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thesis abstract

The mammals of Northern Melanesia: biogeography, systematics and ecology

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Abstract. Northern Melanesia's mammals are poorly known, and perceived deficiencies in faunal records and taxonomic descriptions have, until now, hindered detailed analyses. I examined aspects of biogeography, systematics and ecology in the region's mammalian faunas. Generalized linear models (GLMs) were used to test for differences in rates of persistence in four orders of mammal on continental shelf islands. Ochiai and endemism indices were used to delineate regions of high endemism and influential biogeographic boundaries. A non-parametric multivariate regression tree and GLMs were used to identify the influences of abiotic variables on mammalian species richness. Genetic sequencing, microsatellite genotyping, morphological and ecological data were used to determine evolutionary relationships among the widespread insectivorous bat family, Hipposideridae. Northern Melanesia's islands support mammalian faunas that reflect the poor over-water dispersal abilities of non-volant mammals; lower rates of long-term persistence in dasyuromorphs and diprotodonts; pronounced diversification of the Family Pteropodidae; and comparative lack of speciation in insectivorous bat families. Analyses produced a clear hierarchical classification of Northern Melanesia's islands based on their physical attributes and mammal assemblages, providing the first empirical analyses of Northern Melanesia's and New Guinea's mammalian zoogeography, and adding to biogeographic theory at both regional and local scales.

Keywords. Dasyurid, evolution, extinction, *Hipposideros*, island, mammal, Melanesia, Pacific, speciation, zoogeography.

Introduction

Northern Melanesia is an ideal location for biogeographic studies. Analyses of the region's avifauna have contributed major advances toward theories of evolution and zoogeography including Mayr's biological species concept (Mayr 1942, 1963), and Diamond's ideas on dispersal, gene flow and speciation (Diamond 1970, 1974; see Mayr and Diamond 2001 for a compilation of similar works). Studies of Northern Melanesia's birds continue to spur fundamental advances in biogeographic and evolutionary theory (e.g., Filardi and Moyle 2005, Uy et al. 2009).

In comparison, the mammals of Northern Melanesia are poorly known. Authors of previous mammalian biogeographic studies for this region have typically deferred from empirical tests of biogeographic patterns (Koopman 1979, Flannery 1995a, 1996). The majority of analyses have in-

stead been restricted to qualitative descriptions of species distributions and diversity. This is primarily due to the perceived deficiencies in the faunal record and taxonomic descriptions for the region.

Almost 20 years following the most comprehensive of biogeographic studies, the mammalian fauna of Northern Melanesia remains poorly documented, and gaps exist in the inventories of islands large and small. Despite important advances in faunal survey and taxonomy that have occurred since 1995 (e.g. Helgen and Flannery 2004b, Helgen 2005b, Aplin and Opiang 2011), a comprehensive understanding of the region's mammalian diversity remains elusive. In the meantime, rapid alterations to Melanesia's natural environments are occurring due to mineral and timber extraction. Also, animal species and environments throughout Oceania are particularly vulnerable to extinction and decline (Woinarski 2010), and an-

thropogenic disturbance has the potential to greatly alter species distributions and biogeographic processes.

Biogeographic studies of Northern Melanesia's mammals present opportunities for novel insight given the unusual dominance of marsupials within adjacent continental source pools. The region also contains a variety of islands, including continental shelf islands, oceanic islands and recently defaunated volcanic islands. These offer vast opportunities to dissect the roles of abiotic island variables in shaping mammalian biogeography.

My thesis research (Lavery 2014b) combined biogeography with systematics and ecology to better define the distributions of mammals in Northern Melanesia (defined as comprising the Admiralty, Bismarck, D'Entrecasteaux, Louisiade, Solomon and Trobriand Archipelagos; Fig. 1). I addressed four topics: (1) long-term persistence of

non-volant taxa on continental shelf islands; (2) biogeographic patterns across Northern Melanesia's oceanic and continental shelf islands; (3) phylogenetics of Northern Melanesian Hippidae; and (4) evolutionary relationships of two sympatric and one allopatric species of the *Hippidae diadema* species group in Solomon Islands. In sum, these studies contribute several advances in the understanding of biogeographic patterns, and processes that have led to observed patterns, in the mammals of Northern Melanesia.

