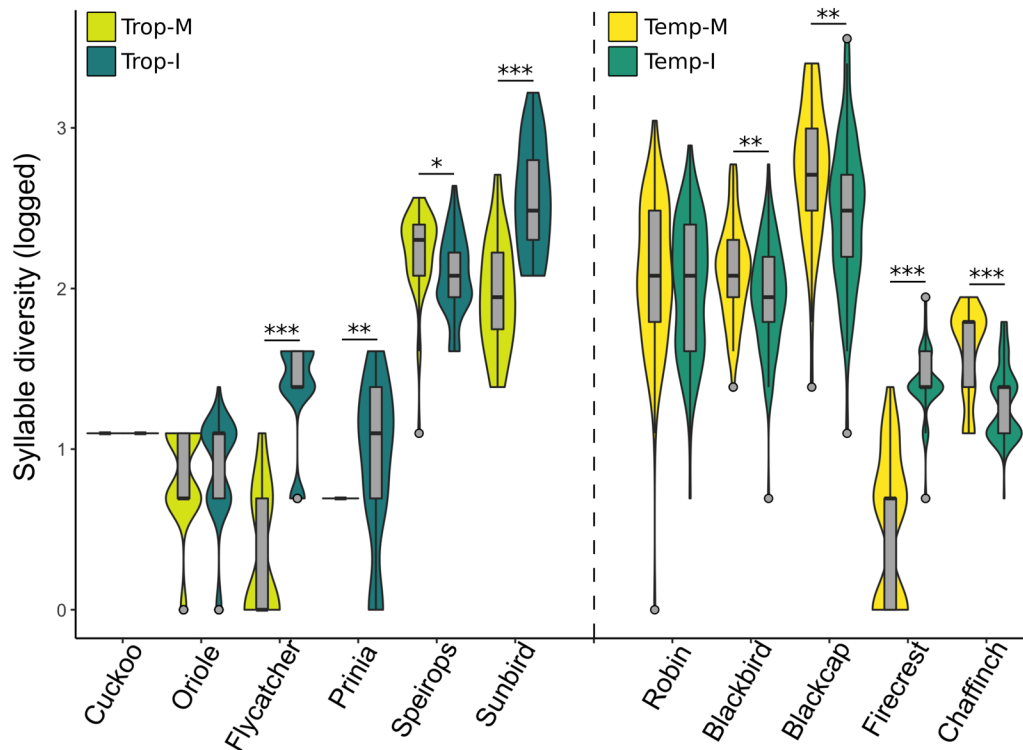


Figure 3. Syllable diversity (log) of the song of 11 focal bird species, from the tropical (Trop, left) and the temperate (Temp, right) zone and respective mainland (M) and islands (I). Symbols associated with p-values for paired t-tests: no symbol: non-significant, $^{\circ} < 0.1$, * < 0.05 , ** < 0.01 , *** < 0.001 . Shape of the violin plot show the probability density of the data at different values and boxplot indicate quartiles of the distribution.

established (Drăgănoiu et al. 2002, Catchpole and Slater 2008, Byers et al. 2015, Podos and Sung 2020).

Patterns of lower vocal performance on islands are thus susceptible to be driven by reduced intersexual selection on islands which could be due to three factors. First, insular populations are of small size and are created stochastically from small subsets (individuals colonising the island) of mainland populations. As such, they have lower levels of genetic diversity than mainland populations, relatedness levels being a priori higher (Frankham 1997). Secondly, parasite pressure is lower on islands (Pérez-Rodríguez et al. 2013 for an example in Macaronesian blackcaps *Sylvia atricapilla*, and Loiseau et al. 2017 for bird communities in the Gulf of Guinea). Both lower genetic diversity and reduced parasite pressure should reduce the indirect benefits of mate choice (benefits of passing ‘good genes’ to offspring) on islands and thus the strength of sexual selection. For instance, Petrie et al. (1998) showed that when males are genetically similar, levels of extra-pair paternity (EPP) – which maximise the probabilities of passing genes to the next generation – are lower, and such patterns have indeed been found in island passerines (Griffith 2000), further supporting reduced sexual selection in insular communities. A third process could lead to less stringent mate choice on islands. Insular species have higher survival and probably higher longevity than mainland species (Covas 2012, Novosolov et al. 2013). This could be associated with a lower divorce rate, longer pair bonds (Botero and Rubenstein

2012) and, hence, lower sexual selection because of reduced variance in mating success (Figuerola and Green 2000).

