Advertising displays of male Musk Ducks indicate population subdivision across the Nullarbor Plain of Australia

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Acoustic advertising displays (n=75) of male Musk Ducks *Biziura lobata* were analysed at ten widely spaced geographic localities in South Australia, Victoria, and Western Australia. Vocalisations differed in a fixed, non-overlapping pattern between allopatric Musk Duck populations in southeastern and southwestern Australia. These findings suggest that Musk Duck populations are subdivided by the Nullarbor Plain, the arid treeless desert at the head of the Great Australian Bight. Three vocalisations performed by male Musk Ducks not previously reported in the literature were documented also. Vocalisations of captive Musk Ducks collected from different geographic regions (southeast and southwest) differed between regions from which captives originally were collected and were unlike those performed by wild birds. Based on calls of immature Musk Ducks, acoustic variation within regional populations and the apparent inability of captive Musk Ducks reared in isolation to develop the wild type adult call, regional dialects seemingly are acquired in a social context by repeated observance of adult males and some combination of social imprinting, learning, or practice.

Key Words: Australia, biogeography, *Biziura lobata*, Musk Duck, Nullarbor Plain, population subdivision, vocalisation

Musk Ducks *Biziura lobata* are large-bodied diving ducks endemic to deep-water wetlands, river systems, and coastal waters of temperate Australia (Frith 1967; Marchant & Higgins 1990; Johnsgard & Carbonell 1996). In addition to exhibiting extreme sexual size dimorphism and peculiar male secondary sexual traits, including a leathery lobe on the lower mandible and a musky odor, Musk Ducks also display an unusual array of behavioural traits (Frith 1967; Marchant & Higgins 1990; McCracken *et al.* 2000). Most notable among these are splashing displays performed by males, frequently in a lek (eg Serventy 1946; Stranger 1961; Johnsgard 1966; Frith 1967). A ritualised series of vocalisations accompany these displays, and vocalisations reportedly differ east to west across the geographic range of Musk Ducks in Australia (Robinson & Robinson 1970; **Figure 1**).

In southeastern Australia, male Musk Ducks perform three display components, which correspond to three escalating levels of intensity of the same display (Johnsgard 1966; Fullagar & Carbonell 1986; Marchant & Higgins 1990). These include: (1) a non-vocal display called the *paddle-kick*, (2) a non-vocal display called the *plonk-kick*, and (3) a vocal display called the *whistle-kick*. The *paddle-kick* usually is performed at the beginning of display bouts, with the tail held flat against the surface of the water, the lobe turgid, and the head held close to the water. With a strong backward kick of the feet and loud smack, water is kicked upward 1-2m and to the rear, propelling the bird forward. The *plonk-kick* typically follows a series of *paddle-kicks*, but in contrast the splash is smaller and directed vertically while the duck remains stationary or rotates. Throughout the *plonk-kick,* the tail is raised vertically, fanned, and alternately dropped to the surface of the water at the end of each *plonk-kick*. The final and most intense component of the southeastern display repertoire is the *whistle-kick*. The *whistle-kick* resembles the *plonk-kick*, but splashes water to both sides rather than vertically. The tail also is cocked completely over the back, and two vocalisations are given. The first vocalisation is a low frequency percussion sound, and the second vocalization is a piercing whistle.

Musk Duck displays are similar in southwestern Australia, but vocalisations given during displays differ (Serventy 1946; Stranger 1961; Robinson & Robinson 1970). Robinson & Robinson (1970) described two vocalisations from Western Australia that differed from vocalisations in the southeast, a *plonk-kick* call and a *whistle-kick* call (Robinson & Robinson 1970; Figure 2b, d). The *whistle-kick* published by Robinson & Robinson (1970) shows similarities to southeastern *whistle-kick* calls, but since the *plonk-kick* is not accompanied by vocalisation in the southeast (vocalisations accompany only the *whistle-kick* in the southeast; Johnsgard 1966), it is questionable whether the *plonk-kick*

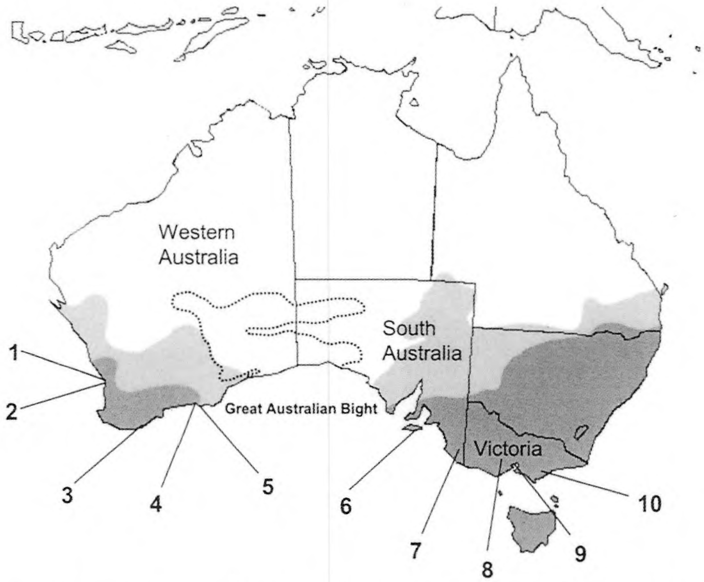

Figure 1. Geographic range of Musk Ducks based on Blakers *et al.* (1984), including recording localities (n=10) in southeastern and southwestern Australia visited between 29 August 1996 and 20 November 1997. Recording localities were: (1) Lake Monger, 31°56'S, 115°51'E, (2) Yangebup Lake 32°07'S, 115°50'E, (3) Seppings Lake 35°00'S, 117°55'E, (4) Lake Warden 33°48'S, 121°52'E, (5) Mullet Lake 33°48'S, 122°56'E, (6) Murray Lagoon 35°55'S, 137°25'E, (7) Bool Lagoon 37°07'S, 140°42'E, (8) Lake Wendouree 37°20'S, 143°31'E, (9) Werribee Ponds 37°35'S, 144°25'E and (10) Sale 38°04'S, 147°02'E. Dark gray areas indicate main breeding range; no breeding records are known from the light gray area of range. Nullarbor Plain and adjacent Great Victoria Desert are indicated by dotted line.

