

distributed across several landscapes. Alternatively, relatively small, isolated populations can segregate and accumulate phenotypic differences if range expansion is not constant through time or if the direction of dispersal changes. Outcomes may vary, depending on the number of independent radiations, differences in diversification rates, rate and pattern of gene flow, and rapidity of species radiation following a wave of dispersal (Mayr and Diamond 2001, Moyle et al. 2009, Cibois et al. 2011).

Inferring the geographic origin and temporal diversification of organisms is an essential part of biogeography and depends on an accurate estimate of evolutionary relationships among species (Rosen 1978, Filardi and Moyle 2005). In the case of birds, enabled by flight to disperse long distances, the spatiotemporal patterns of diversification can be challenging to analyze, especially when shallow radiations on islands generate differential morphological traits that obscure evolutionary affinities (Filardi and Moyle 2005, Irestedt et al. 2013). Dispersal and adaptation together are important drivers of insular diversification of many bird groups (Pratt 2005, Grant and Grant 2008) and account for much of the diversity that we find today in archipelagos (Trewick and Gibb 2010, Trewick 2011). Colonization of islands sometimes involves loss of the capability for further long-distance dispersal, when flight is not integral to foraging, social interaction, or predator avoidance (McNab 1994, McNab and Ellis 2006, Steadman 2006). Reduction, and even loss, of flight capacity can be an adaptive response to island life, and some speciation may occur with adaptation of flightlessness, as a result of altered selective environments (Milá et al. 2010, Sly et al. 2011, Alonso et al. 2012, Runemark et al. 2012).

Family Rallidae (Aves: Gruiformes) is diverse and cosmopolitan. It includes common species that are good dispersers, as well as regional and island endemics. Many oceanic islands that were naturally without terrestrial mammal predators appear to have favored reversion to a terrestrial lifestyle after colonization and speciation by flying ancestors (Ripley 1977, Steadman 2006). This combination of high dispersal and high endemism associated with the loss of flight makes them interesting subjects for evolutionary analysis. In particular, the large, flamboyant purple swamphens (genus *Porphyrio*) demonstrate extraordinary dispersal capabilities, with evidence of multiple invasions, apparently spaced out in time, that resulted in divergences of size, color, and other traits (Ripley 1977, Remsen and Parker 1990, Trewick 1996). Seven species of purple swamphens are currently recognized, 4 of which are or were present in the Oceania region (Trewick 1996, Taylor 1998). Principal among these is the widespread “supertramp” Purple Swamphen (*Porphyrio*

instructions and standard procedures for aDNA (Cooper and Poinar 2000, Rohland and Hofreiter 2007). DNA from bones was extracted using decalcification with EDTA and proteinase K digestion in Tris-buffered saline, followed by purification with phenol–chloroform. DNA from fresh tissues was extracted in a laboratory geographically separated from the aDNA laboratory, using either Tissue DNeasy kit (Qiagen; following the manufacturer's instructions) or incubation at 55°C with proteinase K and a CTAB buffer (2% Hexadecyl trimethyl ammonium bromide, 100 mM Tris–HCl, pH 8.0, 1.4 M NaCl, 20 mM EDTA), followed by a combined phenol–chloroform–isoamyl alcohol (25:24:1) cleanup.

Mitochondrial and Nuclear DNA Amplification

We sequenced 2 mitochondrial genes and 1 nuclear gene for population genetic analyses of *P. porphyrio* in Australia and New Zealand: mitochondrial control region (CR) and cytochrome oxidase b (cyt b), plus a fragment of the

TABLE 1. χ^2 test of independence for the relationship between gender and the number of children in the household.

Gender	1 child	2 children	3 children	4 children	5 children	Total
Male	10	15	20	10	5	60
Female	15	20	15	10	5	65
Total	25	35	35	20	10	125

TABLE 1.

Species	G		b		G		ADG
	11	12	11	12	11	12	
<i>palliatus</i>							
<i>pelewensis</i>							
<i>poliocephalus</i>							
<i>porphyrio</i>							
<i>pulverulentus</i>							
<i>samoensis</i>							
<i>seistanicus</i>							
<i>vitiensis</i>							
<i>P. p. melanoitus</i>							<i>P. p. indicus</i>
<i>P. p. caledonicus</i>							

were resolved using PHASE implemented in DnaSP version 5.0 (Librado and Rozas 2009) with the default parameters. To test for intralocus recombination in BFG-7, we used the PHI test (Bruen et al. 2006) implemented in SplitsTree. This is a robust test that can reliably detect recombination and report few false positives (Martin et al. 2011). We calculated the following summary statistics for genetic variation of each population in DnaSP: number of haplotypes (h), nucleotide diversity per site (ρ), number of



FIGURE 2. A

diversity (ρ) at sampling localities with n

attributable among populations. Population geographic structure was evident in the mitochondrial and nuclear haplotype networks (Figure 2B, 2C), and the Mantel test showed a significant correlation between genetic and geographic distances among populations ($r = 0.508$, $P < 0.05$), even though only ~26% of genetic divergence was explained by geographic distance.

DISCUSSION

Biogeography and Evolution of Swampheims

Our phylogenetic analyses and molecular dating support independent and temporally nonoverlapping colonization events among *Porphyrio* species. This interpretation is, however, based on surviving or recently extinct lineages only; other colonizations are represented by fossils on Oceanic islands (Steadman 1988, 2006, Steadman et al. 1999) or have left no trace at all. The most likely area of origin of *Porphyrio* is Africa, with colonization westward into the Americas and several other colonizations north-eastward (Europe, Asia, and Oceania) during the Miocene and Pleistocene. The oldest split among the currently recognized *P. porphyrio* lineage (Figure 1C, clade A) occurred in the Late Miocene (~37.1955–37.3–49.75 Ma) (0.05–0.05) [0.4(S)57(as)-8((U)on)]

P. melanotus of south Western Australia (Figure 1C, clade B) show exceptional and not subtle differentiation in plumage color pattern (Whittell 1934). The current nominate subspecies *P. p. bellus* in south Western Australia has a prominently brighter blue breast and throat color than *P. p. melanotus* (see images in Figure 2A). Differences in color, size, and other traits are evident among other lineages within the melanotus clade (Ripley 1977) and in other clades. For instance, within the poliocephalus clade, the Middle Eastern



Erythropitta erythrogaster

APPENDIX B

Short Sequences

l G , l ll lll
l
l

. Porphyrio porphyrio porphyrio
G G G G G G G
GG GG GG G
G GG G G G G G

. Porphyrio porphyrio pelewensis
GGG G G GG
G G G
G G G G G
G GG GG G
G G G G
G G G

. Porphyrio porphyrio palliatus
GGG G G GG
G G G G

G G G G G
G GG GG G G GG G
G G G G
G G G

. Porphyrio porphyrio poliocephalus
G G G G G
G G G G G G
G GG GG G G GGGG G
GGG G

. Porphyrio porphyrio caledonicus
G G G G G
G G G G G G
G GG GG G G GGGG G
GGG G

. Porphyrio mantelli