



Local prior information and mainland overflow explain avian colonisation in a major land-bridge island

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Abstract

Aim: The relative roles of intrinsic and extrinsic factors, and those of local and regional variables, in island colonisation, remain major biogeographical questions. Thus, we analysed avian colonisation records of a large land-bridge island, defining successful colonisation as the occurrence of breeding during at least 3 consecutive years, at species level with the aim of identifying the main determinants of island colonisation by birds.

Location: Mallorca (Balearic Islands, western Mediterranean).

Major Taxa: All avian species recorded in Mallorca Island.

Methods: We performed logistic regression by fitting generalised linear mixed models to data. We explored seven explanatory variables and performed model selection based on Akaike's information criterion.

Results: A total of 26 bird species colonised the island during the study period, a rate of ca. 0.7 colonising species/year. Only seven species were found to attempt colonisation unsuccessfully. Bird species with the highest colonisation probabilities were those with growing population trends on the mainland and a previous status as wintering species on the island (0.58), followed by wintering species with a stable population trend on the mainland (0.37).

Main Conclusions: The high rate of colonisation indicates that the process of incorporation of new species has been very dynamic. Colonisation was dependent on a local factor (having prior information about the island) and a regional factor (density dependence on the nearby continent). However, it was not influenced by body size, diet, habitat or IUCN level of threat. Based on the results of our modelling, we present a predictive list of likely future colonisers.

KEYWORDS

Balearic Islands, density dependence, determinants of colonisation, land-bridge island, mainland population trends, overwintering, prior information

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1 | INTRODUCTION

Great vagility allows birds to colonise remote areas, with greater ease than other non-flying vertebrate taxa, including humans. For example, the island of Pascua and New Zealand were not colonised by humans until just 700 years ago (Quintana-Murci, 2022). The island of Mallorca (a major and heterogeneous land-bridge western Mediterranean Island, the largest of the Balearic Islands) was colonised by humans also very recently (ca. 4150–4500 a.E.C.; Alcover et al., 2001; Guerrero, 2007; Micó, 2005), most likely due to the difficulty of navigating from the mainland to the island against marine currents (Alcover 2008). On the contrary, birds do not have these constraints, and in fact many non-breeding bird species arrive to Mallorca annually, where they are present during migration or as winter visitors in the large variety of habitats present on the island. Despite that, Mallorca has a comparatively lower density of breeding species than nearby mainland regions of similar size and comparable habitat heterogeneity (i.e. Alicante province, with 5817 km², has 179 breeding bird species vs. 117 species in Mallorca with 3640 km²; De Juana & García, 2015; Grup Balear d'Ornitologia, 1997, 2010; López, 2015; Rebassa et al., 2021). This observation leads to wondering about the relative roles of local and regional factors for a successful colonisation, as well as about the relative weights of selective colonisation versus selective extinction as driving mechanisms of island richness and species composition at any point in time.

In this study, we aim to analyse the determinants of recent bird colonisation of Mallorca based on two assumptions, namely that (a) habitat availability is not a limiting factor (i.e. there is appropriate and abundant habitat for many bird species that are not present on the island despite breeding in the closest mainland since the island is large and heterogeneous), and (b) arrival to the island is not limiting (as many bird species get to the island annually in large numbers as migrants or winter visitors). For that purpose, we defined colonisation in a conservative way as achieving successful reproduction on the island (at species level) at least during 3 consecutive years. We will also analyse what set of species have been recorded to colonise as breeders, but have remained so for <3 consecutive years (i.e. unsuccessful colonisers), what we will consider an event of failed colonisation or breeding extinction.

The initial trigger of this study was the realisation that many instances of colonisation seemed to be associated with previous overwintering species, while preparing two recent books to the birds of Mallorca (Rebassa et al., 2018, 2021). We wondered if this was a true pattern, if migrant species could also colonise the island, and if the knowledge provided by expending several months a year as a winter visitor could represent an advantage for future colonisation. Hence, we hypothesised that avian colonisation of Mallorca could be affected both by intrinsic and extrinsic factors (see e.g. Martínez-Abraín et al., 2005), and by local and regional variables, including body size, breeding habitat, diet, previous knowledge of the island (i.e. wintering, migrant or wintering/migrant status), IUCN level of threat, and population trend of the species on the

nearest mainland qualitatively and quantitatively analysed (i.e. stable, increasing, decreasing), as species with increasing trends could be affected by density dependence and be forced to send propagules out of the mainland, in a large-enough number and with the adequate sex and age composition to allow a successful island colonisation. Hence, our main working hypothesis was that colonising bird species would be those having some feature promoting dispersal from the mainland (i.e. either being a common species or having positive population trends during the last decades) and/or favouring colonisation (i.e. either having prior knowledge of the island as wintering species, being a dweller of agro-ecosystems, as these are the dominant ecosystems on the island, or having an omnivorous diet, and hence not being restricted to any particular habitat).