Besides reduced intersexual selection, life history trade-offs could also explain the lower syllable rate in island species. Parental care and investment in offspring survival are higher in island species than in their mainland relatives (Covas 2012). A trade-off between sexually secondary traits (and thus mate attraction) and parental care has been shown in bird coloration (Figuerola and Green 2000) and bird song (at least between male song and paternal care; Smith 1995, Rytkonen et al. 1997). In relation to the song, these trade-offs are susceptible to impact all sexually selected features such as syllable rate.

Evolutionary trade-offs could also occur between song features and concur to explain the documented change. In particular, Podos (1996, 1997) identified a negative link between frequency bandwidth and trill rate in Emberizidae. In the two species that sing trills in our data set (chaffinch and sunbird), the syllable rate may be equivalent to trill rate. The aforementioned trade-off is, however, unlikely to explain the observed decrease, as the frequency range of the chaffinch song decreases, rather than increases, on the island, whereas it does not change for the sunbirds (Robert et al. 2021b). Moreover, we show a global decrease of syllable rate in insular species even for species pairs with the same frequency bandwidths on islands.

Finally, beak size and shape are known to directly influence song characteristics and, in particular, vocal performance.

For instance, larger beaks are associated with songs produced at a slower pace in Darwin finches (Podos 2001) or in Meliphagidae (Friedman et al. 2019). Here, we do not have data on beak morphologies, but because beak size has been shown to change in insular environments (Grant 1998, Blondel 2000, Scott et al. 2003, Eloy de Amorim et al. 2017), it will be a factor to explore by future studies trying to understand changes observed on islands. Similarly, body size measures were not taken on the recorded birds, but rather from species means, which could obscure any possible effects of morphology on the song parameters analysed.

Song duration in islands species

Contrary to our expectation, relatively to the mainland, songs were longer on the tropical island but were similar in length on the temperate one. As explained above, trade-offs or correlations between acoustic traits may counterbalance the predicted effect of insularity on song and explain why we did not find the expected results. Trade-offs between frequency ranges and trill rate (Podos 1997) and between amplitude (loudness) and syllable diversity (Mota and Cardoso 2009) are documented in the literature. Yet, to the best of our knowledge, there is no evidence of a trade-off between frequency range or syllable rate and song duration. By contrast, our data showed that song duration is partly correlated to syllable diversity ($r=0.45$, $p < 0.001$) probably simply because of structural reasons as in longer songs there should be more opportunity to include more syllables. Thus, selective pressures towards greater syllable diversity on tropical islands may have driven the increase in song duration that we documented in some tropical island species. Six out of 11 species showed similar patterns of island–mainland differences in song duration and syllable diversity (both variables increased on the island for three species pairs (paradise-flycatcher, sunbird and firecrest), and both variables decreased on the island for three species pairs (speirops, blackbird and blackcap pairs).

As longer continuous singing may pose ventilation challenges (Suthers and Zollinger 2008), song duration likely reflects a component of vocal performance. However, physiological mechanisms of song production are not fully understood, and it is a less-established proxy of vocal performance than the syllable rate. Morinay and coworkers (2013) did not find any significant pattern of song duration reduction on islands in a study comparing the online-library songs of 49 island passerines and of their closest mainland relatives. Our documented difference in the tropics and lack thereof in the temperate region are difficult to interpret without more evidence of the communication function of song duration in each of the study species, especially as negative results could be due to the inadequacy of the metric chosen for the study species (Cardoso 2017). As explained in the introduction, past studies in the temperate region suggested that song duration is an adequate proxy for song complexity due to its role in mate choice and male–male competition. This role was demonstrated for most of the temperate species we studied here, but it remains to be tested in tropical species.

Finally, contrasting results in vocal performance proxies could also be explained by cultural drift during colonisation that is susceptible to draw unpredictable island–mainland differences.

Song complexity on islands

We found that island syllable diversity was, as expected, lower in the temperate area, but against our expectations, it was higher in the tropical area. Apart from the structural correlation with song duration we discussed above, this pattern could be due to changes in several selective factors that are expected to differ across latitudes, including distinct biogeographic histories of different islands and/or different degrees of relaxation of sexual selection on islands. Three explanations can be proposed to explain the lower song complexity on the temperate island of Madeira contrasting with the higher song complexity on the tropical island of São Tomé.

