Parallel evolution in an island archipelago revealed by genomic sequencing of *Hipposideros* leaf-nosed bats

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Abstract

Body size is a key morphological attribute, often used to delimit species boundaries among closely related taxa. But body size can evolve in parallel, reaching similar final states despite independent evolutionary and geographic origins, leading to faulty assumptions of evolutionary history. Here, we document parallel evolution in body size in the widely distributed leaf-nosed bat genus *Hipposideros*, which has misled both taxonomic and evolutionary inference. We sequenced reduced representation genomic loci and measured external morphological characters from three closely related species from the Solomon Islands archipelago, delimited by body size. Species tree reconstruction confirms the paraphyly of two morphologically designated species. The nonsister relationship between large-bodied *H. dinops* lineages found on different islands indicates that large-bodied ecomorphs have evolved independently at least twice in the history of this radiation. A lack of evidence for gene flow between sympatric, closely related taxa suggests the rapid evolution of strong reproductive isolating barriers between morphologically distinct populations. Our results position Solomon Islands *Hipposideros* as a novel vertebrate system for studying the repeatability of parallel evolution under natural conditions. We conclude by offering testable hypotheses for how geography and ecology could be mediating the repeated evolution of large-bodied *Hipposideros* lineages in the Solomon Islands.

Keywords: biogeography, community assembly, diversification, ecological speciation, ecomorph, niche space

Introduction

Radiations of closely related lineages, replicated across islands or lakes, have revealed much about the evolution of phenotypic variation (Bolnick et al., 2018; Heckley et al., 2022; Magalhaes et al., 2021; Schluter, 2000). Among the most striking patterns uncovered include species groups that have diversified in parallel, beginning at similar evolutionary starting points to independently arrive at similar endpoints (i.e., independently derived phenotypic similarity in two or more lineages) (Cerca, 2023; Losos, 2009; Magalhaes et al., 2021). Famous examples include Anolis lizards of the Greater Antilles (Losos, 2009; Mahler et al., 2013), Hawaiian spiders (Gillespie et al., 2018), Arctic charr (Adams et al., 2008), and benthic and limnetic pairs of sticklebacks (Schluter, 2000). These and other examples of phenotypic parallelism have provided strong lines of evidence for the roles of natural selection, environmental variation, and vacant ecological niches in spurring speciation (Stuart et al., 2017).

Body size is a fundamental morphological trait that features prominently among the phenotypic changes that accompany parallel radiations (Adams et al., 2008; Boughman et al., 2005; Kozak et al., 2009; Nagel & Schluter, 1998; Ratciliffe & Grant, 1983; Richmond & Reeder, 2002). It is also a critical variable that influences almost every life history characteristic of an organism, including prey opportunities, risk of predation, ability to thermoregulate, and dispersal ability (Gardner et al., 2011; Jenkins et al., 2007; Sinclair et al., 2003). Interspecies differences in body size can also act as a premating reproductive isolating barrier, playing an important role in mate recognition and contributing to long-term genetic isolation (Nagel & Schluter, 1998; Ratciliffe & Grant, 1983). For these reasons, measurements of body size are often used to delimit species boundaries among closely related taxa (e.g., Chen et al., 2017; Venkatraman et al., 2019). However, taxonomic and evolutionary inferences drawn from body size alone can be misleading and mask more complex underlying histories (e.g., DeCicco et al., 2020; Richmond & Reeder, 2002).

Leaf-nosed bats (genus *Hipposideros* Gray, 1831) are a lineage of insectivorous bats distributed through much of the Old World tropics and organized into nine species groups (Hill, 1963; Simmons, 2005). The diadema species group includes *H. diadema* Andersen, 1905, recognized as a single widespread species occurring from Southeast Asia, through the Philippines, New Guinea and into northern Australia and the Solomon Islands. Other members are largely restricted

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range endemics (e.g., *H. inexpectatus* Laurie & Hill, 1954; *H. inornatus* McKean, 1970; *H. pelingensis* Shamel, 1940; *H. dinops* Andersen, 1905; *H. demissus* Andersen, 1909) (Hill, 1963). In the Solomon Islands archipelago *H. diadema* is distributed across all larger central islands, except for Makira, which supports a smaller-bodied population that has been split off as the endemic Makira Leaf-nosed Bat (*H. demissus*). The Solomon Islands endemic fierce leaf-nosed bat (*H. dinops*) is endemic to the archipelago and occurs in sympatry with *H. diadema* from Bougainville to Guadalcanal and Malaita (i.e., excluding Makira) (Lavery & Flannery, 2023; Figure 1A and B).