recorded in the southwest is the same display observed in the southeast. It was also discovered that advertising displays have not been fully described for either population. Many authors have described the advertising displays of Musk Ducks (Serventy 1946; Stranger 1961; Lowe 1966; Johnsgard 1966; Frith 1967), but only Robinson & Robinson (1970) published sonograms. Ogilvie (1975), Carbonell (1983), Fullagar & Carbonell (1986), and Marchant & Higgins (1990) described displays of captive birds. Knowledge of Musk Duck displays is still incomplete, and as Johnsgard & Carbonell (1996) stated, a comparative study of wild birds from both regions, using the same sound recording equipment, would be highly desirable.

Accordingly, acoustic and visual displays of Musk Ducks were recorded at ten widely spaced geographic localities in South Australia, Victoria, and Western Australia. Musk Duck vocalisations differed in a fixed, non-overlapping pattern across the Nullarbor Plain, the arid treeless desert at the head of the Great Australian Bight. Three vocalisations of adult male Musk Ducks that have not been reported previously in the literature also were documented, and recordings of calls made by wild adults with immature males and captive-reared adult males were compared. Finally, findings are discussed in broader contexts of biogeography and population biology, and speculations are made about the process of vocalisation development in Musk Ducks.

Methods

Advertising displays of male Musk Ducks were recorded in southeastern and southwestern Australia between 29 August 1996 and 20 November 1997 (**Figure 1**). Study areas included: (1) Kangaroo Island, South Australia, between 29 August and 19 November 1996 (n=26 recordings, 95.53 min.) and mainland South Australia and Victoria between 27 August and 11 September 1997 (n=17 recordings, 45.62 min.) and (2) Western Australia between 12 November and 20 November 1997 (n=32 recordings, 116.47 min.). A Sennheiser ME 66 shotgun microphone was used (Sennheiser, Wedemark, Germany) attached to a Sony 8mm TR83 video camera (Sony Corporation Tokyo, Japan). Wetland sites were opportunistically searched for displaying Musk Ducks and then recorded continuously at varying distances from 1 to 100m until displays ceased. Prevention of the recording of the same bird twice was attempted, and localities that were sampled repeatedly contained many more displaying Musk Ducks than the number recorded. Measurements of the relative frequency (% of total display) of each display component (*paddle-kick*, *plonk-kick*, *whistle-kick*, etc.) were taken, and time intervals between display components were measured for all recordings (n=75). Fifty-six percent (n=42) of our recordings were of good enough sound quality for sonographic analysis.

For each of these recordings, three replicate sub-samples were analysed for each class of kick display sonographically using Canary 1.2.1 (Cornell Laboratory of Ornithology 1996). Frequency (kHz), frequency range (kHz), energy (dB), elapsed time (s), and duration (s) of vocal and non-vocal display components were measured within each sub-sampled sonogram. Default software settings were used. Clipping level, brightness, and contrast were adjusted to match recording levels. Ranges, means, and standard deviations for each class of kick display within each geographic area were calculated. G-tests, one-way analysis of variance (ANOVA), non-parametric binomial, and two-tailed Mann-Whitney tests (Sokal & Rohlf 1981) were used to test for differences in relative frequency, inter-kick interval, display order, and other measured acoustic characteristics within each region. Sound files analysed in this study are archived in the Australian National Wildlife Collection and are available from the authors on CD-ROM.

Results

Regional differences

Analysis of Musk Duck displays from southeastern Australia revealed four display components associated with three display postures (**Figure 2**). These include the *paddle-kick* and *plonk-kick* described by Fullagar & Carbonell (1986), plus two forms of the *whistle-kick*, one of which was not previously described. In contrast, the analysis from southwestern Australia revealed five display components associated with two display postures

