Predictable evolution toward flightlessness in volant island birds

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Birds are prolific colonists of islands, where they readily evolve distinct forms. Identifying predictable, directional patterns of evolutionary change in island birds, however, has proved challenging. The "island rule" predicts that island species evolve toward intermediate sizes, but its general applicability to birds is questionable. However, convergent evolution has clearly occurred in the island bird lineages that have undergone transitions to secondary flightlessness, a process involving drastic reduction of the flight muscles and enlargement of the hindlimbs. Here, we investigated whether volant island bird populations tend to change shape in a way that converges subtly on the flightless form. We found that island bird species have evolved smaller flight muscles than their continental relatives. Furthermore, in 366 populations of Caribbean and Pacific birds, smaller flight muscles and longer legs evolved in response to increasing insularity and, strikingly, the scarcity of avian and mammalian predators. On smaller islands with fewer predators, birds exhibited shifts in investment from forelimbs to hindlimbs that were qualitatively similar to anatomical rearrangements observed in flightless birds. These findings suggest that island bird populations tend to evolve on a trajectory toward flightlessness, even if most remain volant. This pattern was consistent across nine families and four orders that vary in lifestyle, foraging behavior, flight style, and body size. These predictable shifts in avian morphology may reduce the physical capacity for escape via flight and diminish the potential for small-island taxa to diversify via dispersal.

birds | islands | morphology | flight | island rule

Birds on islands helped to inspire the theory of evolution by natural selection (1, 2), and they continue to illuminate its mechanisms (e.g., ref. 3). Some studies have reported that the bodies and bills of island birds systematically shift in size, reflecting evolution toward a generalist niche in species-poor communities (4–8). The tendency for island taxa to converge toward intermediate body size after colonizing islands is known as the island rule (4), but this ecogeographic rule has proven to be an inconsistent predictor of evolutionary trends in island bird populations (9–12). Detailed studies of island radiations have revealed idiosyncratic patterns of body size and bill size evolution among species, with morphological changes attributable to taxon-specific changes in foraging ecology (e.g., ref. 12). This inconsistency raises the question as to whether there are predictable evolutionary trends that apply generally to island birds.

The most striking evolutionary trend among island birds is the loss of flight. Transitions to flightlessness are rapid and irreversible (13, 14), with each instance involving the substantial reallocation of mass from the forelimbs to the hindlimbs and near elimination of costly flight muscles (15–18). More than 1,000 independent lineages of island birds have lost flight, including rails, parrots, pigeons, owls, waterfowl, and passerines (13–16). Although widespread, the evolution of island flightlessness requires extreme scarcity of predators and the ability to forage without flight (18–20). Thus, tens of thousands of island bird populations have remained volant, and many bird families that are prolific island colonists contain no flightless species (e.g., kingfishers, hummingbirds, whistlers, and white-eyes).

The dichotomous shift from flight to flightlessness may be subject to a tipping point associated with ecological release from predators (18). Alternatively, flightlessness may represent an extreme state of a continuum of morphological variation that reflects locomotory requirements for survival and reproduction. Across a continuum of insularity, from continents to small islands, biotic communities exhibit gradients of species diversity (21) and corresponding ecological pressures (22). If flightlessness is illustrative of island bird evolution in general, reductions in predation pressure associated with increased insularity should trigger incremental shifts in energy allocation from the forelimbs to the hindlimbs. Accordingly, we hypothesize that volant island birds, even those unlikely to become flightless, reduce their investment in the flight apparatus. The amount of morphological change should be proportional to the degree of insularity, with more insular populations exhibiting greater reduction in flight morphology. Consistent with this hypothesis, our previous work showed that five species of birds evolved smaller flight muscles and longer legs on the small island of Tobago (23). In this study, we tested whether island size, landbird species richness, raptor species richness, and the presence of mammalian predators could predict shifts in the relative investment in forelimbs versus hindlimbs in 366 bird populations from 80 islands across the Pacific and Caribbean.

