Diving Activity of Hoary-headed *(Poliocephalus poliocephalus)* and Australasian Little *(Tachybaptus novaehollandiae)* Grebes

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Abstract.—In austral spring 2006, a year of severe drought conditions, we timed 314 and 133 dives and subsequent surface durations of Hoary-headed (*Poliocephalus poliocephalus*) and Australasian Little Grebes (*Tachybaptus novaehollandiae*), respectively, at a freshwater lake in southern Australia. Hoary-headed Grebes stayed submerged for longer (18.5 ± 3.6 s) than Australasian Little Grebes (15.7 ± 4.2 s and 2.1 ± 1.1, respectively). Consequently, Hoary-headed Grebes maintained a high and constant diving efficiency (2.33 ± 0.25)—measured as the dive:pause ratio—throughout the study, suggesting that they are better at facing changes in water level of their lacustrine environment than Australasian Little Grebes, which showed an erratic and lower (1.95 ± 0.48) dive efficiency.

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In comparison with other diving waterbirds, the diving activity of the 19 grebe species (Podicipepidae) has received relatively little attention, especially since the 1980s (cf. data in Ropert-Coudert *et al.* 2006). Here we present the first comprehensive account of the dive and surface durations of breeding Hoary-headed (*Poliocephalus poliocephalus*) and Australasian Little (*Tachybaptus novaehollandiae*) Grebes foraging in the shallow waters of a lake in South Eastern Australia in austral spring 2006. These two species breed in Australia and New Zealand and use similar habitats (Harrisson 1983; Marchant and Higgins 1990). Following Dewar (1924) we measured the diving efficiency of the two species by calculating the dive:pause ratio and monitored the evolution of this value over a month, under increasing drought conditions. Besides temporal variation in dive efficiency we also looked at the variability of the diving duration of grebes in relation to water depth and meteorological conditions.

Methods

Between 14 November and 4 December 2006 we made eleven 20 to 45-min sessions of observation of Hoary-headed and Australasian Little Grebes diving at Swan Lake (38°30'S, 145°09'E), Phillip Island, Victoria, Australia (Fig. 1). Swan Lake is a 32 ha. freshwater lake with clear (turbidity 2 NTU), neutral (pH measured in December 2001 = 7.0) and relatively well oxygenated waters (76-97% saturation in December 2001 and June 2002, respectively, Schiller 2003).

Numbers of Hoary-headed and Australasian Little Grebes varied on a daily basis but we could count up to twelve grebes of both species on a given day. While the study initially focussed on Hoary-headed Grebes we included Australasian Little Grebes in our analysis from the 20th of November. Birds were always monitored by two observers, with the naked eye or using binoculars from two vantage bird hides. One hide is located on southern side of the lake where the bathymetry ranged 80-140 cm (depth increases rapidly from the banks, see Fig. 1) and one is on the northern side where the bathymetry ranged 20-90 cm (the bottom of the lake on this side was always visible throughout the study period). Bathymetry was measured along a series of transects covering the whole surface of the lake, using 10-cm graduated poles, on board canoes. The two hides were visited successively so that both sides of the lake were monitored on each day of observation. Dive and subsequent surfacing times were counted with stopwatches to the nearest second. When possible up to ten consecutive dive and surface durations were timed from the same individual. We only timed grebes that were located sufficiently far from any conspecifics so as to ensure that a series of dives and surface pauses belonged to the same individual. We stopped the series at the end of a bout, i.e. when the grebe stopped diving for >5 min and started to move at the surface of the lake, or when there was a risk of confusion between two individuals. Dives can be separated into foraging, "alarm" (sensu Lawrence 1950) and "ceremony" (sensu Fjeldså 1983) dives. Alarm dives occurred when Swamp Harriers (*Circus approximans*) or Whistling Kites (*Haliastur sphenurus*) were cruising over the lake, startling all the birds on or near the lake. These alarm dives were extremely short and accounted for <1% of all the dives so they were removed from the analysis. Ceremony dives are those dives in-