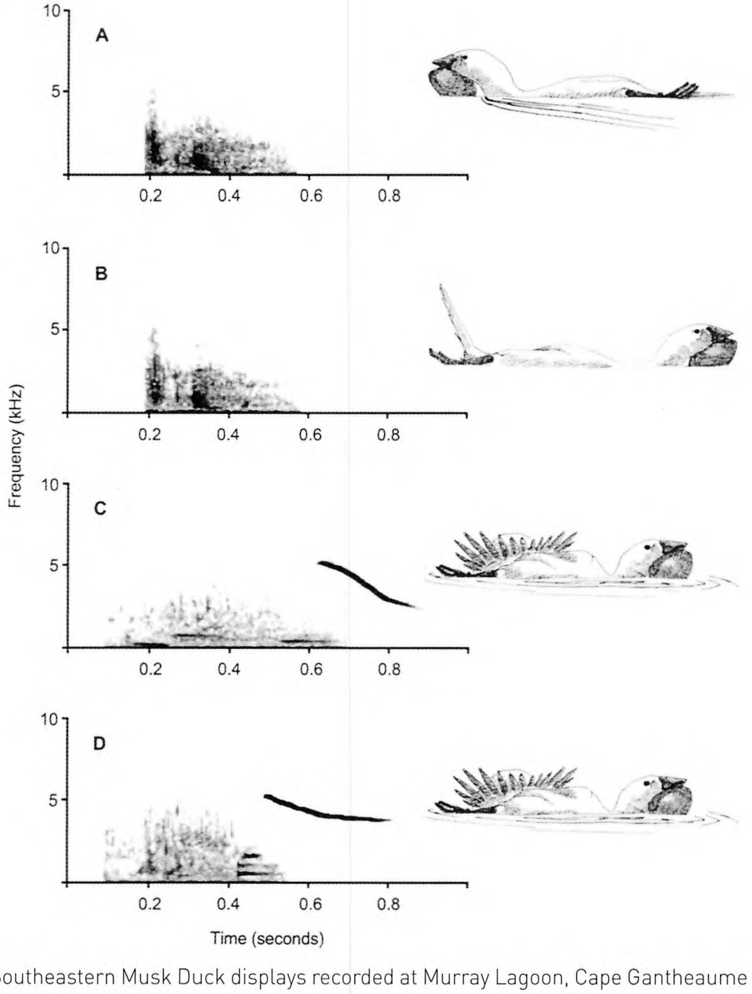

Figure 2. Southeastern Musk Duck displays recorded at Murray Lagoon, Cape Gantheaume Conservation Park, Kangaroo Island, South Australia, 7 October 1996. Sonograms of (A) *paddle-kick*, (B) *plonk-kick*, (C) *low-pitched whistle-kick* and (D) *high-pitched whistle-kick*. Corresponding display postures are depicted at right.

(**Figure 3**). These include the *paddle-kick* and four different vocalisations performed with the *whistle-kick* posture. The four vocalisations from southwestern Australia include two forms of the *plonk-kick* described by Robinson & Robinson (1970) (they described only one *plonk-kick*), a *whistle-kick* (hereafter *western whistle kick*), and a previously undescribed display named the *plunk-kick*.

Paddle-kicks (**Figures 2A, 3A**) are non-vocal (splashing only) in the southeast and southwest. *Plonk-kicks* as described by Johnsgard (1966) and others are non-vocal in the southeast (splashing only) and absent in the southwest (**Figure 2B**). Musk Ducks in the southwest use the *whistle-kick* display posture instead and perform one of two alternative percussion-like vocalisations that are not accompanied by whistles (**Figure 3B, C**). These hereafter are referred to as the low-pitched *poing-kick* and the high-pitched *poing-kick*. The high-pitched *poing-kick* (**Figure 3C**) is the same vocalisation Robinson & Robinson (1970 Figure 2B) incorrectly identified as a *plonk-kick*. Robinson & Robinson (1970) either did not record or overlooked the low-pitched *poing-kick* (**Figure 3B**). *Whistle-kicks* were vocal and performed by birds from the southeast and southwest, but showed very different tonal qualities between the two regions (**Figures 2C, D, 3D**). In the southeast, Musk Ducks performed two forms of the *whistle-kick*, a *low-pitched whistle-kick* and a *high-pitched whistle-kick* (**Figure 2C, D**). Robinson & Robinson (1970: Figure 2C) published the only previously known sonogram of the *low-pitched whistle-kick*, but did not record or overlooked the *high-pitched whistle-kick*. Other authors also apparently overlooked the fact that two *whistle-kicks* are vocalised in the southeast. Musk Ducks performed yet a third form of the *whistle-kick* in the southwest, a *western whistle-kick* (**Figure 3D**) that is distinct from both *whistle-kick* displays performed in the southeast. The *plunk-kick* was observed on two occasions in the southwest (**Figure 3E**).

In brief, three display postures (*paddle-kick, plonk-kick, whistle-kick*) are used by male Musk Ducks (see **Figures 2, 3**). All three postures were recorded in the southeast, but only two postures (*paddle-kick, whistle-kick*) were recorded in the southwest. Vocalisations of birds in the southeast were not performed by birds in the southwest or vice versa. Thus, acoustic differences were fixed and non-overlapping. Since most previous accounts of Musk Duck advertising displays did not publish sonograms or make repeated measurements, and three displays were overlooked, the important acoustic characteristics of each display component is described below.

Southeastern display patterns

Among the four display components performed in the southeast, the *high-pitched whistle-kick* was the most common, followed by the *low-pitched whistle-kick, paddle-kick*, and *plonk kick*