2 | MATERIALS AND METHODS

2.1 | Data sources

To test our hypotheses, we compiled the available records of new breeding presence in the island of Mallorca since the 1980s (Table S1), out of the current total pool of 117 of breeding species, and also about wintering/migrating bird species ($n=87$) that do not breed in Mallorca. We also recorded information on failed breeding attempts. A total of 19 species (out of the total pool of species in Mallorca) were not considered for the analyses either because their colonisation was deemed impossible as the species breed in the tundra (12 shorebirds), were recently translocated by humans (*Aquila fasciata*, *Porphyrio porphyrio*, *Netta rufina*, *Fulica cristata*) or have had an irruptive colonisation (*Gyps fulvus*, *Aegithalos caudatus* and *Streptopelia decaocto*). Information was collected from Grup Balear d'Ornitologia (1997), (2010); Rebassa et al. (2021); De Juana and García (2015). In addition, we consulted issues 1–36 of the Annual Ornithological Record (Anuari Ornitològic Balear) published by the GOB, corresponding to the years 1985–2021.

We also recorded information about habitat, diet and status on the island, body size (i.e. total length) (Mullarney et al., 2001), and also about their recent population trend in Europe (both in quantitative and in qualitative terms) and IUCN threat category (BirdLife International, 2021). All these variables were treated as fixed factors or fixed covariates in our modelling.

2.2 | Modelling

We fitted generalised linear mixed models (with binomial family of errors) to data, to test multiple hypotheses explaining colonisation (0: colonisation not recorded/1: recorded colonisation) as a function of the different explanatory variables considered, controlling by taxonomic family as a random term for phylogenetic control (Table 1). Since we did not have a deep knowledge of the process

TABLE 1 Description of the independent variables considered for the study of the determinants of bird colonisation in Mallorca.

Name	Description
Habitat (breeding habitat)	Freshwater and saltwater ecosystems; islands and coasts with cliffs; meadows; woodlands; scrublands; grasslands and farmlands; urban landscape.
Diet	Carnivorous, granivorous, scavenger, herbivorous, insectivorous, filter feeder, omnivorous, piscivorous.
Status	Wintering; migratory; wintering and migratory
Meanl (Mean length)	Mean body length (cm) of each species
IUCN (IUCN threat category)	Endangered; Vulnerable; Near Threatened; Least Concern.
Indexcuan (Quantitative European population trend)	Mean estimation of the number of mature individuals in Europe
Indexcual (Qualitative European population trend)	Increasing; stable; decreasing

of colonisation beforehand, we built 27 different models combining the explanatory variables chosen either singly or by pairs in additive models, plus a model including all variables considered (i.e. saturated model) and a null model fitted without any variables except for the random term. Additionally, we built five additional models with interaction terms to test some specific biologically sensible hypotheses, such as a differential effect of population trends in relation to status or habitat, as well as between status and habitat (see Table S6 for a complete list of models). All models were fitted using the lme4 package for R. Models were compared simultaneously and selected by means of the loss of theoretical information criteria (Akaike's information criterion [AIC]), duly corrected for small sample size, by means of the R package AICcmoavg. Models with a difference in AIC <3 were considered statistically equivalent (Burnham & Anderson, 2002). Patterns of colonisation were compared among the levels of the factors 'status' and 'qualitative European population trend' using chi-squared tests with Yates' correction, together with its residuals. All analyses were performed using the R software environment (R Core Team, 2022).

2.2.1 | Colonisation probabilities

Colonisation probabilities for all nine combinations of the possible interactions between the three levels of the factor 'status' (i.e. wintering, migrant, both) with the three levels of the factor 'qualitative European population trend' (i.e. stable, increasing, decreasing) were obtained by means of the 'predict' function (type=response) together with the use of 'aggregate' in R.

3 | RESULTS

We found that the model including the qualitative European population trend (stable, increasing, decreasing) and status (wintering, migrant or both) was the most parsimonious one (i.e. had the lowest AIC_c), indicating that it explained the largest amount of deviance with the minimum model complexity (Table 2). Body size, diet, habitat and threat status were not present in the best models (see Tables S2–S5 and Figure S1 in Supporting Information for further details about these non-selected variables).