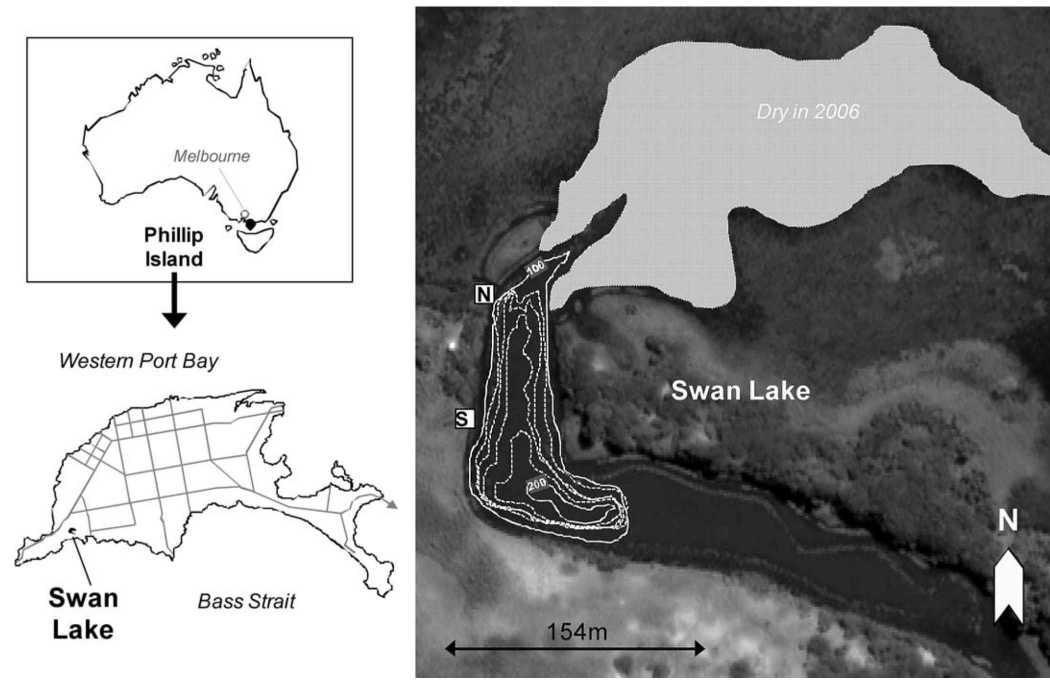

Figure 1. Location of the study site on Phillip Island, Victoria, Australia (map produced using an excerpt from Google Earth beta 4.0.2693, 2006). S and N indicate the Southern and Northern huts, respectively. The 100 and 200 cm bathymetry contours are represented by solid lines, while the 20 cm increment bathymetry contours (between 100 and 200 cm) are represented by dotted lines.

volved in courtship display performed on water but such behavior was not observed during our study period.

It is possible that the same individual was monitored more than twice in an observation period, hereby artificially increasing the number of individuals monitored in a day. To reduce the influence of pseudo-replication, we calculated an average value every time a series of dive and pause variables were positively ascribed to the same individual. Data are subsequently presented as grand mean (the mean of the mean of individuals) ± 1 S.D., except for the relationship between dive and pause durations for which all data were pooled together. Daily weather condition (cloud cover, air temperature, wind strength), measured <500 m from the lake, was obtained courtesy of the Bureau of Meteorology of Victoria (http://www.bom.gov.au/).

RESULTS

We timed a total of 314 and 133 dives/pauses doublets for Hoary-headed and Australasian Little Grebes, respectively. Overall, Hoary-headed Grebes dived for a mean of 18.5 ± 3.6 s followed by a mean 9.1 ± 3.9 s at the water surface, while the equivalent values for Australasian Little Grebes were 15.7 ± 4.2 s and 9.6 ± 6.2 s. The maximum dive durations were 26 and 23 s for Hoary-headed and Australasian Little Grebes, respectively. The dive duration of Hoary-headed Grebes was significantly longer (Student *t*-test, $t_{118} = 4.12$, $P < 0.001$) than that of Australasian Little Grebes (Fig. 2). Australasian Little Grebes had a clear peak of diving at 16 s and a second smaller peak around 18-20 s. In both species, ca. 72% of the surfacing lasted between 5 and 10 s. Surface duration of Hoary-headed Grebes was significantly and positively related to the previous dive duration ($F_{1,312} = 21.3$, $P < 0.001$) but the coefficient of determination explained only 6% of the variability. In contrast, there was no statistical relationship between the dive and surface durations of Australasian Little Grebes ($F_{1,130} = 2.66$, $P = 0.11$). The dive:pause ratio were calculated for each dive, then averaged for each day and a grand average was finally calculated for the two species. These were 2.33 ± 0.25 (range: 0.5-5.8) for Hoary-headed Grebes, which was significantly greater (Student *t*-test, $t_{16} = 2.21$, $P = 0.04$) than for Australasian Little Grebes at 1.95 ± 0.48 (range: 0.2-7.0).

