

1 East-west genetic differentiation in Musk Ducks (*Biziura lobata*) of Australia
2 suggests late Pleistocene divergence at the Nullarbor Plain.

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21 **Running head:** *Phylogeography of the Musk Duck*

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35 **Abstract**

36 Musk Ducks (*Biziura lobata*) are endemic to Australia and occur as two
37 geographically isolated populations separated by the Nullarbor Plain, a vast arid
38 region in southern Australia. We studied genetic variation in Musk Duck populations
39 at coarse (eastern versus western Australia) and fine scales (four sites within eastern
40 Australia). We found significant genetic structure between eastern and western
41 Australia in the mtDNA control region ($\Phi_{ST} = 0.747$), one nuclear intron ($\Phi_{ST} =$
42 0.193) and eight microsatellite loci ($F_{ST} = 0.035$). In contrast, there was little genetic
43 structure between Kangaroo Island and adjacent mainland regions within eastern
44 Australia. One small population of Musk Ducks in Victoria (Lake Wendouree)
45 differed from both Kangaroo Island and the remainder of mainland eastern Australia,
46 possibly due to genetic drift exacerbated by inbreeding and small population size.
47 The observed low pairwise distance between the eastern and western mtDNA lineages
48 (0.36%) suggests that they diverged near the end of the Pleistocene, a period
49 characterised by frequent shifts between wet and arid conditions in central Australia.
50 Our genetic results corroborate the display call divergence and Mathews' (1914)
51 subspecies classification, and confirm that eastern and western populations of Musk
52 Duck are currently isolated from each other.

53

54 Keywords: Arid zone, microsatellite, mitochondrial DNA, nuclear intron, Nullarbor
55 Plain, Waterfowl

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57

58 **Introduction**

59 The Nullarbor Plain, a vast arid region of porous limestone and calcareous sandstone
60 in southern Australia, represents a major biogeographic barrier for east-west dispersal
61 of temperate Australian plant and animal species (e.g. Keast 1981). The avifauna of
62 southern Australia is characterised by an east-west division at the Nullarbor (Cracraft
63 1986), with numerous avian species displaying morphological divergence on either
64 side of the Nullarbor sufficient to suggest subspecific differentiation (Schodde &
65 Mason 1999).

66

67 Because surface water in the Nullarbor drains away rapidly, this region does not
68 support permanent wetlands. The distribution of Australian waterbirds depends on
69 availability of water in the arid zone (Morgan 1954; Frith 1957, 1959; Roshier *et al.*
70 2002; Poiani 2006), and thus the Nullabor is predicted to be an important boundary in
71 the distribution of waterbirds. While the importance of the Nullarbor has been
72 examined using genetic data (Toon *et al.* 2007; Neaves *et al.* 2009; Salinas *et al.*
73 2009), its role as a barrier for dispersal in waterbirds has not been investigated.

74

75 Australian waterfowl (Anatidae) such as Grey Teal (*Anas gracilis*), Australasian
76 Shoveler (*Anas rhynchos*), Pink-eared Duck (*Malacorhynchus membranaceus*) and
77 Freckled Duck (*Stictonetta naevosa*) are highly nomadic and can be found at
78 widespread inland locations after major flooding events (Frith 1967; Briggs 1992).
79 For these species, large scale east-west dispersal seems to occur through the Northern
80 Territory rather than through the Nullarbor (Frith 1962). Other species like Chestnut
81 Teal (*Anas castanea*), Blue-billed Duck (*Oxyura australis*) and Musk Duck (*Biziura*
82 *lobata*) are less nomadic and have regular movement patterns, moving to inland

83 ephemeral wetlands in winter and spring for breeding, and returning to permanent
84 wetlands closer to the coast in summer and autumn (Frith 1967). For the latter three
85 species, the lack of wetlands on the Nullarbor presumably impedes east-west
86 dispersal, but transient flooding may allow some dispersal to occur through the
87 Nullarbor in wet years.

88

89 Musk Ducks are a particularly interesting species among Australian waterfowl,
90 because their distribution does not extend to the Northern Territory. Although fossil
91 records suggest that Musk Ducks were formerly more widely distributed (e.g. Worthy
92 2002), they currently occur as two geographically isolated populations separated by
93 the Nullarbor (Marchant & Higgins 1990). Thus, their east-west dispersal capacity is
94 predicted to depend critically on the availability of water in the Nullarbor. Musk
95 Ducks also occur on Kangaroo Island and in Tasmania (Barrett *et al.* 2003), which are
96 separated from mainland Australia by Backstairs Passage and Bass Strait,
97 respectively.

98

99 Historically, Musk Ducks were thought to be flightless (Ramsey 1867; Campbell
100 1901), but now are known to fly long distances to colonise ephemeral wetlands after
101 inland rain (Frith 1967; Brooker *et al.* 1979; Marchant & Higgins 1990). Band
102 recoveries demonstrate that Musk Ducks disperse locally (Anonymous 1988a; Guay
103 2007). Musk Ducks have been observed on ephemeral wetlands on the Nullarbor
104 after major flooding, but never in large numbers (Brooker *et al.* 1979; Burbidge *et al.*
105 1987). They also occur on, and forage in, marine habitats (Wood 1960; McCracken
106 1999) and have been observed in small flocks on the coast of the Nullarbor
107 (Martindale 1980; Congreve & Congreve 1982, 1985; Barrett *et al.* 2003). These

108 anecdotal sightings suggest that Musk Ducks may move between eastern and western
109 Australia, albeit in low numbers, either inland through connecting ephemeral wetlands
110 or possibly along the coast. Nevertheless, it remains unclear whether there is
111 significant dispersal across the Nullarbor.

112

113 Mathews (1914, 1927) described the eastern populations of Musk Ducks as a separate
114 subspecies (*B. l. menziesi*) distinct from the nominate western populations, although
115 others (Phillips 1926; Hartert 1931; Delacour 1959; Parker *et al.* 1985) considered the
116 species to be monotypic. Display postures and vocalisations of Musk Ducks have
117 been described in detail for populations in eastern and western Australia (Serventy
118 1946; Stranger 1961; Johnsgard 1966; Lowe 1966). Although some or all postures
119 are shared between eastern and western populations (Fullagar & Carbonell 1986),
120 vocalisations differ markedly (Robinson & Robinson 1970; McCracken *et al.* 2002).
121 These differences led Robinson and Robinson (1970) and McCracken *et al.* (2002) to
122 conclude that the two populations probably have been isolated for an extended period.

