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How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes)

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Dispersal ability is a key factor in determining insular distributions and island community composition, yet non-vagile terrestrial organisms widely occur on oceanic islands. The landfowl (pheasants, partridges, grouse, turkeys, quails and relatives) are generally poor dispersers, but the Old World quail (*Coturnix*) are a notable exception. These birds evolved small body sizes and high-aspect-ratio wing shapes, and hence are capable of trans-continental migrations and trans-oceanic colonization. Two monotypic partridge genera, *Margaroperdix* of Madagascar and *Anurophasis* of alpine New Guinea, may represent additional examples of trans-marine dispersal in landfowl, but their body size and wing shape are typical of poorly dispersive continental species. Here, we estimate historical relationships of quail and their relatives using phylogenomics, and infer body size and wing shape evolution in relation to trans-marine dispersal events. Our results show that *Margaroperdix* and *Anurophasis* are nested within the *Coturnix* quail, and are each 'island giants' that independently evolved from dispersive, *Coturnix*-like ancestral populations that colonized and were subsequently isolated on Madagascar and New Guinea. This evolutionary cycle of gain and loss of dispersal ability, coupled with extinction of dispersive taxa, can result in the false appearance that non-vagile taxa somehow underwent rare oceanic dispersal.

1. Introduction

Organisms that are unable to disperse across physical or environmental barriers should be unable to achieve widespread or global distributions. Yet, paradoxically, organisms that lack dispersal capability are still characteristic components of isolated continents and island communities [1–4]. For example, large-bodied and flightless ratite birds (e.g. ostrich, emu) have seemingly colonized distant areas over evolutionary time despite severe dispersal constraints [5–8].

Two hypotheses explain how dispersal-limited organisms reach novel areas: via chance dispersal and vagile ancestors. The chance dispersal hypothesis relies on rare, stochastic events to explain colonization by poor dispersers over evolutionary time [9–11]. Examples include New World monkeys, rodents and salt-intolerant amphibians that rafted between continents or islands on floating debris [12–15]. Alternatively, the vagile ancestor hypothesis posits that non-dispersive lineages are descended from mobile ancestors that reached new islands and continents by colonizing across geographical barriers. Subsequently, parallel or convergent selection towards reduced dispersal abilities and/or increased body size resulted in poorly dispersing descendants. Extinction of the original vagile ancestor lineages over time may then result in the appearance of dispersal-limited groups with relict distributions. This cycle of range expansion, morphological evolution and extinction has recently been favoured to explain
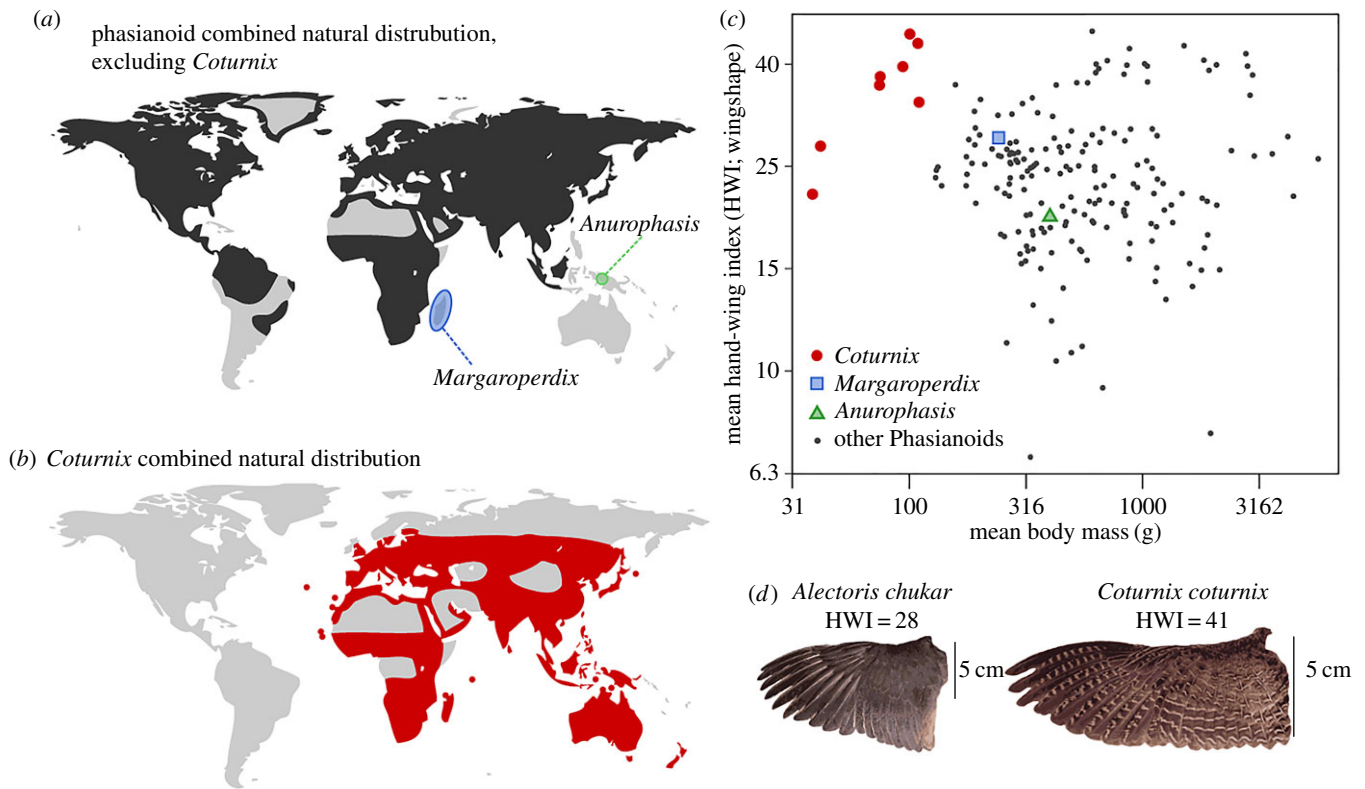
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Figure 1. Maps of (*a*) the combined natural distribution of all phasianoid landfowl excluding *Coturnix* species; phasianoids are limited to continents and islands with recent land connections to Laurasia with the exception of *Margaroperdix* and *Anurophasis*. (*b*) The combined natural distribution of Coturnix, which is found widely throughout the Eastern Hemisphere. (*c*) Bivariate plot of mean body mass and mean hand-wing index (HWI) for phasianoid species; *Coturnix* species occupy a unique area of morphospace, having small body size and short wings. (*d*) Examples of phasianoid wingshape and their hand-wing indices; *Alectoris chukar* has short, broad wings typical of the 'partridge' morphotype, whereas *Coturnix coturnix* has long, narrow wings typical of Old World quail. (Online version in colour.)

