



The island syndrome in birds

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Abstract

The island syndrome is a widespread biological phenomenon that describes a suite of morphological, behavioural, demographic and life-history changes associated with island dwelling. These similar evolutionary responses among disparate groups of animals and plants represent a remarkable case of convergent evolution. Among animals, birds are a highly suitable group to study the island syndrome; they are a comparatively data-rich taxon, are frequent island colonisers, and sometimes display extreme adaptations such as the loss of flight. However, the avian island syndrome literature is fragmented, and multiple components are rarely considered together even though many are inextricably linked. We reviewed multi-species comparative studies, single-species or population-level studies and anecdotal accounts, to summarise and assess the support for individual components of the island syndrome for birds, and to identify suites of traits that should be considered together. The weight of evidence for island syndrome patterns in morphology is substantial, but is more partial or even anecdotal for various aspects of behaviour, life history and physiology. Full validation of the island syndrome in birds will require the less-studied components to be treated in a comparative framework, and for covarying components to be examined in an integrated way. An improved description of the scope of the syndrome will pave the way to understanding its drivers.

KEYWORDS

birds, colouration, ecological naivety, flightlessness, generalism, insularity, island biogeography, island syndrome, life history, morphology

1 | INTRODUCTION

The distinctiveness of island communities and species has captivated generations of biologists (MacArthur & Wilson, 1967). In the 20th century, recurring patterns of change in behaviour, ecology and morphology were noted (Foster, 1964), with the term 'island syndrome' introduced to describe consistent size, behaviour and life-history shifts in island rodents (Adler & Levins, 1994). Components of this biological phenomenon have been

characterised for a variety of organisms, including birds (Clegg & Owens, 2002; Covas, 2012), mammals (Lomolino, 2005; Lomolino et al., 2013), lizards (Novosolov et al., 2013), insects (Leihy & Chown, 2020) and plants (Biddick et al., 2019; Burns, 2019; Nürk et al., 2019). They include changes such as species becoming larger or smaller; producing fewer offspring that take longer to mature and losing defence and escape adaptations such as flight. The taxonomic generality of some island syndrome patterns has been questioned (Itescu et al., 2014; Meiri et al., 2008), as not all

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aspects of the island syndrome are exhibited among taxa to an equal extent (Meiri et al., 2004; Orrock, 2010). Nevertheless, the evidence for the generality of the island syndrome is substantial, and the occurrence of such a widespread pattern is remarkable given differences in latitude, area, topography, isolation and other island attributes (Ali, 2017; Weigelt et al., 2013).

Such extensive convergent evolution has been attributed to the consistent ways in which island communities differ from mainland ones (Adler & Levins, 1994; Burns, 2019; Whittaker et al., 2023). In general, island communities are depauperate compared to mainland ones, with a lower number of species overall (Whittaker et al., 2017). Some functional groups, such as predators, are particularly under- or unrepresented on islands, creating a disharmonic community structure (Whittaker et al., 2023). This can lead to island populations undergoing density-compensation, with higher population densities than are observed on a similar-sized area of mainland (MacArthur et al., 1972; Wright, 1980). These differences extend from the theory of island biogeography (MacArthur & Wilson, 1967) and the dual limitations imposed by land area and geology (Valente et al., 2020; Whittaker et al., 2017), as well as island isolation (Valente et al., 2020), that interact with organismal traits such as dispersal ability and life-history characteristics. The resulting biological communities often have lower predation, lower interspecific competition, lower resource availability and increased intraspecific competition (Lomolino et al., 2012). While a change in magnitude and predominant type of biotic interactions experienced by an island organism is often given as an intuitive explanation of a pattern observed (Lomolino et al., 2012), the relative contributions of drivers are rarely evaluated in a quantitative way. Smaller and more isolated islands should have communities most distinct from continental and hence are thought to favour evolution of the island syndrome (Lomolino, 2005; Lomolino et al., 2012). Indeed, comparative studies of body size in mammals (Benítez-López et al., 2021; Lomolino et al., 2012), and in birds, reptiles and amphibians (Benítez-López et al., 2021) have shown stronger size shifts in smaller and more isolated islands. Furthermore, ecological release, immigrant selection and resistance to climate have also been shown as potential drivers (Lomolino et al., 2012), implying that both evolved differences, as well as filtering for certain traits that favour island colonisation, may contribute to such patterns.

While the original formulation of many of the components of the island syndrome was made using data from mammals (Adler & Levins, 1994; Foster, 1964), birds offer a very suitable case study for assessing widespread patterns and their underlying drivers because they are a well-studied group with a robust understanding of functional traits (Pigot et al., 2020), phylogeny (Jetz et al., 2012), ecology and distribution (del Hoyo & Allen, 2020; Wilman et al., 2014). Approximately 19% (>1900 species) of birds are endemic to islands, and many individual components of the island syndrome have been examined; including size shifts (Benítez-López et al., 2021; Clegg & Owens, 2002), aspects of life history (Beauchamp, 2021; Covas, 2012; Sandvig et al., 2019), dispersal limitations and flightlessness (Wright et al., 2016). Here we provide a review of avian

functional traits on islands from the perspective of the island syndrome. In addition to including literature known to us, we identified studies on established and potential components of the island syndrome by performing simple searches on Web of Knowledge ('island bird' [phenomenon of interest]), and by examining the reference lists of these sources. The resulting comparative and descriptive studies, both neo- and palaeontological, varied in the weight of evidence supporting the patterns, from well to partially supported, down to more anecdotal accounts. While not exhaustive, our review effectively captures four main aspects of bird biology relevant to the island syndrome: morphology (focusing on body size, bill morphology, brain size and flight apparatus), behaviour (predator naivety, ecological niche, mating systems, and tool use and cognition), signalling (vocal and visual signalling), and life history and physiology (parental investment, growth and survival and physiology). Many components of the island syndrome are inextricably linked, for example, body size and pace of life history display covariance within and between species (Sibly et al., 2012; Sibly & Brown, 2007), therefore treating each in isolation inhibits a thorough understanding of the wider phenomenon. Hence, we highlight cases where trait covariation is well-established or intuited to encourage an integrated approach to understanding this phenomenon in birds, and we recommend further steps to better understand the avian island syndrome, and to expand this understanding to other taxa.