Results

To test the hypothesis that island species had evolved smaller flight muscles than their continental relatives, we weighed the two main flight muscles, the *pectoralis major* and the *supracoracoideus*, from more than 8,000 bird carcasses, representing 868 landbird species, 38 of which are restricted to islands (23, 24). With all taxa combined, island-restricted species had smaller flight muscles, relative to body

Significance

Predictable evolutionary trends illuminate mechanisms that affect the diversity of traits and species on the tree of life. We show that when birds colonize islands, they undergo predictable changes in body shape. Small-island bird populations evolve smaller flight muscles and longer legs. These shifts in investment from wings to legs, although often subtle, are qualitatively similar to changes that have occurred in flightless bird lineages. Islands with fewer predator species were associated with more dramatic shifts toward flightlessness, implicating reduced predation pressure as the most likely cause of this trend. These predictable evolutionary changes likely exacerbate the vulnerability of flighted island birds to introduced predators and reduce the potential for small-island species to give rise to subsequent radiations.

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Data deposition: The data are included in *SI Appendix*, have been deposited in figshare (https://dx.doi.org/10.6084/m9.figshare.3123148.v1), and are available, along with all code needed to replicate all results and figures, at https://github.com/coereba/islands.

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mass, than their continental relatives [phylogenetic generalized linear model (PGLS): $P < 0.001$, df: 2 and 866].

To understand the causes of this difference between continents and islands, we examined forelimb and hindlimb investment in bird populations on islands of varying size and ecological characteristics. To achieve this goal, we measured museum skeletal specimens from island taxa in nine families, including taxa that require flight to forage, such as fruit-doves, kingfishers, hummingbirds, monarch flycatchers, and other songbirds. Here, we focus on two measurements: the lengths of the sternal keel (an index of pectoral muscle mass; ref. 23) and the tarsometatarsus, the distal-most long bone in the avian leg. In birds, hindlimb and forelimb size are negatively correlated due to tradeoffs in energetic investment and locomotor function (25). In our dataset, the lengths of the keel and tarsometatarsus were negatively correlated (PGLS: $P < 0.001$, df: 2 and 364; *SI Appendix*, Fig. S1), and this correlation persisted in 13 of 15 focal taxa when analyzed individually (*SI Appendix*, Table S1). We developed an index of hindlimb vs. forelimb investment from a principal component analysis of keel and tarsometatarsus lengths. Larger values of this "forelimb-hindlimb index" indicate larger flight muscles and shorter legs. We used island area, landbird species richness, raptor species richness, and the presence or absence of native mammalian predators as metrics of insularity, because each should be mechanistically related to the intensity of ecological pressures such as competition, predation, and resource diversity (16, 21). Our dataset included islands ranging from 786,000 km^2 and >620 resident landbird species, to atolls of 19 km^2 that support as few as three species. We used PGLS, with island populations as the units of analysis, to test the hypothesis that locomotor morphology evolved predictably with island characteristics.

Smaller flight muscles and longer legs have evolved repeatedly on islands of low species richness and with no mammalian predators (Fig. 1, Table 1, and *SI Appendix*, Figs. S2–S10). Forelimb-hindlimb index was positively correlated with raptor species richness, landbird species richness, and island area across 366 island populations in PGLS analyses (Table 1 and Fig. 1). Raptor species richness and the presence of native mammalian predators provided the greatest explanatory power, whereas island area was the least informative predictor of morphological shifts (Table 1). The correlation between the forelimb-hindlimb index and insularity was evident within 15 focal families and genera in nonphylogenetic analyses (Fig. 2 and *SI Appendix*, Tables S2 and S4) and was statistically significant at $P < 0.01$ for 14 of 15 focal taxa (*SI Appendix*, Table S4). Strikingly, island species richness explained as much as 60% of the variation in forelimb-hindlimb index among individual *Todiramphus* kingfishers on 27 Pacific islands representing 32