the distributions of non-vagile birds as diverse as the flight-less ratites and tinamous [5,7,8], and the mostly flightless New Zealand wrens [16]. However, in these cases, the putative vagile ancestors were purely hypothetical. The only fossil evidence of vagile ratites is from the Palaearctic, where no extant ratites reside [8,17–19]. Similarly, all known fossil New Zealand wrens already feature non-vagile traits [16].

The pheasants, partridges, grouse, turkeys, quail and relatives (Aves: Phasianoidea, Phasianidae, Odontophoridae and Numididae) feature a near-worldwide distribution, being absent only from southern South America, Antarctica, extremely dry deserts and some insular regions (figure 1*a*,*b*). Yet, despite having a broad distribution, phasianoids are among the poorest-dispersing flighted birds. Species are generally heavy-bodied, short-winged and ground dwelling [20]. Most fly only in short bursts to escape predators, or into trees to roost. Phasianoids are generally thought to be incapable of crossing marine barriers [21], and thus are generally limited to continents and continental islands (i.e. islands that had recent dry-land connections to continents during periods of low sea levels or sea-ice connections). Rare overwater movements have been observed in arctic ptarmigan (*Lagopus* spp.) [22] (but see [23,24]), otherwise historical movements of phasianoid lineages between North America and Asia were likely to have been facilitated by the Bering Land Bridge [25].

The Old World quail (*Coturnix*) are a great contrast to most phasianoids in terms of dispersal ability. *Coturnix* are excellent flyers, and their impressive long-distance transcontinental movements were recorded in texts as dating back to the Old Testament (Numbers 11:31–32) and Pliny's *Natural History* (AD 79). Unlike other phasianoids, *Coturnix* exhibit small

body size and high-aspect-ratio wings (figure 1*c*,*d*), both adaptations that improve long-distance flight performance [26]. In addition, *Coturnix* species are widespread on oceanic islands in the Atlantic, Indian and Pacific Oceans, and they have repeatedly crossed major faunal boundaries such as Wallace's and Lydekker's Lines (figure 1*b*).

