



## Trans-equatorial range of a land bird lineage (Aves: Rallidae) from tropical forests to subantarctic grasslands

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Despite the capacity for dispersal, range size varies considerably among birds species. Many species have restricted geographic spread, whilst others routinely travel long distances to reach preferred habitat. These alternatives are well expressed amongst the rails (Rallidae) and a varying tendency for movement results in overlapping distribution patterns. Here, we examine the situation of a particular lineage, the *Lewinia* rails (*L. mirifica*, *L. pectoralis* and *L. muelleri*) that inhabit a very wide spatial and ecological range. *Lewinia* occurs from the Philippines, north of the equator in Oceania, to Australia and the subantarctic Auckland Islands far to the south. Allopatric distribution and differences in plumage colour result in their treatment as distinct species but our mitochondrial molecular analysis (cyt *b* and CR) reveals genetic distances of less than < 1%. The genetic and phylogeographical structure in the *Lewinia* lineage includes shared nuclear sequence alleles and this is consistent with a calibrated multigene phylogeny suggesting trans-hemispheric dispersal since the middle Pleistocene. Despite this recent history, available morphometric data indicates that the subantarctic population has relatively small wings for its mass, and this implies adaptation away from flight. *Lewinia* provides a nice example of the way dispersal and adaptation intersect over short time frames to generate diversity.

Flight enables birds to move horizontally and vertically between habitat patches and take advantage of ephemeral resources. As a result, the ranges that individual species occupy vary from those that undertake seasonal migration (Newton 2008), to those that occupy small islands. Most birds have comparatively small ranges, especially near the equator and on islands in the southern hemisphere (Gaston and Blackburn 1996, Orme et al. 2006). Some sedentary taxa have migratory ancestors (Rolland et al. 2014), and some lineages of sedentary birds have ranges that cross the equator but are not migratory and these provide intriguing insights into the way dispersal and colonisation proceed, even in unlikely circumstances (Newton 2003).

In non-migratory species, individual dispersal is influenced by species attributes (Claramunt et al. 2012), external biotic factors such as competition and predation (Cody and Diamond 1975, Diamond 1975), and physical conditions including wind direction and habitat patchiness. The least likely routes for dispersal are those that cross hostile environments (climatic, ecological or physiological barriers) that do not match current or 'natal' habitats (i.e. hatching site). However, colonisation (cf. dispersal) could be enhanced in such circumstances if there is less chance of encountering competition (Diamond 1970, Newton 2003). Habitats that share attributes may enable colonization and establishment among them, whereas habitats that present adaptive challenges to

colonists might be expected to enhance genetic isolation, if initial colonisation is achieved. In some systems such as the western Pacific where terrestrial habitat is fragmented among large regions of ocean, ephemeral changes in land availability (e.g. seamounts, sea level change) could influence the likelihood of colonisation and thus in situ adaptation (Carlquist 1966, Diamond 1970, 1974). Nonetheless, rare dispersal and establishment between distant habitats is mostly apparent from the disjunct distributions of species or lineages (Gillespie et al. 2012).

A curious instance is that of the rail lineage *Lewinia* that has an unusual range extending across the equator from tropical forests to windswept herbfields of subantarctic islands. The genus is typically treated as three species even though their generic classification has varied (Christidis and Boles 2008). Temminck (1831) assigned them to *Rallus* because of similarity to *R. striatus*, although this is now usually included within *Gallirallus*. Olson (1973) considered *Lewinia* to be generalised, and more 'primitive', than *Gallirallus striatus*, forming part of a pro-*Rallus* stock with the skeletally near-identical *Dryolimnas cuvieri* of Madagascar and Aldabra despite plumage differences (Taylor 1998). Sibley and Monroe (1990), maintained the *Lewinia* super-species as having no relation to *D. cuvieri* but considered only their geographical isolation. Livezey (1998) placed the *Lewinia* group in *Gallirallus*.

Recent phylogenetic analyses of molecular data (Garcia-R et al. 2014) demonstrate that *Lewinia* and *G. striatus* are sister lineages (Fig. 1). The broad ‘*Rallus*’ group (Garcia-R et al. 2014) includes continental species of *Rallus* and *Crex* that range through Africa, Europe and Asia, or the Americas. Notably, there are also many insular species with localised ranges between Oceania and Australasia (Fig. 1). Most are classified as *Gallirallus*, but others include *Dryolimnas*, *Habroptila*, *Diaphorapteryx*, *Nesoclopeus*, *Eulabeornis* and *Aramidopsis*. These, and other extinct taxa, are mostly flightless (Diamond 1991, Trewick 1997b, Steadman 2006). In comparison, the scarcity of volant ‘*Rallus*’ species in the Oceania/Australasia region is very apparent and those that exist have larger ranges spanning continental areas (e.g. *G. striatus*) or island archipelagos (e.g. *G. philippensis*).