First, the character release hypothesis predicts an increase of song complexity in communities encompassing fewer species, as is the case with island communities (Kroodsma 1985, Naugler and Ratcliffe 1994). This hypothesis could explain the increase in syllable diversity we observed on tropical islands. Character release is expected to lead to an increase in song variability at the population level because, on the one hand, males are less strongly selected to accurately reproduce species-specific songs and, on the other hand, a reduction in interspecific competition frees up acoustic space. Thus, in the future, it should be interesting to study changes in repertoire with different metrics such as among-song repertoire size. Some authors have also argued that character release could lead to more complex songs at the individual level (Morinay et al. 2013). If this is the case, an increase of syllable diversity at the individual level could still lead to increased diversity at the intra-individual level, at least in oscines learning their songs from conspecifics. Character release is expected to be more pronounced at low latitudes where there are greater differences in species numbers between the mainland and islands (Robert et al. 2021b); this could explain why we found a higher syllable diversity on the tropical island compared to the tropical mainland.

Secondly, two distinct consequences of founder events also predict reduced song complexity in oscines, for which song is a learned behaviour (in our study, 10/11 species pairs are oscines). Reduced complexity could be the consequence of 1) an interruption of the learning period (Thielcke 1973, Baker 2006), which may occur when islands are colonised by young birds that have not yet fully learned their song. In this case, individuals perform songs that are similar to those of birds raised in laboratories in absence of singing relatives. 2) Cultural drift may occur because oceanic islands are colonised by small numbers of individuals encompassing a small part of the song diversity of the continental population (Parker et al. 2012, Potvin and Clegg 2014). In both cases, a reduction in complexity is expected at the song level because, as previously noticed, a positive correlation is expected in oscines between inter-individual level song diversity and song complexity at

the intra-individual level. Founder effects are expected to be stronger on more remote islands (fewer colonisers) and are more strongly felt after recent colonisation events (Hill and Pawley 2019). In this study, the temperate island was more remote than the tropical one and the temperate pairs represent more recent divergence events than the tropical pairs. As such, the tropical pairs had time to rebuild any song diversity lost after colonisation, in a process similar to the rapid recovery of genetic diversity after founder events (Brekke et al. 2011). These two facts may explain why the reduced diversity has only been found in Madeira, the temperate island. Our pattern of more recent divergence events in the temperate zone follows the pattern observed on the whole bird family. Sister species are older in the tropics than in the temperate region (Schluter and Pennel 2017), although rates of divergence in mating traits (e.g. body size, coloration and song) are often slower in the tropics (Weir and Wheatcroft 2011).

Finally, complex songs are expected to be a product of mate choice (Catchpole and Slater 2008) and, as previously mentioned, intersexual selection is probably lower on islands. A decrease of within-song complexity has been shown in some insular species (e.g. common chaffinch, Baker and Jenkins 1987, reviewed by Price 2008). Intersexual selection is greater at high latitudes where the short breeding seasons increase the importance of male song in mate attraction, whereas a burst of food availability decreases the cost of singing (Irwin 2000). It has been shown that this leads to higher divergence rates in song complexity at higher latitudes (Read and Weary 1992, Martin et al. 2010, Weir and Wheatcroft 2011, Najar and Benedict 2019). Moreover, some of the peculiar ecological conditions of islands (such as lower seasonality or higher food availabilities) are more marked at high latitudes, i.e. on temperate islands (Whittaker and Fernandez-Palacios 2007, Covas 2012). Thus, if syllable diversity is affected by sexual selection, then decreased syllable diversity is expected to be more pronounced on temperate islands than on tropical ones. In our study, this latitude effect may be enhanced by the fact that Madeira is 10° to the south of France while São Tomé is only 4° to the south of Cameroon. Reduction in syllable diversity in the temperate island is well illustrated by the loss of the terminal ‘flourish’ syllable of the common chaffinch (see Supporting information for a spectrogram of a typical song), which has both intersexual (Riebel and Slater 1998) and intrasexual Leitão and Riebel (2003) functions.

Conclusion

Overall, this study confirms some of the predictions on the direction of song evolution on islands but, more importantly, highlights how this process may be affected by several mechanisms that can prevent convergent evolution of song traits on islands. To better understand patterns of changes on islands for song performance and complexity, a larger comparative study is needed. Field data are long to collect but are crucial to control both for latitude and for time since island colonisation. Our study supported previous suggestions that some

aspects of the ‘island effect’ may be stronger on temperate regions. As with genetic variation, studies on the evolution of song complexity on islands will need to distinguish between short-term responses to founder events and long-term adaptations to the island environment. In this respect, studies should sample species pairs across latitudes and spanning a wide time range, from early colonisers to well-differentiated endemic species. Also, it would be important to have more information about mechanisms of vocal production in order to better understand trade-offs or structural correlations that could involve proxies of song performance or song complexity. Overall, our study provides additional elements to the debate regarding the predictability of evolutionary trends on oceanic islands and the possibility of convergent evolution of acoustic signals within the ‘insularity syndrome’.

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Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.3j9kd51k5>> (Robert et al. 2021a).

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