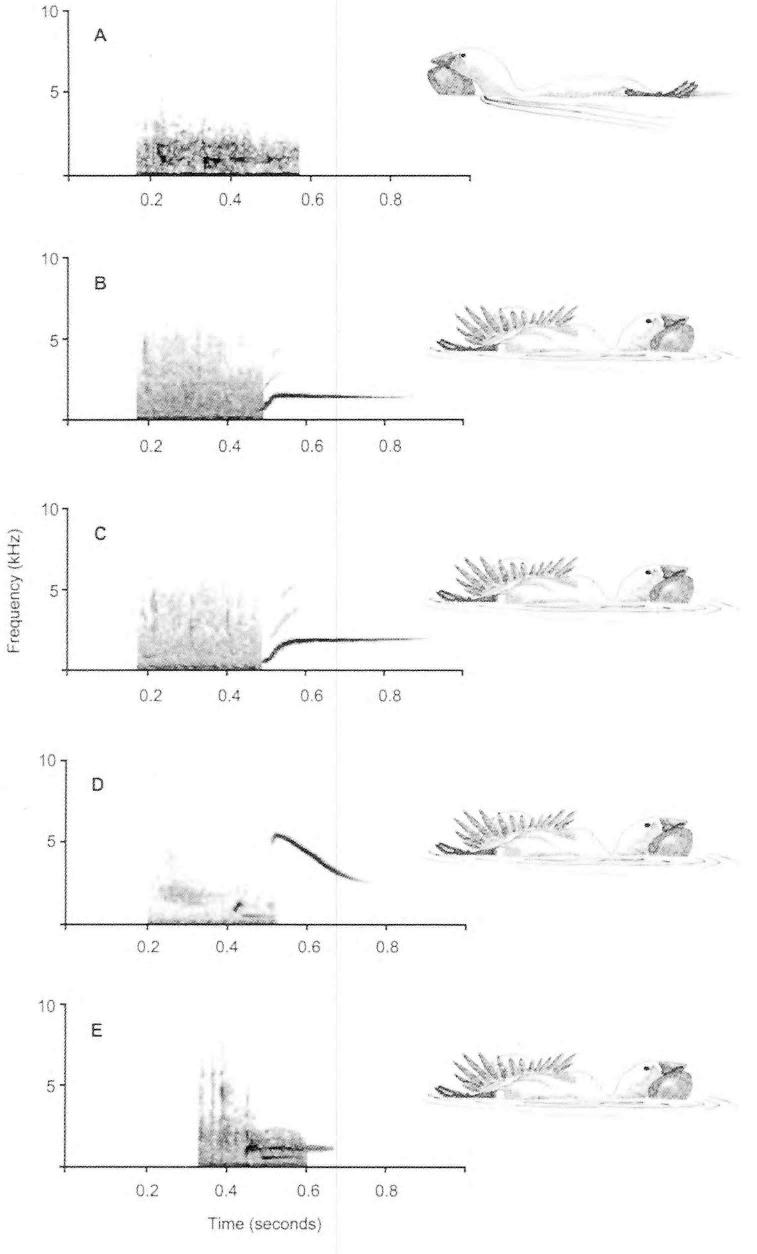

Figure 3. Southwestern Musk Duck displays recorded at Lake Monger, Perth, Western Australia, 12-13 November 1997, and Seppings Lake, Albany, Western Australia, 17 November 1997. Sonograms of (A) *pladdle-kick*, (B) *low-pitched poing-kick*, (C) *high-pitched poing-kick*, (D) *western whistle-kick* and (E) *plunk-kick*. Corresponding display postures are depicted at right.

(G-test for heterogeneity; $G=39.78$, $df=3$, $P<0.05$; **Table 1**). Intervals between kick displays did not differ among kick types (ANOVA; $F=1.48$, $df=3$ and 64, $P>0.22$; **Table 1**). Seventy-five percent of display sequences in which two or more kick types occurred were initiated by a series of *paddle-kicks* (binomial test for random sequence initiation; $n=16$, $z=2.00$, $P=0.023$). Within 11 display bouts, including both *low-pitched* and *high-pitched whistle-kicks*, *low-pitched whistle-kicks* always preceded *high-pitched whistle-kicks* (binomial test for random display sequence; $n=11$, $z=6.63$, $P<0.0001$). Only two series of *plonk-kicks* were recorded, but both were observed between a series of *paddle-kicks* and *low-pitched whistle-kicks* (see also Fullagar & Carbonell 1986; McCracken 1999). The *plonk-kick* as performed in the southeast is a transitional display that occurs between *paddle-kicks* and *whistle-kicks*. No such pattern was observed in Western Australia.

Southeastern *paddle-kicks* and *plonk-kicks* were non-vocal as described by Johnsgard (1966) and Fullagar & Carbonell (1986). The differences between the two displays are the position of the tail, amount of for-

Table 1. Percent of total time spent displaying and time intervals between Musk Duck display components recorded in southeastern and southwestern Australia 1996, 1997.

	Mean ± SD	
Display component	Display (%)	Interval (s)
Southeastern Australia[a]		
Paddle-kick	15.3 ± 28.8	3.7 ± 0.5
Plonk-kick	1.1 ± 5.8	3.2 ± 0.1
Low-pitched whistle-kick	31.3 ± 40.0	3.9 ± 0.8
High-pitched whistle-kick	52.2 ± 44.5	3.8 ± 0.4
Southwestern Australia[b]		
Paddle-kick	5.5 ± 16.2	4.2 ± 2.4
Low-pitched poing-kick	9.1 ± 23.7	5.5 ± 1.1
High-pitched poing-kick	32.4 ± 37.5	4.5 ± 1.3
Western whistle-kick	52.6 ± 38.8	5.2 ± 0.7
Plunk-kick	0.4 ± 2.3	3.0

[a]Advertising displays (n=43) from southeastern Australia were recorded at Murray Lagoon (n=26), Bool Lagoon (n=12), Lake Wendouree (n=1), Werribee Ponds (n=2), and 20km west of Sale, Victoria (n=2).
[b]Advertising displays (n=32) from southwestern Australia were recorded at Lake Monger (n=18), Yangebup Lake (n=1), Seppings Lake (n=7), Lake Warden (n=4) and Mullet Lake (n=2).

ward movement, and height water is splashed upward (**Figure 2A, B**). Elapsed times (±SD) for these two kicks were 338.53±8.80 ms (n=5) and 328.00±3.30ms (n=2) respectively. In contrast, both *whistle-kicks* consisted of one non-vocal splash component produced by the sound of the feet hitting the water, followed by two distinct vocal components (**Figure 2C, D**). In the *low-pitched whistle-kick* (n=7), the first of these two components consisted of a 0.36±0.03 kHz, 129.62±29.25ms, low frequency, percussion sound initiated 349.48±41.82ms after the moment the feet first hit the water. This was followed by a much louder, 5.12±0.15 to 2.58±0.16kHz decrescendo whistle of 226.81±8.43ms initiated 448.90±48.21 ms after the initiation of the display or 30.20ms prior to the completion of the percussion sound. The shape of the low-pitched whistle note was concave down. *High-pitched whistle-kicks* (n=12) were similar (splash + percussion sound + whistle), but the whistle was modulated to a higher frequency. Like the *low-pitched whistle-kick*, the first vocal component of the *high-pitched whistle-kick* consisted of a percussion sound, but in this display the sound consisted of three 0.55±0.02 kHz harmonics; the first and third were the most intense. The sound duration averaged 105.92±34.89ms, and occurred earlier in the sequence, 329.12±60.28ms after the feet hit the water, but did not differ from the *low-pitched whistle-kick* (Mann-Whitney n=19, *P*s>0.05). The loud whistle component also was initiated earlier in the sequence, 401.50±65.07ms after the feet hit the water (n=19, *P*>0.05), but was of significantly longer duration, 320.18±43.63 ms (n=19, *P*<0.05), and higher frequency, 5.23±0.12 to 3.71± 0.04 kHz. The shape of the whistle note was concave up.