The *Lewinia* lineage range extends from the Auckland Islands that are more than 50° south of the equator to Luzon (Philippines) which is 16° north of the equator (Fig. 2A). *Lewinia mirifica* lives in tropical montane forest above 900 m a.s.l. in Luzon and Samar islands of the Philippines (Desmond 2010) where they appear to undertake local interisland migrations (Taylor 1998). *Lewinia pectoralis* is

patchily distributed in the Lesser Sunda Islands and upland Papua New Guinea (above 1000 m a.s.l.) more than 3000 km from the nearest population of *L. mirifica* (BirdLife International 2014). Sporadic populations occur in southwest Australia, the eastern seaboard of Australia and Tasmania, in habitats ranging from subtropical and tropical forest to lakes and marshes below 1000 m a.s.l. (<<http://bie.ala.org.au/species/Lewinia+pectoralis#>>). The few records of movements among habitat patches suggest they occur at night. *Lewinia muelleri* is endemic to two small (~ 64 km<sup>2</sup>) subantarctic islands in the Auckland Islands group (Elliott et al. 1991, Roots 2006) where it lives in low scrub-forest, coastal herbfield, tussock and grassland below 500 m a.s.l. These islands are about 1625 km from the nearest population of *L. pectoralis* in Tasmania.

*Lewinia* species differ morphologically mainly in terms of plumage (Taylor 1998). Some taxonomic treatments recognise seven living and one possibly extinct subspecies in *L. pectoralis* (Taylor 1998), keeping *L. mirifica* and *L. muelleri* separate, but these have also been treated as conspecific within *Rallus pectoralis* (Ripley 1977). In particular, *L. muelleri* has been considered as a subspecies within