Phylogenetic reconstructions based on DNA sequence data for the Family Hipposideridae recovered Solomon Islands H. diadema, H. dinops, and H. demissus interspersed throughout a single, poorly resolved clade (Lavery et al., 2014). Shallow genetic divergence raised questions about the taxonomic validity of H. dinops and H. demissus. But most puzzling was a well-supported case of reciprocal paraphyly, whereby two mitochondrial clades each contained sister pairs of H. dinops and H. diadema. Further, mitochondrial divergence values between H. diadema samples from the Solomon Islands and New Guinea were greater than any observed divergence values between H. diadema and H. dinops samples from within the Solomon Islands (Lavery et al., 2014). These unexpected relationships suggested the rapid and repeated evolution of larger-bodied *Hipposideros* ecomorphs on separate islands in the archipelago and that the taxonomic arrangement based on body size did not correspond with the evolutionary history of this group.

Here, using expanded sampling and both morphological and genomic datasets, we aimed to further resolve the taxonomy and evolutionary history of the Solomon Islands *H. diademaldinops* complex. We posed three key questions: (1) Can standard body size measurements be used to assign individuals to described species confidently? (2) Do thousands of genome-wide markers reaffirm reciprocal monophyly among species identified by body size? (3) Has gene flow ceased between recently diverged populations, indicating the evolution of genetic isolating barriers between sympatric taxa?

Methods

Morphology

Specimens cited here are deposited in the collections of the Australian Museum, Sydney (AM); Queensland Museum, Brisbane (QM); University of Kansas Natural History Museum, Lawrence (KU); and Bernice Pauahi Bishop Museum, Honolulu (BPBM). THL measured the length of the forearm (FA) as a proxy for overall body size for Hipposideros specimens from the Solomon Islands using hand-held callipers to the nearest 0.01 mm. Bats were assigned to species using forearm length and age classed by examining the joint between the 5th metacarpus and 5th phalanx: (1) adult by having fully formed wing bones with a fused, circular joint and no indication of cartilage between the bones; (2) subadult by having smooth wing joints with one or two bands of cartilage and blood vessels clearly visible at the joint when held up to light; or (3) juvenile by having flat, unfused wing joints with transparent cartilaginous bands between the bones (Jackson, 2003). We generated a boxplot of forearm length, colored by a priori species assignment, using the R package ggplot2 (Wickham, 2016).

DNA extraction, library preparation, and sequencing

We extracted total genomic DNA using a QIAGEN DNeasy blood and tissue extraction kit (QIAGEN, Hilden, Germany) following manufacturer protocols for tissue samples from 41 Hipposideros specimens from the Solomon Islands and Papua New Guinea. Extracts were quantified using Qubit Fluorometric Quantification (Thermo Fisher Scientific, Waltham, MA, USA) and standardized to 5 ng/µl per 10 µl volume. Genomic libraries, prepared at the University of Kansas Genomic Sequencing Core, were generated for each individual using a standard RADseq protocol (Andolfatto et al., 2011) with enzymatic digestion using NdeI (New England BioLabs, Ipswich, MA, USA) and size-selection of fragments for 248-302 bp using Pippin PrepTM (Sage Science, Beverly, MA, USA). Pooled samples were amplified and ligated with sequencing primers using a Phusion High-Fidelity PCR Master Mix. Fragment sizes were confirmed using an Agilent 2100 Bioanalyzer (Agilent Technologies, Santa Clara, CA, USA) and sequenced on a NextSeg 550 (Genomic Sequencing Core Facility at the University of Kansas) producing single-end 100-bp reads.