Southwestern display patterns

Among the five displays performed in the west, the *western whistle-kick* was the most common, followed by the *high-pitched poing-kick*, *low-pitched poing-kick, paddle-kick*, and *plunk-kick* (G-test for heterogeneity; G=55.14, df=4, *P*<0.05; **Table 1**). The *plunk-kick* was observed on only one occasion during the study period (and again on 21 November 2000; pers. obs.), but was repeated 28 times by the same adult bird. Mean intervals between kicks did not differ among kick types (ANOVA excluding *plunk-kicks*; *F*=2.18, df=3 and 49, *P*>0.10; **Table 1**). Unlike display components in the southeast, no particular performance order was observed (binomial test for random sequence initiation; n=12 displays initiated with either of two most common kicks; *z*=0.58, *P*>0.28). Birds that performed *low-pitched poing-kicks* were not recorded performing *high-pitched poing-kicks* or vice versa. All Musk Ducks that were recorded performed one display or the other.

Western paddle-kicks (n=4) were 311.00±62.64 ms in duration and did not differ from those in the southeast (n=9, *P*>0.05; **Figure 3A**). Both *poing-kicks* consisted of a non-vocal splash sound followed by a low frequency, metallic, ping-like sound with faint harmonic overtones initiated shortly after the feet hit the water (**Figure 3B, C**). This latter vocal component was initiated 303.93±22.22ms after the feet hit the water in the *low-pitched poing-kick* (n=5), whereupon it lasted for 299.00±34.21ms, rising abruptly from an initial frequency of 0.47±0.03 kHz to a final trailing frequency of 1.4±0.02 kHz. *High-pitched poing-kicks* (n=14) were similar but the vocal components were initiated earlier in the sequence, 249.84±27.43 ms after the feet hit the water (n=19, $P<0.05$), and modulated to a higher final frequency, 0.48±0.4 to 1.80±0.04 kHz. Vocal components averaged 328.43±31.86ms, but did not differ from the *low-pitched poing-kick* (n=19, $P>0.05$). In both displays, the tail was cocked completely over the back throughout the duration of the display, and movements of the feet were directed to the side instead of the rear. *Western whistle-kicks* (n=18) showed the same pattern as southeastern *whistle-kicks* (splash + percussion sound + whistle), but contained one additional, hooked inflection prior to the percussion sound (**Figure 3D**). This inflection consisted of a 0.75±0.03 to 1.25±0.06 kHz sound of 26.16±2.92ms, initiated 260.01±49.54ms after the feet hit the water. It was immediately followed by 0.51±0.02 kHz, 80.16±11.80 ms, low frequency percussion sound with faint harmonic overtones. These two sounds, in turn, were followed by a shrill, 5.52±0.07 to 2.79±0.17 kHz descending whistle of 214.51±20.27ms initiated 355.20±52.53ms into the display. The final display component observed in the western repertoire was the *plunk-kick* (n=1; **Figure 3E**). Comparisons of the various sonograms suggest similarity to the *western whistle-kick*. This was indicated by an overall tonal similarity and an emphasis on the second of a four harmonic, 203.00±11.79ms, percussion sound with a fundamental frequency of 0.55±0.02 kHz (**Figure 3E**). Like the *whistle-kick*, the *plunk-kick* was preceded by an initial splash sound 117.00±3.00ms earlier; however, no whistle note was evident. The *plunk-kick* we observed might have been a truncated *whistle-kick* performed by an adult Musk Duck that had not yet learned the complete vocalisation. Although the *plunk-kick* was observed in only one individual during the study period, the same display was observed 600km distant and three years later, on 21 November 2000 at Lake Warden, Esperance, Western Australia (pers. obs.).

Immature/captive display patterns

While recording vocalisations in Western Australia, two immature males were recorded (as indicated by small overall body size and the size of the pendant lobe below the lower mandible) attempting to perform *western whistle-kicks* (**Figure 4**). Acoustic displays performed by these immatures showed only a rough

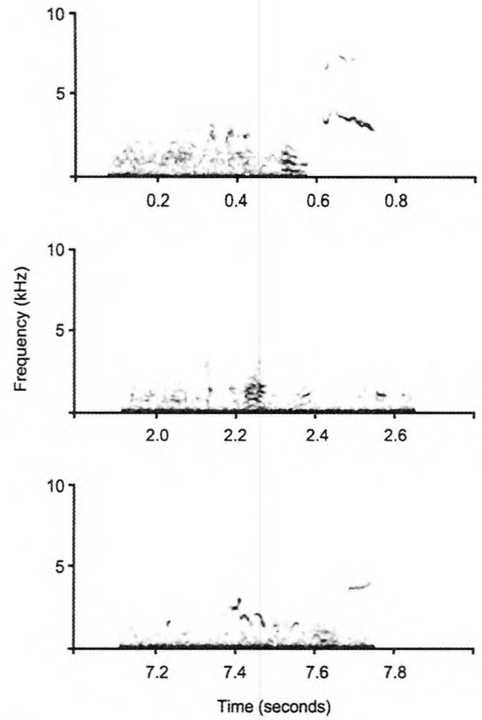

Figure 4. Sonograms of three immature *western whistle-kick* displays recorded at Lake Monger, Perth, Western Australia, 12 November 1997.

resemblance to vocalisations of adults recorded at the same location (**Figure 3D**). In all three sonograms, only rudimentary percussion sounds and whistle notes were evident. Similar rudimentary *whistle-kick* calls also were observed in immatures from southeastern Australia on Kangaroo Island in 1997 but not recorded; no other recordings of immature males are available.