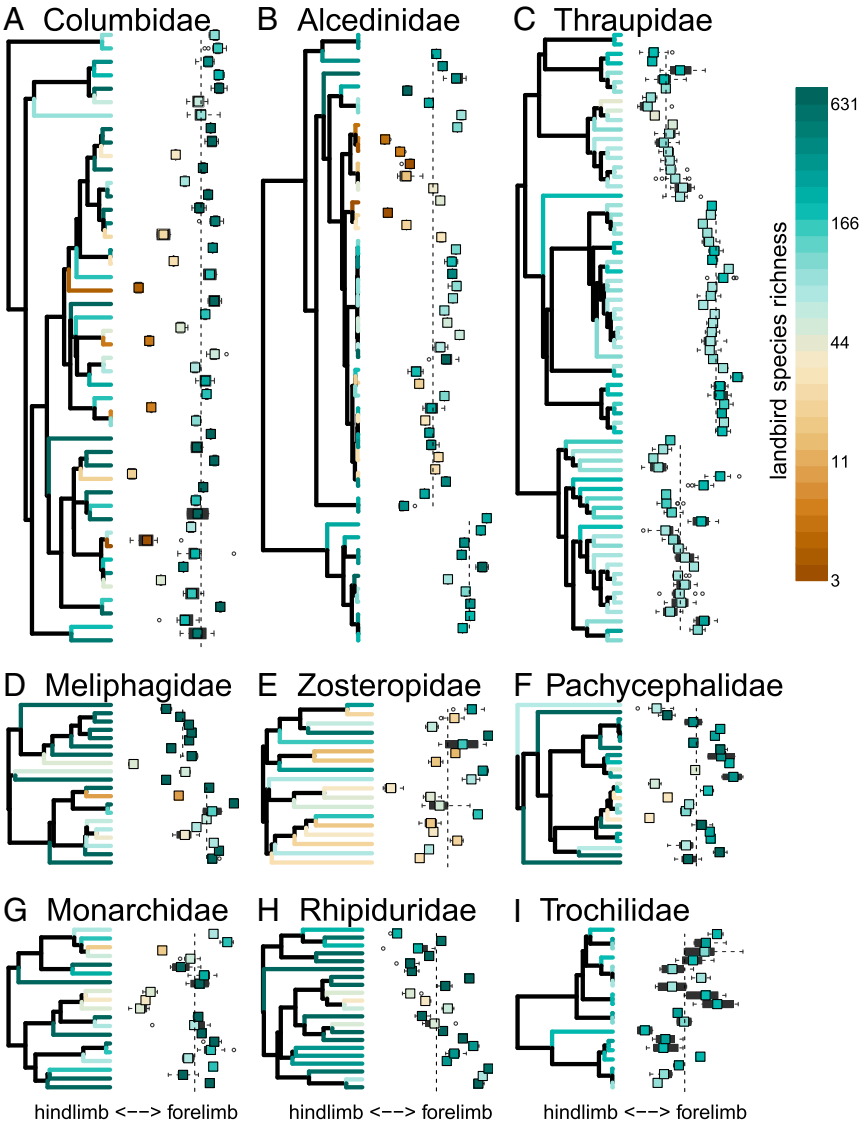

Fig. 1. Avian populations on islands of low species richness have repeatedly evolved smaller flight muscles and longer legs (Table 1 and *SI Appendix*, Table S2). Colors of tree tips and boxes represent island landbird species richness. The positions of colored squares represent population means of the forelimb-hindlimb index, with values further to the right indicating larger flight muscles and shorter legs. Dashed vertical lines represent clade means of the forelimb-hindlimb index. Gray box-and-whisker plots behind the colored squares show the first and third quartiles, with whiskers extending to 1.5 times the inner quartile range or the outermost data point within that range. Tree tips are species (trees A, D, E, G, and H), where differences among species encompass the majority of the variation among islands, or island populations (trees B, C, F, and I). *SI Appendix*, Figs. S2–S10 contain additional details, including island population names and individual keel and tarsometatarsus lengths.

distinct populations (*SI Appendix*, Table S4). Two-thirds of taxa (10 of 15) exhibited sexual dimorphism in forelimb-hindlimb index; thus, models that included sex as a predictor tended to explain significantly more variation (*SI Appendix*, Table S4). There was no interaction between sex and other predictor variables. Analyses with keel length or leg length as the dependent variable, respectively, followed the same general pattern: Keels became smaller and legs longer on islands of low raptor and landbird species richness (Table 1 and *SI Appendix*, Figs. S2–S10 and Tables S3 and S5).