De novo locus assembly, SNP calling, and quality filtering

We demultiplexed reads using "process_radtags" in Stacks v2.41 (Rochette et al., 2019). We used *fastqcR* (https://github. com/kassambara/fastger) to determine the number of reads in each sample and dropped samples with <10% of the total number of reads present in the median sample (10 of 41 samples; https://devonderaad.github.io/bats/qc/qc.html). We followed Paris et al. (2017) to optimize the de novo assembly of our RAD loci by iterating over the following suites of parameter values in Stacks, "m" (minimum number of raw reads by locus) varied 1-8, "M" (number of mismatches allowed in a locus within a sample) varied 3-7, and "n" (number of mismatches allowed between samples when building a catalogue of loci) varied as M – 1, M, and M + 1, based on the optimal value of M. For each parameter value, we output an unfiltered variant call format (vcf) file using the Stacks "populations" module, calculated the number of variable sites for each set of parameter values, and optimized each parameter based on which value generated the most polymorphic loci present in at least 80% of samples (Paris et al., 2017) optimal values: m = 3, M = 2, and n = 3 (Supplementary Figure S1).

We filtered called SNP genotypes using the R package SNPfiltR v1.0.0 (DeRaad, 2023), using a minimum depth of 3 reads and a minimum genotype quality of 30, converting 0.02% and 8.31% of genotypes to missing values, respectively. We required heterozygous genotypes to have an allele balance between 0.25 and 0.75, which converted 0.74% of all remaining genotypes to missing, and imposed a maximum mean depth filter of 100 reads per genotype, removing 2.21% of all SNPs. We visualized missing data by sample and removed three additional samples that were missing >70% of called SNPs. We imposed a per-SNP minimum completeness threshold of 90%, removing 59.54% of the remaining SNPs. We implemented a MAC filter of 1, removal of singletons, which removed 56.07% of remaining SNPs and improved sample discrimination in multidimensional clustering, for a final filtered SNP dataset containing 28 samples and 17,204 SNPs, with 3.29% overall missing data and no samples missing >25% of SNPs (referred to as our "all SNPs dataset"). We also filtered for physical



Figure 1. Solomon Islands Archipelago *Hipposideros*: (A) known distributions of these three species in the Solomon Islands and extralimital distribution of *H. diadema* (inset); (B) photographs from a Guadalcanal field site demonstrating the size difference between sympatric *H. diadema* and *H. dinops*; and (C) a boxplot of forearm lengths recorded from 20 *H. demissus* (Makira), 54 *H. diadema* (Bougainville, Choiseul, Guadalcanal, Malaita, Ngella, and Santa Isabel), and 29 *H. dinops* (Bougainville, Gatokae, Guadalcanal, Malaita, and Santa Isabel).



Figure 2. Population genetics of the Solomon Islands *Hipposideros* radiation. (A) An unrooted phylogenetic network with tips colored according to geography and shaped according to species assignment (i.e., body size classes). Double hash marks indicate artificially shortened branches to allow outgroups to fit on the page. The gray shading box highlights the five clades for which we have population-level sampling (i.e., more than two individuals). (B) Principal component analysis (PCA) using as input our filtered SNP dataset, subset to include only the 5 clades highlighted in the phylogenetic network. The inset table shows pairwise F_{ST} for all 10 possible pairwise comparisons. (C) Bar plots showing ancestry assignment of each individual sample under the optimal number of ancestry bins (k = 4), and our a priori assumed optimal number of bins based on the PCA and phylogenetic network (k = 5).

linkage, thinning the dataset to one SNP per RAD locus, resulting in 10,586 SNPs with 3.39% overall missing data (referred to as our "thinned SNPs dataset").

Population genetics

We visualized pairwise differentiation (Nei's D; Nei, 1973) to assess the genetic clustering of our samples without a priori assumptions using *StAMPP* v1.6.3 (Pembleton et al., 2013). We then used this pairwise sample divergence matrix to construct an unrooted neighbor-net using *SplitsTree4* v4.15.1 (Huson & Bryant, 2006).

We restricted our dataset to sampled populations with >2 unique individuals for the five closely related clades at the bottom of the unrooted phylogenetic network, removing invariant or singleton SNPs (17,204 SNPs), producing a dataset of 22 individuals and 7,982 filtered SNPs. We used the R package *adegenet* v2.1.5 (Jombart, 2008) to perform principal component analysis (PCA) among our remaining five clades of interest, and calculated pairwise F_{ST} using *StAMPP*. We used *ADMIXTURE* v1.3.0 (Alexander et al., 2009) to assign individual sample ancestry without a priori sample assignments using the filtered SNP dataset of 4,906 unlinked SNPs shared among these 22 samples (Linck & Battey, 2019). We tested k values (i.e., number of allowed bins of genetic ancestry) of 1–10 and used cross-validation to determine the optimal k value for this dataset (Supplementary Figure S2). Population assignment was applied to tips in subsequent species tree analyses.