2 | THE FUNCTIONAL SPAN OF THE ISLAND SYNDROME IN BIRDS

We discuss the evidence for the island syndrome in species traits considered separately, because most studies focus on single traits. However, many of these traits evolve in tandem, responding to the same pressures or driving change in each other (Figure 1; Table S1). The nature of covariation among traits will influence the order and magnitude of shifts and as such, the island syndrome should not be considered an 'all-or-nothing' phenomenon within or across species. Below, we summarise the existing evidence for morphological, behavioural, signalling, life history and physiological traits; with the caveat that covariation among these traits should always be considered.

3 | MORPHOLOGY

Changes in morphology in island taxa are wide-ranging. They include changes in body size, proportional bill size, brain size and limbs, along with resultant changes in flight ability. While evolution of body size is expected to also result in allometric change in multiple aspects of morphology, allometric relationships often break down in island forms with traits being exaggerated or diminished relative to body size. Body size evolution and reduction/loss of flight are perhaps the best supported general trends of the avian island syndrome, though neither is ubiquitous. Islands are also known for the evolution of

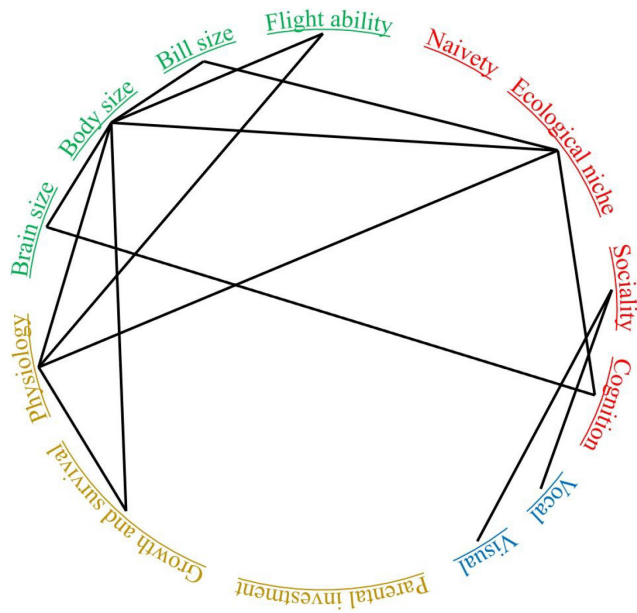


FIGURE 1 Examples of trait covariation that have been either explicitly investigated in the context of the island syndrome, or have been implied as highly likely in publications about the island syndrome. Trait covariation is depicted by black lines. Links are based on example studies cited in Table S1.

some highly specialised morphologies, rarely found in continental birds (Mayr, 2017), such as wing clubs in the extinct Rodrigues Solitaire *Pezophaps solitaria* (Hume & Steel, 2013) and Jamaican Ibis *Xenicibis xympteticus* (Longrich & Olson, 2011), hypothesised to have been used for fighting (Hume & Walters, 2017). The frequency and form of specialised morphological traits have not been comparatively assessed.

3.1 | Body size

The pattern referred to as the 'island rule', originally described in mammals (Foster, 1964) describes a tendency to evolve towards medium body size on islands; species with large continental ancestors become smaller, and vice versa (Lomolino et al., 2013). The island rule is thought to occur due to nearly the full scope of proposed explanations for the island syndrome: resource limitations, release from predation and competition, and filtering during dispersal (immigrant selection), all acting in tandem to determine the extent of change in size (Lomolino et al., 2012). While controversial as a ubiquitous pattern (Lomolino et al., 2013; Meiri et al., 2008), it is currently well-verified in land vertebrates (Benítez-López et al., 2021) and plants (Biddick et al., 2019). Body size evolution in island birds has been studied using large comparative datasets as well as species and population comparisons of continent-island pairs, and a diversity of size indices, including mass (e.g. Clegg & Owens, 2002), and indices derived from body measurements such as principal components (e.g. Bell, 2018). Multiple comparative studies have shown that birds on islands follow

the island rule, a pattern most pronounced on remote, small islands (Bell, 2018; Benítez-López et al., 2021; Boyer & Jetz, 2014; Clegg & Owens, 2002). Furthermore, a recent study of 120 island-continental bird species pairs has demonstrated that the island rule shows a stronger pattern in the absence of predators, supporting the traditional idea of the role of this biotic interaction (Ponti et al., 2023). The island rule is also apparent in comparisons of the same species occurring on both islands and continents: among subspecies [e.g. Varied Tit *Poecile varius* (Fujita et al., 2014), Emu *Dromaius novaehollandiae* (Heupink et al., 2011), Silvereye *Zosterops lateralis* (Estandía et al., 2023)]; and among populations [e.g. Coal Tit *Periparus ater* (Norberg & Lindhe Norberg, 2015), Grey Jay *Perisoreus canadensis* (Strickland & Norris, 2015)], even those recently introduced to islands [e.g. Great Kiskadee *Pitangus sulphuratus* (Mathys & Lockwood, 2009)]. Some exceptions occur, for example, White-fronted Chat *Epthianura albifrons* populations not changing in size as expected (Major, 2012). However, the generality of the island rule in birds is robustly supported among hundreds of species (see Benítez-López et al., 2021).