Biogeography

(1) Long-term persistence of non-volant taxa on continental shelf islands

An outstanding question relates to the persistence of non-volant lineages on continental shelf islands following isolation by rising sea level. Flannery (1995a) hypothesized that marsupials have lower rates of long-term persistence than placental

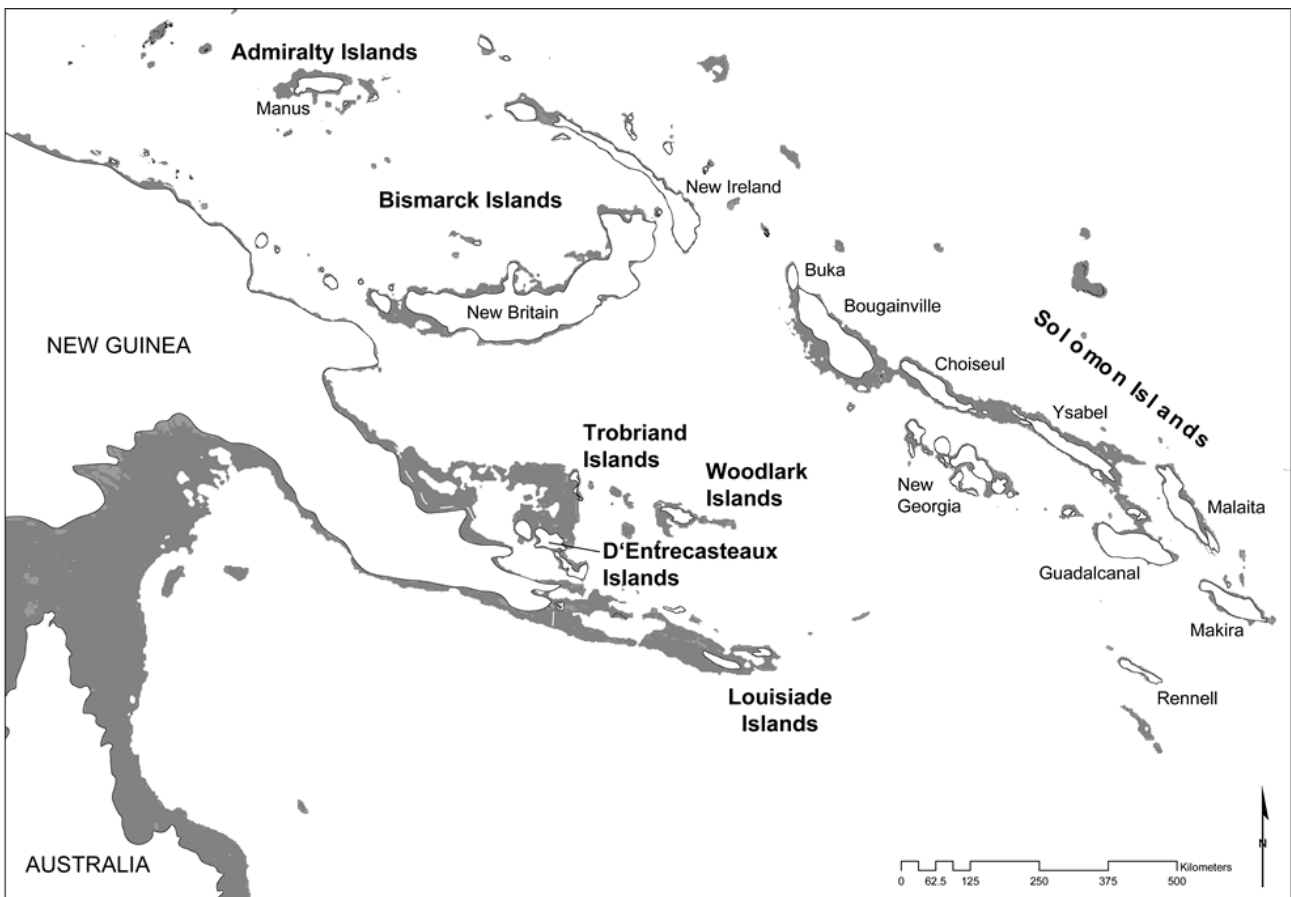


Figure 1. The region of Northern Melanesia. Archipelagos and selected islands discussed in the text are labelled. Grey shading indicates the approximate configurations of land bridges at a sea level of 120 metres below the present day level. Bathymetry data used in this reconstruction was sourced from Amante and Eakins (2009).

mammals. To test this hypothesis I compared the species richness of Dasyuromorphia, Diprotodontia, Peramelemorphia and Rodentia on Australian and Papuan continental shelf islands to that present within adjacent mainland source pools (mammalian zoogeographic provinces; Lavery et al. 2013a).