To test the island rule, we examined whether island birds evolved toward intermediate body size as they became more hindlimb-dominant. Most of our study taxa were small-bodied birds (median body size: 14.5 g; range: 2.6–915 g). The island rule predicts that small taxa should become larger on smaller, more insular islands. Following this prediction, in PGLS analysis including all taxa with island population as the unit of analysis, body size was negatively correlated with island species richness and island area, albeit weakly (Table 1). Individual lineages, however, showed no consistent patterns of directional body size change. Body size correlated negatively with island species richness in 5 of 15 focal taxa and positively in another five taxa in nonphylogenetic analyses (*SI Appendix*, Tables S3 and S5). We tested whether body size predicted the direction of body-size evolution on islands by examining how the slope of the regression of body size vs. island species richness within each focal taxon correlated with its mean body size. The island rule predicts a positive relationship, with larger taxa evolving smaller body sizes on small islands and small taxa evolving in the opposite direction (*SI Appendix*, Fig. S11). We found no significant relationship between the magnitude or direction of body size changes on islands and mean body size (*SI Appendix*, Figs. S12–S14).

Discussion

These results suggest an ecogeographic rule for birds that relates to shape rather than size: Island birds evolve reduced flight muscles and larger legs in response to the ecological pressures associated with small, species-poor islands. This trend toward reallocation of energy from the forelimbs to the hindlimbs is evident in separate analyses of nine avian families and four orders, representing a range of lifestyles, diets, foraging behaviors, flight styles, and body plans. The pattern holds regardless of whether we focus on differences among individuals, populations, or species, with or without accounting for phylogenetic relationships. It is consistently supported for birds on continental or oceanic islands, and in Caribbean or Pacific archipelagoes.

Island raptor species richness and the presence of mammalian predators were the best predictors of forelimb-hindlimb index, keel length, and tarsometatarsus length (Table 1). Landbird species richness was slightly less informative than raptor richness, whereas island area explained substantially less variation (Table 1 and *SI Appendix*, Tables S3–S5). Although species richness and island area were correlated ($P < 0.001$, adjusted $R^2 = 0.42$, df: 1 and 78) and are expected to be mechanistically linked (21), the islands in this study vary in remoteness, archipelago size, geologic history, and topography. These size-independent factors affect the complexity of ecological communities, including species richness of landbirds and raptors (16, 21, 26). Accordingly, the repeated evolution of reduced flight muscles and longer legs

Table 1. PGLS comparisons for island population means ($n = 366$) of forelimb-hindlimb index, keel length, tarsometatarsus length, and body size

Dependent variable	Predictor variable(s)	AIC	*P* value	R^2
Forelimb-hindlimb index	Raptor richness + mammal predators	76	<0.001	0.50
Forelimb-hindlimb index	Raptor richness	82	<0.001	0.49
Forelimb-hindlimb index	Landbird richness + mammal predators	83	<0.001	0.46
Forelimb-hindlimb index	Landbird richness	86	<0.001	0.45
Forelimb-hindlimb index	Mammal predators + area	100	<0.001	0.39
Forelimb-hindlimb index	Mammal predators	122	<0.001	0.29
Forelimb-hindlimb index	Area	128	<0.001	0.28
Keel length	Raptor richness + mammal predators	1,899	<0.001	0.45
Keel length	Raptor richness + landbird richness	1,900	<0.001	0.45
Keel length	Raptor richness	1,901	<0.001	0.46
Keel length	Landbird richness + mammal predators	1,906	<0.001	0.41
Keel length	Landbird richness	1,908	<0.001	0.41
Keel length	Area + mammal predators	1,921	<0.001	0.33
Keel length	Area	1,938	<0.001	0.27
Keel length	Mammal predators	1,943	<0.001	0.23
Tarsometatarsus length	Raptor richness + mammal predators	1,024	<0.001	0.37
Tarsometatarsus length	Landbird richness + mammal predators	1,026	<0.001	0.34
Tarsometatarsus length	Raptor richness + landbird richness	1,035	<0.001	0.34
Tarsometatarsus length	Landbird richness	1,036	<0.001	0.32
Tarsometatarsus length	Raptor richness	1,038	<0.001	0.34
Tarsometatarsus length	Area + mammal predators	1,040	<0.001	0.30
Tarsometatarsus length	Mammal predators	1,059	<0.001	0.24
Tarsometatarsus length	Area	1,073	<0.001	0.18
Body size	Landbird richness	530	0.004	0.03
Body size	Mammal predators	533	0.027	0.01
Body size	Raptor richness	533	0.023	0.02
Body size	Area	535	0.02	0.0