Adult male Musk Ducks raised in captivity produce sounds very different from any of the six vocal displays recorded under natural conditions in either the southeast or southwest. The basic elements of a *whistle-kick* are evident in captives originally obtained from the mainland southeast (**Figure 5A**), but sonographic analysis reveals no similarity to any wild-type vocalisations. In place of a percussion sound, captive Musk Ducks from southeastern Australia substitute an unstructured swoosh-like sound. The whistle note, which also differs, spans the combined frequency ranges of both *low-pitched* and *high-pitched whistle-kicks* and resembles components of neither display more closely than the other.

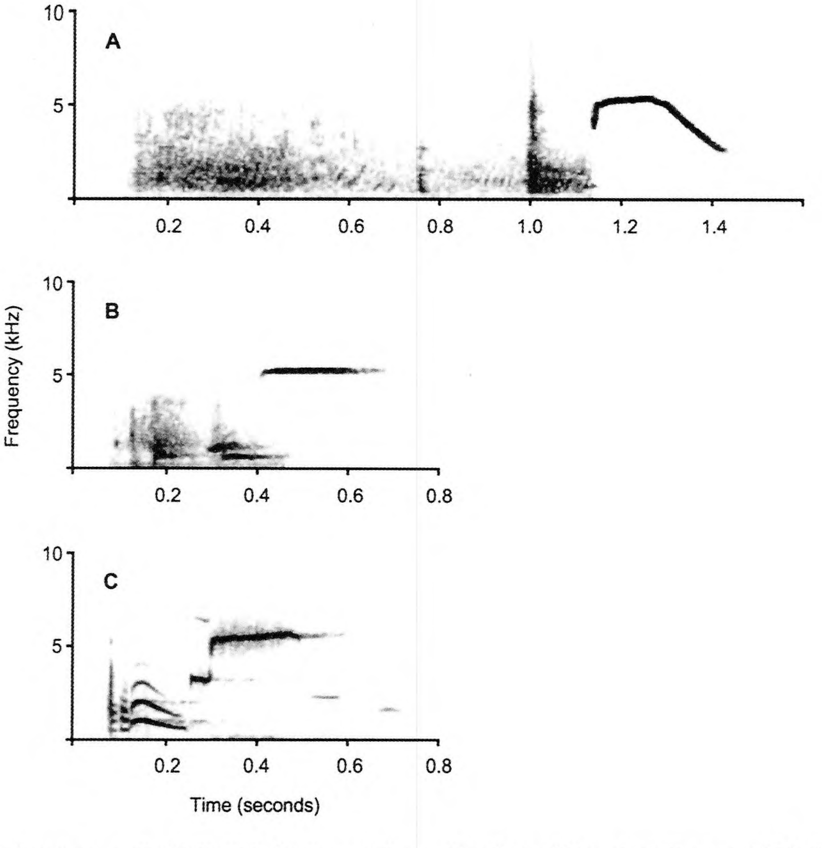

Figure 5. Sonograms of *whistle-kick* displays performed by three different captive-raised Musk Ducks taken from southeastern and southwestern Australia. (A) Southeastern Australia-origin Musk Duck recorded at Serendip Wildlife Research Station, Lara, Victoria, 1984 (ANWC X115), (B) Western Australia-origin Musk Duck recorded at The Wildfowl & Wetlands Trust, Slimbridge, UK, 1986, and (C) Western Australia-origin Musk Duck recorded at Pensthorpe Waterfowl Park and Nature Reserve, Norfolk, UK, 1988.

Captive Musk Ducks from southwestern Australia perform yet another *whistle-kick call* (**Figure 5B, C**) that differs from southeastern captives (**Figure 5A**) and wild-type calls from both regions (**Figures 2, 3**). Musk Ducks also have demonstrated remarkable abilities to mimic calls of other waterfowl and mechanical and human sounds (Marchant & Higgins 1990). Examples from two captive Musk Ducks include mimicry of female Pacific Black Ducks *Anas superciliosa* (**Figure 6A**), a closing cage door (**Figure 6B**), and the words "you bloody fool" (**Figure 6C**).