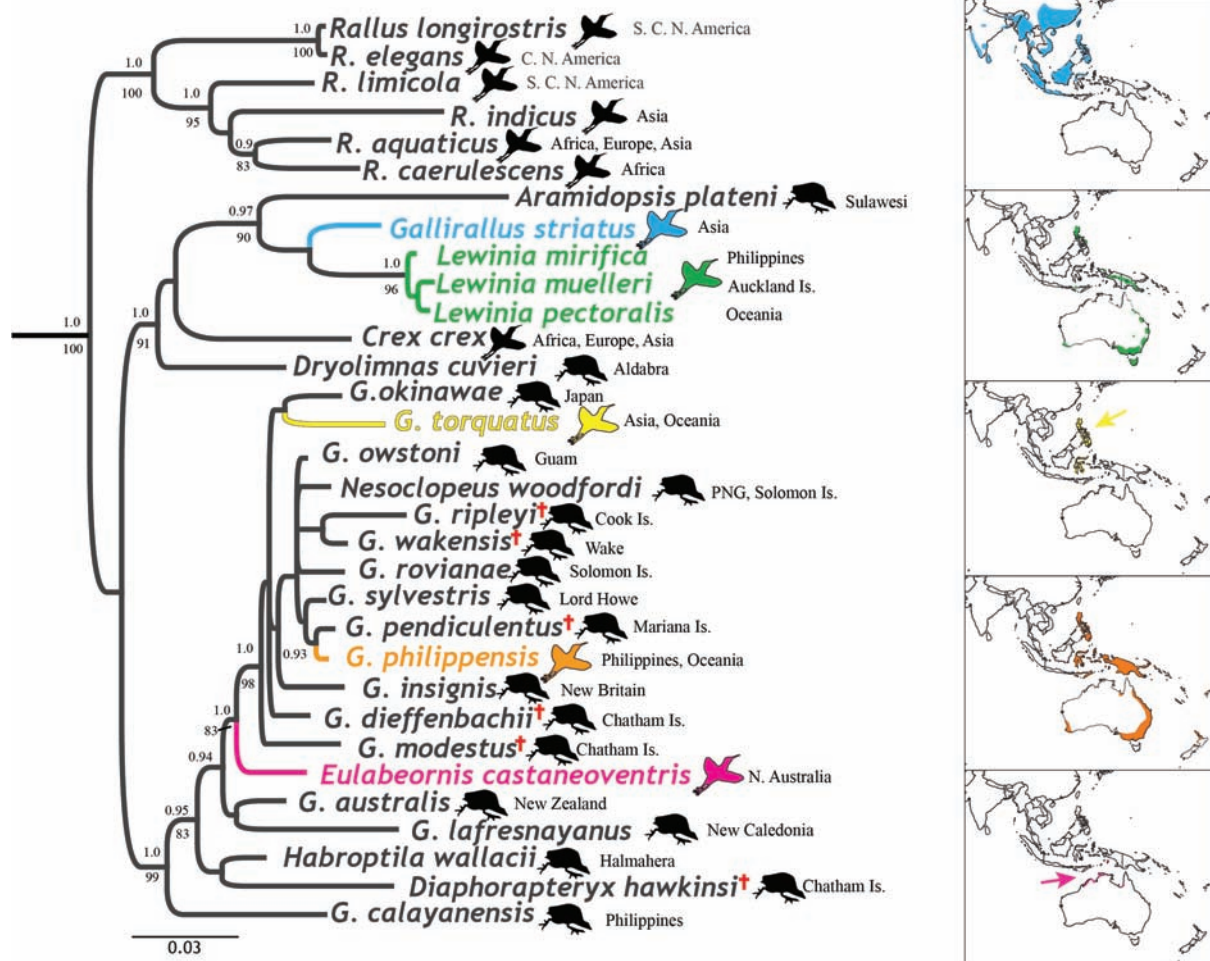


Figure 1. Bayesian phylogenetic inference of the ‘*Rallus*’ clade based on concatenated gene analysis. Posterior probabilities over 0.90 and ML bootstrap supports over 80% are indicated above and below each node, respectively. Cross symbols (†) next to names indicate extinct species. Flying species are shown with a winged-bird icon and flightless species with a walking-bird icon. Geographic range of each species is indicated. Coloured branches correspond to geographic range maps of volant species in the southwestern Pacific/Australasian/Oceania region (right).

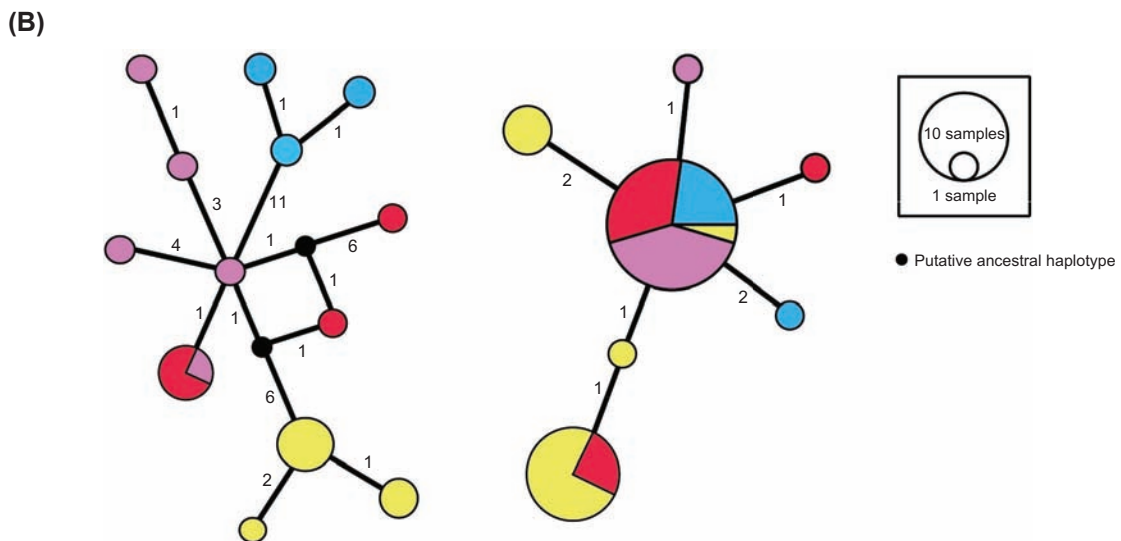
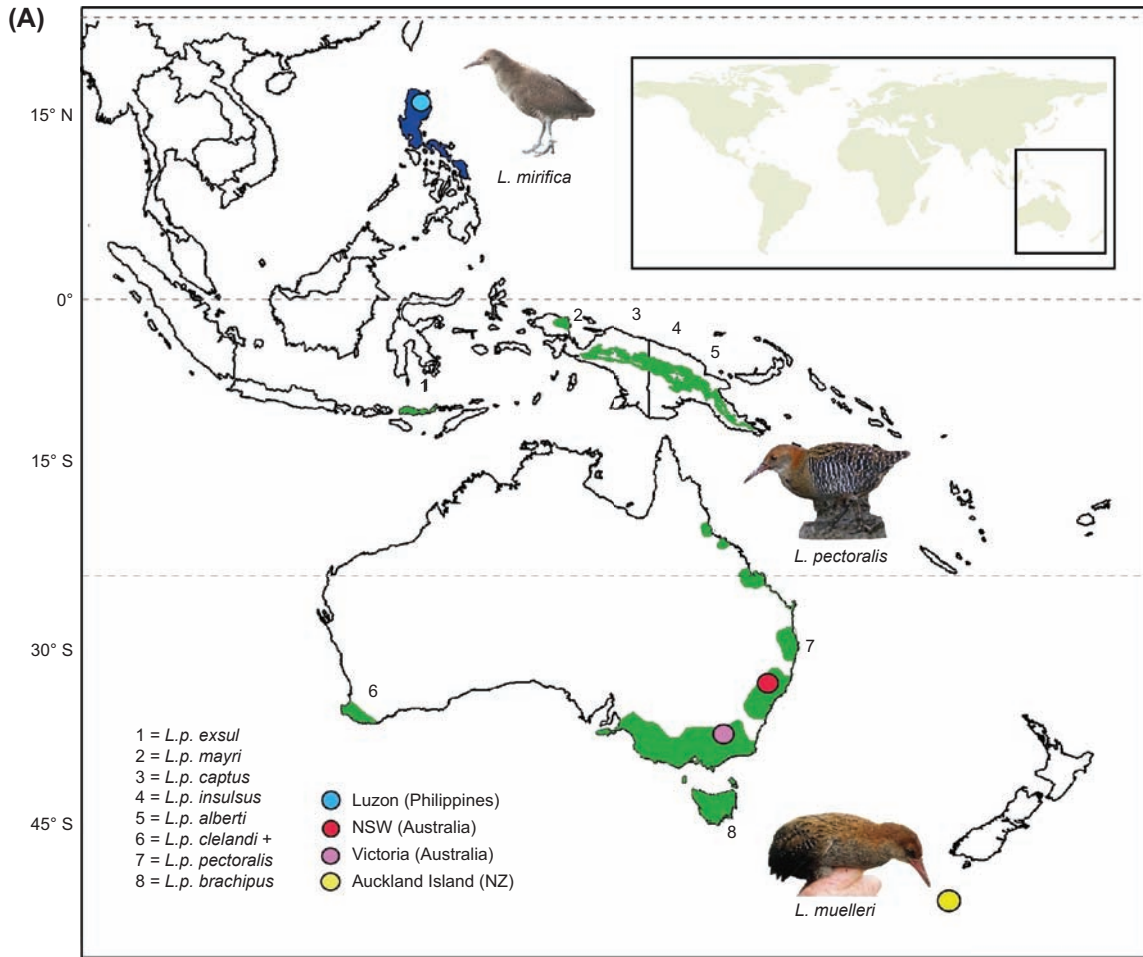