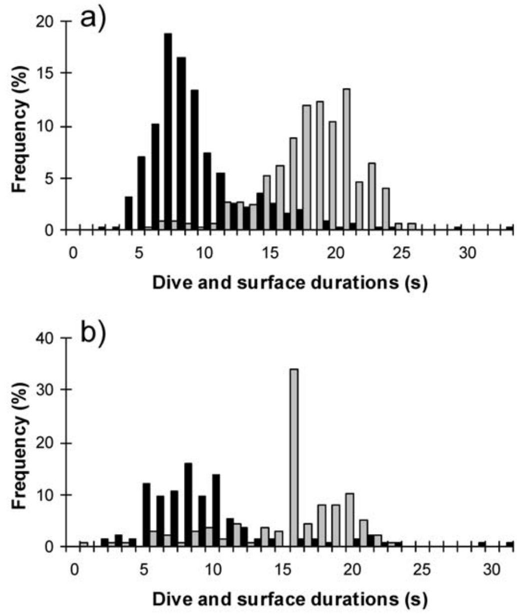

Figure 2. Frequency distribution of dive (grey bars) and surface (black bars) durations of a) Hoary-headed Grebes, and b) Australasian Little Grebes.

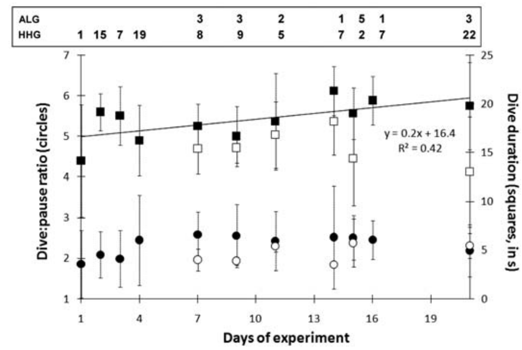

Figure 3. Temporal evolution over the study period (14 November to 4 December 2006) of the dive:pause ratio (circles) and dive duration (squares) of the Hoary-headed Grebes (black) and Australasian Little Grebes (white). The numbers above the graph represent the sample size for each species (number of individuals, ALG: Australasian Little Grebes, HHG: Hoary-headed Grebes).

Although the dive durations were not different (t_{16} = -0.58, P = 0.57), the dive:pause ratio of Australasian Little Grebes was significantly greater (Paired t-test, t_{16} = -2.70, P = 0.016) in shallow water (the northern side of the lake, 2.3 ± 0.5, n = 9 individuals) than in deep water (the southern side of the lake, 1.6 ± 0.5, n = 9 individuals). Conversely, Hoary-headed Grebes dived significantly longer (t_{99} = 4.21, P < 0.0001) in deep water (20.5 ± 0.4 s, n = 39 individuals) than in shallow water (18.4 ± 2.8 s, n = 62 individuals) but their dive:pause ratios were not different (t_{99} = 0.52, P = 0.61, deep: 2.3 ± 0.9, shallow: 2.4 ± 0.7).

Over the whole study period, the dive durations of Hoary-headed Grebes significantly increased (DiveDur = 0.2*day - 7790.5, R^2 = 0.42, $F_{1,9}$ = 6.52, P = 0.03) with time (Fig. 3) and their dive:pause ratio remained high and constant, although it increased slightly in the first few days and started to decrease towards the end of the study period. In contrast, the dive duration of Australasian Little Grebes showed no statistical trend but this may be the result of the relatively small number of days where data could be collected for this species. Their dive:pause ratio was much more erratic but remained lower than that of Hoary-headed Grebes (except on the last day of monitoring).

Heavy cloud covers (provided in eights) occurred principally around the beginning of the study period, with maximum cover observed on the 14th and 15th of November, accompanied by light to heavy rainfalls (hail on the 15th) and strong wind. All the other days, the cloud cover was light and the temperature became increasingly warm. Essentially because of our small sampling period (eleven days), there was no statistically significant relationship between the diving efficiency of the two grebe species and the meteorological parameters collected but diving efficiency of the two grebe species tended to decrease with increasing cloud cover (r^2 = 0.26 and 0.14 for Hoary-headed and Australasian Little Grebes, respectively).