123

124 While numbers of Musk Duck seem stable in Western Australia (Saunders & Ingram
125 1995) and Tasmania (Bryant & Jackson 1999; S. Blackhall, unpublished data), they
126 have decreased in mainland eastern Australia (e.g. Parker *et al.* 1985; Davey 1989;
127 Paton *et al.* 1994). Musk Ducks are currently listed as vulnerable in Victoria
128 (Victorian Department of Sustainability and Environment 2007) and rare in South
129 Australia (Robinson *et al.* 2000), but are yet to be listed in New South Wales. Little
130 information on population size is available, but the combined eastern and western
131 population is estimated to be 20,000 to 50,000 individuals (Wetlands International
132 2006). Major threats to the population include habitat loss due to drainage for

133 agriculture and possible competition for food with introduced European carp
134 (*Cyprinus carpio*) in the Murray Darling Basin (McCracken 2005). Decreased habitat
135 availability over the last decade, due to a long lasting drought in southeastern
136 Australia, probably has contributed to recent population declines. Because numbers
137 of Musk Ducks are not declining nationally, conservation or recovery efforts have not
138 been initiated. Conservation efforts should not be limited to species or subspecies, but
139 rather target populations that are ecologically and/or genetically distinct (Moritz 1994;
140 Crandall *et al.* 2000). Understanding patterns of divergence and gene flow between
141 eastern and western Australia is therefore essential for the proper management of the
142 species.

143

144 We investigated genetic variation in Musk Ducks in the mitochondrial DNA
145 (mtDNA) control region, two nuclear introns, and eight microsatellite loci, to estimate
146 levels of population connectivity. We analysed genetic structure at a coarse scale
147 (eastern versus western Australia) and at fine scales (four populations within eastern
148 Australia). We predicted that genetic structure between eastern and western Australia
149 would be consistent with display divergence, but that the dispersive ability of Musk
150 Ducks would limit structure within eastern Australia.

151

152 **Methods**

153 *Sample collection*

154 We collected blood and/or feather samples from 89 Musk Ducks captured or collected
155 from eastern and western Australia between 1995 and 2005 and obtained an additional
156 71 samples from museum tissue collections and from historical museum specimens
157 dating as far back as the late 1800s (Appendix 1). We grouped samples

158 geographically into five populations (Figure 1): Western Australia (WA; $n = 16$),
159 Kangaroo Island (KI; $n = 47$), Tasmania (TAS; $n = 8$), mainland eastern Australia
160 (SE; $n = 55$) and Lake Wendouree (LW; $n = 34$).

161

162 *Sampling and study sites*

163 Most of the live captures took place on two wetlands: Murray Lagoon, Cape
164 Gantheaume Conservation Park, Kangaroo Island, South Australia ($35^{\circ}54'S$,
165 $137^{\circ}24'E$; 1995-1997; $n = 46$) and Lake Wendouree in Ballarat, central Victoria
166 ($33^{\circ}33'S$, $143^{\circ}49'E$; 2003-2004; $n = 34$).

167

168 Murray Lagoon is a 750-1,000ha natural wetland on Kangaroo Island which greatly
169 increased in size after flooding in 1995 (McCracken *et al.* 2000). Musk Ducks breed
170 on Murray Lagoon (Baxter 1989; McCracken *et al.* 2000). The population fluctuates
171 seasonally, and between 1995 and 1997 numbers peaked in early to mid-October
172 (McCracken 1999). We captured Musk Ducks on Murray Lagoon using night-
173 lighting, baited traps, and walk-in-nest-traps (McCracken *et al.* 2003).

174

175 Lake Wendouree is an artificial wetland maintained by the Ballarat city council for
176 recreational purposes. The lake was traditionally topped up in summer, but water
177 restrictions imposed by a recent drought meant that this practice was abandoned in
178 2003. In 2005, the lake dried up entirely for the first time in 50 years. Musk Ducks
179 bred regularly and, prior to 2005, were sedentary on Lake Wendouree (Thomas &
180 Wheeler 1983; Anonymous 2000; Guay & Mulder 2007). We captured Musk Ducks
181 on Lake Wendouree by hand or using a hand net after they were enticed to the shore
182 using bread morsels (Guay & Mulder 2007).

183

184 *Mitochondrial DNA and intron sequencing*

185 We extracted DNA from blood samples using the salting out method (Bruford et al.
186 1992) and from feathers, tissue and toe-pad samples using the DNeasy Tissue Kit
187 (Qiagen, Valencia, CA). Only DNA isolated from feathers, muscle tissue or toe-pad
188 samples was used for amplification of mtDNA, and DNA isolated from blood or
189 tissue was used to amplify nuclear introns and microsatellites. We amplified the
190 5'end of the mitochondrial genome control region (positions 82-773 in the chicken
191 genome), intron 4 of ornithine decarboxylase (ODC1) and intron 7 of beta-fibrinogen
192 (FGB). Primers included L81 (TATTTGGTTATGCATATTCGTGCAT; M. D.
193 Sorenson unpublished), H493 (Sorenson & Fleischer 1996) and H774 (Sorenson *et al.*
194 1999) for control region, ODC1-5F and ODC1-6R (McCracken *et al.* 2009) and FGB-
195 7F (CTCAGAAGACTGGAGCTCATTG; M. D. Sorenson unpublished) and FGB-
196 7R (CCRCCRTCTTCTTTNGARCACTG; M. D. Sorenson unpublished). We
197 performed polymerase chain reactions (PCR) on a Corbett Research PC-960C
198 thermocycler using standard recipes. Betaine (1.0M) was added to PCR reactions of
199 samples from study skin feathers and toe-pads (Johnson & Dunn 2006). We
200 performed PCR amplification as follows: one cycle of 7min at 94°C followed by 45
201 cycles of 94°C for 20s, 56°C for 20s and 72°C for 60s, and one cycle of 72°C for
202 7min. PCR products were separated by agarose gel electrophoresis, gel purified using
203 the QIAquick Gel Extraction Kit (Qiagen, Valencia, CA), and sequenced either
204 commercially (Macrogen, Seoul, Korea) or with the BigDye Terminator kits on ABI
205 3100 Genetic Analyzers (Applied Biosystems, Foster City, CA). We sequenced both
206 strands of the mtDNA, but nuclear introns were only sequenced in one direction

207 unless the individual was found to be heterozygous for an insertion/deletion (indel), in
208 which case both strands were sequenced to resolve the indel (e.g. Peters *et al.* 2007).

209

210 We sequenced 652bp from the 5' end of the mtDNA control region of birds collected
211 for this study and 373bp from most recent samples obtained from museum study
212 skins. All but one of the variable sites were located within the first 244 bp from the 5'
213 end of the sequence. The only variable site outside the first 244bp was a transition at
214 position 250; this transition was unique to two specimens from Tailem Bend, South
215 Australia (SAMA B25005 and SAMA B23004) that also shared a unique haplotype
216 within the first 244bp. Thus, we designed an internal primer (H364;
217 GCATGAGTAATGGGAGGTAGC) to amplify the first 244bp of the control region
218 from older specimens for which amplification using both L81/H774 and L81/H493
219 had failed. Finally, we sequenced 363bp from ODC1 and 450bp from FGB.

220 Sequences from complementary mtDNA strands were reconciled and double peaks in
221 intron sequences were coded with IUPAC degeneracy codes and treated as
222 polymorphisms using SEQUENCHER 3.1 (Gene Codes, Ann Arbor, USA).