Figure 2. (A) Spatial range of the three species of *Lewinia*. Subspecies of *L. pectoralis* are indicated by numbers. A cross symbol (†) indicates an extinct subspecies in *L. pectoralis*. Coloured circles indicate approximate sampling localities of specimens used in phylogeographic analysis. Dashed lines delimit the tropical region, bounded by latitudes 23.5°N and 23.5°S. (B) Median-joining haplotype networks of mitochondrial (*cyt b* and CR data) and nuclear ( $\beta$ fib-7) sequences (left and right, respectively). The number of mutational steps is indicated on each branch. Circle size is proportional to the number of individuals found for each haplotype.

*L. pectoralis* (Elliott et al. 1991), but by virtue of inhabiting a remote island and ‘softer plumage and indications of degeneration of the wing formula’ (Ripley 1977) it is maintained as a separate species (Taylor 1998). *Lewinia pectoralis* has noticeable streaks in plumage of the head and hindneck (Taylor 1998) and with *L. muelleri* has prominently dark-streaked upperparts, barred upperwings and black flanks (Parkes and Amadon 1959).

Here, we use mitochondrial and nuclear DNA sequences and morphological information to explore population connectivity of *Lewinia* across this unusual range. Although limited sample sizes constrain definitive estimates of gene flow among populations, we use phylogenetics, phylogeography and available morphological characters for quantitative comparisons of these taxa. Is *Lewinia* a remnant of an older and formerly more widespread lineage or is it a taxonomic anomaly that actually represents the result of recent dispersal and adaptation?

## Material and methods

### Taxon sampling for molecular data collection

Tissue samples of *Lewinia mirifica* ( $n = 3$ ) were obtained from the Field Museum of Natural History (USA). These samples were collected from Luzon, Philippines. Samples of *Lewinia pectoralis* ( $n = 10$ ) came from the Australian National Wildlife Collection, Australian Museum and Victoria Museum (Australia). All samples were collected from Victoria ( $n = 5$ ) and New South Wales ( $n = 5$ ) in Australia and represent subspecies *L. p. pectoralis*. Blood samples of *Lewinia muelleri* ( $n = 7$ ) were collected during summer expeditions in 2011 and 2012 on Adams Island (Auckland Islands group) using live trapping and preserved in ethanol (Elliott et al. 1991). See Fig. 2A for sampling localities.