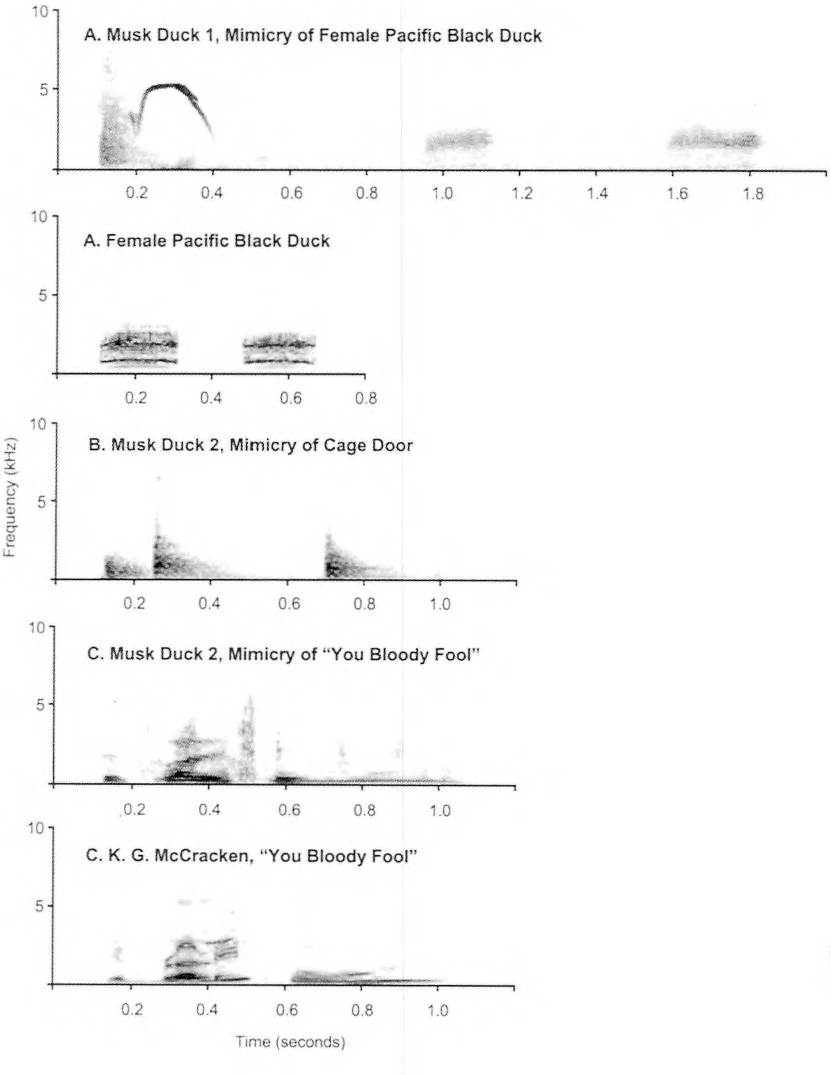

Figure 6. Examples of vocal mimicry by two different male Musk Ducks. (A) Sonogram of male 1 mimicking female Pacific Black Duck vocalisations at Tidbinbilla Nature Reserve, ACT, 2000; a sonogram of female Pacific Black Duck vocalisations is shown for comparison. Sonogram of male 2 mimicking (B) a closing cage door at Tidbinbilla Nature Reserve, ACT, 1984 (ANWC X142). Sonogram of male 2 (same male as **Figure 6B**) mimicking (C) the words "you bloody fool" at Tidbinbilla Nature Reserve, ACT, 1984 (ANWC X142); a sonogram of the words "you bloody fool" spoken by K.G. McCracken is shown for comparison.

Discussion

The Nullarbor Plain, which sprawls across the head of the Great Australian Bight and divides the geographic range of Musk Ducks in two, is one of the world's most formidable edaphic barriers and a major zoogeographic barrier (eg Keast 1981). The Nullarbor is composed primarily of porous limestone and sandstones (Lowry & Jennings 1974), thus surface water on the Nullarbor drains away rapidly resulting in few wetlands for waterbirds. The Nullarbor also was dried to the margin of the continental shelf and flooded repeatedly by the expansion and contraction of the sea (Galloway & Kemp 1981; Nelson 1981). Thus, Musk Ducks probably evolved with the arid characteristics of the Nullarbor largely in place or inundated by the Southern Ocean. Consequently, it is not surprising that Musk Ducks show a non-overlapping pattern of acoustic variation in southeastern and southwestern Australia. Among Australian birds, about one in five species (n=124; including 68% of Australia's waterfowl) exhibit geographic ranges completely or partly divided by the Nullarbor Plain (Blakers *et al.* 1984).

Musk Ducks have been observed in small numbers at sea near the Eyre Bird Observatory on the western edge of the Nullarbor Plain (Blakers *et al.* 1984; Congreve & Congreve 1985), and they were found in 1978 on the northwestern Nullarbor following major flood events (Brooker *et al.* 1979), but such sightings are uncommon. It is not known whether or how often Musk Ducks disperse across the Nullarbor. Dispersal via the Southern Ocean might be easier than by land, but heavy wing-loading and the absence of protected coastal bays and inlets between Fowlers Bay, South Australia, and Israelite Bay, Western Australia, probably make this trip uncommon.

Fixed, non-overlapping patterns of acoustic variation in southeastern and southwestern Australia also are consistent with Mathews's (1910-27) recognition of two Musk Duck subspecies based on morphological differences, *B. l. lobata* for Western Australia and *B. l. menziesi* for southeastern Australia (but see Parker *et al.* 1985). Further assessment of population subdivision using molecular markers and morphological characters are needed. Insular populations in southeastern Australia (Tasmania, Kangaroo Island) might be reproductively isolated from mainland populations, and assortive mating on the basis of regional call types also might exist.

The findings from this study raised questions about how immature male Musk Ducks develop adult advertising calls. Waterfowl vocalisations generally are not believed to be learned but inherited, such that adult calls are delivered from an early age with little or no social imprinting (Sharpe & Johnsgard 1966; but see Dane & van der Kloot 1964; Korschgen & Frederickson 1976; Afton & Sayler

1982). Calls of immature, wild Musk Ducks (**Figure 4**) show only a rough resemblance to vocalisations of adult males and suggest that some combination of social imprinting, learning, or practice is involved in vocal transmission from one generation to the next. Recordings of captive-reared Musk Ducks from southeastern and southwestern Australia (**Figure 5**) also suggest that a genetic basis for regional dialects may exist. Calls of captive Musk Ducks differ notably depending on the region from which they originally were collected (compare **Figure 5A** and **Figure 5B, C**), and when reared in isolation from wild Musk Ducks performing adult calls, captives never develop the wild type call, even after as many as 25 years (P. J. Fullagar pers. obs.). Finally, Musk Duck calls also show obvious levels of variation within populations. For example, male Musk Ducks from Western Australia performed *low-pitched poing-kicks* or *high-pitched poing-kicks* and never were observed performing both displays in the same display sequence. The two versions of the *poing-kick* are variations of the same display, and differences may be attributable to factors such as experience or age.