Data exploration showed a higher proportional colonisation by 'wintering' birds ($\chi^2 = 6.81$; $p < 0.05$; Figure 1; Table S2), and also by birds whose European population trend was 'increasing' ($\chi^2 = 11.17$; $p < 0.01$; Figure 2; Table S2).

The highest colonisation probability corresponded to wintering birds with increasing European population trend (0.58; Table 3), followed by wintering birds with stable European population trend (0.37; Table 3).

Colonisations were equally allocated by year (none or one colonisation per year) except for 2 years (1997 and 2008) in which three species colonised Mallorca respectively. A total of 18 years out of 40 considered (45%) had at least one colonisation.

While 26 species colonised successfully, only 7 species were found to have attempted colonisation unsuccessfully since the 1980s (*Anas querquedula*, *Circus pygargus*, *Falco subbuteo*, *Larus melanocephalus*, *Athene noctua*, *Saxicola rubetra*, *Spinus spinus*). Some other older attempts of punctuated reproduction were recorded in the 1970s (*Asio flammeus*, *Oriolus oriolus*) and in the 1920s and 1930s (*Charadrius hiaticula*, *Sternula albifrons*, *Sylvia hortensis*, *Sylvia borin*, *Serinus citrinella*; De Juana & García, 2015; GOB, 1997, 2010; Rebassa et al., 2021).

Considering information on status, trends in the continent and previous breeding attempts, we built a predictive list of likely future colonisers (Table 4). The list includes 19 species of birds whose colonisation of Mallorca in the following decades is deemed possible. Most species are linked to forest and wetland habitats and belong to 12 different families (7 non-passeriforms and 5 passeriforms). Species with the highest chances of colonising as breeders are *Coccothraustes coccothraustes*, *Turdus philomelos* and *Phalacrocorax carbo*.

4 | DISCUSSION

Despite Mallorca is one of the most remote islands in the Mediterranean (located ca. 200km off the mainland), reaching it is not a limiting factor for birds. Every year the island receives and holds huge contingents of many migrant and/or wintering bird species that do not breed in the island (see e.g. Rebassa et al., 2021). Breeding bird species composition of Mallorca has been found to be a very dynamic process. Far from being stabilised around a theoretical equilibrium, the number of species has changed substantially at the scale of a few decades (i.e. a few bird generations), with as

TABLE 2 Multiple hypotheses contrast of the effects of the explanatory variables considered on the colonisation/non colonisation of Mallorca by birds.

Models	K	Log-lik	AICc	Δ AIC	w_i	r^2
Colonisation~indexcual + status	6	-51.83	116.45	0	0.35	0.18
Colonisation~indexcual	4	-54.76	117.90	1.45	0.17	0.13
Colonisation~indexcuan + status	5	-54.01	118.59	2.13	0.12	0.10
Colonisation~indexcual * status	10	-48.49	119.14	2.69	0.09	0.22
Colonisation~indexcual + meanI	5	-54.55	119.67	3.21	0.07	0.15
Colonisation~indexcuan * status	7	-52.48	120.05	3.59	0.06	0.13
Colonisation~indexcuan	3	-57.18	120.58	4.13	0.04	0.04
Colonisation~indexcuan + meanI	4	-57.14	122.67	6.21	0.02	0.04
Colonisation~indexcual + IUCN	7	-54.13	123.32	6.87	0.01	0.13
Colonisation~indexcual + habitat	10	-50.67	123.50	7.05	0.01	0.17
Colonisation~indexcuan + habitat	9	-51.87	123.52	7.06	0.01	0.12
Colonisation~habitat + status	10	-51.08	124.32	7.86	0.01	0.17
Colonisation~status	4	-57.70	126.76	7.31	0.01	0.09
Colonisation~1	2	-60.50	125.11	8.65	0.00	0.07

Note: Models are listed in descending order in Akaike weights; only models with Akaike weights >0.01 (out of the 34 total models, see Table S6) are shown. The null model (Colonisation~1) is shown in the last row for comparison. The most parsimonious models are shown in bold (AICc<3). The Akaike weight of the most parsimonious models sum up to 0.73. K=number of estimable parameters; AICc, Akaike information criterion corrected by small size; log-lik, Log-likelihood; r^2 , proportion of variation explained by the model in total, including both fixed-effects and random-effects factors. All models include the random term (1|Family) for phylogenetical control by means of generalised linear mixed models with binomial family of errors.