### Laboratory techniques

Genomic DNA was extracted using either the Qiagen Tissue DNeasy kit (Qiagen) or standard phenol-chloroform methods. For phylogeographic analysis genomic DNA was PCR amplified using primers (Supplementary material Appendix 1, Table A1) that target fragments of the mitochondrial DNA genes cytochrome *b* (*cyt b*) and Control Region (CR), and the nuclear DNA  $\beta$ -fibrinogen intron 7 ( $\beta$ fib-7). Amplification reactions contained 2.0 mM  $MgCl_2$ , 2.0 mM dNTPs, 0.2  $\mu$ M of each Primer, 0.04 U of Taq polymerase and 10 ng of DNA. Negative controls were used to monitor potential contamination. Amplification products were purified with ExoI/SAP digestion and analyzed on an ABI 3730XL automated DNA sequencer (Applied Biosystems) using Big-Dye Terminator ver. 3.1 reagents. GenBank accession numbers are given in Supplementary material Appendix 1, Table A2.

### DNA sequences analysis

Phylogenetic analyses were performed using a concatenated alignment of sequences of mitochondrial (*cyt b*, COI, 16S and CR) and nuclear ( $\beta$ fib and RAG-1) genes previously reported (Fain et al. 2007, Ozaki et al. 2010, Kirchman 2012,

Garcia-R et al. 2014) for the ‘*Rallus*’ clade that includes *Lewinia* (Supplementary material Appendix 1, Table A3). Each of 30 ingroup species was represented by data from one individual with an outgroup comprising *Rallina fasciata* and *Rallina tricolor*. Bayesian and maximum likelihood hypotheses were inferred using MrBayes and RAxML, respectively. MrBayes was implemented in Geneious ver. 6.0.5 using a general time reversible model with gamma distribution (GTR +  $\Gamma$ ), 10 million generations and 10% burn-in. A burn-in of 10% gave optimal results, and we obtained effective sample sizes (ESS) > 200 for 98% of the parameters. Convergence and diagnostics of the Markov process were visualized using Tracer ver. 1.6. (<<http://tree.bio.ed.ac.uk/software/tracer/>>). ML analysis used a GTR +  $\Gamma$  model implemented in RAxML via the Cipres portal (Miller et al. 2010). The model was estimated in ModelTest ver. 3.7 using the Akaike information criterion (Posada and Crandall 1998).

*Lewinia* sequences obtained for phylogeographic analysis were edited and aligned using the MAFFT aligner implemented in Geneious ver. 6.05 (Drummond et al. 2012) and checked by eye. Nucleotide and inferred amino acid sequences of *cyt b* were checked to verify the absence of indels and stop codons. Sequence ambiguities at heterozygous sites in  $\beta$ fib-7 were resolved using PHASE implemented in DnaSP ver. 5.0 (Librado and Rozas 2009). We calculated maximum pairwise divergence (p-distances) of concatenated mitochondrial loci (*cyt b* and CR) using the number of nucleotide changes of the haplotypes between species and correcting for within group variation in MEGA ver. 5.2.2 (Tamura et al. 2011). Haplotype networks were constructed in PopArt (<<http://popart.otago.ac.nz>>) using median joining to visualize the relationship among haplotypes within *Lewinia* and their geographical distribution.

### Morphological data collection

We compiled available data of morphological characters of the currently retained taxa (Mayr and Gilliard 1951, Junge 1952, 1953, Parkes and Amadon 1959, Leicester 1960, Gilliard and Lecroy 1961, Falla 1967, Harrison 1975, Ripley 1977, Elliott et al. 1991, Round and Allen 2010), including anatomical and histological traits compiled by Livezey (1998). Means, standard deviations and coefficient of variation of bill, tarsus, toe, wing, tail, culmen lengths (mm) and weight (g) were calculated for each of the currently recognised *Lewinia* species and bivariate plots were used to reveal shape trends. To test for morphological differentiation between species using the available data we performed one-tailed t-tests. A minimum of two (culmen length in *L. muelleri*) and a maximum of 82 (wing length in *L. pectoralis*) specimens were obtained and included in these analyses (Table 1 and Supplementary material Appendix 1, Table A4). Statistical analyses were performed in the R programming environment (R Development Core Team).

## Results

### Molecular

Phylogenetic analysis showed strong support for a shared common ancestor of *Lewinia* with *Gallirallus striatus* within

Table 1. Mean ( $\bar{x}$ ), standard deviation (SD) and coefficient of variation (CV) of linear measurements (mm) and weight (g) of *Lewinia mirifica*, *L. pectoralis* and *L. muelleri*. Mean, standard deviation and coefficient of variation in *L. pectoralis* were calculated using data available for all subspecies (Supplementary material Appendix 1, Table A4). p-values indicate support for difference between means of each taxon where \*\* = < 0.001; \* = 0.01 < p < 0.05; ns = no significant.