In addition to a general tendency to evolve medium body size on islands, there is also the more frequent occurrence of 'giants' or 'dwarfs' (defined as large scale deviations from size of most congeners) on islands than on continents (Meiri et al., 2011). Neither phylogeny or ecology appears to account for the evolution of insular giants and dwarfs; both are scattered throughout the avian phylogeny, and they represent a wide variety of forms with respect to the original ecological niche. Island giants have experienced high extinction rates, likely due to their extreme specialisation (Fromm & Meiri, 2021), including flightlessness (Sayol et al., 2020), and are well known from fossils and subfossils. Island dwarfs may once have been more common, and experienced similar extinctions, but as small fossils are less likely to survive, there may be a taphonomic bias in the record of size distributions of extinct island birds. Additionally, there may be a publication bias towards charismatic island giants. Alternatively, because birds are overall quite small in size relative to other vertebrates (Pigot et al., 2020) there may be more scope for gigantism given a particular starting point. Many of the largest known members of bird families, or higher taxonomic levels, are island endemics (e.g. Dodo *Raphus cucullatus* among Columbidae, South Island Takahē *Porphyrio hochstetteri* among Rallidae, Hercules Parrot *Heracles inexpectatus* among parrots [Worthy et al., 2019]). The hummingbirds (Trochilidae), which account for much of the lower end of mass distribution of birds (Tobias et al., 2022), only have 19 out of 353 species as island endemics (including the smallest known bird, the Bee Hummingbird *Mellisuga helenae*). Outside of hummingbirds, the four smallest bird species (the Pygmy Bushtit *Aegithalos exilis*, Handsome Sunbird *Aethopyga bella*, Lovely Sunbird *Aethopyga shelleyi*, and the Flamecrest *Regulus goodfellowi*) are all island endemics. However, island dwarfism has received limited attention in birds (but see Meiri et al., 2011), and evolution of avian size extremes would merit a more comparative approach, as has been recently done in plants (Burns, 2022).

3.2 | Bill size and shape

Changes in overall body size might be accompanied by concomitant changes in other traits due to allometric scaling, but there may also be changes in relative proportions as allometric relationships are decoupled. Bills have received significant attention due to their role in adaptation to feeding niches, signalling and thermoregulation (Friedman et al., 2019; Pigot et al., 2020), with early studies describing non-allometrically longer, wider and deeper bills in insular birds versus their continental counterparts (Grant, 1965). However, the inclusion of species with a greater range of starting sizes revealed that bills follow island rule-like patterns with changes in feeding being a potential driver (Clegg & Owens, 2002) (see 'Behaviour: Ecological release' and 'Tool use and cognition' sections below). Multiple studies have noted that passerines on islands have longer or larger (deeper and wider) billed forms such as reed warblers *Acrocephalus* (Bell, 2018; Leisler & Winkler, 2015); white-eyes *Zosterops* (Clegg et al., 2007; Dutson, 2008); Hawaiian honeycreepers (Fringillidae) (Lovette et al., 2002); New Holland Honeyeaters *Phylidonyris novaehollandiae* (Myers et al., 2010); Great Kiskadees *Pitangus sulphuratus* (Mathys & Lockwood, 2009); Song Sparrows *Melospiza melodia* (Greenberg & Danner, 2013); Yellow Warblers *Setophaga petechia* (Luther & Greenberg, 2014); Dark-eyed Juncos *Junco hyemalis* (Aleixandre et al., 2013); Eurasian Jays *Garrulus glandarius* (Aoki et al., 2021); towhees *Pipilo* (Olson & Wingate, 2012) and Gulf of Guinea thrushes *Turdus* (Melo et al., 2010). Smaller bills in island passerines, despite increased body size, have also been noted, for example, in Superb Fairywren *Malurus cyaneus* (Dudaniec et al., 2011). Among other bird families, a tendency for longer bills has been found in pigeons (Andrade et al., 2021; Heathcote et al., 2021), oystercatchers (Collar et al., 2021) and herons (Kushlan, 2009), but not in some moorhen subspecies (DesRochers et al., 2010). In addition to size changes, cases of highly modified bills evolving in insular contexts include the Dodo *Raphus cucullatus* and the Rodrigues Solitaire *Pezophaps solitaria* (Mayr, 2017), adzebills (Mayr, 2017; Worthy et al., 2011), Hawaiian honeycreepers (Navalón et al., 2020) and vangas (Jønsson et al., 2012). While examples focusing on individual populations/subspecies, and sometimes bird families, are common, island bird bill size and shape trends could be revisited with a comparative approach, especially in the light of novel availability of trait data for all bird species (Tobias et al., 2022).

3.3 | Brain size

Island birds have relatively larger brains than continental relatives, providing another example of a deviation in allometric relationships (Sayol et al., 2018). The pattern found from examining 1931 species of birds from across the avian phylogeny represented in situ evolution on islands, as island-colonisers were not more likely

to originate from large-brained groups. In this study, brain size was correlated with increased behavioural flexibility and slower pace of life, highlighting covariation between island syndrome traits (Sayol et al., 2018). In other studies, brain size has been linked to many phenotypes common in island endemics, including flightlessness (Nakao et al., 2022), being resident (Sol et al., 2010) and higher territoriality (Hardie & Cooney, 2023). Local modifications of brain structure are also described for island birds, though their taxonomic extent may be more limited. These include modifications of the olfactory bulbs and optic lobes in the elephant birds of Madagascar (Aepyornithiformes) (Torres & Clarke, 2018), the kiwis (Apterygidae) (Witmer et al., 2017) and Rodrigues Owls *Otus murivorus* (Duhamel et al., 2020) and expansions of somato-sensory systems as in the Mole Duck *Talpanas lippa* (Iwaniuk et al., 2009; Witmer et al., 2017). These result in olfaction and tactile sense-driven sensorics, as opposed to vision as is more common in birds (Martin et al., 2007). Therefore, evolution of the proportionally larger brain size as part of the island syndrome appears well supported, however focusing on finer details of evolution of brain anatomy could reveal further patterns associated with sensory systems.