Forelimb-hindlimb index indicates the size of the flight muscles relative to the legs. We tested all possible combinations of the four predictor variables and eliminated models that contained uninformative variables (55). R^2 values are for the models after phylogenetic signal has been taken into account. "Mammal predators" refers to the presence or absence of native mammalian predators of landbirds on the island. Body size variable is the first principal component from a PCA of skeletal measurements (coracoid, humerus, femur, and tarsometatarsus).

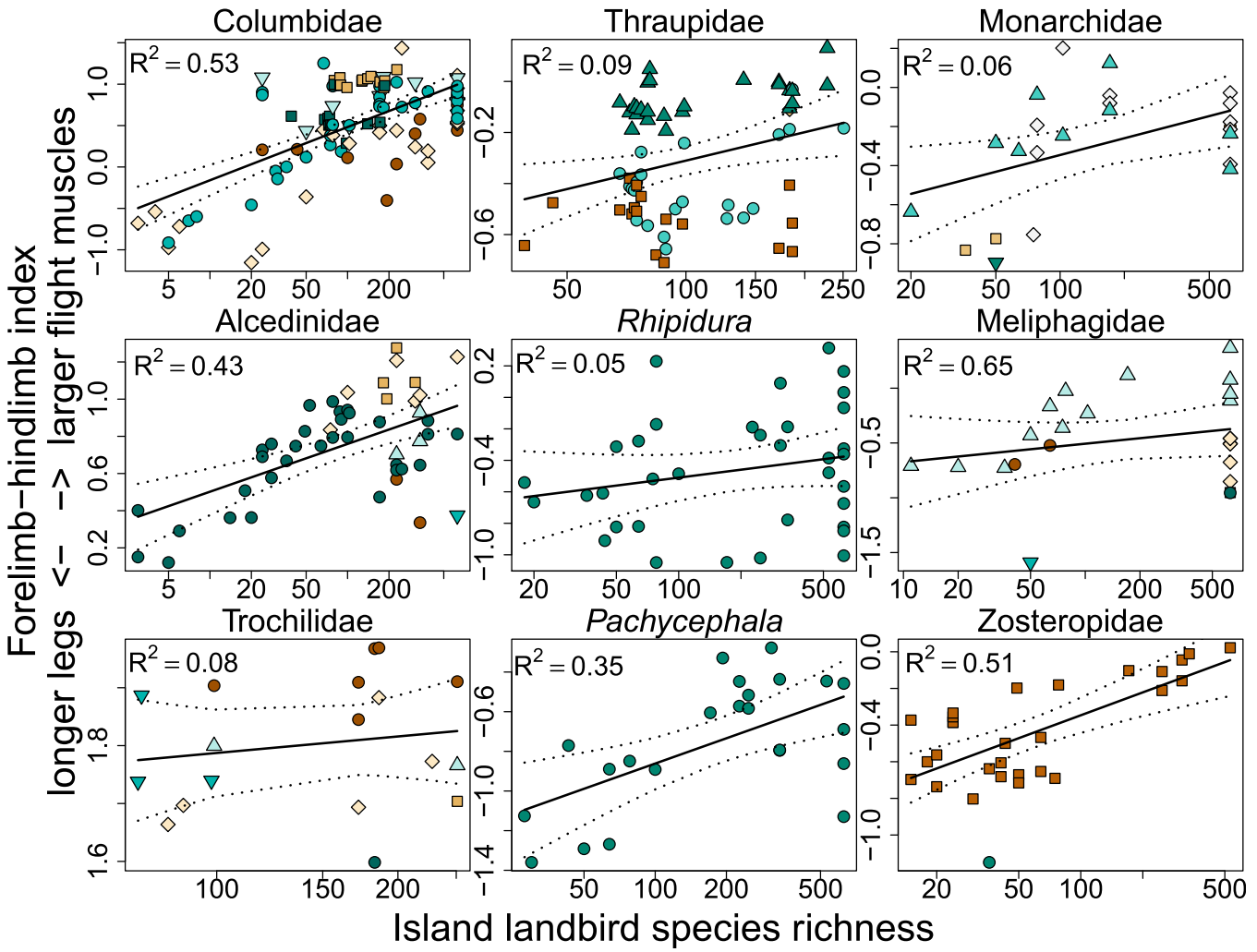

Fig. 2. Larger flight muscles and shorter legs are positively correlated with island species richness (Table 1 and *SI Appendix*, Table S2). Each point is a population mean. Solid black lines are linear regression lines and dashed lines are 95% confidence bands. R^2 values are partial R^2 for landbird species richness in linear regressions that include genus as a predictor variable where applicable (*SI Appendix*, Tables S2 and S4). That is, they estimate the proportion of variation explained by species richness that cannot be explained by genus alone. Differently colored and shaped points within a family indicate different genera (see *SI Appendix*, Fig. S15 for a key to genera).

is most likely attributable to depauperate ecological communities rather than the physical properties of small islands.

Lower predation pressure on islands with low raptor species richness and no mammalian predators might release landbirds from the need for large, powerful flight muscles that facilitate rapid escape. Islands of lower species richness tend to have less diverse sets of competitors, predators, habitats, and food sources (16, 21, 27). Raptor species richness and overall landbird species richness were tightly correlated ($P < 0.001$, $R^2 = 0.90$, df: 1 and 78), but raptor species richness was consistently the best predictor of changes in keel and leg lengths (Table 1). Additional reduction in the forelimb-hindlimb index of island birds was attributable to the absence of native mammalian predators (Table 1). Raptor species richness is likely an informative index of the predation pressure that raptors exert on island birds because when only one or a few raptor species are present on an island, those species tend to be generalist predators; whereas, raptors that specialize on eating birds tend to occur only on islands of high species richness (16, 27). Specialized predators likely exert stronger pressure to maintain rapid escape abilities. Hence, the lack of bird-specialist predators on islands with few raptor species may allow for reduced energetic investment in flight muscles and concomitant increase in hindlimb size.