	<i>L. muelleri</i> (A)				<i>L. pectoralis</i> (B)				<i>L. mirifica</i> (C)				A-B	A-C	B-C	Overall CV
	n	$\bar{x}$	SD	CV	n	$\bar{x}$	SD	CV	n	$\bar{x}$	SD	CV	p	p	p	
Bill	9	27.78	4.35	0.16	45	34.3	2.14	0.06	10	27.2	1.71	0.06	**	ns	**	0.09
Tail	8	34.35	4.94	0.14	41	39.24	3.1	0.08	9	44.6	2.13	0.05	**	**	**	0.09
Weight	9	80.8	14.91	0.18	2	68	14.14	0.21	9	62.9	6.18	0.10	ns	*	ns	0.17
Tarsus	11	28.69	1.3	0.05	55	30.8	1.87	0.06	17	29	0.76	0.03	**	ns	**	0.04
Toe	11	31.17	1.78	0.06	10	36.18	2.52	0.07	7	35.71	1.8	0.05	**	**	ns	0.06
Wing	8	80.12	3.76	0.05	82	100.11	4.21	0.04	16	108.9	4.03	0.04	**	**	**	0.04
Culmen	2	26.5	2.12	0.08	76	34.18	3.19	0.09	7	25.43	0.98	0.04	**	ns	**	0.07

the broad ‘*Rallus*’ clade. Closely related with this group are two flightless insular endemic species found in the western Pacific (*Aramidopsis plateni*) and Indian (*Dryolimnas cuvieri*) Oceans. Also, in this subclade is the widespread volant species *Crex crex* that occurs in Europe, Asia and Africa but is only a rare vagrant in Oceania and Australasia. Members of *Gallirallus* and other monotypic genera form the sister group (Fig. 1).

For phylogeographic analysis the complete alignment of three gene fragments contained 2089 bp, comprising 892 bp of *cyt b*, 596 bp of CR and 601 bp of  $\beta$ fib-7. No premature stop codons were detected in the protein-coding *cyt b* gene. The sampled *Lewinia* did not share mtDNA haplotypes between locations (Fig. 2B), except for the *L. pectoralis* sampled from Victoria and New South Wales on the Australian mainland. The network of  $\beta$ fib-7 sequences revealed a pattern of incomplete lineage sorting among the three taxa (Fig. 2B). Maximum uncorrected pairwise genetic distances among these species using concatenated mitochondrial genes was highest between *L. mirifica* and *L. muelleri* ( $0.01 \pm 0.003$ ), less between *L. mirifica* and *L. pectoralis* ( $0.008 \pm 0.002$ ), and smallest between *L. pectoralis* and *L. muelleri* ( $0.006 \pm 0.002$ ). Pairwise distance between populations of *L. pectoralis* in Victoria and NSW was 0.002 ( $\pm 0.001$ ). Concatenated sequences therefore differed by less than 1% within *Lewinia*.

## Morphology

Despite limitations of sample size, variation in data collection methods and detailed information about specimens (e.g. sex and maturity stage), the available *L. muelleri* sample comprised birds that had on average the shortest wings, tails, bills, tarsus and toes but the highest body weights of the *Lewinia* measured (Table 1 and Supplementary material Appendix 1, Table A4). Tail and wing are the most significantly different traits among the three *Lewinia*. Comparisons of mean wing lengths confirm that *L. mirifica* and *L. pectoralis* had significantly ( $p < 0.001$ ) longer wings than *L. muelleri* specimens (Table 1). *Lewinia muelleri* has the higher coefficient of variation in bill and tail ( $> 10\%$ ). *Lewinia muelleri* and *L. pectoralis* are quite similar in culmen ( $\sim 20\%$ ) and weight ( $\sim 8\%$ ), however, weight is the trait with higher overall variation (17%) across all species (Table 1). Bivariate plots between variables indicate that these species show within and between

population variations in wing length (Fig. 3 and Supplementary material Appendix 1, Fig. A1).

From 570 osteological, myological and integumentary characters (Livezey 1998) just four characters were found to differ among *Lewinia* taxa. All are subtle differences in colouration: the region orbitalis colour in *L. mirifica* and *L. pectoralis* is red while it is brown in *L. muelleri*; the penna of dorsum has blackish stripes along rachises in *L. pectoralis* and *L. muelleri* but these are absent in *L. mirifica*; *Lewinia*