Curiously, even within the putative 'non-vagile' phasianoids (all but *Coturnix* and perhaps *Lagopus*), two species are found on landmasses across marine barriers from continental sources: Madagascan partridge (*Margaroperdix madagarensis*) of Madagascar and Snow Mountain quail (*Anurophasis monorthonyx*) of New Guinea. *Anurophasis* and *Margaroperdix* have medium-sized bodies and short, rounded wings similar to various other partridges and francolins (figure 1*c*). However, previous authors have noted some similarities between *Margaroperdix*, *Anurophasis* and *Coturnix*, including plumage characters of their downy chicks [20]. Molecular data now support close relationships between *Margaroperdix* and *Coturnix* [27–29]. Yet, because several *Coturnix* species and *Anurophasis* lack DNA sequence data, relationships in the group remain uncertain.

Continental vicariance of Madagascar and Australasia far preceded diversification of phasianoids [30] and modern birds in general [31–33], meaning *Margaroperdix* and *Anurophasis* ancestors must have crossed permanent marine barriers. How did these 'non-vagile' phasianoids come to inhabit their present insular distributions? Are they examples of rare, chance dispersal across oceanic barriers by generally non-vagile birds? Alternatively, are they descended from small-bodied, dispersive *Coturnix* stock, which evolved into 'island giants' once isolated in unique insular environments? Previous studies have identified great plasticity in phasianoid morphotypes,

with 'pheasant' (large-bodied, long-tailed), 'partridge' (medium-bodied, short-tailed) and 'quail' (small-bodied, short-tailed) morphologies evolving repeatedly across the tree [28,34].

To understand if body size and wing shape evolution influenced marine dispersal propensity in phasianoids, we sequenced genome-wide markers from *Margaroperdix*, *Anurophasis*, all extant *Coturnix* species and a wide variety of phasianoids to place them in a phylogenetic framework. We then used mensural data to characterize ancestral morphological states of phasianoids to test topological and morphological predictions of the 'chance dispersal' and 'vagile ancestor' hypotheses.

2. Material and methods

(a) DNA sequencing and data processing

We extracted DNA from fresh tissues and toepad clips from museum specimens, including *Anurophasis*, *Margaroperdix* and all extant *Coturnix* species (electronic supplementary material, table S1). Target capture libraries of 5060 ultraconserved elements loci using 5472 probes [35] were performed by RAPiD Genomics (Gainesville, FL). In total, 150 nt paired-end sequence reads were generated on an Illumina HiSeq 3000. We removed PCR duplicates from demultiplexed reads with PrinSeq-lite 0.20.4 [36], trimmed and error corrected raw reads with QuorUM [37], and read-mapped to known UCEs sequences from published *Gallus*, *Meleagris* and *Coturnix* genomes with Bowtie2 2.2.5 [38]. We then assembled quality-controlled reads with Trinity r20131110 [39]. We aligned the novel UCEs to those from other galliforms (Cracidae, Megapodiidae) and an anseriform outgroup, and data generated from previous studies [25,29,30], resulting in 115 total sampled taxa. We extracted UCEs from contigs with PHYLUCE 1.5 [40] and aligned each UCE locus with MAFFT 7 [41]. We trimmed ends of alignments when 35% of cells were missing across a 20 bp sliding window.

(b) Phylogenetic inference

We concatenated all loci recovered in more than 50% of taxa and obtained the maximum-likelihood (ML) estimate of phylogeny using RAxML 8.2.8 [42] and the GTRGAMMA model with partitioning. We selected the optimal partitioning scheme using the Bayesian information criterion and the rclusterf algorithm [43] in PartitionFinder 2.0-pre11 [44], and quantified support with 100 thorough bootstrap replicates. We implemented MCMCtree (PAML 4.8 [45]) using a relaxed clock and six galliform fossil calibrations [30,46] to calibrate minimum node ages (electronic supplementary material, table S2) and infer an ultrametric, time-calibrated phylogeny. We restricted analysis to the largest single DNA sequence partition identified by PartitionFinder to reduce among-site rate heterogeneity and computation time. We also estimated a phylogeny statistically consistent under the multispecies coalescent model with 100 SVDquartets bootstraps [47], each sampling 10 000 000 quartets, in PAUP* 4a150 [48].