Definition of Australo-Papuan zoogeographic provinces required the amalgamation of an existing classification for Australia (Burbidge et al. 2008) with my own, similar classification for New Guinea. To classify New Guinea's zoogeographic provinces I compiled 4194 distributional records for 264 of New Guinea's native mammals from Flannery (1995b), Hitchcock (1997, 1998), Bonaccorso (1998), Flannery and Groves (1998), Aplin et al. (1999, 2010), Van Dyck (2002), Helgen and Flannery (2004a), Helgen (2005a,c, 2007a), Woolley (2005), Helgen et al. (2008, 2010, 2011), Musser et al. (2008), Helgen and Helgen (2009) and Musser and Lunde (2009). Records were allocated to existing mapped bioregions (Wikramanayake et al. 2001) and cluster analysis was then used to allocate bioregions to zoogeographic provinces. Generalized linear models using the procedure GENMOD in SAS 9.3 (SAS Institute Inc., Cary, NC) were used to determine rates of island persistence in the four mammalian orders as proportions of the species present within adjacent zoogeographic provinces. We used the extreme value function (Williams 1995) that employs a complementary log–log distribution to estimate intercept (k), slope (y) and maximum likelihood (ML). Proportions of species (S_p) present on islands were modelled as a binomial response variable on island area (A):

$$S_p = 1 - \exp[k + y \times \log(A)] \quad (1)$$

The order Dasyuromorphia had the lowest rate of persistence overall and within all but two of the individual provinces. Within Northern Melanesia, the rate of persistence did not differ between dasyuromorphs, peramelemorphs and rodents, but diprotodontids did exhibit a lower rate of persistence than rodents. The observed result that overall, dasyurids have lower persistence on Australo-Papuan islands was unexpected, yet intu-

itive. Dasyuromorphs are a carnivorous and insectivorous lineage, whereas rodents, diprotodonts and peramelemorphs are largely herbivorous. Carnivores require far larger home ranges than herbivores to obtain sufficient resources (Kelt and Van Vuren 2001). The implications of this are lower animal densities, smaller populations and reduced species survival rates on islands (Heaney 1984). This finding is not only a noteworthy and previously unacknowledged pattern in the Australo-Papuan insular fauna, but also has significant implications for mammalian conservation. Australia's islands are often used as *arks* to isolate populations of threatened mammals from mainland threats. Such measures have also been implemented for conservation of dasyurids such as Tasmanian devils *Sarcophilus harrisii* (Jones et al. 2007) and dibbler *Parantechinus apicalis* (Moro 2003). Acknowledgement of this result will greatly benefit long-term conservation planning for dasyurids.

(2) Biogeographic patterns across Northern Melanesia's oceanic and continental shelf islands

A second outstanding question concerns empirically describing biogeographic patterns in the mammalian fauna across the islands of Northern Melanesia. Using my own surveys, museum databases and the published literature (Koopman 1979, Flannery and Wickler 1990, Flannery and White 1991, Flannery 1995a, 1996, Bowen-Jones et al. 1997, Bonaccorso 1998, Anthony 2001, Emons and Kinbag 2001, Heinsohn 2003, Helgen and Flannery 2004b, White 2004, Heinsohn 2005, Helgen 2005b, 2007b, Read and Moseby 2006, Helgen 2007b, Heinsohn 2010, Aplin and Opiang 2011, Lavery et al. 2013b, 2014, Almeida et al. 2014, Lavery 2014a) I compiled mammal inventories for 74 islands found within Northern Melanesia. Ochiai and endemism indices used by Mayr and Diamond (2001) were employed to enable comparisons with patterns in the avifauna of the region. I defined the species-area relationship for all mammals, as well as separately for volant and non-volant groupings. Direct comparisons of family compositions were made between Northern

Melanesia and a defined New Guinea source pool, and Ochiai and endemism indices were used to determine regions of high endemism, and boundaries where mammalian faunas changed markedly between adjacent island groups.