The apparent inability to develop mature wild-type calls in the absence of adult Musk Ducks and variation within populations suggests that young Musk Ducks must listen to mature adult calls and practice repeatedly in a social context. The duration of the vocal development period is unknown, but probably is more than one year, and possibly two or three years (age of first-breeding is unknown). If this is true, it might explain why male Musk Ducks spend a considerable time intently observing the advertising displays of other male Musk Ducks (McCracken 1999). An unusually long period of social development coupled with asymptotic body growth beyond the first year of life (McCracken *et al.* 2000) also might have factored importantly in the evolution of the Musk Duck's relatively large brain size (Iwaniuk & Nelson 2001). The ability of Musk Ducks to mimic the vocalisations of other waterfowl, mechanical sounds, and complex human sounds (Marchant & Higgins 1990) further underscores social aspects of their biology. Similar examples of mimicry are evident in the acoustic display repertoires in other arena-performing birds, such as lyrebirds (Menuridae; Smith 1968) and bowerbirds (Ptilinorhynchidae; Cooper & Forshaw 1977; Bradley 1987). For future research on these topics, the roles that heritable and social environment factors play in the development of Musk Duck vocalisations could be teased apart by transplanting eggs between southeastern and southwestern populations using controlled experiments (eg James 1983) and following Musk Ducks through two to three years of social, behavioural, and physical development.

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References

Afton, A.D. & Sayler, R.D. 1982. Social courtship and pairbonding of Common Goldeneyes Bucephala clangula, wintering in Minnesota. *Canadian Field Naturalist* 96: 295-300.

Blakers, M., Davies, S.J.J.F. & Reilly, P.N. 1984. *The atlas of Australian birds*. R.A.O.U., Melbourne University Press, Melbourne.

Bradley, J.M. 1987. Vocal behaviour and annual cycle of the Western Bowerbird *Chlamydera guttata*. Australian Bird Watcher 12: 83-90.

Brooker, M.G., Ridpath, M.G. Estbergs, A.J., Bywater, J., Hart, D.S. & Jones, M.S. 1979. Bird observations on the north-western Nullarbor Plain and neighboring regions, 1967-1978. *Emu* 79: 177-190.

Carbonell, M. 1983. Comparative studies of the stiff-tailed ducks (tribe Oxyurini, Anatidae). Ph.D. Dissertation, University College, Cardiff, Wales.

Congreve, D.P., & Congreve, P. 1985. *Birds: Eyre bird observatory report 1981-1983*. R.A.O.U. Report No. 9: 20-42.

Cooper, W. T., & Forshaw, J.M.. 1977. *The Birds of Paradise and Bowerbirds*. Collins, Sydney.

Cornell Laboratory of Ornithology. 1996. Canary 1.2.1: the Cornell bioacoustics workstation. Cornell Laboratory of Ornithology, Ithaca, New York.

Dane, B., & van der Kloot, W.G. 1964. An analysis of the display of the Goldeneye duck *Bucephala clangula [L.]*. *Behaviour* 22: 282-328.

Frith, H.J. 1967. *Waterfowl in Australia.* East-West Center Press, Honolulu.

Fullagar, P.J., & Carbonell, M. 1986. The display postures of the Musk Duck. *Wildfowl* 37: 142-150.

Galloway, R.W., & Kemp, E.M. 1981. Late Cainozoic environments in Australia. In: *Ecological biogeography of Australia* (A. Keast, ed.). W. Junk, The Hague, Netherlands, pp 51-80.

Iwaniuk, A.N. & Nelson, J.E. 2001. A comparative analysis of relative brain size in waterfowl (Anseriformes). *Brain, Behavior and Evolution* 57: 87-97.

James, F.C. 1983. Environmental component of morphological differentiation in birds. *Science* 221: 184-186.

Johnsgard, P.A. 1966. Behaviour of the Australian Musk Duck and Blue-billed Duck. *Auk* 83: 98-110.

Johnsgard, P.A., & Carbonell, M. 1996. *Ruddy Ducks and other stifftails: their behavior and biology.* University of Oklahoma Press, Norman, Oklahoma.

Keast, A. 1981. *Ecological biogeography of Australia.* W. Junk, The Hague, Netherlands.

Korschgen, C.E. & Frederickson, L.H. 1976. Comparative displays of yearling and adult male Wood Ducks. *Auk* 93: 793-807.

Lowe, V.T. 1966. Notes on the Musk Duck, *Biziura lobata. Emu* 65: 279-290.

Lowry, D.C., & Jennings, J.N. 1974. The Nullarbor karst, Australia. *Zeitschrift fur Geomorphologie* 18: 35-81.

Marchant, S. & Higgins, P.J. 1990. *Handbook of Australian, New Zealand, and Antarctic birds.* Oxford University Press, Oxford.

Mathews, G.M. 1910-27. *The birds of Australia.* Witherby, London.

McCracken, K.G. 1999. Systematics, ecology and social biology of the Musk Duck *Biziura lobata* of Australia. Ph.D. Dissertation. Louisiana State University, Baton Rouge, Louisiana.

McCracken, K.G., Paton, D.C. & Afton, A.D. 2000. Sexual size dimorphism of the Musk Duck. *Wilson Bulletin* 112: 457-466.

Nelson, E.C. 1981. Phytogeography of southern Australia in: *Ecological biogeography of Australia* (A. Keast, ed.). W. Junk, The Hague, Netherlands, pp 733-759.

Ogilvie, M.A. 1975. The Musk Duck. *Wildfowl* 26: 113.

Parker, S.A., Eckert, H.J. & Ragless, G.B. 1985. *An annotated checklist of the birds of South Australia 2A.* South Australian Ornithological Association, Adelaide.

Robinson, F.N., & Robinson, A.H. 1970. Regional variation in the visual and acoustic signals of the male Musk Duck, *Biziura lobata. CSIRO Wildlife Research Report* 15: 73-78.

Serventy, D.L. 1946. Display of the Musk Duck. *Emu* 5: 318-321.

Sharpe, R.S., & Johnsgard, P.A. 1966. Inheritance of behavioral characters in F2 Mallard x Pintail *Anas platyrhynchos L. Anas acuta L.* hybrids. *Behaviour* 27: 259-272.

Smith, L.H. 1968. *The Lyrebird.* Lansdowne Press, Melbourne.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry: the principles and practice of statistics in biological research*. W. H. Freeman and Co., New York.

Stranger, R. H. 1961. Display of the Musk Duck. *Western Australia Naturalist* 7: 210-211.