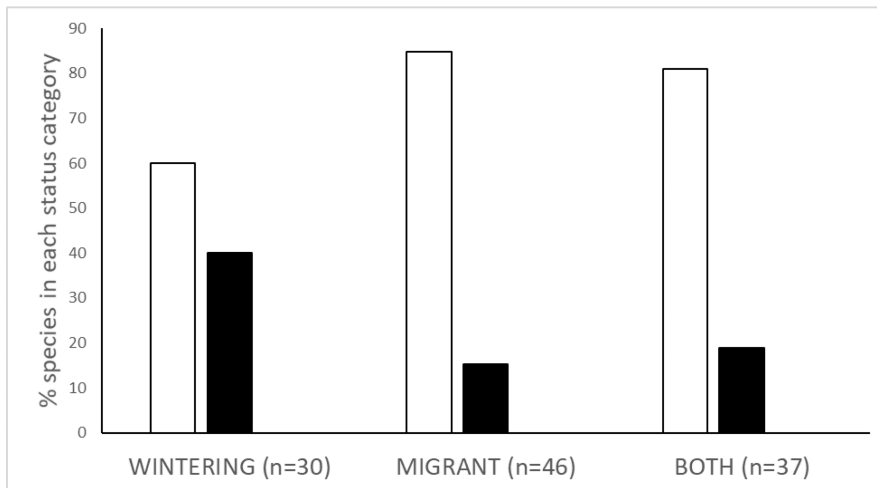


FIGURE 1 Percentage number of species colonising (black bars) or not colonising (white bars) Mallorca as a function of status (wintering, migrant or both).

many as 26 new breeders from 18 taxonomic families recorded. We have only worked at the timescale of a few decades and found a high rate of successful colonisation (0.7 species/year). It is possible that this rate could be higher now than in the past due to the current low levels of direct wildlife persecution associated with the process of rural flight that took place some 60 years ago (Martínez-Abraín et al., 2020, 2021). Previously intense bird persecution, within a subsistence farming-based economy, could have prevented the colonisation of many species. However, we cannot be certain. The rate of failed colonisations (i.e. extinctions as breeders) was much lower than that of successful colonisations (7 cases detected in 40 years, 0.17 species/year), although we acknowledge the difficulty of detecting such cases and hence this rate could be somewhat higher.

Our results indicate that having been previously a wintering species is a condition promoting colonisation. Wintering species may spend a long time on the island (several months a year), and can get to explore its resources in depth, collecting large amounts of prior information that can be used to evaluate whether a future breeding attempt could be successful or not. This concept, termed informed dispersal, has been found to be instrumental for social species (see Blanchet et al., 2010; Clobert et al., 2009; Oro, 2020; Oro et al., 2021), although the concept also seems to be valid for non-social species relying on private information, according to our results.

On the other hand, not all wintering birds are in the position of shifting from wintering to resident status. Wintering species whose populations were showing a growing population trend in the nearest

FIGURE 2 Percentage number of species colonising (black bars) or not colonising (white bars) Mallorca as a function of qualitative population trend on the nearest mainland (stable, increasing, decreasing).

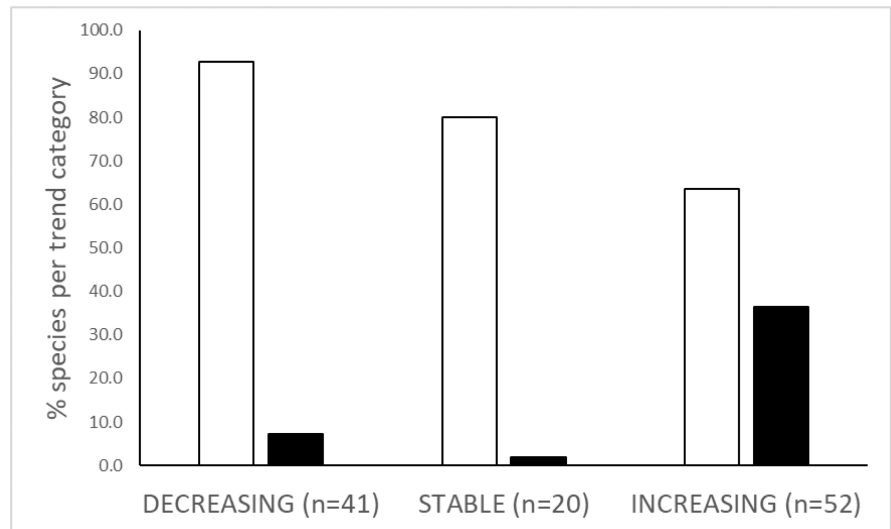


TABLE 3 Probabilities of colonising Mallorca by bird species depending on the combination of the type of qualitative population trend in Europe and the type of status.