3.4 | Flightlessness and reduced flight ability

Flightlessness, defined as complete or near-complete loss of flight, evolved up to 150 independent times across the bird phylogeny (Sayol et al., 2020) and is predominantly an island phenomenon, with 468 of 581 known flightless species occurring on islands. Loss of flying ability is closely linked to variation in body size, as flightlessness tends to evolve in tandem with increased body size, and breaking of allometric scaling with evolution of shorter wings relative to body size (Livezey, 2003). Some bird clades have a particular proclivity to evolve flightless species, and these tend to be island endemics (Sayol et al., 2020). These include gruiforms (cranes and rails, especially Rallidae rails) (Boast et al., 2019; Garcia-R et al., 2014; Livezey, 2003; Oswald et al., 2021) and anseriforms (Iwaniuk et al., 2009; Williams, 2015; Witmer et al., 2017). Even passerine birds (Passeriformes) have flightless representation, especially New Zealand wrens Acanthisittidae, but also buntings Emberizidae (Millener, 1988; Rando et al., 1999, 2010). Biological traits that might predispose a taxon to evolve flightlessness on islands remain uncertain, though ideas include having shorter wings than expected for body size (McCall et al., 1998) and exhibiting simultaneous moult (Terrill, 2020).

Island-dwelling birds may not experience drastic loss of flying ability, but rather a general shift in the proportions of wings, legs and pectoral muscles, resulting in greater hindlimb over forelimb investment, reduced flight ability and hence reduced dispersal capacity (Wright et al., 2016). Examples include Eurasian Blackcaps (*Sylvia atricapilla*) and Common Snipe (*Gallinago gallinago*) in the Azores (Andrade et al., 2015; Rodrigues et al., 2018); Grey Jays (*Perisoreus canadensis*) on Anticosti Island (Strickland &

Norris, 2015) Guadalupe Junco (*Junco hyemalis insularis*) (Alexandre et al., 2013) and São Tomé Short-Tail (*Motacilla bocagii*) (Alström et al., 2015). These changes occur even in clades with no flightless members, such as kingfishers or tanagers (Wright et al., 2016). Therefore, loss of flight ability seems to be strongly supported across multiple comparative studies, but may be underestimated due to frequent lack of incorporation of palaeobiological data. The gradient of changes in flight ability may evolve in the face of the same drivers—as predation becomes less likely, the maintenance of expensive flight apparatus may be too costly. As there is evidence of a tendency to have slower metabolism in island birds (see the 'Life history and physiology: Physiology' section), both complete and partial weakening of flying ability may be an energy-saving strategy, with the outcome dependent on other aspects of species' biology, such as body size change, moult and diet.

A large comparative study revealed that the wing aspect ratio, as measured by hand-wing index (HWI), is higher in island species (Sheard et al., 2020). HWI is interpreted to represent flight capacity, therefore this result is contrary to what is known from behavioural and other morphological studies. A degree of flightlessness can even occur without morphological change, due to the phenomenon of behavioural flightlessness (Diamond, 1981), where a bird is reluctant to fly, either completely or over longer geographical distances. This results in loss of dispersal and migratory propensity and has been suggested as a precursor to morphological flightlessness (Diamond, 1981). Loss of distant dispersal and migration ability may be extreme on islands, as exemplified by the non-migratory Polynesian Sandpipers *Prosobonia* (De Pietri et al., 2020), which belong to the highly migratory family Scolopacidae. However, losses of migratory behaviour or other examples of behavioural flightlessness have not been quantified beyond these anecdotes in island species, and would merit further natural history study to generate comparative data.

4 | BEHAVIOUR

In comparison to morphology, behaviour has received less attention in terms of the island syndrome. While island species have frequently been included in bird behaviour studies, a more comparative approach has rarely been used other than for sociality and reproductive behaviours. Colonising and establishing on an island can be a significant challenge for birds, likely requiring behavioural flexibility and novel ways to exploit resources (Gavriilidi et al., 2022). A range of behavioural traits may be exploited to meet these challenges, and altered landscapes of biotic interactions may cause rapid behavioural responses (Gavriilidi et al., 2022; Tebbich et al., 2010). In birds, behavioural traits covary with each other (e.g. dispersal and aggressive behaviour, other aspects of biology, including body size, brain size, bill size and pace of life (see Table S1 and references therein).

4.1 | Predator naivety

Tameness and predator naivety are often associated with island species, and attributed to the absence or reduction in the predator threat (Hume & Walters, 2017) because maintaining anti-predator responses is energetically expensive (Cooper & Blumstein, 2015). However, empirical studies are few, with the common perception of 'naïve' island endemics mostly stemming from older travel accounts (Hume & Walters, 2017). Some evidence that island birds change their behaviour comes from studies of flight initiation distance (FID), the distance at which a bird can be approached before it flies away, frequently used as a proxy of fear (Blumstein, 2003). However, the evidence is mixed. In the Small Ground Finch (*Geospiza fuliginosa*) of the Galapagos Islands, FID is much lower in pristine habitats as opposed to those with invasive predators (Gotanda, 2020). In the Bull-headed Shrike (*Lanius bucephalus*) that established breeding populations on the Ryukyu islands in 2012, higher FID occurs on islands (Hamao et al., 2020). However, quantitative comparative studies of flight initiation distance or other measures of naivety are lacking in island birds (but see Cooper et al., 2014 for one such study in lizards). In the absence of such studies at this point, extinctions on islands may serve as a proxy of whether predator naivety was common or not (Berger et al., 2001). Bird extinctions are positively correlated with numbers of introduced predators to islands (Blackburn et al., 2004). At least 22 avian extinctions on islands can be directly attributed to novel predators (Medina et al., 2011), and other negative impacts are particularly common with threats unique on islands such as generalist ground mammals (e.g. rats) (Harper & Bunbury, 2015). Therefore, it can be assumed that predator naivety may be a common aspect of the island syndrome in birds, but confirmation requires comparative data, keeping in mind that species displaying extreme naivety are more likely to have suffered anthropogenically driven extinctions.

