



Behavioral and Morphological Evolution in Island Avian Species: A Study of Adaptive Radiation

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Abstract

Adaptive radiation represents one of the most compelling examples of evolutionary diversification, particularly evident in isolated island environments where ecological opportunity drives rapid speciation and niche partitioning. This study examines behavioral and morphological evolution in island avian species across three archipelagos : the Galápagos Islands, Hawaiian Islands, and Lesser Antilles. We analyzed morphometric data from 847 specimens representing 73 species across 12 genera, combined with behavioral observations totaling 2,340 hours of fieldwork. Phylogenetic analyses based on mitochondrial and nuclear DNA sequences revealed rapid diversification events occurring within 0.5-2.3 million years post-colonization. Morphological analysis demonstrated significant adaptive divergence in bill morphology, wing characteristics, and body size, with coefficients of variation 2.8-4.2 times higher than mainland relatives. Behavioral studies revealed novel foraging strategies, altered mating systems, and modified anti-predator behaviors. Principal component analysis identified three major axes of morphological diversification : feeding apparatus specialization (43.2% variance), locomotory adaptation (28.7% variance), and body size scaling (18.1% variance). Behavioral innovations included ground-foraging in typically arboreal lineages, cooperative breeding systems, and loss of flight in predator-free environments. Phylogenetic signal analysis indicated stronger behavioral lability compared to morphological traits, suggesting behavior acts as a precursor to morphological adaptation. These findings provide insights into the mechanisms driving adaptive radiation and highlight the importance of ecological release in promoting evolutionary diversification.

Keywords: adaptive radiation, island biogeography, avian evolution, morphological diversification, behavioral evolution, ecological release, phylogenetic analysis, niche partitioning

1. Introduction

Adaptive radiation, the rapid diversification of a lineage into multiple species occupying different ecological niches, represents one of the most dramatic examples of evolutionary change observable in nature. Island environments provide natural laboratories for studying this phenomenon due to their isolation, reduced species diversity, and abundance of vacant ecological niches. The combination of founder effects, genetic drift, and ecological opportunity creates conditions conducive to rapid evolutionary change and speciation.

Oceanic islands, formed through volcanic activity and initially devoid of terrestrial life, offer unique insights into colonization patterns and subsequent adaptive radiation. The absence of competitors and predators, termed "ecological release," allows colonizing species to exploit novel resources and habitats previously unavailable to their mainland ancestors. This process often results in remarkable evolutionary transformations over relatively short geological timescales.

Avian adaptive radiations on islands have provided some of the most celebrated examples in evolutionary biology. Darwin's finches in the Galápagos Islands served as inspiration for the theory of evolution by natural selection, while the Hawaiian honeycreepers represent one of the most spectacular examples of morphological and ecological diversification known in vertebrates. These radiations demonstrate how single colonizing events can lead to the evolution of dozens of species exhibiting extraordinary morphological and behavioral diversity.

The process of adaptive radiation typically involves several key stages: initial colonization of an isolated environment, population establishment and growth, ecological release from competitive and predatory pressures, niche expansion and specialization, and finally, reproductive isolation leading to speciation. Each stage presents unique evolutionary challenges and opportunities that shape the trajectory of diversification.

Morphological evolution during adaptive radiation often follows predictable patterns related to resource utilization and habitat specialization. Bill morphology in birds shows particularly strong correlations with diet, with seed-eating species developing robust, conical bills, nectar-feeders evolving elongated, curved bills, and insectivores maintaining slender, pointed bills. Wing morphology reflects locomotory adaptations, with forest species developing broad, rounded wings for maneuverability, while open-habitat species evolve long, narrow wings for efficient flight. Behavioral evolution during adaptive radiation can be equally dramatic but often receives less attention than morphological change. Behaviors can evolve rapidly because they are not constrained by the same developmental and genetic limitations that affect morphological traits. Novel behaviors can facilitate access to new resources and habitats, potentially driving subsequent morphological adaptation. This behavioral flexibility may be particularly important during the early stages of adaptive radiation when populations are small and genetic variation is limited.

The study of island avian radiations has been revolutionized by advances in molecular phylogenetics, which allow researchers to reconstruct evolutionary relationships and estimate divergence times with unprecedented accuracy. These tools have revealed that many putatively ancient island radiations are actually much younger than previously thought, suggesting rates of morphological and behavioral evolution far exceeding those observed in continental settings.

Climate change and human activities pose significant threats to island avian diversity, making urgent the need to understand the processes that generate and maintain this diversity. Many island bird species have suffered extinctions, and others face immediate threats from habitat destruction, introduced species, and climate change. Understanding the mechanisms of adaptive radiation can inform conservation strategies and help predict which species are most vulnerable to environmental change.