(c) Comparative analyses

To determine if trans-oceanic colonization is predicted by dispersal and body mass evolution, we compiled information on body mass and wing morphometrics to produce an index of flight ability: the hand-wing index (HWI). HWI is related to wing aspect/ratio, an important metric in flight performance [26,49]. Wings with high aspect ratio/high HWI are longer, narrower and produce greater lift than wings with low aspect ratio/low HWI. HWI correlates strongly with dispersal capabilities [49–51]. We calculated mean HWI for phasianoids and outgroups based on measurements from traditional museum skins with the wings prepared folded on the body. Although direct measurement of wing aspect ratio and additional flight performance metrics from spread wing specimens, skeletons and anatomical specimens would be preferable [1], spread-wing specimens and skeletal specimens of *Anurophasis* and many other phasianoid species do not exist. To calculate HWI, we measured wing chord to the longest primary and wing chord to the longest secondary from a minimum of four specimens per species (two male, two female) of all available phasianoids and outgroups. We used mean body mass estimates from the literature [20] because many older museum specimens lacked body mass data. We used the R package geiger 2.0.6 [52] to test phylogenetic signal (Blomberg's K) and various evolutionary models for HWI, body mass (log-transformed) and HWI scaled to log-transformed body mass (electronic supplementary material, table S3). We also tested for potential correlation between body mass and HWI. We computed continuous ancestral states for HWI, body mass and HWI to body mass ratio under the best-fit evolutionary model with R package phytools [53].

3. Results

(a) Phylogenetic inference

We identified 4021 suitable UCE loci (1.67 million bp) that met our criteria for phylogenetic analysis. ML phylogeny was well resolved (figure 2; electronic supplementary material, figure S4); only five nodes received less than 100% bootstrap support. The SVDquartets topology was similarly well resolved and corroborated the ML topology, although SVDquartets bootstrap support was slightly lower than the ML support (electronic supplementary material, figure S4). We inferred a crown age of Galliformes at 55–78 Ma (95% HPD) and a crown age of Old World quail at 16–27 Ma (95% HPD).

Both *Margaroperdix* and *Anurophasis* were nested within the *Coturnix* clade (figure 2, inset; electronic supplementary material, figure S4). *Margaroperdix* was sister to a clade of five *Coturnix* species: *C. coturnix*, *C. japonica*, *C. pectoralis*, *C. coromandelica* and *C. delegorguei*. *Anurophasis* was sister to *C. ypsilophora*; *Anurophasis* + *C. ypsilophora* was sister to the small 'blue' quails *C. chinensis* and *C. adansonii*. All relationships within the enlarged *Coturnix* clade were supported with 100% ML and SVDquartets bootstraps. The *Coturnix* clade was sister to the small partridge *Ammoperdix*, rather than other small-bodied, quail-like galliforms such as bush-quail (*Perdicula*) or New World quail (Odontophoridae, the sister group to Phasianidae).