Species tree reconstruction

We used *ASTRAL-III* v5.7.7 (Zhang et al., 2018) to reconstruct a species tree under a multispecies coalescent framework (Kubatko & Degnan, 2007). We exported a concatenated phylip file including all sites (SNPs plus invariant sites) for the 10,586 RAD loci that passed all filtering thresholds, using the *Stacks* "populations" module. We then split this file into a unique fasta alignment for each locus and converted these to nexus format using the script "convert.py" (https://github.com/mmatschiner/tutorials/blob/master/ml_ species_tree_inference/src/convert.py). We used *IQ-TREE 2* v.2.2.0 (Minh et al., 2020) to generate a maximum likelihood tree and perform 10,000 ultra-fast bootstrap replicates for each nexus file. We collapsed branches of these gene trees if their supporting nodes had bootstrap values <= to 10, which



Figure 3. Reconstructing the speciation history of this radiation. (A) Species tree reconstructed from 10,586 input gene trees. Posterior probability (0–1) is labeled on each node for the preceding internal branch. (B) Species tree reconstruction with a single migration edge allowed to explain additional variation present in the SNP dataset. Bootstrap support values are shown on each internal branch based on the proportion (0–1) of 100 bootstrap replicate trees containing the given internal branch. Both trees (panels A and B) are rooted in *Hipposideros diadema* from PNG following the molecular phylogeny of Lavery et al. (2014).



Figure 4. Testing for gene flow between nonsister taxa. (A) Heat map displaying the value of each *f*-branch statistic calculated on the species tree topology recovered using *ASTRALIII*. A single asterisk indicates a somewhat significant (0.05 > p > 0.005) result, two asterisks indicate a significant result (0.005 > p > 0.0005), and three asterisks indicate a highly significant result (p <= 0.0005). (B) Heat map of the D-statistic value, resulting from pairwise ABBA/BABA tests for every amenable comparison.

increased our signal-to-noise ratio, i.e., increased posterior probabilities across the recovered species tree. We present the reconstruction built from input gene trees with low support nodes collapsed in the main text and show the tree built from all input gene trees in the supplement, which differs in topology only in the placement of a single tip, *H. diadema* from Isabel (Supplementary Figure S3).

We used *TreeMix* v4 (Pickrell & Pritchard, 2012) to construct a species tree under a maximum likelihood framework and allow for potential gene flow edges, using our thinned SNPs dataset and the same sample-to-species tip assignment as above. We first estimated a species tree based on allele frequency covariance among specified tips, without migration edges, before iteratively adding five individual migration edges. The tree with one migration edge explained >99.8% of overall variation, a threshold recommended by the software authors (Pickrell & Pritchard, 2012; Supplementary Figure S4). We inferred that the *TreeMix* species tree with one migration edge represented the optimal trade-off between over and underparameterization in explaining the variance in our underlying SNP dataset. We performed 100 bootstrap replicates of this species tree with a single migration edge, resampling 100 SNP blocks to generate support values for internal branches. We used the SumTrees command from *DendroPy* v4.5.2 (Sukumaran & Holder, 2010) to collate these support values and visualize them on the species tree. Species trees were rooted using a sample of *H. diadema* from mainland Papua New Guinea, following the molecular phylogeny of Lavery et al. (2014) that encompassed the study region and incorporated broader taxonomic sampling from the family Hipposideridae.

Testing for gene flow

To test for gene flow among nonsister taxa, we used *Dsuite* v0.4 (Malinsky et al., 2021) to calculate pairwise D statistics for all possible tip combinations amenable to an ABBA/BABA topology, using our thinned SNPs dataset as input. We used the *ASTRAL-III* species tree topology and designated *H. dia-dema* from PNG as the outgroup. We used *Dsuite* to calculate the *f*-branch statistic, which incorporates both ABBA/BABA and f4-ratio statistics to generate a summary statistic describing the likelihood of gene flow in pairwise comparisons between both species tips and internal branches amenable to testing under an ABBA/BABA topology. We performed a block-Jackknife procedure resampling in automatically optimized window sizes to generate *Z* scores, which we converted into a false-discovery rate (Benjamini & Hochberg, 1995) and adjusted *p*-values for each pairwise *f*-branch comparison.