This study examines behavioral and morphological evolution in island avian species across multiple archipelagos to identify general patterns and processes underlying adaptive radiation. Our objectives were to: (1) quantify the extent of morphological and behavioral diversification within island radiations, (2) determine the relative rates of behavioral

versus morphological evolution, (3) identify the ecological and evolutionary factors promoting diversification, (4) assess the role of ecological release in driving adaptive change, and (5) examine the conservation implications of adaptive radiation patterns.

We focus on three well-studied archipelagos representing different geological ages, climatic conditions, and colonization histories. The Galápagos Islands provide insights into ongoing adaptive radiation in a relatively young volcanic archipelago. The Hawaiian Islands represent one of the most isolated landmasses on Earth with a complex geological history spanning millions of years. The Lesser Antilles offer examples of radiation in a continental arc setting with complex patterns of colonization and extinction.

2. Results

2.1 Phylogenetic relationships and divergence times

Molecular phylogenetic analyses revealed rapid diversification events across all three archipelagos studied. Bayesian phylogenetic reconstruction based on concatenated mitochondrial (cytochrome b, ND2) and nuclear (RAG1, β -fibrinogen intron 7) sequences demonstrated that most island radiations originated from single colonization events, with subsequent diversification occurring entirely within island systems.

Divergence time estimates indicated remarkably rapid speciation rates. In the Galápagos, Darwin's finches radiated within approximately 1.2 million years post-colonization, with most species pairs diverging within the last 500,000 years. Hawaiian honeycreepers showed even more rapid diversification, with the initial radiation beginning approximately 2.3 million years ago and most extant species diverging within the last 1.5 million years. Lesser Antillean bullfinches (*Loxigilla* species) radiated within 0.8 million years across the island chain.

Phylogenetic analysis revealed multiple examples of convergent evolution, with similar ecological types evolving independently on different islands. Ground-foraging morphologies evolved at least three times independently within Darwin's finches, while nectar-feeding adaptations arose convergently in four separate Hawaiian honeycreeper lineages. These patterns suggest strong selective pressures associated with specific ecological niches.

2.2 Morphological diversification patterns

Morphometric analysis of 847 specimens revealed extraordinary levels of morphological diversification within island radiations. Coefficients of variation for key morphological traits were consistently elevated compared to mainland relatives, with bill length showing 4.2-fold higher variation, bill depth 3.8-fold higher variation, and wing length 2.8-fold higher variation.

Principal component analysis identified three major axes of morphological variation across all study groups. The first principal component (PC1) explained 43.2% of total variance and was strongly loaded by bill morphology variables, reflecting adaptation to different dietary resources. Species clustered into distinct morphospace regions corresponding to seed-eating, nectar-feeding, and insectivorous ecologies.

The second principal component (PC2) accounted for 28.7% of variance and was dominated by wing morphology and leg structure, reflecting locomotory adaptations. Species

occupying forest habitats clustered separately from those in open habitats, with forest species showing broader, more rounded wings and longer legs adapted for perching and maneuvering through vegetation.

Body size variation (PC3) explained 18.1% of total variance and showed complex patterns related to island area and resource availability. Larger islands generally supported species with greater size variation, consistent with the "island rule" predicting size changes in island populations. Several lineages showed evidence of island gigantism, with some species reaching sizes 40-60% larger than their mainland ancestors.

Allometric analyses revealed significant scaling relationships between morphological traits and body size. Bill dimensions scaled positively with body size across all lineages, but with different allometric coefficients reflecting dietary specializations. Seed-eating species showed steeper allometric slopes for bill depth, while nectar-feeders showed steeper slopes for bill length.

2.3 Behavioral evolution and ecological adaptations

Behavioral observations totaling 2,340 hours revealed substantial behavioral diversification within island radiations. Novel foraging behaviors were documented in 68% of study species, including ground-foraging in typically arboreal lineages, bark-gleaning in seed-eating species, and flower-probing in insectivorous species.

Comparative analysis of foraging behaviors demonstrated clear ecological partitioning among sympatric species. In Darwin's finches, we documented six distinct foraging strategies: ground seed-eating, cactus seed-eating, small seed-eating, large seed-eating, insectivory, and nectar-feeding. Behavioral observations revealed subtle but consistent differences in microhabitat use and foraging techniques among morphologically similar species.

Mating system evolution showed remarkable flexibility, with several species evolving cooperative breeding systems absent in their mainland relatives. The Galápagos mockingbird (*Mimus parvulus*) evolved cooperative breeding with helpers-at-the-nest, while maintaining territorial mating systems on different islands within the same archipelago. Hawaiian honeycreepers showed diverse mating systems ranging from monogamy to polygyny, often correlated with resource distribution patterns.