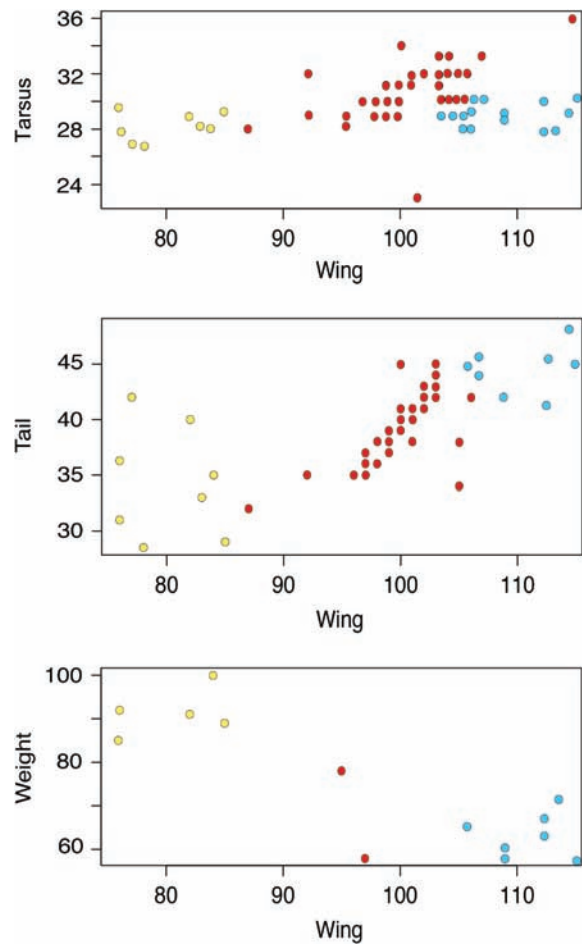


Figure 3. Shape differences of *Lewinia* species depicted by the interaction between wing and tarsus length, tail length and body weight. Yellow = *L. muelleri*, red = *L. pectoralis* and blue = *L. mirifica*.

*mirifica* and *L. pectoralis* have bars throughout the vexilla of penna and white markings in the tectrices dorsales caudae and both characteristics are absent in *L. muelleri*.

## Discussion

Despite its unusual distribution, extending over 60 degrees of latitude, the estimated crown age of the *Lewinia* species trio dates to the last 1 mya (Garcia-R et al. 2014), which is much more recent than the formation of islands in the region (Neall and Trewick 2008). Over-water dispersal and subdivision of *Lewinia* populations between Philippines and Sunda islands and between Papua New Guinea and Australia might have occurred during the sea-level changes of the Pleistocene climate cycling (Voris 2000, Wurster et al. 2010, Lohman et al. 2011), but, this does not explain the presence of *L. pectoralis* and *L. muelleri* in Australia and the Auckland Islands on either side of the Tasman Sea. There are no modern or fossil records of *Lewinia* in nearer mainland New Zealand and there is no evidence for occurrence or historical extinctions of *Lewinia* on other islands between Australia and the Auckland Islands. Absence of *Lewinia* from New Zealand is strongly indicated by their absence from the wealth of Holocene bird fossils that includes the remains of several other rail species (Olson 1975, Cooper and Millener 1993, Steadman 1995, 2006, Holdaway et al. 2001). This suggests that the large gap in distribution today reflects the circumstances in which the current range was established.

The dynamic ranges of bird species and their success at establishment in new habitats must be dependent on fecundity, resource limitation and the conditions between habitat patches (Veech et al. 2011, Weber and Agrawal 2012). Establishment of late-arriving colonists may be influenced by ecological factors, including competition with earlier arrivals, or involve expansion through marginal habitats that reflect progressive specialization to novel conditions (Wilson 1959, Erwin 1981). Colonisation of the distant and relatively young (~ 12 mya) volcanic Auckland Islands by *Lewinia* might have been facilitated by the absence of congeners, relatively low diversity of interspecific competitors for food or nesting locations and low number of predators there. This small group of islands (~ 600 km<sup>2</sup>) is tenanted by 15 breeding land bird species (Heather and Robertson 1997, O'Connor 1999) including parakeet *Cyanoramphus novaeseelandiae*, pippet *Anthus novaeseelandiae*, snipe *Coenocorypha aucklandica* and teal *Anas aucklandica*, a variety of ground nesting seabirds including albatross *Diomedea antipodensis*, shag *Phalacrocorax colensoi* and yellow-eyed penguin *Megadyptes antipodes*, two potential avian predators, the sub-antarctic skua *Catharacta antarctica* and New Zealand falcon *Falco novaeseelandiae*, and no occurrence of mammals on Disappointment and Adams Island (Elliott et al. 1991). This contrasts with much more diverse vertebrate assemblages in other parts of the *Lewinia* range. Australia, New Guinea, Lesser Sundas and Philippines have high bird and mammal diversity including species of the same clade as *Lewinia* (*Gallirallus striatus*, *G. philippensis*, *G. calayanensis*, *G. torquatus*, *Eulabeornis castaneovenstris*). Mainland New Zealand also has two species from the same clade (*G. philippensis* and *G. australis*). This might constrain abundance and habitat range

expansion of *Lewinia* in those areas (Diamond 1975, Webb et al. 2002, Sanderson et al. 2009, Connor et al. 2013).