4.2 | Ecological release

The term ecological release encompasses both niche widening and niche shifts that occur when biotic constraints such as interspecific competition are removed (Herrmann et al., 2021). Island birds undergo ecological release in that they tend to have wider ecological niches than mainland counterparts (Diamond, 1970; Scott et al., 2003). Wider niche availability is afforded by having fewer interspecific competitors and lower risk of predation. A wider population-level niche can be achieved by all individuals having a broad niche, or each individual having a narrower but different niche (Bolnick et al., 2003). Few studies have examined how niche expansion is achieved at the individual level, but generalist populations consisting of individual specialists have been reported for several island bird populations (Price, 1987; Scott et al., 2003; Werner & Sherry, 1987). The distinction is important in the context of the island syndrome because feeding ecology may influence multiple morphological components including body and bill size (Clegg &

Owens, 2002), as well as brain size (Hardie & Cooney, 2023). Niche shift patterns are also known from numerous observational studies (Alström et al., 2015; Diamond, 1970). Niche width and niche shift patterns on islands have not been investigated in a large comparative or phylogenetic framework. Because of the relative ease and long history of collecting bird feeding observations and habitat associations, it is likely that a treasure-trove of quantitative data could be extracted from dispersed sources (e.g. from classic texts Lack & Gillmor, 1971; Mayr et al., 2001 and older papers, Diamond & Marshall, 1977). However, the manner in which individual variation influences the nuances of niche expansion on islands requires further data collection from a range of species to determine generalities.

4.3 | Mating systems and sociality

Changes in mating systems and the breeding biology of island birds manifest in a number of ways, and comparative studies have demonstrated clear differences between island and continental species. Lower levels of extra-pair paternity in island passerines were previously reported (Griffith, 2000) and some of the lowest levels of extra-pair paternity in birds are found in the island-rich Madagascar and Oceania zoogeographical realms (Valcu et al., 2021). However the accumulation of studies showing that some island species have similar or higher rates of extra-pair paternity than nearest mainland relatives suggests that the comparative pattern should be revisited [see for example: African Blue Tits (*Cyanistes teneriffae*) (Garcia-Del-Rey et al., 2012), Eurasian Blue Tits (*Cyanistes caeruleus*) (Charman-tier & Blondel, 2003), Hihi (*Notiomystis cincta*) (Brekke et al., 2011), Seychelles Warblers (*Acrocephalus sechellensis*) and Chatham Islands Black Robins (*Petroica traversi*) (Forsdick et al., 2021)].

Co-operative breeding occurs more frequently on islands (Covas, 2012). In a sample of 237 species pairs, 17.3% of island species bred cooperatively compared to 9% on continents, and additionally they were more frequently found to be living in family groups (19% on islands compared to 14.8% on mainlands) (Covas et al., 2022). Exceptions occur, for example, in insular White-Winged Fairy-Wrens (*Malurus leucopterus*), where populations are socially monogamous rather than co-operative breeders as seen on the mainland (Rathburn & Montgomerie, 2003). Social monogamy is generally common among birds (Lack, 1968), and examples of well-characterised socially monogamous breeding systems on islands also show genetic monogamy like in the Capricorn Silvereye (*Zosterops lateralis chlorocephalus*) (Robertson et al., 2001), New Zealand Saddlebacks (*Philesturnus carunculatus*) and New Zealand Robins (*Petroica australis*) (Taylor et al., 2008). The occurrence of bi-parental care between island and continental species is similar (Covas, 2012). While these conclusions are largely based on comparative analyses, they rely on just two papers, and therefore investigation into differences between island and continental bird species sociality and mating systems should be continued and expanded. Suggested selective drivers for an increase in the occurrence of co-operative breeding on islands include a combination of restricted resources, high-density

populations; and higher survival of island birds (Covas, 2016) (and see 'Life History and Physiology' section below), however these ideas require investigation.

4.4 | Tool use and cognition

Due to increased brain size, birds on islands may display more innovative and flexible behaviours (Sayol et al., 2018). Tool use in the wild appears more common in island bird species (Gavrillidi et al., 2022) except for nest construction and prey-dropping (Switzer & Cristol, 1999). There are multiple examples of foraging-based tool use in island birds. The Woodpecker Finch (*Camarhynchus pallidus*) uses cactus needles to pry insects out of wood (Tebich et al., 2002). The Hawaiian Crow (*Corvus hawaiiensis*) and the New Caledonian Crow (*Corvus moneduloides*) fashion elaborate tools for the same purpose (Hunt & Gray, 2004; Rutz et al., 2016). In parrots, Goffin Cockatoos (*Cacatua goffini*) of the Tanimbar Archipelago (Auersperg et al., 2012), and the New Zealand Kea (*Nestor notabilis*) (Goodman et al., 2018) show a range of innovative tool uses. Additionally, the New Zealand Kākā (*Nestor meridionalis*) has been recently observed to engage in potential anti-predatory tool use by throwing wood on a falcon (Burns, 2021). Overall, the topic of cognition in island birds remains relatively unexplored and requires further natural history observation (Gavrillidi et al., 2022), but new reports on tool use are appearing frequently, for example, Fayet et al., 2020 which may allow comparative analyses in the future.