(b) Comparative analyses

A simple bivariate plot (figure 1*c*) demonstrates that *Coturnix* occupy a unique area of morphological space within the Phasianoidea, having both small body size and large HWI. Conversely, *Margaroperdix* and *Anurophasis*, have moderate body sizes and HWI similar to many continental phasianoid species, such as partridges (e.g. *Perdix*, *Arborophila*) and francolins (e.g. *Francolinus*, *Pternistis*). Model testing indicated that Brownian motion was the best-fit evolutionary model for HWI, body mass and HWI scaled to body mass, given the phylogeny (electronic supplementary material, table S3); and was therefore chosen in subsequent analyses. Blomberg's K indicated significant phylogenetic signal for HWI ($p < 0.00001$, $K = 0.73$) and body mass ($p < 0.00001$, $K = 0.86$). The HWI/body mass ratio ($p < 0.00001$, $K = 0.92$) had greater
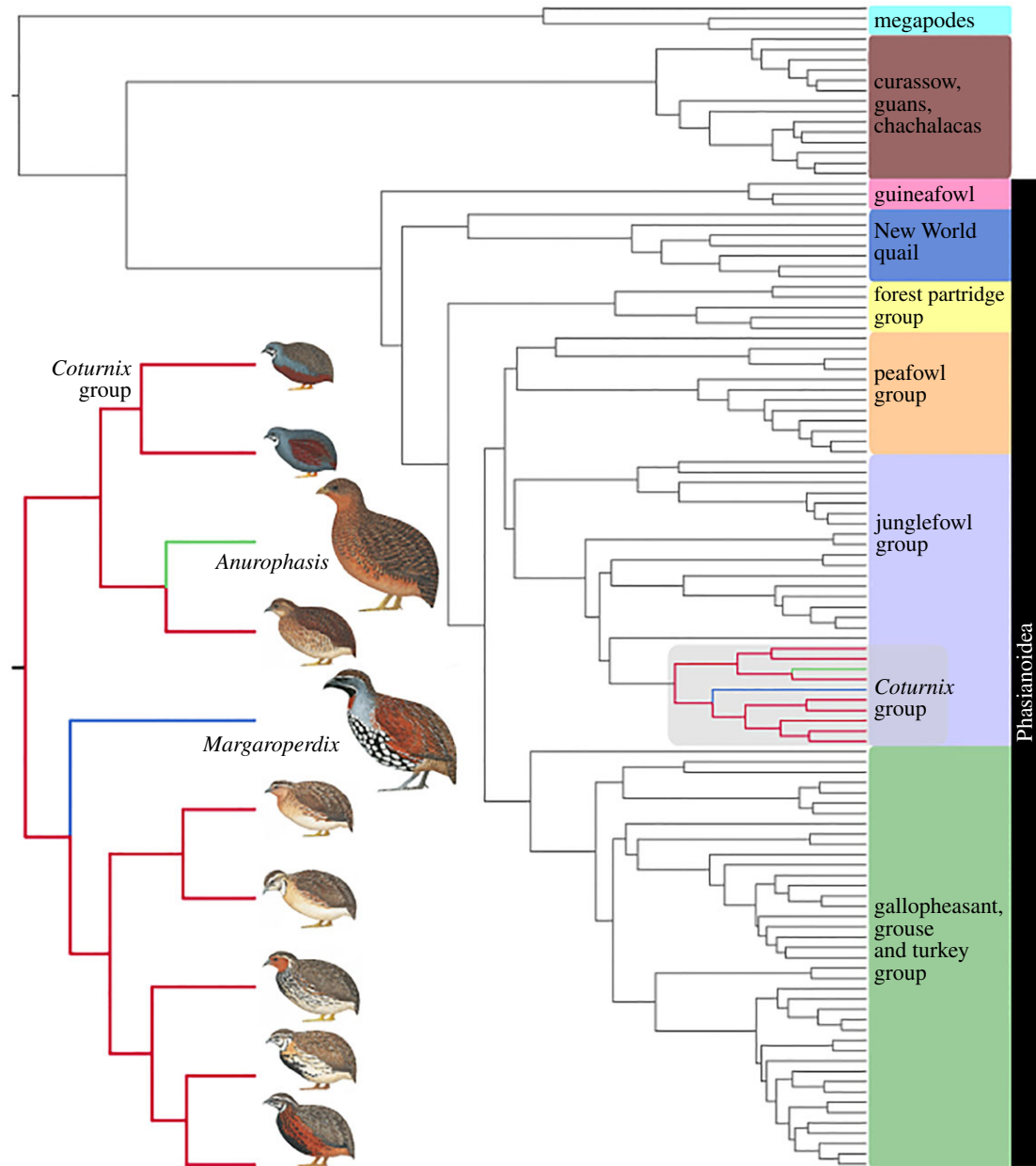
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Figure 2. Time-calibrated ultrametric phylogeny of landfowl inferred from UCE markers. Inset is the clade containing *Coturnix*, as well as *Margaroperdix* and *Anurophasis*. *Coturnix* group illustrations by Norman Arlott, © HBW Alive, reproduced with permission. A detailed version of this figure including tip labels and node support calculated from maximum-likelihood (RAxML)/SVDquartets (SVDq) bootstrapping can be found in electronic supplementary material online, figure S4. (Online version in colour.)

phylogenetic signal than either variable alone. Body mass and HWI were not significantly correlated across the phylogeny (Spearman $p = 0.3$, $r = 0.096$).