Smaller flight muscles likely result in slower maximal flight speeds and slower takeoffs, with longer legs potentially compensating for small flight muscles (25, 28–30). Birds use a leg thrust to generate initial forward velocity during takeoff (28, 29). Flight is extremely costly at airspeeds close to zero, and power requirements decrease as velocity increases to moderate flight speeds (30). Birds' leg thrusts allow their wings and flight muscles to begin generating lift at airspeeds significantly greater than zero, thereby reducing the overall power required for lift production (30). Longer legs provide a longer lever, increasing force generation during the leg thrust that initiates takeoff. Theoretically, this change should reduce the power required from the flight muscles while also reducing the overall speed of escape from a predator, although this prediction has yet to be experimentally tested. Longer legs may have evolved as a result of this functional (28, 29) and/or energetic tradeoff with flight muscle size, because similar tradeoffs occur across the bird phylogeny and within individuals across ontogeny (25). In this way, selection for reduced flight muscles may have indirectly caused leg length to increase. An alternative explanation for longer legs on

depauperate islands is that they may have been directly favored via selection for perch generality and ground foraging (5, 12). Birds on islands of low species richness tend to use a wider variety of habitats, food sources, and perch types (5, 31, 32). Songbirds have been found to evolve longer legs on islands in association with variable perch types (5, 12). Similarly, longer legs are associated with increased terrestriality and walking. If reduced interspecific competition resulting in the use of greater perch variety is the primary driver of the evolution of longer legs on islands of low species richness, we would expect to see this pattern exclusively in birds that use perches in a variety of ways while foraging (e.g., clinging, hanging, hopping, or walking). Instead, even hummingbirds and kingfishers, which tend not to cling, hang, hop, or walk, have longer legs on islands of lower species richness. This phenomenon suggests that biomechanical compensation for small flight muscles is an important cause of elongated legs in volant island birds.