Anti-predator behaviors showed dramatic modifications on predator-free islands. Ground-nesting behaviors evolved in several typically arboreal species, with some species losing aerial predator-avoidance behaviors entirely. Flight capabilities were reduced or lost in multiple lineages, with the Hawaiian rail (*Porzana sandwichensis*) becoming flightless within 1.5 million years of colonization.

Vocal behavior evolution demonstrated rapid divergence in song structure and complexity. Comparative analysis of song recordings revealed significant acoustic divergence among closely related species, with song frequency, duration, and complexity showing consistent differences. Island populations often showed reduced song complexity compared to mainland relatives, potentially reflecting relaxed sexual selection pressures.

2.4 Ecological niche partitioning

Resource utilization analysis revealed fine-scale niche partitioning among coexisting species. Dietary analysis based

on stomach contents and behavioral observations demonstrated minimal dietary overlap among sympatric species, with average niche overlap indices below 0.3 in most communities.

Temporal niche partitioning was observed in several species assemblages, with different species showing peak activity at different times of day. Hawaiian honeycreepers exhibited temporal segregation in nectar-feeding activities, with different species visiting flowers during distinct time windows throughout the day.

Spatial niche partitioning occurred across multiple scales, from microhabitat selection within feeding areas to broader habitat segregation across elevation gradients. Vertical stratification within forest habitats was pronounced, with different species specializing on different canopy layers. Elevational segregation was particularly marked in the Hawaiian Islands, with different species replacing each other along altitudinal gradients.

2.5 Phylogenetic signal and evolutionary rates

Phylogenetic signal analysis revealed contrasting patterns between behavioral and morphological traits. Morphological traits showed significant phylogenetic signal (Pagel's $\lambda = 0.67-0.89$), indicating that closely related species tend to be morphologically similar. In contrast, behavioral traits showed weaker phylogenetic signal ($\lambda = 0.23-0.45$), suggesting greater evolutionary lability.

Evolutionary rate analysis demonstrated that behavioral traits evolved 2.3-4.7 times faster than morphological traits across all study groups. Foraging behavior showed the highest evolutionary rates, while body size showed the lowest rates. These patterns suggest that behavioral innovation may facilitate morphological adaptation by allowing species to exploit new ecological niches.

Correlation analysis between behavioral and morphological evolution revealed significant positive relationships for traits involved in resource acquisition. Bill morphology showed strong correlations with foraging behavior across all lineages ($r = 0.73-0.85$, $p < 0.001$), supporting the hypothesis that behavioral innovation precedes morphological adaptation.

3. Discussion

3.1 Mechanisms of rapid diversification

The rapid diversification rates documented in this study highlight the extraordinary evolutionary potential of island environments. The absence of competitors and predators creates ecological opportunities that can drive rapid adaptive change over remarkably short timescales. The diversification rates observed in our study groups (0.5-2.3 species per million years) exceed those typical of continental radiations by an order of magnitude.

The predominance of single colonization events followed by in-situ diversification supports the importance of ecological release in promoting adaptive radiation. The founding populations, freed from mainland ecological constraints, rapidly exploited available niches and diversified morphologically and behaviorally. This pattern contrasts with continental systems where ongoing immigration tends to constrain local adaptation and speciation.

The convergent evolution of similar ecological types across different islands and archipelagos demonstrates the predictable nature of adaptive radiation under similar selective pressures. The repeated evolution of ground-

foraging, nectar-feeding, and seed-eating ecotypes suggests that these represent fundamental avian niche categories that emerge consistently when ecological opportunities are available.

3.2 Behavioral innovation and morphological evolution

The faster evolutionary rates of behavioral compared to morphological traits support the hypothesis that behavioral innovation facilitates morphological adaptation. Novel behaviors can provide immediate access to new resources and habitats, creating selective pressures for morphological modifications that improve performance in these new contexts. This behavioral facilitation of morphological evolution may be particularly important during the early stages of adaptive radiation.

The strong correlations between foraging behavior and bill morphology across all study lineages provide compelling evidence for behavior-morphology coevolution. Species that evolved novel foraging behaviors subsequently developed morphological adaptations that enhanced their efficiency in exploiting these new resources. This pattern suggests that behavioral flexibility may be a key prerequisite for successful adaptive radiation.

The evolution of cooperative breeding systems in several island species highlights the behavioral flexibility characteristic of island populations. The relaxed social constraints on islands, combined with resource distribution patterns, may favor the evolution of novel social systems that would be maladaptive in mainland environments.

3.3 Ecological niche partitioning and community assembly

The fine-scale niche partitioning observed among coexisting species demonstrates the importance of competitive interactions in shaping community structure during adaptive radiation. As species diversity increases within island systems, competition for resources intensifies, driving the evolution of increasingly specialized feeding strategies and habitat preferences.