	Probabilities
Increasing + wintering	0.58
Increasing + migratory	0.27
Increasing + migratory&wintering	0.29
Stable + wintering	0.37
Stable + migratory	0.14
Stable + migratory&wintering	0.15
Decreasing + wintering	0.15
Decreasing + migratory	0.04
Decreasing + migratory&wintering	0.05

Note: The three highest probabilities are highlighted in bold.

mainland were the ones with higher chances of colonising. This may be due to extrinsic factors such as an urge for overflowing species to escape from competition on the continent, confirming an important role of density dependence in the process of long-distance dispersal and colonisation (Elton, 1971; Ye et al., 2022; see Veit et al. 2022 for a role of vagrant birds as colonisers). However, it also suggests a likely role of limiting local (island dependent) factors such as arriving to the island with a well-balanced population regarding sexes and age classes, as well as with the right percentage of individuals having a bold personality to allow colonisation. Bolder birds are known to be more prone to explore, compete and colonise and be less afraid of novelties (i.e. having less neophobia) (e.g. Martínez-Abraín et al., 2022; Miller et al., 2022). Birds with a stable trend but a previous wintering status showed a relatively high probability of colonising, which indicates that wintering status (prior information availability) may be the main driver of colonisation. Even wintering species with a decreasing trend on the nearby continent had some chances of colonising.

However, we do not know if wintering birds colonising are juveniles or adults (see Skórka et al., 2016 for differential response of

young and adult birds to the same environmental variables). In case it is juveniles (following natal dispersal), long-term previous experience would still count if juveniles follow adults to their wintering sites. We hypothesise the likely existence of a trade-off between the need of having previous knowledge for successful colonisation, and the urge to achieve first reproduction, which would be modulated by the longevity of each species. Longer-lived species, which take several years to achieve sexual maturity, could invest several years in prospecting via natal dispersal before making a decision to colonise, whereas shorter-lived species could be forced to make a decision sooner, likely with greater risk of failure. Whatever the case, it appears less likely that adult individuals with successful breeding experience elsewhere are inclined to change their breeding grounds to their wintering quarters, except perhaps in the case of highly nomadic species, more prone to perform adult breeding dispersal (see e.g. Martínez-Abraín et al., 2003) or in the event of a major perturbation. As a rule, dispersal tendency decreases with age, that is, natal dispersal is more frequent than breeding dispersal both in long-lived (Bullock et al., 2002; Clobert et al., 2012) and short-lived species (Andreu & Barba, 2006).

Colonisation was not monopolised by any bird taxon in particular, but rather many different taxa were involved, and no influence of body size was detected either, with colonising species ranging from herons to small song birds. Most colonising birds were wetland birds and least concern species, although habitat and IUCN level of threat were not included in the best models. From an applied perspective, the role of mainland overflow suggests that the consequences of conservation (or of changing socio-economic factors) on mainland bird population sizes can influence the composition and diversity of the land-bridge islands located along the mainland coasts.

4.1 | Considerations on ancient colonisation and extinction

If the observed colonisation rate of ca. 0.7 species/year was also valid for the past centuries, this would imply that most bird species

TABLE 4 Predictive list of likely colonising species in the near future considering the results of our modelling, accounting for previous isolated attempts of reproduction by some species.