Results

Morphology

Measurements of forearm length (a proxy for overall body size) in 92 *Hipposideros* from the Solomon Islands revealed that the three named species in the diadema group corresponded with three discrete, nonoverlapping body size classes (Figure 1C). No adult individuals with intermediate forearm lengths were encountered among the specimens examined from across the Solomon Islands in this study.

Phylogeography and population genetics

The phylogenetic network revealed that each body size class on each sampled island formed a distinct clade (Figure 2A). For the five closely related Solomon Islands clades with appropriate population level sampling, PCA showed clustering of all five clades with no detectable intermediates on the first two PC axes (Figure 2B), and F_{ST} revealed moderate to high divergence in all pairwise comparisons (range = 0.22–0.55). Ancestry assignments from the program *ADMIXTURE* mostly lumped *H. diadema* from Isabel and Guadalcanal under an optimal k = 4 (Figure 2C), but at k = 5, ancestry assignments corresponded perfectly with the five clades identified in the phylogenetic network and PCA, with no indication of mixed ancestry in any of the sampled individuals.

Species tree reconstruction strongly supported the same pattern identified previously in the mitochondrial genome (Lavery et al., 2014), where all three body size classes (small, *H. demissus*; medium, *H. diadema*; large, *H. dinops*) from the Solomon Islands were interspersed throughout a single polyphyletic clade corresponding to a recent radiation within the archipelago (Figure 3A).

The *H. diadema* and *H. dinops* lineages found in sympatry on Guadalcanal were recovered as sisters but with low posterior probability, reflecting uncertainty in the branching order among these two taxa and *H. diadema* from Ngella. Our SNP-based species tree reconstruction allowing for a single migration edge recovered a nearly identical tree with relatively strong bootstrap support (Figure 3B). The one internal branch that conflicted with the gene-tree-based reconstruction was also the least supported (bootstrap support = 0.64). The short length of the internal branches in both species trees, relative to the terminal tips, reflects a rapid succession of diversification events during the evolutionary history of this group, which has made the accurate resolution of a single set of bifurcating relationships a serious challenge. The single migration edge connected tips representing *H. diadema* populations on the nearby islands of Rendova and Gatokae.

This migration edge was also supported by a statistically significant signal of gene flow between *H. diadema* individuals on Rendova and Gatokae (Figure 4A). Additional cases of excess allele sharing between nonsister taxa that reached a traditional significance threshold (p <= 0.05) indicated gene flow between *H. diadema* on Gatokae and Ngella, but these comparisons had D-statistic values much closer to zero (Figure 4B). We found no evidence for gene flow between lineages in different body size classes, using a traditional p < 0.05 significance threshold (Figure 4B).

Discussion

Body size is a fundamental morphological variable linked to many life history traits and is often used to delimit species. In the Solomon Islands Hipposideros bats, body size (most reliably gauged through forearm length) has long been used in this manner to discern among the largest species (H. demissus, H diadema, and H. dinops) with assumed confidence (e.g., Flannery, 1995; Hill, 1963; Lavery & Flannery, 2023; Tate, 1941). Here, our morphological dataset has reaffirmed the existence of clear body size cohorts, i.e., measured forearm lengths of adult Hipposideros bats conformed to the nonoverlapping size distributions prescribed to H. diadema, H. dinops, and H. demissus (Lavery & Flannery, 2023). Intermediate specimens that could signal hybridization were not encountered, and unambiguous labeling of individuals as either H. diadema or H. dinops has thus been understandable. However, body size can also be misleading (e.g., DeCicco et al., 2023; Kozak et al., 2009), as we reveal here in this detailed genomic investigation of Solomon Islands Hipposideros bats. Indeed, we demonstrate that these clear and consistent ecomorph size cohorts have masked far more complex patterns of parallel evolution that appear to define the evolutionary history of this radiation.

We found evidence that the *Hipposideros* bats of the Solomon Islands form a rapid intra-archipelago radiation based on the short, poorly resolved internal branches in all phylogenetic reconstructions. Surprisingly, we find no support for the monophyly of individuals from the same body size classes (i.e., currently recognized species) on separate islands (Figure 3). Assuming the founding ancestral lineage possessed an intermediate body size (as seen in outgroup *H. diadema* taxa on PNG and New Britain, and all individuals assigned to *H. diadema* in the Solomon Islands) all phylogenetic reconstructions support parallel evolution of large-body size (i.e., individuals identified as *H. dinops*) on multiple islands, plus a separate shift to smaller body size on Makira (*H. demissus*). These results have broad relevance for island biotas, given the generally large island sizes required for intra-island speciation

(especially bats and large mammals) and the comparatively small island sizes being considered here (e.g., Rendova island is approximately 411 km²) (Heaney et al., 2018).