5 | SIGNALLING

We consider two aspects of signalling, songs (and calls) and colouration, in relation to the island syndrome. We have separated signalling from behaviour despite partial overlap. Signalling will be very closely linked to other behavioural traits that may impact how signals are generated, along with morphology and physiology that determine the size, shape, form and quality of signals (Hamilton & Zuk, 1982). Both song and colouration of island forms have been investigated with comparative approaches. Studies have ranged from tens or hundreds of comparisons, and examination of different facets of these complex traits, and consistent patterns have not always emerged.

5.1 | Vocal communication

Bird song is a highly conspicuous, well-studied and important signal used by birds in interacting with other individuals, including in terms of sexual and territory advertisement (Catchpole et al., 2008). Song can diverge following island colonisation as a result of population bottlenecks during founding, cultural drift, acoustic adaptation to new environments and/or changed sexual selection regimes (Potvin & Clegg, 2015). Furthermore, changes in body size alter the qualities of songs as larger species tend to produce lower frequency

songs (Mikula et al., 2021), while changes in mating systems and loss of migratory behaviour may also cause song divergence (Read & Weary, 1992). Morinay et al. (2013) found in a study of 49 species pairs that song on islands are less likely to include potentially aggressive elements, such as rattles and buzzes, but did not significantly differ in complexity metrics, such as syllable diversity. A comparison of 11 species pairs from mainland Africa with species on São Tomé and Madeira found no significant differences in syllable diversity, delivery rate or song duration (Robert et al., 2022). Reudink et al. (2021) examined species pairs for 731 species of Meliphagidae (honeyeaters), Fringillidae (finches) and Monarchidae (monarch flycatchers), and reported no significant differences in aspects of song complexity or performance, though birds inhabiting smaller islands tended to have fewer syllables in their songs. In the Eurasian Chaffinch (*Fringilla coelebs*) there is progressive loss of song structure from continental Africa to more remote islands in Macaronesia (Lachlan et al., 2013). Song complexity in island populations or subspecies changes in variable ways. For example, it decreases in Red-Capped Robins (*Petroica goodenovii*) and Singing Honeyeater (*Gavialis virescens*) on Rottneest Island, Australia (Baker et al., 2006), in the Japanese Bush Warbler (*Horornis diphone*) on Ogasawara Islands (Hamao & Ueda, 2000) and in the Zebra Finch (*Taeniopygia guttata*) on Timor (Lansverk et al., 2019), but increases in complexity in the Western Gerygone (*Gerygone fusca*) on Rottneest Island (Baker et al., 2006) and in the Guadalupe Junco (*Junco hyemalis insularis*) (Alexandre et al., 2013). Time since colonisation has been shown to affect patterns of song diversity as the influence of different drivers change (Potvin & Clegg, 2015). Initial changes to song may be largely due to population bottlenecks associated with island colonisation, but syllable innovation and acoustic adaptation to island environments may proceed with time. This may partially explain why the results of both large-scale comparative studies and single-case studies have reported variable results. While there is a considerable body of comparative work on song, clearly further investigation is needed to ascertain the direction of changes. As bird song and calls are now readily available for nearly all bird species on databases such as xeno-canto, studies encompassing the full suite of bird diversity could search for the most consistent pattern of vocal evolution in island birds. Studies below the species level likely require the collection of more recordings to quantify population variability.

5.2 | Colouration

Colouration is a complex trait, that can be used actively and passively in signalling, and be moderated by both morphology and behaviour. In the island syndrome literature, there has been a long-held notion that birds on islands are less colourful—and this is supported by recent large-scale comparative studies. Doutrelant et al. (2016) found that birds on islands tend to be less bright and colourful, and males also have a significantly decreased number of colour patches, related to lower number of same-family sympatric species. Particular examples include reduced brightness in island male wildfowl

(Figuerola & Green, 2000), increased dullness of island species in Western Palearctic birds (Fitzpatrick, 1998), increased uniformity of male colour of *Terpsiphone* flycatchers on islands (Fabre et al., 2012), and decreased male colouration (but increased female colouration) in Pacific Robins (*Petroica* sp.) (Kearns et al., 2020). While the pattern generally holds, there are some cases where particularly colourful groups occur in insular settings, such as birds of paradise (Paradisaeidae), predominantly occurring in New Guinea, with some species also found in Australia. Recent studies have shown that fewer predators occurring on islands are correlated with evolution of more colourful plumage in a sample of 110 species pairs (Bliard et al., 2020). In birds of paradise specifically, aspects of mating systems, and the unique displays of these birds, affect the degree of sexual dichromatism and colouration as well (Miles & Fuxjager, 2018). However, the ways in which the evolutionary trend to increase in colour with fewer predators interacts with the general tendency towards duller plumage, potentially promoted by relaxed species recognition requirements in lower diversity communities (Doutrelant et al., 2016), is currently unclear. Because evolution of colouration will be affected by an interplay of sexual selection, the need for separation from other species, and interaction with predators, it would particularly benefit from investigation of further drivers, some of which may currently be unknown.

Melanism (darker colouration) patterns are known to systematically vary in some groups. A tendency for repeated evolution of melanism on islands has been observed, for example, in *Monarcha* flycatchers (Uy & Vargas-Castro, 2015). Some well-known melanistic forms occur exclusively on islands, including melanistic Tahiti Reed-Warblers (*Acrocephalus caffer*) (Cibois et al., 2012), Canarian Oystercatcher (*Haematopus meadewaldoi*) (Collar et al., 2021) (but note that within *Haematopus* there are multiple continental and island species in the Southern Hemisphere, so biogeographic origin may matter), or the 'Veiled' Eurasian Blackcap (*Sylvia atricapilla*) morph of Macaronesia (Berthold et al., 1997). In contrast, within the Barn Owl complex (39 taxa of *Tyto alba* ssp. or *Tyto* sp.) island owls tend to be lighter with less eumelanistic (dark) colouration, and more pheomelanistic colours (brown and rufous) than continental forms (however as islands become smaller birds become darker than on larger islands) (Romano et al., 2021; Roulin & Salamin, 2010). The possibility of increased melanism as an island syndrome component warrants a wider comparative approach, as current examples are too few and phylogenetically disparate.