We found that wing shape (i.e. HWI) has evolved substantially in phasianoids (figure 3a). From an average ancestor, relatively short wings have evolved in the great argus (*Argusianus argus*), peacock-pheasants (*Polyplectron*), bush-quails (*Perdicula*), tragopans (*Tragopan*) and some pheasants (*Crossoptilon*). Long wings have also evolved multiple times, in snowcocks (*Tetraogallus*), *Coturnix* quails, grouse and ptarmigan (Tetraoninae). Similarly, evolution of body size in phasianoides has been dynamic (figure 3b). From a relatively large-bodied ancestor, body size increased in the curassows, guans and chachalacas, argus and peafowl (*Argusianus* and *Pavo*), snowcocks (*Tetraogallus*), turkeys (*Meleagris*) and caper-caillies (*Tetrao*). Smaller body sizes evolved independently in the New World quail (Odontophoridae), forest partridges (Arborophilinae), bush-quail (*Perdicula*) and the *Coturnix*

quail. However, *Coturnix* is unique in having long, high-HWI wings and small body sizes in concert (figure 3c). These traits reversed in insular *Margaroperdix* and *Anurophasis*, having similar values to various partridges and francolins.

4. Discussion

Phylogeny and ancestral reconstructions reject the hypothesis that non-*Coturnix* phasianoids are capable of rare, trans-marine colonization events. Rather, the 'partridges' *Margaroperdix* of Madagascar and *Anurophasis* of New Guinea are actually 'giant quail'. These species evolved body sizes an order of magnitude larger than their highly vagile *Coturnix*-like ancestors, and have converged upon a morphotype defined by moderate body size, short broad wings and a short tail. This 'partridge' morphotype has evolved multiple times across Phasianoidea,
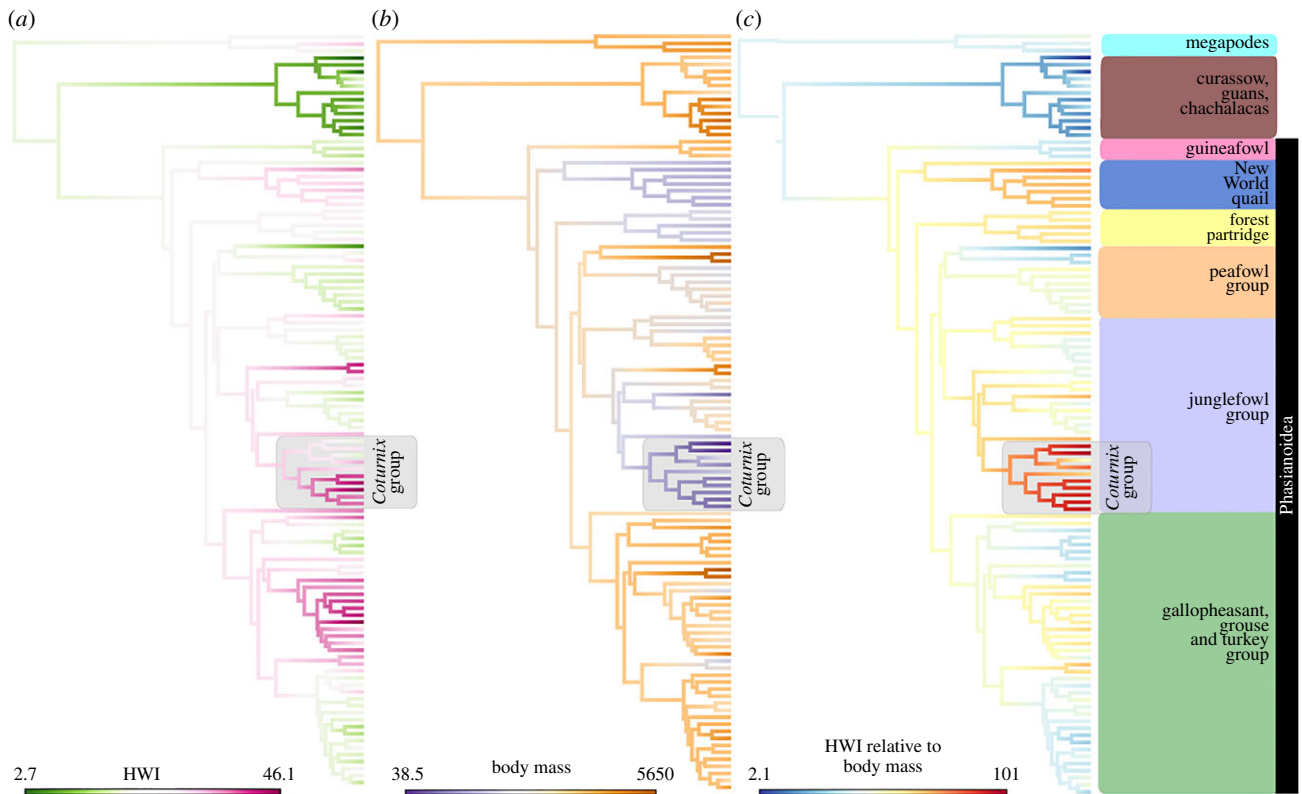
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Figure 3. Ancestral state reconstructions of mean hand-wing index (HWI), mean body mass and HWI relative to body mass across the landfowl tree of life. *Coturnix* feature large HWI and small body mass relative to other landfowl, and their large HWI relative to body mass is unique. However, these traits reverse in 'island giants' *Margaroperdix* and *Anurophasis*, which are nested within *Coturnix* quails but are morphologically convergent with the various partridges. (Online version in colour.)