Generalized linear models in R version 3.2.0 (R Development Core Team 2015) and a non-parametric multivariate regression tree (LINKTREE) implemented in PRIMER (PRIMER-E) were used to identify the influences of abiotic variables on mammalian species richness. The LINKTREE procedure constructs a hierarchical dendrogram that relates environmental variables to patterns in mammalian assemblage, whereby each binary division in the LINKTREE is characterised by one or more discriminating variables (Clarke et al. 2008). Abiotic variables tested were: island size, island height, linear distance to New Guinea, and measures of isolation within 25 km, 50 km, 75 km, 100 km and 200 km buffers.

Northern Melanesia's islands support few species of marsupial, and a moderate diversity of insectivorous bats with few endemics. The region holds a diverse, highly endemic pteropodid bat fauna that exceeds the species richness present in the adjacent source pool region of New Guinea. The Solomon Islands support an outstanding proportion of endemic mammals.

Generalized linear models revealed island size as the single best explanatory variable for inter-island variation in species richness of all mammals and bats. The linear distance to New Guinea was the single best explanatory variable for variation in species richness of non-volant mammals. The multivariate regression tree identified a clear hierarchical classification of islands according to their physical attributes and mammal assemblages. The mammalian faunas of Northern Melanesia's islands were dictated primarily by island size. The first three divisions in the dendrogram grouped islands above 1300 km², between 1300–600 km², and between 600–200 km² in area. The last four divisions grouped islands smaller than 200 km² according to their isolation, firstly by the area of land present with a 100 km island buffer (>18%, and between 18% and 9.5 %), and lastly by the area of land present with a 50 km island buffer

(>2.5%, and <2.5%).

Systematics and Ecology

(3) Phylogenetics of Northern Melanesian Hipposideridae

A paradox exists concerning speciation of bats in Northern Melanesia (Flannery 1995a, Heads 2002). Whilst Family Pteropodidae is diverse and has undergone *in situ* diversification with numerous endemics, insectivorous families show limited diversification with few endemics. Within at least one of these families (Hipposideridae), phylogenetic studies have commonly identified cryptic diversity in other insular regions (e.g., Murray et al. 2011). Hipposiderid bats are relatively common throughout Northern Melanesia, with at least one endemic genus (*Anthops*) and two endemic species present: *Hipposideros dinops* and *H. demissus* (Lavery et al. 2014). Hence, I considered it a possibility that the observed pattern may merely reflect the presence of additional, unappreciated diversity rather than a genuine disparity in levels of speciation and endemism.

I used sequences of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and the nuclear recombination activating gene 1 (RAG1) to reconstruct molecular phylogenetic relationships for hipposiderid species. A total of twenty-five specimens from eight species sampled across eleven localities in Northern Melanesia and Cape York Peninsula, Australia, were sequenced and combined with published sequences from Southeast Asia (Murray et al. 2011).

I used JMODELTEST version 1 (Posada 2008) to determine the best available evolutionary models of nucleotide substitution. We tested for congruence between our two datasets using partition homogeneity test in PAUP* (Farris et al. 1994, 1995). There was no significant difference between data partitions ($P = 0.96$), so Bayesian and maximum likelihood analyses were performed on the concatenated dataset using the models and parameters identified by JMODELTEST. Phylogenetic reconstructions using Bayesian inference were implemented in MRBAYES version 3.1.2 (Ronquist and Huelsenbeck 2003), and reconstructions using Maximum Likelihood were implemented in RAxML version 2.2.3 (Stamatakis 2006). I also employed molecular clock analysis using the Bayesian

approach implemented in BEAST version 1.5.2 (Drummond and Rambaut 2007) to determine approximate dates for the most recent common ancestors of hipposiderid lineages in the region.

Results of the molecular clock analysis indicated an extended presence of Hipposideridae in Northern Melanesia, and divergence appears to have occurred there (the most recent common ancestor of *Hipposideros* and *Anthops ornatus* was estimated at 22.3 MYA, CI \pm 5.6). Phylogenetic analyses also revealed the presence of undescribed diversity in northern Australia. *Hipposideros ater* was polyphyletic and separated specimens into three well supported clades: Australia, Borneo, and the Philippines. Sequence divergence for the mitochondrial gene ND2 was 12.4–12.8% and 13.2–13.6% between Cape York specimens and specimens from Borneo and the Philippines, respectively, with the most recent common ancestor having occurred some 13.7 million years ago.