223

224 *Microsatellite genotyping*

225 Individuals were genotyped at eight Musk Duck-specific microsatellite loci (*Blm2*,
226 *Blm3*, *Blm4*, *Blm5*, *Blm7*, *Blm9*, *Blm11* and *Blm12*; Guay & Mulder 2005). In all
227 eight cases, one primer of each pair was attached with an M13 tail
228 (CACGACGTTGTAAAACGAC) to allow for universal dye labelling (Boutin-
229 Ganache *et al.* 2001). PCR reactions were performed on a Corbett Research PC-960C
230 thermocycler as described by Guay and Mulder (2005). Fragments were separated on
231 a CEQ 8000 automatic DNA sequencer (Beckman Coulter) and fragment size was

232 estimated using the CEQ 8000 Genetic Analysis System software (Beckman Coulter,
233 2004; version 8.0.52). Genotyping was repeated for 10% of the individuals and in all
234 cases confirmed that allelic designations were accurate.

235

236 *Statistical Analysis – sequence data*

237 Two specimens showed a single transition polymorphism in their mtDNA, suggesting
238 heteroplasmy (QVM:1963/2/28 and LSUMZ 34777 from Tasmania and Kangaroo
239 Island respectively). Both haplotypes for these two specimens were considered
240 separately in the analysis. Gametic phase of introns was resolved using PHASE 2.1
241 (Stephens *et al.* 2001). PHASE uses a Bayesian algorithm to infer haplotypes from
242 diploid genotypic data with recombination and the decay of LD with distance. Each
243 data set was analyzed using the default values (100 main iterations, 1 thinning
244 interval, 100 burn-in) followed by 1,000 main iterations and 1,000 burn-in (-X10
245 option) for the final iteration. Analysis was performed three times, and all pair
246 probabilities were 1.00 for both loci.

247

248 We used FSTAT 2.9.3 (Goudet 1995) to test both introns for deviation from the
249 Hardy-Weinberg equilibrium and for evidence of linkage disequilibrium between loci.

250 We calculated haplotype (h) and nucleotide diversity (π) using ARLEQUIN 3.01
251 (Excoffier *et al.* 2005). We calculated unrooted networks using the software
252 NETWORK 4.2.0.1 (Fluxus Technology).

253

254 *Statistical analysis – microsatellites*

255 Number of alleles (A) and observed (H_O) and expected (H_E) heterozygosity were
256 calculated using GENALEX 6 (Peakall & Smouse 2006). We also calculated allelic

257 richness (R_s ; El Mousadik & Petit 1996) and the inbreeding coefficient (F_{IS}) using
258 FSTAT 2.9.3. We tested each locus in each population for deviation from the Hardy-
259 Weinberg equilibrium and tested each pair of loci in each population for linkage
260 disequilibrium using GENEPOP 1.2 (Raymond & Rousset 1995). We performed
261 Hardy's (2003) test using SPAGEDI 1.2g (Hardy & Vekemans 2002) to evaluate
262 which of the two measures of population differentiation (F_{ST} or R_{ST}) was more
263 appropriate to use with our dataset. As part of Hardy's test, allele size permutation is
264 performed to calculate simulated R_{ST} (pR_{ST}). If observed R_{ST} is larger than pR_{ST} ,
265 mutation plays an important role in population differentiation and R_{ST} should be used
266 (Slatkin 1995). Otherwise drift is the main driving force of population and F_{ST} should
267 be used (Hardy et al. 2003). R_{ST} and pR_{ST} were not significantly different in our data
268 set ($P > 0.10$). We therefore used F_{ST} for the analysis of population differentiation.

269

270 *Genetic structure analysis*

271 We analysed genetic structure at two levels: 1) coarse scale (east versus west), and 2)
272 fine scale (within eastern Australia). For the coarse scale analysis, samples from
273 eastern Australia were compared to samples from Western Australia. To avoid
274 potential biases from over-representation of samples from either Lake Wendouree or
275 Kangaroo Island within the eastern Australia sample, we randomly selected eight
276 samples from each of these two populations, as this was the maximum number of
277 sequences from any other population in eastern Australia. For the fine-scale analysis,
278 we compared samples from Kangaroo Island to samples from Tasmania and to
279 samples from mainland eastern Australia (including eight randomly selected samples
280 from Lake Wendouree). Finally we compared samples from Lake Wendouree to
281 samples from Kangaroo Island and the remainder of mainland eastern Australia.

282 Samples from Tasmania were only used for analysis of mtDNA because of low
283 sample size due to poor PCR amplification success of nuclear markers from old
284 museum specimens.

285

286 The HKY model (Hasegawa et al. 1985) was identified as the best-fit model of
287 nucleotide substitution for both mtDNA and nuclear introns in our dataset using
288 MODELTEST 3.7 (Posada & Crandall 1998). We thus calculated pairwise Φ_{ST}
289 values for mtDNA and introns using the closely related K80 (Kimura 1980)
290 nucleotide substitution model in ARLEQUIN 3.01, as the HKY model is not available
291 in this software. For both mtDNA and the introns, we also calculated F_{ST} based on
292 the haplotype frequencies using ARLEQUIN 3.01. We estimated pairwise F_{ST} for the
293 eight microsatellite loci combined using FSTAT 2.9.3. Significance values for all
294 pairwise Φ_{ST} and F_{ST} calculations were adjusted using sequential Bonferroni
295 correction to avoid type I error (Holm 1979). Sample sizes varied between markers
296 and populations. Uneven sample size can bias F_{ST} leading to Type I error (Scribner *et*
297 *al.* 2001). To test for biases in cases where sample size differed between populations
298 and we found significant F_{ST} or Φ_{ST} , we repeated the analysis using a random
299 subsample of the largest population of equal sample size to that of the other
300 population. This procedure was repeated ten times for each population/locus
301 combination. To determine the level of divergence between eastern and western
302 Australia, we calculated the net mitochondrial average pairwise distance (D_A)
303 between eastern and western Australia using ARLEQUIN 3.01.

304

305 *Intra-population analysis within eastern Australia*

306 To investigate the potential impacts of inbreeding and small population size on
307 Kangaroo Island and Lake Wendouree (the populations with the two largest sample
308 sizes in the southeast), we estimated theta from mtDNA haplotypes and both average
309 pairwise relatedness and effective population size (N_e) using microsatellite data.
310 Theta was calculated using DnaSp 5.10 (Librado & Rozas 2009). We calculated
311 averaged pairwise relatedness (Queller & Goodnight 1989) and performed a
312 permutation test (9999 permutations and 10000 bootstraps) using GENALEX 6. We
313 estimated effective population size (N_e) from microsatellite data using the Linkage
314 Disequilibrium Method (Bartley et al. 1992) implemented in the software
315 NeESTIMATOR 1.3 (Peel et al. 2004). Finally, we tested for evidence of a recent
316 bottleneck in either population using BOTTLENECK (Piry et al. 1999).

317

318 **Results**

319 *Mitochondrial sequences*

320 We found 13 variable sites (all transitions) and a single base pair indel in 15 distinct
321 haplotypes (Figure 2A). Haplotype diversity (h) within populations varied between
322 0.250 and 0.692 and nucleotide diversity (π) varied between 0.00103 and 0.00557
323 (Table 1). In both cases, the lowest diversity was observed in Tasmania and the
324 highest in western Australia.