and is characteristic of genera including *Perdix, Francolinus, Pternistis, Arborophila* and others [28,34].

Evolution of body size has been suggested as an adaptation in populations following insular colonization [54–56], although whether or not it is a predictable, general pattern remains controversial [57,58]. In theory, island gigantism (i.e. organism body size increase on islands) is due to multiple factors including ecological release from mainland predation and character displacement from insular competitors [59,60]. Whether or not predation is a credible factor in phasianoid body size evolution is difficult to ascertain because of little direct evidence. Madagascar and New Guinea are both large islands that support numerous mammalian and raptorial predators. The Madagascar harrier (*Circus macrosceles*), Madagascar sparrowhawk (*Accipiter madagascariensis*) and the fossa (*Cryptoprocta ferox*) are known to prey on *Margaroperdix* [20]. Predation pressure upon *Anurophasis*, like most aspects of its ecology and natural history, is virtually unknown [20].

Some evidence exists for character displacement in insular Old World quails. Both *Margaroperdix* and *Anurophasis* are found on the same islands as other *Coturnix* species. *Margaroperdix* is sympatric with resident *Coturnix coturnix* populations on Madagascar, and *Anurophasis* is found at elevations above populations of its sister taxa *C. ypsilophora*, as well as *C. chinensis*, on New Guinea. Extinct *Coturnix gomera* [61] from the Canary Islands provides a third likely example of convergent gigantism among quails on islands. *Coturnix gomera* was larger and more robust than sympatric *C. coturnix*, although it was perhaps at an earlier stage of divergence and morphological distinctiveness than *Margaroperdix* or *Anurophasis*.

The increased body size in *Margaroperdix* and *Anurophasis* could be related to co-distribution with *Coturnix* relatives and character displacement as predicted by the taxon cycle

hypothesis, where lineages alternate between phases of range expansion and contraction over time [62–64]. Migratory and dispersive quail species qualify as lineages in a state of distributional expansion, whereas large-bodied insular forms with reduced HWI are in a state of contraction. Under the taxon cycle hypothesis, larger body sizes of *Margaroperdix* and *Anurophasis* would be interpreted as character displacement to avoid competition, and loss of dispersal capability as an adaptation to reduce metabolic cost of large flight muscles— simultaneously reducing dispersal capability [63,65,66]. Maintenance of flight muscle mass needed for long dispersal flights is energetically demanding [66], and insular bird populations tend to evolve towards reduced dispersal if there is not strong connectivity with nearby populations [1,50,67]. In extreme cases, this selection pressure can lead to complete flightlessness [68]. The character displacement/taxon cycle hypothesis is also congruent with the lack of size evolution in the recently extinct New Zealand quail (*Coturnix novaezelandiae*). It was only naturally occurring *Coturnix* on New Zealand, and it was approximately the same size as its sister taxon, *C. pectoralis* of Australia.