Our results provide new perspective on the evolution of flightlessness. Previous workers have focused on the causes and consequences of the evolution of flightlessness on islands (e.g (15, 16, 19, 33, 34), but the possibility that volant species are subject to similar mechanisms has not been addressed. We suggest that the profound shape change exhibited during the transition to flightlessness is the extreme manifestation of a predictable pattern of avian evolution in response to ecological release from predators. Certain taxa, like rails, are more likely to reach the extreme state (15, 16, 18). The majority of landbirds that colonize islands, however, appear to be affected similarly, even those that are destined to never evolve flightlessness. Taxa including fruit doves, monarch flycatchers, tanagers, white-eyes, whistlers, fantails, honeyeaters, kingfishers, and hummingbirds exhibited morphological changes along the trajectory toward flightlessness, despite flight ability being integral to their modes of foraging and breeding. The range of variation in the forelimb-hindlimb index reflects a continuum of locomotory modes, from highly aerial to flightless. In insular communities, a shift in the balance of directional selection pressures causes incremental changes along this continuum. Consistent with this idea, McCall et al. (33) found that flightlessness is most likely to evolve in taxa that already have short wings relative to their body mass.

Our results have two major implications for mechanisms of diversification. First, the vulnerability of volant island birds to introduced predators, partly attributable to an evolved reduction in vigilance ("island tameness"; refs. 35 and 36), is exacerbated by reduced physical capacity for escape via flight, increasing extinction risk (37). Second, systematic reduction in flight muscle size could propel taxon cycles (38) by reducing the probability of over-water dispersal from small-island populations. The latter would inhibit interisland gene flow, causing island populations to evolve on independent trajectories, each with reduced probability of undergoing subsequent expansion and diversification.

Materials and Methods

Data Collection. For the comparison of continents versus islands, we used bird specimens that were collected by us and many colleagues using standard museum methods (23, 24). Each bird was weighed, and the pectoralis major and supracoracoideus muscles were extracted and weighed. Flight muscle mass scaled isometrically with body mass; accordingly, we calculated relative flight muscle size by dividing total flight muscle mass by body mass. Species values were obtained by taking the mean of the average male measurement and average female measurement. All mass data were associated with specimens archived at the Museum of Southwestern Biology (University of New Mexico), Centro de Ornitología y Biodiversidad (Lima, Peru), or Florida Museum of Natural History (University of Florida).

To address forelimb and hindlimb dimensions in island bird populations across a range of insularity, we used museum skeletal specimens from historic to modern collections, focusing on 15 well-represented taxa: Trochilidae; *Macropygia*, *Ducula*, *Ptilinopus*, *Columbina*, and *Zenaida aurita* (Columbidae); Alcedinidae; Zosteropidae; *Rhipidura* (Rhipiduridae); Meliphagidae; Monarchidae; *Pachycephala* (Pachycephalidae); *Coereba flaveola*, *Tiaris*, and *Loxigilla* (Thraupidae). Because the flight muscles attach to the sternal keel, keel size is closely related to flight muscle size. A single measurement, the diagonal length of the keel, which encompasses both length and depth, was the best predictor of flight muscle size and correlated strongly with flight muscle mass both within and among species (*SI Appendix, SI Materials and Methods*). We measured all available skeletal specimens of our focal island taxa at five natural history museums with large avian skeletal collections. One person (N.A.W.) made all of the following measurements from each skeletal specimen: diagonal keel length and the lengths of the coracoid, humerus, femur, and tarsometatarsus. Specimens missing any of these elements were excluded from analyses.

Data on island area, landbird species richness, and raptor species richness were compiled from the literature (16, 27, 39–42) for each island from which we had bird skeletal measurements. We included regularly occurring resident or migrant species, but excluded vagrants and rarities. We coded islands for the presence/absence of native mammals that might predate birds.