325

326 No mitochondrial haplotypes were shared between eastern and western Australia. The
327 two lineages were separated by a single transition (Fig. 2A). Thus, there was
328 substantial genetic structure between eastern and western Australia for mtDNA ($\Phi_{ST} =$
329 0.747; Table 2). In contrast, no significant structure was detected within eastern

330 Australia (Table 2). A low net average pairwise distance (D_A) of 0.36% separated the
331 eastern and western lineages.

332

333 *Intron sequences*

334 We found six variable sites and a single base pair indel in ODC1 and six variable sites
335 in FGB. Seven alleles were inferred for ODC1 (Figure 2B), and five alleles for FGB
336 (Figure 2C). Neither intron deviated from Hardy-Weinberg equilibrium, and no
337 evidence of linkage disequilibrium between loci was detected when populations were
338 analysed separately or pooled together. Haplotype diversity (h) varied between 0.611
339 in western Australia and 0.770 on Lake Wendouree and nucleotide diversity (π)
340 varied between 0.00415 on mainland eastern Australia and 0.00557 on Lake
341 Wendouree for ODC1 (Table 1). For FGB, haplotype diversity (h) varied from 0.603
342 on Lake Wendouree to 0.723 in western Australia and nucleotide diversity (π) varied
343 from 0.00341 in mainland eastern Australia to 0.00434 on Kangaroo Island (Table 1).

344

345 Many haplotypes were shared between populations for both ODC1 (Fig. 2B) and FGB
346 (Fig. 2C). Genetic structure was detected between eastern and western Australia (Φ_{ST}
347 = 0.193; F_{ST} = 0.157; Table 2) for ODC1. Random resampling yielded significant
348 Φ_{ST} ($P < 0.007$) in nine out of ten replicates. Within eastern Australia, no significant
349 Φ_{ST} values were observed, but significant pairwise F_{ST} values were observed between
350 Lake Wendouree and both Kangaroo Island and mainland eastern Australia for ODC1
351 (Table 2). In both cases, random resampling yielded identical results. Although
352 marginally significant Φ_{ST} and F_{ST} were detected with FGB, no significant structure
353 was detected with FGB at any level of analysis after Bonferroni correction (Table 2).

354

355 *Microsatellite loci*

356 None of the eight microsatellite loci deviated from Hardy-Weinberg equilibrium, and
357 no evidence of linkage disequilibrium was observed. The average number of alleles
358 per locus ranged from 7.0 in western Australia to 9.1 in Kangaroo Island, and the
359 number of private alleles per population varied between 2 for mainland eastern
360 Australia and 11 for Kangaroo Island (Table 3).

361

362 Using microsatellites, significant F_{ST} values were observed between eastern and
363 western Australia ($F_{ST} = 0.035$, $P = 0.001$; Table 4). All random samples from
364 eastern Australia also yielded significant F_{ST} (all $P < 0.002$) with western Australia.
365 Within eastern Australia, we found significant pairwise F_{ST} between Lake Wendouree
366 and both Kangaroo Island ($F_{ST} = 0.050$, $P < 0.001$; Table 4) and mainland eastern
367 Australia ($F_{ST} = 0.042$, $P < 0.001$; Table 4). In both cases, sub-sampling did not
368 change the result. Kangaroo Island also differed from mainland eastern Australia (F_{ST}
369 $= 0.018$, $P = 0.001$; Table 4). Identical results were obtained with ten random
370 samples to control for uneven sample size (all $P < 0.02$).

371

372 *Intra-population analysis within eastern Australia*

373 Theta per site (Theta-W) estimated from mtDNA was significantly larger for
374 Kangaroo Island (0.00373; 95% C.I.: 0.00314–0.00434) than for Lake Wendouree
375 (0.00203; 95% C.I.: 0.00152–0.00254). Similarly, the effective population size of the
376 Kangaroo Island population (118.7; 95% C.I.: 73.0–279.0) was larger than that of the
377 Lake Wendouree population (31.2; 95% C.I.: 24.6–41.1). Furthermore, the Lake
378 Wendouree population had a larger inbreeding coefficient (F_{IS} ; 0.018) than did

379 Kangaroo Island (-0.055), average pairwise relatedness was higher in Lake
380 Wendouree than on Kangaroo Island (0.053 vs 0.014 ; permutation test: $P < 0.05$), and
381 in all but one microsatellite locus, heterozygosity was equal or larger in the Kangaroo
382 Island population compared to Lake Wendouree. We found no evidence of a recent
383 bottleneck in either the Kangaroo Island or Lake Wendouree population.

384

385 **Discussion**

386 *Genetic diversity*

387 We observed low mtDNA genetic diversity ($h = 0.25$ – 0.69 %, $\pi = 0.10$ – 0.56) in Musk
388 Ducks as compared to two other species of Australian waterfowl, Grey Teal (*Anas*
389 *gracilis*; $h = 0.99$ %, $\pi = 1.4$) and Chestnut Teal (*Anas castanea*; $h = 0.97$ %, $\pi = 1.3$;
390 Joseph et al. 2009). This suggests recent population decline or long-term low
391 effective population size for Musk Ducks possibly exacerbated by their highly
392 polygynous lek mating system (Johnsgard & Carbonell 1996). Although our
393 microsatellite data do not suggest a recent bottleneck event, Musk Ducks were
394 previously more widely distributed (Worthy 2002). Alternatively, the low genetic
395 diversity of Musk Duck may be due to their relatively smaller population size. At an
396 estimated 20,000–50,000 (Wetlands International 2006), the global population of
397 Musk Ducks is much lower than the estimate of >1 million for Grey Teal or 105,000
398 for Chestnut Teal (Wetlands International 2006).

399

400 *Genetic structure*

401 We found no shared mtDNA haplotypes and substantial genetic structure between
402 eastern and western Australia. The Φ_{ST} for the 5' end of the mtDNA control region of
403 Musk Ducks was greater than that observed using the same marker between eastern

404 and western populations of North American Wood Ducks (*Aix sponsa*; Φ_{ST} : 0.31;
405 (Peters et al. 2005) or between North American and Eurasian Mallards (*Anas*
406 *platyrhynchos* Φ_{ST} : 0.41–0.0.50; (Kulikova et al. 2005). In contrast, haplotype
407 sharing was extensive between eastern and western Australia for both ODC1 and
408 FGB. While ODC1 displayed significant genetic structure, FGB did not. Within
409 eastern Australia, no significant Φ_{ST} were detected between any two populations for
410 ODC1, but significant pairwise F_{ST} was detected for both ODC1 and microsatellites
411 between Lake Wendouree and both Kangaroo Island and mainland eastern Australia.
412 This suggests that genetic drift rather than mutation may be responsible for
413 differentiation within eastern Australia. Our results yielded no evidence of mtDNA
414 gene flow across the Nullarbor Plain. Although our sampling in Western Australia
415 was limited, the sampling in eastern Australia was extensive and presumably
416 sufficient to detect moderately low levels of shared mtDNA haplotypes if
417 introgression had occurred west to east.