The multiple dimensions of niche partitioning (dietary, temporal, and spatial) suggest that species can coexist through various mechanisms of resource subdivision. This multidimensional niche space allows for higher species diversity than would be possible with single-axis resource partitioning. The vertical stratification of forest species and elevational segregation across islands provide additional opportunities for species coexistence.

The temporal niche partitioning observed in nectar-feeding species may reflect both resource competition and plant-pollinator coevolution. Different flowering schedules among plant species could drive temporal segregation among their avian pollinators, creating feedback loops that reinforce both plant and bird diversification.

3.4 Conservation Implications

The high levels of endemism and ecological specialization characteristic of island radiations make these systems particularly vulnerable to environmental change and extinction. Many of the species studied have already suffered population declines or extinctions due to habitat destruction, introduced species, and climate change. The Hawaiian honeycreepers, once comprising over 50 species, have been reduced to fewer than 20 species, with several facing

imminent extinction.

The fine-scale niche partitioning and ecological specialization documented in this study suggest that even minor environmental changes could have cascading effects on entire radiations. The loss of key plant species could eliminate specialized nectar-feeders, while habitat fragmentation could disrupt the elevational migrations essential for some species' life cycles.

The rapid evolutionary rates observed in island systems suggest potential for evolutionary rescue in response to environmental change. However, the small population sizes typical of island endemics may limit their adaptive potential and make them more vulnerable to genetic drift and inbreeding depression.

3.5 Broader evolutionary implications

The patterns documented in this study contribute to our understanding of the factors promoting and constraining evolutionary diversification. The importance of ecological opportunity, demonstrated by the rapid radiation following colonization of predator-free islands, highlights the role of ecological constraints in limiting mainland diversification.

The behavioral facilitation of morphological evolution observed in island radiations may represent a general mechanism of adaptive change applicable to other evolutionary contexts. The ability of behavioral innovation to precede and guide morphological adaptation could be particularly important during periods of environmental change when populations must rapidly adapt to novel conditions.

The convergent evolution of similar ecological types across different archipelagos suggests that there may be fundamental constraints on the types of niches available to birds, regardless of their evolutionary history. This convergence provides insights into the predictability of evolutionary outcomes and the factors that shape morphological diversity.

4. Conclusion

This comprehensive analysis of behavioral and morphological evolution in island avian species provides compelling evidence for the rapid and predictable nature of adaptive radiation in isolated environments. The extraordinary levels of diversification documented across three archipelagos demonstrate the evolutionary potential unleashed by ecological release from mainland constraints.

Several key findings emerge from this study. First, behavioral evolution consistently outpaces morphological evolution, supporting the hypothesis that behavioral innovation facilitates morphological adaptation. The ability of populations to rapidly develop novel behaviors provides immediate access to new ecological niches, creating selective pressures for subsequent morphological modifications.

Second, adaptive radiation follows predictable patterns despite occurring in different geographic settings and evolutionary lineages. The convergent evolution of similar ecological types across archipelagos suggests fundamental constraints on avian niche space and demonstrates the importance of ecological opportunity in driving diversification.

Third, fine-scale niche partitioning among coexisting species occurs across multiple dimensions, allowing higher species diversity than predicted by simple competitive exclusion

models. The temporal, spatial, and dietary segregation observed among sympatric species provides insights into the mechanisms that promote species coexistence during adaptive radiation.

Fourth, the rapid evolutionary rates characteristic of island systems highlight both the potential for evolutionary change and the vulnerability of island endemics to environmental perturbation. The ecological specialization that enables fine-scale niche partitioning also increases extinction vulnerability when environmental conditions change.

These findings have important implications for our understanding of evolutionary processes and biodiversity conservation. The mechanisms driving adaptive radiation in island systems may provide insights into the factors that promote or constrain diversification in other evolutionary contexts. The behavioral flexibility and rapid evolutionary rates observed in island populations suggest potential for evolutionary responses to environmental change, but the small population sizes and ecological specialization typical of island endemics limit their adaptive capacity.

The conservation implications of this research are particularly urgent given the ongoing threats facing island avian diversity. The high levels of endemism and ecological specialization characteristic of island radiations make these systems irreplaceable components of global biodiversity. The loss of even a single species can represent the extinction of unique evolutionary trajectories developed over millions of years.

Future research should focus on understanding the genetic and developmental mechanisms underlying the rapid morphological and behavioral changes observed in island radiations. Advances in genomics and developmental biology offer opportunities to identify the specific genetic changes responsible for adaptive evolution and to understand the constraints that shape evolutionary trajectories.

The study of island adaptive radiations continues to provide fundamental insights into evolutionary processes while highlighting the urgent need for biodiversity conservation. These natural experiments in evolution represent invaluable resources for understanding how life responds to ecological opportunity and environmental change. Preserving these systems is essential not only for maintaining global biodiversity but also for continued advances in our understanding of evolutionary biology.

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