Species	Family	European population trend	Status	Comments
<i>Accipiter nisus</i>	Accipitridae	Stable	Migrant and wintering	
<i>Spinus spinus</i>	Fringillidae	Increasing	Migrant and wintering	Ancient occasional breeding
<i>Chlidonias hybrida</i>	Sternidae	Increasing	Migrant	Some breeding displays lately
<i>Ciconia Ciconia</i>	Ciconiidae	Increasing	Migrant	Some wintering birds lately
<i>Coccothraustes coccothraustes</i>	Fringillidae	Increasing	Wintering	
<i>Croicocephalus genei</i>	Laridae	Increasing	Migrant	Some wintering birds lately
<i>Egretta alba</i>	Ardeidae	Increasing	Migrant and wintering	Increasing as a wintering bird Some summering birds lately
<i>Hippolais polyglotta</i>	Acrocephalidae	Increasing	Migrant	
<i>Larus melanocephalus</i>	Laridae	Increasing	Migrant and wintering	Ancient occasional breeder. Increasing as a wintering bird
<i>Milvus migrans</i>	Accipitridae	Increasing	Migrant and wintering	Increasing as a wintering bird
<i>Pernis apivorus</i>	Accipitridae	Increasing	Migrant	
<i>Phalacrocorax carbo</i>	Phalacrocoracidae	Increasing	Wintering	
<i>Phoenicopterus roseus</i>	Phoenicopteridae	Increasing	Migrant and wintering	Ancient occasional breeder. Increasing as a wintering bird
<i>Phoenicurus ochruros</i>	Muscicapidae	Increasing	Migrant and wintering	
<i>Prunella modularis</i>	Prunellidae	Decreasing	Migrant and wintering	
<i>Sterna nilotica</i>	Sternidae	Increasing	Migrant	Some breeding displays lately
<i>Thalasseus sandvicensis</i>	Sternidae	Increasing	Migrant and wintering	
<i>Turdus philomelos</i>	Turdidae	Increasing	Wintering	
<i>Turdus viscivorus</i>	Turdidae	Increasing	Migrant and wintering	

Note: Species with the highest probability of colonisation (0.58) are highlighted in bold.

currently present in Mallorca as breeders could be relatively recent colonisers, as a consequence of such a high rate. In fact, just a small number of species has differentiated locally as subspecies (*Muscicapa tyrrhenica balearica*, *Loxia curvirostra balearica*, *Cyanistes caeruleus balearicus* and *Regulus ignicapilla balearica*). This is also consistent with the fact that only a couple of species (*Puffinus mauretanicus* and *Sylvia balearica*) are deep-time endemic species (Alcover et al., 1992), that survived the human colonisation of the island, which took place ca. 4150–4500 a.E.C depending on the author (Alcover et al., 2001; Guerrero, 2007; Micó, 2005).

Based on the island fossil record (Alcover et al., 1992), we can also suggest that some bird groups currently have disharmonic representations in Mallorca due to selective (i.e. non-random) extinction. This is the case of Corvidae with several species present in Pleistocene times (at least *Corvus monedula*, *Corvus corone*, *Pyrrhocorax graculus*, *Pyrrhocorax pyrrhocorax*), whereas only *Corvus corax* is present currently (not found in the fossil record). A second consideration is that some bird groups (such as reed bed passerines, from the genus *Acrocephalus*, *Locustella*, *Cettia*) only have slightly disharmonic faunas presently, thus either showing a great colonisation potential or low rates of extinction over long-timescales (unknown genus in the local fossil record). This is also

the case of *Sylvia* warblers, with a wide array of species currently present as breeders, but with no signal in the fossil record. Judging only from the fossil record can provide a misleading idea of the roles of extinction and colonisation regarding past and current island richness and species composition, because many old colonisers (extant species or not) may have not left behind any trace in the fossil record. Certainly, the Mallorca avifauna should not be seen as the remains of an old fauna that has been losing species over time. Colonisation most likely has been a major structural component of diversity at any time.

Finally, our colonisation model, developed for a land-bridge island, should be contrasted with similar information from oceanic (volcanic) islands, to verify whether the same deterministic drivers apply or not. The process of island colonisation could be more random in oceanic islands that emerge rapidly from the ocean floor, and that do not count necessarily with a long geological history, contrary to the case of the Balearic Islands, which constitute an undersea continuation of main mountain ranges from the Iberian Peninsula and Northern Africa. However, it could also be argued that Mallorca may be acting, to some extent, as an oceanic island, due to the extinction of many bird species linked to human action over the last few thousand years. Our results should also be

contrasted in other land-bridge islands throughout the globe, with variable features and histories of human occupation, to test the generalisation of the role of the factors identified by us in avian island colonisation.

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CONFLICT OF INTEREST STATEMENT

No, there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in this study are available as [Table S7](#) in Supplementary Material.

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BIOSKETCH

The authors are concerned with the interaction between population/community ecology and conservation biology. A large part of our past work has involved wetland and island birds. We are interested in the changes in abundance, distribution and behaviour of vertebrate species associated with the current paradigm of profound changes in land uses linked to rural abandonment.

Author contributions: AMA generated the initial idea and wrote the first draft of the manuscript. JC performed the analyses and built the figures. MR provided original data and expert ornithological advice. All authors contributed to the improvement of the initial manuscript.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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