418

419 In contrast to the mtDNA, the nuclear introns showed numerous shared alleles.
420 Similar results are evident for other waterfowl species (e.g. Sonsthagen *et al.* 2009).
421 Such contrasts between mitochondrial and nuclear markers may result from high
422 female philopatry and/or incomplete lineage sorting (e.g. Funk & Omland 2003).
423 Female Musk Ducks may exhibit higher natal site fidelity as male Musk Ducks are
424 more often sighted at sea (McCracken 1999). While we cannot rule out gene flow
425 across the Nullarbor mediated by males, east-west movement is likely to be limited
426 because we found significant, albeit small, F_{ST} values using microsatellite markers.
427 Alternatively, the lack of differentiation in nuclear introns may be the result of
428 incomplete lineage sorting. Because its effective population size is four times larger,

429 nuclear DNA requires longer to sort to reciprocal monophyly (Moore 1995; Palumbi
430 et al. 2001). Thus, although eastern and western Musk Duck populations have been
431 isolated for an extended period of time, and have attained reciprocally monophyletic
432 mtDNA, they likely have not been isolated long enough to have reciprocally
433 monophyletic nuclear DNA at these loci.

434

435 *Possible causes of genetic differentiation at Lake Wendouree*

436 The Kangaroo Island and Lake Wendouree populations differ markedly in their
437 ecology. For example, the Kangaroo Island population exhibited seasonal movements
438 (McCracken 1999), whereas the Lake Wendouree population, prior to the lake drying
439 out in 2005, was sedentary (Thomas & Wheeler 1983). This difference may have
440 influenced the genetic structure of these two populations. Compared to Kangaroo
441 Island, the Lake Wendouree population had larger F_{IS} , larger average pairwise
442 relatedness, lower theta and effective population size and lower heterozygosity. This
443 suggests that the Lake Wendouree population was both smaller and more inbred than
444 was the Kangaroo Island population. Although immigration to Lake Wendouree was
445 probably taking place, our sample may have been biased toward resident birds, which
446 were easy to capture because they were habituated to take food from humans (Biro &
447 Dingemase 2009). Since genetic drift occurs more rapidly in small populations (Nei
448 & Takahata 1993), the genetic differentiation we observed between Lake Wendouree
449 and the rest of eastern Australia may thus have been the result of drift resulting from
450 small population size and inbreeding.

451

452 *Timing of isolation*

453 The average mtDNA pairwise distance between the eastern and western Australia
454 populations was low at 0.36%. Based on a rate of divergence of 9.7% per million
455 years for the 5' end of the mtDNA control region in ducks (Peters et al. 2005),
456 divergence between the two lineages is recent and likely dates to the late Pleistocene.
457 This is considerably more recent than the late Pliocene aridification of the Nullarbor
458 that has been suggested to have led to the initial differentiation of the southern
459 Australian avifauna (Cracraft 1986). In Australia, the Pleistocene was characterised
460 by major fluctuations in precipitation regime (Ayliffe et al. 1998). The availability of
461 surface water during periods of increased precipitation could have allowed wetland
462 connectivity through the arid interior and favoured east-west dispersal of Musk
463 Ducks. Musk Ducks are known to disperse long distances to colonise ephemeral
464 wetlands in the arid zone (Frith 1967; Brooker et al. 1979; Marchant & Higgins 1990;
465 Todd 1997). The last wet period occurred between 55 and 35 kyr ago and was
466 characterised by lower temperature and higher lake levels in the semi-arid region of
467 southeastern Australia (Bowler et al. 1986; Bowler & Teller 1986; Nanson et al. 1992;
468 Miller et al. 1997). The amount of surface water may have been higher during these
469 wet periods and thus perhaps connectivity was increased at that time. Since the end of
470 the last wet period, 35 kyr bp, the Nullarbor has been drier, restricting movement
471 between isolated populations that are now differentiated.

472

473 The Nullarbor is a well defined isolating barrier (Cracraft 1986; Ford 1987). It was
474 formed in the mid-Miocene (11-15 my bp) when the sea retreated (Wasson 1982). It
475 is characterised by mallee and shrub vegetation and thus constitutes a strong
476 geographical dispersal barrier for mesic species of southeastern and southwestern

477 Australia (Ford 1971; Specht 1981). Similarly to our results, phylogeographic work
478 on Australian magpies (*Gymnorhina tibicen*; Toon et al. 2007) and Southern Emu-
479 wrens (*Stipiturus malachurus*; Donnellan et al. 2009) revealed divergent
480 monophyletic lineages on either sides of the Nullarbor. This pattern is not limited to
481 birds and has also been observed in other vertebrates (Spencer et al. 2001; Chapple et
482 al. 2004; Keogh et al. 2005).

483

484 *Conservation implications*

485 The taxonomic level (i.e. species, subspecies, population) to target for conservation
486 efforts is often debated. Moritz (1994) advocated independent management of
487 monophyletic populations, whereas others have suggested that even in the absence of
488 genetic differentiation, ecologically distinct populations should be preserved (Crandall
489 et al. 2000). Although their mtDNA lineages are not highly differentiated, our data
490 demonstrate that the eastern and western mtDNA haplotype groups are monophyletic,
491 and other studies have demonstrated that eastern and western populations differ in
492 display behaviour (Robinson & Robinson 1970; McCracken et al. 2002).

493 Accordingly, the two Musk Duck populations satisfy both criteria of evolutionarily
494 significant units. Our data are also consistent with Mathews' (1914, 1927) split of
495 Musk Ducks into eastern (*B. l. menziesi*) and western (*B. l. lobata*) subspecies.

496

497 Musk Duck populations appear stable in Western Australia (Saunders & Ingram 1995)
498 and Tasmania (S. Blackhall, unpublished data), but they have decreased in mainland
499 eastern Australia (e.g. Parker et al. 1985; Davey 1989; Paton et al. 1994), where they
500 are now listed as vulnerable in Victoria (Victorian Department of Sustainability and
501 Environment 2007) and rare in South Australia (Robinson et al. 2000). This decrease

502 corresponds with habitat loss through decreased rainfall and wetland drainage. About
503 one third of Victoria's wetlands have been drained since European settlement
504 (Anonymous 1988b) and 60% of wetlands in coastal New South Wales have also been
505 lost (Goodrick 1970). Musk Ducks may also be threatened by the introduction of the
506 European carp (*Cyprinus carpio*), with whom they compete for food, in river systems
507 (Paton et al. 1994; McCracken 2005). A management plan for protection of Musk
508 Ducks has not been completed to date, probably because they appear stable in
509 Western Australia (Saunders & Ingram 1995). Our results indicate that the eastern
510 and western Musk Duck populations are genetically distinct, and that wildlife
511 agencies should consider managing them separately.