However, there was no cryptic diversity detected in Northern Melanesian specimens when compared to conspecifics from Southeast Asia and Australia. On the contrary, phylogenetic reconstructions indicated that three recognised species from the Solomon Islands (*Hipposideros diadema*, *H. dinops* and *H. demissus*) exhibited genetic divergence below that typically used to infer species (corrected genetic distances of 0.74 – 6.93%). With regard to *H. diadema* and *H. dinops* this was most unexpected. The two species differ remarkably in morphology, occur syntopically and have never been regarded as conspecifics.

(4) Evolutionary relationships of two sympatric and one allopatric species of the *Hipposideros diadema* species group in Solomon Islands

Focussing on a finer geographic and temporal scale, DNA sequencing was combined with microsatellite genotyping, and with morphological and ecological data, to determine the evolutionary relationships of *Hipposideros diadema*, *H. demissus* and *H. dinops*. An additional seven specimens from six localities in Solomon Islands were sequenced with additional genes from the mitochondria (Cytochrome-*b*) and nuclear gene introns (signal transducer and activator of transcription

5A, and thyrotropin beta chain precursor). Ten microsatellites were genotyped from populations of *H. diadema* and *H. dinops* that occupy the same cave on Guadalcanal to determine if the two are reproductively isolated. Echolocation calls were recorded from the three species using an Echo Meter EM3 Ultrasonic Bat Detector (Wildlife Acoustics Inc., Concord, MA, USA) and one hundred and twelve specimens from the three taxa were examined and reproductive condition, external body measurements and/or skull morphological variables were measured.

Genetic sequencing revealed *Hipposideros diadema* and *H. dinops* are separated by less than 2% genetic divergence in Cytochrome-*b*, and even less among nuclear genes. However, syntopic populations of *H. diadema* and *H. dinops* from Guadalcanal clearly separate by morphology and echolocation call. The morphological attributes that can be used to distinguish the different species are also independent of the extreme differences in body size. Microsatellite genotyping indicated populations occupying the same cave are reproductively isolated from each other.

The larger species *H. dinops* appears to have evolved rapidly, most likely via a combination of morphological plasticity in *Hipposideros diadema* and disruptive natural selection in a newly colonised environment. The results provide a novel example of speciation in mammals (Bradley and Baker 2001), and an example of what I have referred to as *genetically cryptic species*. The results presented suggest that ecological and not geographic influences have prompted speciation in Solomon Island leaf-nosed bats.

Conclusions

These projects have advanced the understanding of mammalian biogeography in Northern Melanesia. Despite the constraints of unresolved taxonomies and incomplete inventories, the research successfully used quantitative data to critically confirm patterns previously described qualitatively by other authors (Koopman 1979, Flannery 1995a, 1996).

In broad terms, the mammalian fauna of Northern Melanesia is a consequence of the poor

over-water dispersal abilities of non-volant mammals; lower persistence rates of dasyuromorphs and diprotodonts on continental shelf islands; significant rates of speciation in pteropodid bats; and comparative lack of speciation in insectivorous bats.

The lower rates of speciation and limited endemism in insectivorous families when compared to pteropodid bats are possibly the most intriguing biogeographic patterns. The notion that the larger, more mobile lineage Pteropodidae should demonstrate more localised patterns of endemism than smaller bats seems counterintuitive and difficult to explain. I suspect it is a situation that may be theoretically related to the paradox of *the great speciators* (Diamond et al. 1976).

These findings are based on additional relevant scientific knowledge via three appendices (Lavery 2014b). Appendix A contributes fundamental distributional data and an analysis of species richness for mammals and all other groups of vertebrates on what I consider are some of Australia's most understudied continental shelf islands, the Torres Strait islands. These data have contributed records of several mammals previously unknown from these islands (Lavery et al. 2012). Appendix B provides the first reproductive record for a little known, Solomon Island endemic bat, the flower-faced bat *Anthops ornatus* (Lavery et al. 2013b). Appendix C reassesses the type locality for a Solomon Island endemic rodent *Solomys salomonis*, known only from the holotype (Lavery 2014a).

The results presented have reaffirmed the usefulness of Northern Melanesia's islands for studying biogeography and evolution. The findings provide a foundation upon which future biogeographic, systematic and ecological studies of Melanesia's mammals can continue to be built.

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