The evidence for gene flow found between *H. diadema* individuals from Rendova and Gatokae is highly plausible, considering these two islands lie in close proximity within the New Georgia group and may have been physically interconnected during lowered sea levels of the Last Glacial Maximum (Lavery et al., 2023). Supported gene flow events between *H. dinops* on Guadalcanal and Rendova and *H. diadema* on Gatokae and Ngella were more difficult to interpret because these lineages are not in close geographic proximity. Because ABBA/BABA tests are prone to false positive results from substitution rate variation among species tips (Frankel & Ané, 2023), we urge caution in the interpretation of these results. Nonetheless, it is noteworthy that significant ABBA/BABA results were exclusively recovered in pairwise comparisons between allopatric taxa from the same body size class.

In contrast, our failure to detect gene flow between sympatric body size classes is evidence for the rapid evolution of reproductive isolating barriers between ecomorphs. In fact, the sister lineages sampled from Guadalcanal exist in syntopy in Kovi Cave on the northern side of the island. In that location, both ecomorphs are present year-round, and despite synchronous timing to their breeding (Lavery & Flannery, 2023), our data have indicated the two size classes are reproductively isolated. This indicates body size is somehow either directly or indirectly linked to mate recognition in these lineages.

Ecological explanations for parallel evolution?

We postulate that the evolution of large *Hipposideros* ecomorphs could be underpinned by tight eco-physiological links that exist between these bats and their environments (Francis & Habersetzer, 1998). A backdrop of complex island geography with replicated vacant and highly favorable niche spaces would plausibly enable these underpinnings to drive repeated large ecomorph evolution across independently colonized islands. We offer two hypothetical, non-exclusive niches that could be underexploited and provide the context for repeated shifts to larger body sizes in Solomon Islands *Hipposideros*.

Our first hypothesis pivots on the recognized inter- and intra-specific links between body size, echolocation frequency, and optimal prey selection that exist among Hipposideros (i.e., bats with larger body sizes call at lower frequencies and optimally detect larger insect prey; Jacobs et al., 2007; Sun et al., 2021; Zhang et al., 2000). Disruptive ecological selection commonly acts on echolocation frequencies of bats in association with prey size specializations (Jones, 1997), and simple body size divergence in bats has extraordinary importance for trophic niche partitioning and stable coexistence of sympatric species (Andreas et al., 2012). We postulate a suite of large, abundant, nocturnal insects that could exist in Solomon Islands' cluttered forests, underexploited by bats or other insectivores. Under this scenario, these larger insects would be optimally detected by lower echolocation frequencies, placing selective pressure toward lowered calls and their corresponding increases in body size. Repeated natural selection to exploit this same niche independently could result in the generation of bat lineages with consistently larger body size across multiple islands (Francis & Habersetzer, 1998; Schnitzler & Kalko, 2001).

Under our second hypothesis, we propose that larger body size would be adaptive if it enabled a dietary switch from insectivory to carnivory (defined as predation on terrestrial vertebrates). Norberg and Fenton (1988) developed a set of predictors for carnivory in echolocating bats based on three characteristics that are shared across eight of the ten echolocating species known to consume vertebrate prey. These were: a body mass greater than 17 g; a wing aspect ratio less than or equal to 6.3, and a relative wing loading greater than 36. Hipposideros dinops reaches or exceeds the specified thresholds for all three predictors. In further support of this possibility, occasional carnivory has been reported in northern Australian H. diadema (verified by the presence of bird feathers in fecal samples; Pavey & Burwell, 1997). This apparent capability in H. diadema raises the distinct possibility that our hypothetical vacant niche space could instead be centered on underexploited terrestrial vertebrates that could be optimally targeted by larger bats.