512

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539

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809 **Table 1.** Genetic diversity estimates for the mtDNA control region, ornithine decarboxylase
810 (ODC1), and beta-fibrinogen (FBG) including sample size (N), number of haplotypes (H),
811 number of private haplotypes (Pri), haplotype diversity ($h \pm S.E.$), and nucleotide diversity
812 ($\pi \pm S.E.$) for western Australia (WA), Kangaroo Island (KI), Tasmania (TAS), mainland
813 eastern Australia (SE), and Lake Wendouree (LW).

Pop	N	H	Pri	$h \pm S.E.$	π
<u>Mitochondrial control region</u>					
WA	16	4	4	0.692 ± 0.018	0.00557 ± 0.00102
KI	47	7	4	0.537 ± 0.010	0.00388 ± 0.00044
TAS	8	2	0	0.250 ± 0.064	0.00103 ± 0.00052
SE	49	6	4	0.419 ± 0.012	0.00311 ± 0.00037
LW	33	2	0	0.409 ± 0.013	0.00338 ± 0.00048
<u>ODC1</u>					
WA	14	5	1	0.611 ± 0.018	0.00556 ± 0.00067
KI	46	6	1	0.728 ± 0.003	0.00489 ± 0.00033
SE	25	5	0	0.668 ± 0.008	0.00415 ± 0.00040
LW	34	5	0	0.770 ± 0.003	0.00557 ± 0.00043
TAS	1	2	0	—	—
<u>FBG</u>					
WA	13	5	0	0.723 ± 0.011	0.00381 ± 0.00050
KI	43	5	0	0.655 ± 0.003	0.00434 ± 0.00030
SE	12	3	0	0.627 ± 0.010	0.00341 ± 0.00048
LW	34	4	0	0.603 ± 0.005	0.00382 ± 0.00030
TAS	2	2	0	—	—

814 **Table 2.** Pairwise Φ_{ST} values and F_{ST} values for mtDNA and introns (P -values in
815 parenthesis). Bold text indicates a significant comparison after Bonferroni correction.

Pairwise comparison	Φ_{ST}	F_{ST}
<u>Mitochondrial DNA control region (mtDNA)</u>		
Eastern vs western Australia	0.747 (<0.001)	0.509 (<0.001)
Tasmania vs mainland eastern Australia	-0.042 (0.769)	-0.013 (0.487)
Tasmania vs Kangaroo Island	0.047 (0.219)	0.057 (0.183)
Kangaroo Island vs mainland eastern Australia	0.046 (0.036)	0.025 (0.092)
Kangaroo Island vs Lake Wendouree	-0.025 (0.980)	-0.015 (0.639)
Lake Wendouree vs mainland eastern Australia	0.041 (0.068)	0.008 (0.253)
<u>Ornithine decarboxylase (ODC1)</u>		
Eastern vs western Australia	0.193 (<0.001)	0.157 (0.002)
Kangaroo Island vs mainland eastern Australia	-0.001 (0.406)	-0.004 (0.611)
Kangaroo Island vs Lake Wendouree	0.019 (0.078)	0.057 (0.002)
Lake Wendouree vs mainland eastern Australia	0.022 (0.095)	0.091 (0.003)
<u>Beta-fibrinogen (FBG)</u>		
Eastern vs western Australia	-0.002 (0.373)	0.057 (0.027)
Kangaroo Island vs mainland eastern Australia	0.035 (0.037)	0.041 (0.018)
Kangaroo Island vs Lake Wendouree	0.046 (0.018)	0.040 (0.118)
Lake Wendouree vs mainland eastern Australia	0.081 (0.030)	0.030 (0.039)

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Table 3. Genetic diversity estimates for eight microsatellite loci, including number of individuals (N), number of alleles (A), allelic richness (Rs), observed (H_O) and expected heterozygosity (H_E), F_{IS} for western Australia (WA), Kangaroo Island (KI), mainland eastern Australia (SE) and Lake Wendouree (LW), and average number of alleles (N_A) and private alleles (P_{VA}), and F_{IS} summed over all loci.

Locus		Populations				All	Mean
		WA	KI	SE	LW		
Blm2	N	13	39	12	34	98	8.8
	A	7	11	8	9	15	
	Rs	6.490	7.076	7.725	7.850	8.342	
	H_O	0.85	0.87	0.83	0.82		
	H_E	0.79	0.80	0.82	0.87		
	F_{IS}	-0.075	-0.091	-0.021	0.052		
Blm3	N	11	39	10	34	94	6.8
	A	6	8	6	7	8	
	Rs	5.723	6.342	6.000	5.450	6.266	
	H_O	0.64	0.85	0.80	0.71		
	H_E	0.66	0.81	0.79	0.79		
	F_{IS}	0.038	-0.045	-0.019	0.105		
Blm4	N	12	36	12	34	94	10.5
	A	8	12	10	12	16	
	Rs	7.639	8.539	9.266	9.025	9.599	
	H_O	0.75	0.92	1.00	0.88		
	H_E	0.83	0.87	0.85	0.88		
	F_{IS}	0.096	-0.053	-0.176	0.000		
Blm5	N	12	39	12	34	97	7.5
	A	8	8	7	7	11	
	Rs	7.599	6.074	6.665	5.846	6.839	
	H_O	0.83	0.82	0.92	0.82		
	H_E	0.79	0.78	0.82	0.79		
	F_{IS}	-0.053	-0.057	-0.119	-0.038		
Blm7	N	13	39	12	34	98	6.0
	A	6	8	6	4	10	
	Rs	5.308	5.452	5.333	3.160	4.782	
	H_O	0.85	0.77	0.67	0.35		
	H_E	0.69	0.66	0.64	0.41		
	F_{IS}	-0.222	-0.169	-0.038	0.135		
Blm9	N	13	39	12	34	98	9.0
	A	8	10	10	8	11	
	Rs	7.615	8.210	9.284	6.580	8.289	
	H_O	0.92	0.90	0.83	0.79		
	H_E	0.82	0.87	0.85	0.81		
	F_{IS}	-0.122	-0.037	0.016	0.014		

Blm11	N	12	39	12	34	97	7.3
	A	7	9	7	6	9	
	R _S	6.601	6.612	6.496	4.670	6.418	
	H _O	0.75	0.90	0.83	0.71		
	H _E	0.72	0.79	0.75	0.63		
	F _{IS}	-0.038	-0.132	-0.116	-0.124		
Blm12	N	12	38	12	34	96	7.0
	A	6	7	6	9	10	
	R _S	5.954	5.253	5.663	6.689	6.710	
	H _O	0.83	0.71	0.75	0.88		
	H _E	0.80	0.73	0.74	0.82		
	F _{IS}	-0.048	0.021	-0.014	-0.083		
N _A		7.0	9.1	7.5	7.7		
P _{VA}		4	11	2	6		
F _{IS} All		-0.009	-0.055	-0.017	0.018		

823 Table 4. Pairwise F_{ST} for microsatellite loci (P -values in parenthesis). Bold text
824 indicates a significant comparison after Bonferroni correction.