The history of insular colonization and morphological evolution in *Coturnix* quail provides an empirical example of a general framework, explaining how 'non-vagile' organisms disperse across marine barriers (figure 4). If ecological specialization on islands reduces dispersal ability, then vagility evolves in relation to the taxon cycle. Phases of this dispersal cycle are: (i) a truly non-vagile ancestor; (ii) evolution of vagility, including gains of morphological, physiological or behavioural traits that increase dispersal potential; (iii) the newly dispersive species colonizes novel areas unavailable to its non-vagile relatives; (iv) colonizing lineages become isolated from the dispersive ancestor, and selection for reduced
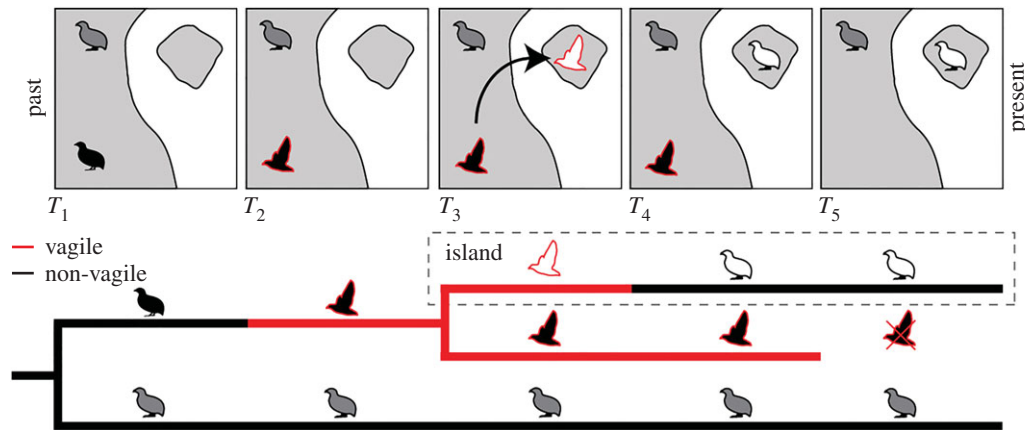
Figure 4. Phases of the dispersal cycle, which occurs when specialization on islands results in reduced dispersal capability. The upper panels represent trait evolution and diversification in geographical space across discrete time slices, whereas the phylogeny represents trait evolution and diversification over continuous time. (T_1) Non-vagile mainland lineages, (T_2) evolution of vagility in a mainland lineage, (T_3) the newly dispersive species colonizes novel areas, (T_4) colonizing lineages become isolated from the dispersive ancestor because of selection for reduced dispersal, (T_5) in some instances, extinction of the widespread dispersive results in relictual distributions of non-vagile taxa distributed across marine barriers. (Online version in colour.)

dispersal on islands reverses morphology, physiology and behaviour to non-vagile states. In some instances, the differential extinction of widespread dispersive species in primarily non-vagile clades, along with survival of mainland and insular species with reduced dispersal ability, result in the confusing impression that they must have colonized their island ranges by marine dispersal despite being poorly adapted to do so. This results in a fifth stage: relictual distributions of non-vagile taxa distributed across marine barriers.

In the example of quail, the key innovations resulting in increased dispersal were evolution of small body size, long wings and perhaps migratory behaviour. Various *Coturnix* lineages are at stages two (*C. coromandelica*, *C. delegorguei*, *C. adansonii*) or three (*C. coturnix*, *C. japonica*, *C. ypsilophora*, *C. pectoralis*, *C. novaezelandiae*), whereas *Margaroperdix*, *Anurophasis* and perhaps *C. gomerae* reached the fourth stage. Hypothetical extinction of all dispersive *Coturnix* species, along with persistence of the *Margaroperdix*/*Anurophasis* lineages, would result in the fifth stage, which could easily be misinterpreted as marine dispersal by these non-vagile species. Examples of 'stage five' in this framework include relictual lineages such as ratites [5,7], New Zealand wrens [16] and the New Caledonian kagu [69]. However, without a fossil record, dispersive ancestors in these and other stage-five examples can only be inferred.

5. Conclusion

Our phylogenetic and morphometric analyses confirm that *Margaroperdix* and *Anurophasis* are nested within the *Coturnix*

clade, and offer clear examples of island gigantism and evolutionary reversion to non-vagile adaptations in resident insular lineages arising within a vagile clade, rather than cases of rare dispersal by non-vagile taxa. Previous studies have reported increased body size [55], as well as rapid losses of dispersal ability [1], in lineages colonizing oceanic islands. Our results extend these findings to galliforms, and suggest that evidence for rare marine dispersal events by non-vagile taxa should be treated with caution, even when apparent cases derive from largely non-vagile clades.

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