In general, migratory behaviour is uncommon amongst rails but sporadic dispersal appears to occur widely in the family. For example, American coots *Fulica americana* make seasonal movements and frequently aggregate in winter (Terres 1980, Udvardy 1994, McKnight and Hepp 1998), and dispersal in Brazilian wood rail *Aramides mangle* appears to involve cyclic range expansion and retraction (Marcondes et al. 2014). The corncrake *Crex crex* is notable among Rallidae for its reproductive range that requires seasonal migration between Europe/Asia and southern Africa (Taylor 1998, Walther et al. 2013). Other species that have extensive ranges that have been achieved in recent times include the Eurasian coot *Fulica atra* and purple swamp hen *Porphyrio porphyrio*. Fossils and living populations indicate that some lineages have expanded their ranges less recently resulting in the evolution of island endemics in the Oceania region (Trewick 2011, Garcia-R et al. 2014, Garcia-R and Trewick 2015). Within this region, some members of the 'Rallus' group (e.g. *Gallirallus philippensis*) have ranges that extend across ocean between islands and are phylogenetically nested among flightless insular relatives (Fig. 1). The *Lewinia* lineage appears to be an example that bridges these two scenarios; a widespread relative does not overly the ranges of the three species.

The sporadic tendency of sedentary and dispersal behaviour has resulted in several lineages occupying territories across widely spaced habitat patches and oceanic islands, especially in the Oceania region (Garcia-R et al. 2014, Garcia-R and Trewick 2015). Volant species within the 'Rallus' clade have been successful at inhabiting different habitats in Australasian archipelagos despite their recent arrival (Kirchman 2012, Garcia-R et al. 2014). This suggests that, contrary to a negative relationship of dispersal and diversification rates (Weeks and Claramunt 2014), dispersal should be high to reach several islands in short time. To offset the potential mixing resulting from high gene flow we propose that dispersal is episodic, occurring in waves and at different places. This would mean that time is not the limiting factor in speciation rates of 'Rallus' in Australasia; an apparent negative relationship is perhaps a product of an inaccurate dispersal index or lineages in different evolutionary phases (Weeks and Claramunt 2014). However, the age of the entire clade is correlated with geographical range and species richness in a broader context (McPeck and Brown 2007). Ecology and geography are strongly linked in evolutionary time and consistent with diversification because older clades in Rallidae have had more time to expand and accumulate species (Garcia-R et al. 2014).

Morphological changes after colonization of oceanic islands has been observed in diverse vertebrate groups and is thought to be the result of strong selective force (Trewick 1997b, Clegg and Owens 2002, Lomolino 2005, Boyer and Jetz 2010) with an opportunity for diversification of the colonizing taxa. The relative body/wing size of *Lewinia* species indicates that selection has occurred but in a timeframe too short to allow completion of lineage sorting at a nuclear locus. Despite limited data there appears to be allometric differences of *Lewinia* consistent with the likely population sizes and their locations. *Lewinia pectoralis* and *L. mirifica*

are the most similar in shape whereas the Auckland Island *L. muelleri* is disproportionately heavy for the size of its wings. This suggests an adaptive response that channels resources away from flight. Clearly the presence of *Lewinia* populations in such spatially and ecologically disparate places must be the product of recent colonisation. The fact that the populations are sufficiently morphologically distinct to warrant separate species names while having such mitochondrial divergence and sharing nuclear sequence alleles (Fig. 2B) attests to recent evolutionary change. Genetic drift is expected to drive fixation of neutral differences in small isolated populations, but even the small *L. muelleri* population on the Auckland Islands shares nuclear alleles with the others. Morphological differences are therefore most likely the result of natural selection.

Features associated with flightlessness were the main traits used by taxonomists to place several species within monotypic genera in this clade. However, evolution of flightlessness is likely a by-product of adaptation to the limited resources on islands and intraspecific competition that reduced the basal rate of metabolism (McNab 1994, 2002). Low competition and lack of ground predators mean colonists can forage on the ground and not expend energy on flight and flight muscles; selection for ground foraging and against the production of large wings and muscles would be favoured. This is likely the key to rail success on islands. New environmental conditions can produce shifts in ecology and trigger changes in behaviour that lead to rapid morphological shifts such as reduction of pectoral muscle (Trewick 1997a), but the underlying adaptive paradox in rails persist. Despite sedentary behaviour in most volant species, rails retain flight capacity that allows not only escape from predators but also permits dispersal. A sedentary disposition pre-adapts rails to take advantage of novel resource opportunities where flight does not offer a significant benefit. The small genetic distances found in this study indicate that the morphological differences of heavier body and shorter wings originally used to separate southern *Lewinia* rails are of recent origin, and likely an adaptive response to the local environmental.

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Supplementary material (Appendix JAV-00804 at <www.avianbiology.org/readers/appendix>). Appendix 1.