Pairwise comparison	F_{ST}
Eastern vs western Australia	0.035 (0.001)
Kangaroo Island vs mainland eastern Australia	0.018 (0.001)
Kangaroo Island vs Lake Wendouree	0.050 (<0.001)
Lake Wendouree vs mainland eastern Australia	0.042 (<0.001)

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826 **Figure 1.** Geographic distribution of sampling sites within the five populations of
827 Musk Ducks. The shaded area in the southern part of the continent
828 corresponds to the Nullarbor Plain.
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831 **Figure 2.** Unrooted haplotype networks for (A) mtDNA, (B) ODC1 and (C) FGB sequences. Open circles represent samples from eastern
832 Australia, black circles samples from western Australia. KI: Kangaroo Island; EA: mainland eastern Australia; LW: Lake Wendouree; TA:
833 Tasmania; WA: Western Australia. Open squares represent ancestral haplotypes that were not sampled.
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835 **Appendix 1.** Localities for the specimens used in this study

Catalogue number ^a (Field number) <i>Band number</i>	Sex	Date	Locality
<u>Western Australia</u>			
ANWC 50286	M	31 May 2004	Lake Carabundup, MW of Mt Baker, WA, 34°28'S, 117°18'E
ANWC 50287	M	31 May 2004	Lake Carabundup, MW of Mt Baker, WA, 34°28'S, 117°18'E
ANWC 50288	F	31 May 2004	Lake Carabundup, MW of Mt Baker, WA, 34°28'S, 117°18'E
ANWC 50289	F	31 May 2004	Lake Carabundup, MW of Mt Baker, WA, 34°28'S, 117°18'E
ANWC 50384	M	7 June 2004	Lake Namming, c. 15km S of Cataby, WA, 30°54'S, 115°35'E
ANWC 50385	M	7 June 2004	Lake Namming, c. 15km S of Cataby, WA, 30°54'S, 115°35'E
UAM 11882	M	19 November 2000	Coolgardie, WA, 33°27'S, 121°44'E
UAM 15016	M	20 November 2000	Warden Lake, WA, 33°49'S, 121°53'E
UAM 22312	M	21 November 2000	Warden Lake, WA, 33°49'S, 121°53'E
WAM A18748	F	14 January 1940	Torbay, WA, 35°02'S, 117°38'E
WAM A4333	M	29 March 1933	Harvery Estuary, WA, 32°42'S, 115°41'E
WAM A7419	M	1 June 1954	Floreat Park, WA, 31°56'S, 115°47'E
WAM A36076	M	4 October 2005	Cracker Swamp, Coldat, WA, 30°54'S, 115°35'E
WAM A36077	M	4 October 2005	Cracker Swamp, Coldat, WA, 30°54'S, 115°35'E
(PJG 290) <i>132-20301</i>	M	1 October 2005	Lake Joondalup, Perth, WA, 31°45'S, 115°47'E

(PJG 294) <i>132-20302</i>	M	1 October 2005	Lake Joondalup, Perth, WA, 31°45'S, 115°47'E
			<u>Kangaroo Island</u>
LSUMZ 34096 <i>131-88701</i>	M	11 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34097 <i>131-88702</i>	M	11 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34098 <i>131-88703</i>	M	11 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34099 <i>131-88704</i>	F	12 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34100 <i>131-88705</i>	F	12 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34101 <i>131-88706</i>	F	12 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34102 <i>131-88707</i>	F	15 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34103 <i>131-88708</i>	M	15 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34104 <i>131-88709</i>	F	15 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34105 <i>131-88710</i>	F	15 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34106 <i>131-88711</i>	M	16 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34107 <i>131-88712</i>	M	16 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34108 <i>131-88713</i>	M	22 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34109 <i>131-88714</i>	F	23 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34110 <i>131-88715</i>	F	23 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34111 <i>131-88716</i>	M	25 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E

LSUMZ 34112	131-88717	M	25 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34113	131-88718	M	25 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34114	131-88719	M	26 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34115	131-88720	M	26 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34764	131-88721	M	26 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34765	131-88722	F	26 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34767	131-88724	M	27 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34768	131-88725	M	27 September 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34769	121-41101	F	23 October 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34770	121-41102	F	24 October 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34771	131-88727	M	25 October 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34772	131-88728	M	27 October 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34773	131-88729	M	4 November 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34774	121-41103	F	8 November 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34775	121-41104	F	10 November 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34776	121-41105	F	11 November 1995	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34777	121-41106	F	27 September 1996	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34778	131-88730	M	28 September 1996	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E

LSUMZ 34779 131-88731	M	18 October 1996	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34780 131-88732	M	18 October 1996	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34781 131-88733	M	20 October 1996	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34782 131-88734	M	21 October 1996	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34783 131-88735	M	5 October 1997	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34784 131-88736	M	12 October 1997	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34785 121-41108	F	14 October 1997	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34786 131-88737	M	15 October 1997	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34787 131-88738	M	17 October 1997	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34788 131-88739	M	18 October 1997	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
LSUMZ 34789 131-88740	M	19 October 1997	Murray Lagoon, Kangaroo Island, SA, 35°55'S, 137°24'E
SAMA B46336	U	18 September 1990	Nepean Bay, Kangaroo Island, SA, 36°39'S, 137°42'E
<u>Tasmania</u>			
AMNH 734151	M	November 1914	Colebrook, TAS, 42°32'S, 147°21'E
ANWC 47623	F	11 March 1989	Hobart, TAS, 42°52'S, 147°19'E
QVM:1963/2/28	F	17 April 1961	Moulting Lagoon, TAS, 42°02'S, 148°10'E
QVM:1969/2/7	F	1 March 1969	Flinders Island, TAS, 39°51'S, 147°54'E
QVM:1969/2/8	M	9 March 1969	Needles, TAS, 41°32'S, 146°33'E

QVM:1988/2/102	M	16 September 1988	Painted Post, Greens Beach, TAS, 41°05'S, 146°44'E
TM B2080	F	1800s	Richmond, TAS, 42°44'S, 147°26'E
TM B3360	F	7 March 1971	Sanford Lagoon, TAS, 42°56'S, 147°29'E
<u>Mainland South East</u>			
AMS O.42017	M	1 October 1962	Keepit Dam, Tamworth, NSW, 30°52'S, 150°30'E
AMS O.45232	F	13 December 1974	Barren Box Swamp, Griffith, NSW, 34°09'S, 145°49'E
AMS O.45233	M	13 December 1974	Barren Box Swamp, Griffith, NSW, 34°09'S, 145°49'E
AMS O.45465	F	30 August 1975	Myall Lakes, NSW, 32°25'S, 152°22'E
AMS S.720	M	4 September 1899	Sydney, NSW, 33°46'S, 150°46'E
ANWC 10793	F	24 September 1964	Barren Box Swamp, Griffith, NSW, 34°09'S, 145°49'E
ANWC 15647	M	28 August 1964	Barren Box Swamp, Griffith, NSW, 34°09'S, 145°49'E
ANWC 15648	F	29 August 1964	Barren Box Swamp, Griffith, NSW, 34°09'S, 145°49'E
ANWC 15654	F	No collection date	Barren Box Swamp, Griffith, NSW, 34°09'S, 145°49'E
ANWC 22655	M	6 June 1905	Lake Cowal, NSW, 33°30'S, 147°22'E
ANWC 22658	F	12 June 1905	Stranger Pond, Bonython, ACT, 35°26'S, 149°05'E
ANWC 50091	M	18 February 2004	Deadmans Creek, E of Mathoura, NSW, 35°50'S, 144°56'E
ANWC 50099	F	19 February 2004	Duck Lagoon, Moira State Forest, NSW, 35°52'S, 144°52'E
ANWC 50180	F	26 March 2004	Mullawoolka Basin, Tonga Station, NSW, 30°29'S, 143°47'E