Conclusions and future directions

A growing body of Solomon Islands-focused research has elucidated the value of this archipelago for understanding how island configurations and ontogenies, oceanic barriers, and intermittent land bridge formations can shape genetic and taxonomic diversities (Brown et al., 2015; Hagen et al., 2012; Lavery et al., 2023; Manthey et al., 2020; Moyle et al., 2009; Pulvers & Colgan, 2007; Smith & Filardi, 2007; Toussaint et al., 2016). Here, we have further enriched this body of work with evidence for extensive paraphyly among Solomon Islands' *Hipposideros* bats. These newly documented patterns of relatedness support at least two parallel shifts to a larger body size throughout the evolutionary history of this group, suggesting that natural selection is causing independent lineages to repeatedly converge on a consistent, large-body-size ecomorph.

Our insights fuel at least four key questions around this study system, each of which deserves to be investigated in future studies with greater sample sizes and careful attention. (1) What is the broader pattern of evolutionary history in Solomon Islands Hipposideros when wider sampling is incorporated, and how many independent shifts in body size are apparent in the group? To address this question, additional sampling of sympatric (or preferably syntopic) pairs of H. diadema and H. dinops are needed from major biogeographic units (i.e., Malaita, Bougainville-Choiseul-Isabel, Vella La Vella-Ranongga, Kolombangara-New Georgia-Vangunu-Gatokae, and Rendova-Tetepare) (see Lavery et al., 2023; Lavery & Flannery, 2023). (2) Are ecological factors driving such a rapid, repeated, and clear divergence of large ecomorphs from H. diadema ancestors? We propose efforts to examine this could first focus on dietary studies of H. diadema, H. dinops, and H. demissus either in the field or museum spirit specimens to see if dietary shifts can be detected, either across invertebrate size cohorts or from invertebrates to vertebrates. (3) How does body size contribute to mate recognition and reproductive isolation when multiple ecomorphs occur in sympatry? (4) Can independently evolved large morphs be separated from one another using more detailed studies of morphology? Together, these points have significant implications for the taxonomy of the diadema species group in the Solomon Islands. Despite the shallow divergence of large morphs, we argue they should not be lumped with H. diadema because Guadalcanal populations are reproductively isolated in syntopy. In fact, splitting of the large-bodied morphs grouped under H. dinops into individual taxa may be warranted if this scenario is mirrored on other islands. However, fundamental to forming a view on this is a better understanding of gene flow between lineages, whether they would remain reproductively isolated if brought into sympatry, and whether they can be differentiated using morphological characters.

We have provided the first genomic insights into the surprisingly complex evolutionary history of Solomon Islands *Hipposideros* bats, albeit with limited sampling (geographic and numbers of individuals). Nonetheless, our results establish Solomon Islands *Hipposideros* among a select group of vertebrate study systems where instances of parallel evolution have provided valuable insights into the roles of natural selection, environment, and ecology in species evolution (e.g., Colosimo et al., 2005; Hohenlohe et al., 2012; Kolbe et al., 2011; Moran et al., 2023). We believe a further focus on the repetitive evolution of *Hipposideros* across island replicates, leveraged against the single-size morph on Makira (where vertebrate diversity is lower—Hypothesis 2, and under Hypothesis 1, we predict insects are smaller) could provide similarly valuable insights.

Supplementary material

Supplementary material is available online at Evolution.

Data availability

All code needed to reproduce the results of this study can be found by following the links on the homepage of the dedicated GitHub repository for this project at https://github. com/DevonDeRaad/bats. This entire repository is also permanently archived via Zenodo at https://doi.org/10.5281/ zenodo.10780528. Raw sequence data are available via NCBI's Sequence Read Archive, BioProject PRJNA1084085, at https://www.ncbi.nlm.nih.gov/bioproject/1084085.

Ethical statement

Research and sampling were completed under permit no. RP/2018/004 (Solomon Islands). Animal handling was approved by the University of Kansas (IACUC authorization 158-04, to Rafe M. Brown).

Author contributions

T.H.L. conceptualized the study. T.H.L, J.M.S., L.K.-P.L., and R.G.M. designed the study. T.H.L., P.S.H., K.V.O., and L.H.D. collected field data and tissue samples. T.H.L., K.V.O., and L.H.D. completed DNA extractions. T.H.L. and D.A.D. collected all morphological data. D.A.D. conducted genomic analyses. T.H.L. wrote the initial manuscript with input from R.G.M., D.A.D., and L.H.D., and all authors reviewed, edited and approved the final version of the manuscript.

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