6 | LIFE HISTORY AND PHYSIOLOGY

Changed selective pressures on islands will significantly affect life history, and concurrently physiology. Firstly, as the environment is expected to favour competitive individuals, slower pace of life focusing on quality, not quantity, is likely to evolve. Secondly, changes across morphology and behaviour are also likely to be intertwined with a shift towards slower life histories. Slower pace of life generally translates into smaller clutches of larger-sized offspring, longer

developmental periods, increased survival and higher longevity (Stearns, 1992). Despite the popularity of birds as models with which to study life history, relatively little of it has been studied in an island context. Only some aspects of avian life histories and physiology have been examined comparatively, often with relatively small species sample sizes.

6.1 | Investment in offspring

Comparative studies reveal that island birds generally have smaller clutch sizes after accounting for latitudinal effects (Covas, 2012; Jetz et al., 2008). Specific examples include community-wide decreases in clutch size in Sri Lankan passerines relative to other regions of the Indian subcontinent (Padmanabhan & Yom-Tov, 2000), and island populations of Japanese Bush Warblers (*Horornis diphone*) (Hamao & Hayama, 2015), rails (Rallidae) (McNab & Ellis, 2006), Southern House Wren (*Troglodytes aedon chilensis*) (Ippi et al., 2012), Eurasian Blue Tits (*Cyanistes caeruleus*) (Blondel et al., 1992), African Blue Tits (*Cyanistes teneriffae*) and Ma'oma'o (*Gymnomyza samoensis*) (Stirnemann et al., 2016). Exceptions occur such as the Eastern Bluebirds (*Sialis sialis*) of Bermuda, which show comparable clutch size to mainland populations (Matson et al., 2014). Smaller clutch sizes are associated with increased egg size in birds (Blackburn, 1991), resulting in more parental investment per offspring. Specific studies of egg size in island forms show variable support for the expectation of larger eggs in island birds. In the extinct Emu subspecies (*Dromaius novaehollandiae* ssp.) egg sizes of the smaller-sized island subspecies were within the range of the continental Emu (Hume & Robertson, 2021), hence egg size is increased relative to body mass. However, a study of birds introduced to New Zealand found that, for those species where egg size changed, smaller eggs were produced (Congdon & Briskie, 2010). While island clutch size patterns are generally well established, a broader taxonomic perspective would help to identify exceptions and mechanisms. The subsequent expectation of larger egg sizes associated with smaller clutches remains to be tested in a comparative framework.

6.2 | Growth, development and survival

Other stages of life history show consistent patterns of slow-down in island birds. Slower developmental periods in island birds are evidenced by longer incubation times [36 species pairs (Covas, 2012)], and a tendency for slower growth rates [264 altricial bird species, including 33 island growth rates (Sandvig et al., 2019)]. Longer brood-rearing time is known from single-species cases, for example, 59–63 days in Hawaiian Hawks (*Buteo solitarius*) compared to average of 43 days for temperate congeners (Griffin et al., 1998). Annual survival for both juvenile and adult life stages is higher in island birds [adult survival rates from 697 species including 154 island species (Beauchamp, 2021); juvenile

survival rates from 342 species including 51 island species (Beauchamp, 2022)]. Wasser and Sherman found that longevity of island species is almost twice that of continental counterparts [longevity data on 470 species including 76 island species (Wasser & Sherman, 2010)]. In many of these studies, the proportion of island species was relatively low, reflecting the lack of life history studies in island populations. Thus, increased survival as part of the island syndrome is considerably well supported across a diversity of species. However, the pace of growth needs more examination, as while the patterns are tentatively promising, they are based on too few species to be certain of generality.

6.3 | Physiology—metabolism and immune function

Multiple examples of slower metabolic rates are known for both flightless and volant island birds, likely related to an increase in size and the slowing down of life histories. A shift to flightlessness allows energy conservation achieved via lower flight muscle mass and basal metabolic rate, and therefore strongly links with slower overall metabolism, as seen in kiwis (*Apterus* sp.) (McNab, 1994), Kakapos (*Strigops habroptilus*) (McNab & Salisbury, 1995), flightless rails Rallidae (McNab & Ellis, 2006) and flightless ducks Anatidae (McNab, 2003). Examples of volant island birds with very low metabolic rates compared to continental relatives include flighted Anatidae of New Zealand (McNab, 2003) and pigeons Columbidae of the South Pacific (McNab, 2000). Exceptions have been noted, such as the honeyeater Tūi (*Prothemadera novaeseelandiae*) endemic to New Zealand, that has a similar basal metabolic rate relative to other honeyeaters Meliphagidae of the Australian mainland (McNab, 2016). Another dimension of lower rates of metabolism on islands may stem from nutritional stress, as has been shown for Red-billed Choughs (*Pyrrhocorax pyrrhocorax*), where Canary Islands populations show clear signs of nutritional stress attributed to low insect abundance, and a subsequent shift to fruit-eating (Blanco et al., 2014). As interpretations about metabolic rate changes on islands stem from mostly species-specific papers, with a comparative perspective only for New Zealand taxa, further empirical work is needed.