DISCUSSION

The average dive durations of the two species of grebe in this study are within the range given in the literature, i.e. 8-20 s for Australasian Little Grebes (Fjeldså 1988), but slightly longer than the 8-15 s range observed over six dives of a Hoary-headed Grebe in New Zealand (Best 1976). However, Fjeldså (1988) gave maximum duration much greater than that observed in our study (66 s). Both Hoary-headed and Australasian Little Grebes are small-sized Podicipedidae and their diving ability is in accordance with what is expected from their body mass BM in g (Fig. 4, cf. Ropert-Coudert *et al.* 2006, Maximum dive duration = 0.035*BM - 6.05, $R^2 = 0.63$, $F_{1,6} = 10.16$, $P = 0.019$, note the data were not controlled for water depth and represent absolute maxima for each species).

One of the predictions of optimal foraging theory states that dive duration increases with diving depth for bottom-feeding species (cf. Houston and Carbone 1992). We did observe an increase in dive duration when Hoary-headed Grebes fed in deeper water, which suggests that they would preferentially forage close to the bottom of the lake. The reverse would thus apply for Australasian Little Grebes suggesting that this species uses the whole water column. This assumption is partly supported by our observation that Hoary-headed Grebes on the shallow side of the lake were visible throughout their dives and foraged close to the bottom of the lake in all instances. In addition, this finding is consistent with what is known in the literature of the feeding ecology of these species. Hoary-headed Grebes feed on a great diversity of prey, although the core of their diet (± 90%) consists of arthropods and tiny larvae but could occasionally (3%) contain fish up to 4-cm long (Fjeldså 1983; del Hoyo *et al.* 1992). Their favorite prey type would, therefore, be found close to the bottom. In contrast, Australasian Little Grebes feed mainly in open water, like the majority of grebes, and their diet contains mainly fish, snails and arthropods (Marchant and Higgins 1990; Hobbs 1958). According to a survey conducted in spring 2001 (Schiller 2003), 68% of the invertebrate fauna of Swan Lake is dominated by gastropod spp. (34.8%), oligochaeta spp. (22%) and the amphipod *Austrochiltona australis* (11.2%). The same survey showed that the fish population was limited to introduced Brown Trout and Common Galaxias *Galaxias maculatus.* With regard to the dietary preferences of the two species of grebes, such limited fish abundance would tend to favour Hoary-headed Grebes and their invertebrate-dominated diet while affecting negatively the Australasian Little Grebes and their mixed diet.

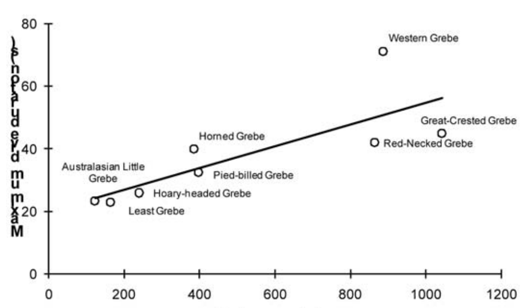

Figure 4. Relationship between the body mass and the maximum dive duration of various Podicipedidae (data taken from Ropert-Coudert *et al.* 2006).

Dive:pause ratio is often used as an index of diving efficiency in waterbirds (cf. Dewar 1924). Our averaged dive:pause ratios are intermediate between the values for other grebe species given in the literature (e.g., 1.41 for Western Grebe, *Aechmophorus occidentalis*, Lawrence 1950; 2.7 for Horned Grebes, Dow 1964). Hoary-headed Grebes were able to maintain a constant and high diving efficiency despite drought conditions becoming more and more severe over the study period. Following a near total absence of rain in the period from August to November, this was the second driest spring averaged over Victoria since 1900 (data from the Bureau of Meteorology of Australia). Consequently, the water depth of the lake had decreased by ca. 30-40 cm over the time of the study but the regularity of the Hoary-headed Grebes' dive:pause ratio suggests that this species is able to maintain a high diving efficiency despite the changes occurring in its environment, while Australasian Little Grebes are less able to do so (at least in our study site). One possible explanation could lie in the differential feeding strategy of the two species. Although the progressive drying of the lake may have contributed to concentrating the prey of Australasian Little Grebes in the water column, the target depth for Hoary-headed Grebes was certainly less affected by a modification in the volume of water as they fed near the bottom of the lake. More importantly, an extensive drying up of Swan Lake has been noted in the past (during the 2001-2002 season) and was associated with a massive fish extinction, which would reduce the array of prey available to Australasian Little Grebes. In other words, invertebrate feeders like Hoary-headed Grebes would be, at least to a certain extent, more resistant to environmental changes than Australasian Little Grebes and may out compete them in the habitats they share. In light of the recent climatic trends in Australia and progress towards drier and drier conditions, it appears necessary to conduct further studies over longer periods and in different sites to confirm this possibility.

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