BBM B.lobata1	F	1 February 1981	Bool Lagoon, SA, 37°07'S, 140°41'E
BBM B.lobata2	M	23 February 1997	Bool Lagoon, SA, 37°07'S, 140°41'E
BBM B.lobata3	M	23 February 1997	Bool Lagoon, SA, 37°07'S, 140°41'E
NMV B.5102	M	11 July 1951	King's Billabong, Mildura, VIC, 34°14'S, 142°13'E
NMV B.5188	U	No collection date	Middle Park Beach, Port Phillip Bay, VIC, 37°51'S, 144°57'E
NMV B.7738	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7739	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7742	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7743	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7744	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7746	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7747	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7748	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.7749	U	17 October 1961	Kerang, VIC, 35°43'S, 143°55'E
NMV B.9078	M	6 October 1967	Little Ranker Ck, Keera Stn, VIC, 34°16'S, 141°43'E
NMV B.13775	M	2 March 1985	Kerang, VIC, 35°43'S, 143°55'E
NMV B.18358	M	19 March 1988	Kerang, VIC, 35°43'S, 143°55'E
NMV B.19134	M	14 March 1987	Lake Martin, VIC, 35°05'S, 143°36'E

NMV B.19198	M	12 November 1986	Beechworth, VIC, 36°21'S, 146°41'E
NMV B.19227	F	14 March 1987	Lake Martin, VIC, 35°05'S, 143°36'E
NMV B.19229	F	12 November 1986	Beechworth, VIC, 36°21'S, 146°41'E
NMV B.19288	M	14 March 1987	Lake Martin, VIC, 35°05'S, 143°36'E
NMV B.25089	M	14 March 1987	Lake Murdeduke, VIC, 38°10'S, 143°54'E
NMV B.31571	F	26 April 1993	Lake Bael Bael, VIC, 35°31'S, 143°44'E
NMV MV785	U	19 March 1989	Kerang, VIC, 35°43'S, 143°55'E
NMV W15085	M	No collection date	Lake Purrumbete, near Colac, VIC, 38°16'S, 143°13'E
QMO 666	M	No collection date	Kalbar, QLD, 27°56'S, 152°37'E
QMO 9335	F	16 June 1962	Lake McKenzie, Fraser Island, QLD, 25°27'S, 153°04'E
SAMA B23004	M	1 December 1942	Tailem Bend, SA, 41°05'S, 146°44'E
SAMA B23710	F	17 April 1947	Tailem Bend, SA, 41°05'S, 146°44'E
SAMA B23883	M	13 March 1947	Lake Albert, SA, 35°37'S, 139°18'E
SAMA B25005	F	1 December 1942	Tailem Bend, SA, 41°05'S, 146°44'E
SAMA B38100	F	2 September 1979	Merbein, VIC, 34°10'S, 142°03'E
SAMA B48312	F	30 January 1984	Ulbanda Res., Colwell, Eyre Peninsula, SA, 33°32'S, 136°57'E
(PJG 054)	U	21 March 2005	Kitty Miller Wetland, Philip Island, VIC, 38°30'S, 145°10'E
(PJG 231) <i>132-20261</i>	M	5 September 2004	Western Treatment Plant, Werribee, VIC, 38°00'S, 144°34'E

(PJG254)	U	17 August 2005	Western Treatment Plant, Werribee, VIC, 38°00'S, 144°34'E
(PJG 308)	U	30 October 2005	Western Treatment Plant, Werribee, VIC, 38°00'S, 144°34'E
(PJG 321)	M	4 July 2005	Bool Lagoon, SA, 37°07'S, 140°41'E
(PJG 331)	M	28 December 2005	Western Treatment Plant, Werribee, VIC, 38°00'S, 144°34'E
(PJG 341)	M	16 June 1988	Port Augusta, SA, 32°29'S, 137°46'E

Lake Wendouree

(PJG 200) <i>121-49551</i>	F	1 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 201) <i>121-49552</i>	F	24 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 202) <i>121-49553</i>	F	10 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 203) <i>121-49554</i>	F	24 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 204) <i>121-49555</i>	F	14 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 205) <i>121-49556</i>	F	24 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 206) <i>121-49557</i>	F	12 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 207) <i>121-49558</i>	F	24 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 208) <i>121-49559</i>	F	20 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 209) <i>121-49560</i>	F	20 August 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 210) <i>121-49561</i>	F	3 December 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 211) <i>121-49562</i>	F	27 August 2004	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E

(PJG 212) <i>121-49563</i>	F	4 December 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 213) <i>121-49564</i>	F	3 December 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 214) <i>121-49565</i>	F	3 December 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 215) <i>121-49566</i>	F	25 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 216) <i>121-49567</i>	F	14 October 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 217) <i>121-49568</i>	F	4 December 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 218) <i>121-49569</i>	F	16 October 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 219) <i>121-49570</i>	F	14 October 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 220) <i>121-49571</i>	F	7 December 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 221) <i>132-20251</i>	F	29 August 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 222) <i>132-20252</i>	M	29 August 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 223) <i>132-20253</i>	M	6 October 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 224) <i>132-20254</i>	F	11 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 225) <i>132-20255</i>	M	13 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 226) <i>132-20256</i>	F	11 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 227) <i>132-20257</i>	M	31 August 2004	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 228) <i>132-20258</i>	M	7 October 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJG 229) <i>132-20259</i>	F	11 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E

(PJM 230) <i>132-20260</i>	M	7 November 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJM 232) <i>140-52811</i>	M	1 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJM 233) <i>140-52819</i>	M	13 September 2003	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E
(PJM 234) <i>121-49572</i>	F	4 November 2004	Lake Wendouree, Ballarat, VIC, 37°33'S, 143°50'E

836 ^a Catalogue number for vouchered specimens from the American Museum of Natural History (AMNH), the Australian Museum (AMS), CSIRO
837 Sustainable Ecosystems, Australian National Wildlife Collection (ANWC), the Bourne's Bird Museum (BBM), Louisiana State University Museum
838 of Natural History (LSUMZ), Museum Victoria (NMV), the Queensland Museum (QMO), the Queen Victoria Museum and Art Gallery (QVM), The
839 South Australian Museum (SAMA), the Tasmanian Museum (TM), the University of Alaska Museum (UAM) and the Western Australian Museum
840 (WAM).

line figure

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