Analyses. We tested whether island-restricted species have evolved smaller flight muscles than their continental relatives by conducting PGLSs in R with packages ape and nlme (43–45) using a phylogenetic tree for birds (46) and species averages of relative flight muscle sizes. Species found on both continents and islands (including migrants) were coded as continental. We coded species as "island-restricted" if they were not regularly found on any continent or island larger than 200,000 km^2. We chose this cutoff because large islands are continent-like in their ecology (e.g., New Guinea has roughly the same landbird species richness as Australia) and because this cutoff was a natural break point in the data. Our dataset included species restricted to islands larger than 450,000 km^2 and smaller than 200,000 km^2, but none in between (Dataset S1). We restricted analyses to landbirds only (i.e., excluded ducks, seabirds, shorebirds, and grebes). Our dataset included average relative flight muscle sizes for 868 species, of which 59 of were restricted to islands, and 38 were restricted to islands smaller than 200,000 km^2.

To test whether flight muscle size and leg lengths were related to landbird species richness, raptor species richness, mammalian predators, or island area, we analyzed skeletal measurements multiple ways. We used principal component analysis on length measurements of the coracoid, humerus, femur, and tarsometatarsus to account for body size, because the first principal component (PC1) of this analysis included all four variables, loading roughly equally and in the same direction. We used the residuals of a linear model of the skeletal element of interest (i.e., keel length and tarsometatarsus length) by PC1 as a body size-corrected estimate of the character. All results presented are these body size-corrected estimates rather than raw values. Because in most cases keel length and leg length were evolving in concert and were strongly negatively correlated (*SI Appendix*, Fig. S1 and Table S1), we created a shape index to characterize small flight muscles and long legs. This forelimb-hindlimb index was the second principal component (PC2) from a principal component analysis on keel length and leg length measurements. Both keel and leg length loaded equally and in the same direction in PC1, and in opposite directions in PC2. PC2 explained 25% of the variation when analyzed across the entire dataset.

We conducted PGLS analysis on the entire skeletal dataset, with island population as the unit for analysis and island population means calculated from individual-level data (Dataset S2). This analysis required a phylogenetic tree that included relationships among island populations. Therefore, we patched hypothesized relationships among island populations into a species-level tree from Jetz et al. (46), largely derived in its major clades from Hackett et al. (47). We used published phylogeographic studies (48–54) as the basis for hypothesized relationships among island populations. For taxa without published phylogeographic studies, we hypothesized relationships based on subspecies differentiation, relationships among populations of similar species on the same islands, and geographic proximity of islands (see *SI Appendix*, Figs. S2–S10 for resulting phylogenetic trees). We performed AIC model selection to test which combination of four variables (raptor species richness, landbird species richness, island area, or presence/absence of mammalian predators) best predicted morphology, eliminating models with uninformative parameters (55).

We also conducted nonphylogenetic linear regression analyses with each morphological character of interest as a function of landbird species richness and island area, respectively, using both population-level means and individuals as units of analysis. We conducted these analyses within each genus or, where sampling within one particular genus was limited, within a family (e.g., Trochilidae, Monarchidae, Meliphagidae). Taxa for which we only had a few island populations were excluded to allow for more clade-specific analyses (e.g., members of Alcedinidae outside of the genus *Todiramphus*).

The resulting 15 focal taxa for the nonphylogenetic analyses included 339 (93%) of the 366 island populations analyzed above.

To test predictions of the island rule as traditionally defined (4), we examined how the slope of the regression of body size vs. island species richness within each genus correlates with mean body size across genera. For each genus with sample $n \geq 10$ and island populations $n > 3$, we performed a linear regression between body size (PC1) and species richness ($n = 19$ genera). We regressed the coefficient of the relationship between body size and species richness against mean body size of the genus. We repeated the analysis with the slope set to 0 for taxa in which the linear regression of body size by species richness was not statistically significant at $P < 0.05$. We performed this analysis for all taxa together, and also for Columbidae and Passeriformes separately. If the taxa in our study follow the island rule, we would expect the relationship to be positive: Small-bodied species should have negative relationships between island species richness and body size, whereas large-bodied taxa should become smaller as island species richness decreases (*SI Appendix*, Fig. S11).

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