Isolated islands and archipelagos can provide an evolutionary refuge from parasites and disease. The maintenance of immune function is costly (Hanssen et al., 2005; Martin et al., 2003), and a loss of immune function and high susceptibility to disease have been observed in some of the most isolated island avian communities, such as in the Galapagos (Wikelski et al., 2004), or among Hawaiian honeycreepers Mohoidae (LaPointe et al., 2012) where historical introductions of diseases have had devastating consequences. In less isolated situations, reduced parasite loads are sometimes (Loiseau et al., 2017), but not always (Ishtiaq et al., 2010) observed. Following from this, patterns of immune function shifts are varied. Barthe et al. (2022) showed that among immunity-related genes in 34 species of birds including 20 island cases, only major histocompatibility complex II showed evidence

of relaxed selection, while major histocompatibility complex I, toll-like receptors and beta-defensins showed no such signals. Similarly, immune indices measured from 25 species, encompassing continental and island populations in the Nearctic, showed no obvious attenuation in island populations, and even increases in some (Matson, 2006). Finally, across 21 species comparisons of populations on the islands of São Tomé and Príncipe versus continental West Africa, the island populations had lower immunoglobulin levels, but no significant change in haptoglobins (Lobato et al., 2017). Immune function is a complex trait and can change along various axes (Matson, 2006). Information from many more island species would help to reveal if there are general or specific changes in immune capabilities of island birds.

7 | CONCLUSION

The aim of this review was to draw together disparate empirical and anecdotal evidence regarding the evolution of avian traits on islands. We have collated a large number of examples that highlight patterns consistent with the current understanding of the island syndrome, exceptions to these patterns, and components that with more data, might form part of the island syndrome. With this framework, shortfalls in the scope of traits studied are apparent. Only body size has received a somewhat comprehensive treatment, where significant proportions of avian diversity have been compared for differences between island and continental taxa. Comparative treatments have been applied to other aspects of morphology, mating systems and sociality, song, reproduction, growth strategies and immunological differences, but all of these considered a limited number of taxa. Few studies examine more than 100 species on islands, which corresponds to less than 5% of island avian diversity, and not all treat the data in a phylogenetic or paired comparison framework (but see Benítez-López et al., 2021; Clegg & Owens, 2002; Covas, 2012; Sayol et al., 2018; Wright et al., 2016). A much larger proportion of bird diversity will need to be examined to ascertain the generality of the patterns observed in smaller comparative studies. In some traits, such as occurrence of unique morphological structures, predator naivety, widened use of ecological resources, tool use, colouration, egg size or physiology, the evidence for an island syndrome mostly relies at single-family or lower taxonomic level studies, and broader generality requires further empirical data and comparative treatment. Additionally, the island syndrome literature generally neglects marine birds such as shearwaters and petrels, because their lifestyle connects them to the open seas. However, they are very frequently island breeders, and the pressures on these parts of their life history likely have some parallels with terrestrial island birds, for example, behavioural naivety to nest predators, and components of life history variation. Therefore, they warrant inclusion in studies of the island syndrome.

A more comprehensive characterisation of patterns in individual traits should also consider covariation among traits, which will

ultimately shed light on the drivers of the island syndrome. Relatively few studies of the island syndrome have focused on how traits evolve in concert, as traits are frequently studied separately. We have highlighted likely links among traits and suggested drivers for the components of the island syndrome that could be investigated further. While we have a general appreciation for the suite of drivers underlying the island syndrome (Lomolino et al., 2012), the relative importance of changed biotic interactions requires quantification from multiple systems. Furthermore, the role of immigrant selection at colonisation needs further attention. The direction of shifts in some traits appears broadly supported, but traditional ideas for particular traits have been challenged or are only weakly or inconclusively supported by the available data. Hence, the way that drivers interact could be more idiosyncratic than previously appreciated.

The amount of information available on birds continues to grow and be collated [e.g. avian functional variation has been characterised (Pigot et al., 2020; Tobias et al., 2022)], while other aspects of biology such as behaviour, diet, and life histories have been painstakingly collected by professionals and citizen scientists alike, for example, in *Birds of the World* (Billerman et al., 2020). Distributions of birds are mapped in unparalleled detail (BirdLife International and Handbook of the Birds of the World, 2020; del Hoyo & Allen, 2020), and phylogenetic and genomic data are increasingly available (Feng et al., 2020; Jetz et al., 2012). With these tools, more detailed phylogenetically controlled studies can be performed that will fill in the gaps in avian island syndrome research. However, it is paramount that palaeobiological data are included, where trait types allow it. Many of the examples we have collated refer to extinct taxa. With regards to IUCN-classified species, about 8% of all endemic species of island birds are now extinct (Matthews et al., 2022). However, island extinctions have been occurring well before timescales considered by the IUCN (1500 CE) (Hume & Walters, 2017; Steadman, 2006), and 22% of all species known to have lived in the past 125,000 years are extinct (Matthews et al., 2022). In addition, it is likely that there are many unknown anthropogenic bird extinctions. For example, estimates suggest that in the Pacific islands alone, 731–1332 species of non-passerine birds have gone extinct during the time of human habitation (Duncan et al., 2013). The Pacific Ocean is particularly island-rich, but if these numbers reflect potential scales of extinction elsewhere, then possibly nearly half of the endemic island birds that co-occurred with humans may have gone extinct. These extinctions are problematic for the further study into the island syndrome, as they cause loss of data that will result in statistical biases. Already, it has been shown that not including extinct species would underestimate the rate of evolution of flightless birds, the majority of which are island endemics, four-fold (Sayol et al., 2020). This issue will be significant for other traits, including size, as the largest bird species on islands are the most likely to be extinct (Fromm & Meiri, 2021). In mammals, both larger size, and having undergone the largest island rule-related shifts, predispose species to extinction (Rozzi et al., 2023). Furthermore,

traits that do not fossilise—such as behaviour or many elements of life history, may be forever beyond the reach of scientific study. Therefore, the investigation into the island syndrome is urgent, and island birds provide a rich seam of information to more fully characterise this widespread phenomenon, and ultimately to understand its drivers in birds and other species.

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AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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SUPPORTING INFORMATION

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

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