

CARDIAC RESPONSE TO VOLUNTARY DIVING IN TUFTED DUCKLINGS (*AYTHYA FULIGULA*)

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Summary

Heart rate was monitored in tufted ducklings during first-ever and subsequent voluntary whole-body dives. Although the cardiac response to first-ever dives varied between individuals, the average response to these dives, to the following 20 dives, and to dives of longer duration closely resembled the response seen in adult tufted ducks. These results indicate that the cardiac response to voluntary diving in the tufted duck does not result from habituation of the classical bradycardia seen during involuntary diving.

Introduction

The cardiac response to both voluntary and involuntary (forced) diving in adult aquatic birds is well documented (for reviews see Butler, 1982; Butler & Jones, 1982). During involuntary submersion, adult birds show a progressive reduction in heart rate below the resting value (bradycardia), with the rate of reduction being greater in diving ducks than in dabbling ducks. During voluntary diving, there is no maintained bradycardia. There is a pre-dive cardiac acceleration, particularly before the first dive of a series. Heart rate falls from this elevated pre-dive level to its lowest value immediately upon submersion and then starts to increase until it reaches a maintained level which is similar to that seen when the duck is at the surface.

Forced submersion causes profound bradycardia in juvenile dabbling ducks (Rey, 1971; West, 1981; Jones & Butler, 1982), but nothing is known about the response to voluntary diving in juvenile diving ducks. In some species, ducklings start to dive at a very early age. White-headed ducks (*Oxyura leucocephala*) start diving for food when they are 1 day old and spend 13% of their time on this activity (Matthews & Evans, 1974). Tufted ducklings spend 6% of their time diving from hatching up to 5 days of age (Hill & Ellis, 1984). In both species, first dives last approximately 5 s, after which there is a gradual increase in dive duration with age, until the adult mean dive duration is reached when the ducks are approximately 7 weeks old.

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Repetitive involuntary submersion of adult diving and dabbling ducks causes a gradual reduction in the degree of bradycardia (Gabrielsen, 1985; Gabbott & Jones, 1987). As discussed by Stephenson & Butler (1987), it is possible that this habituation is the reason for the different cardiac responses during voluntary and involuntary dives (see also Gabbott & Jones, 1986). The present study was undertaken to establish whether the cardiac response during voluntary diving of tufted ducklings differs from that seen in adult ducks, i.e. to determine whether habituation may be involved.

Materials and methods

Six tufted ducklings (*Aythya fuligula*), three males and three females, were used in this study. They were hatched in an incubator, hand-reared and kept in the room of one of us (EK) in a circular tray (diameter 0.6 m) to become fully accustomed to human presence. Heat lamps were used to provide extra warmth during the first week after hatching. Drinking water was supplied only in very shallow bowls (water depth 0.5 cm) to prevent the ducklings from submersing their beaks, and they were fed on chick-rearing crumbs (Heygates Ltd). At 9–10 days old they had grown large enough for a miniature radiotransmitter to be implanted (under halothane anaesthesia; 1–2 % Fluothane, ICI Ltd, in a 40 % O₂ 60 % N₂ mixture) into the abdominal cavity to monitor cardiac activity. This transmitter is a further miniaturization of the one described by Butler & Woakes (1982a). Fully encapsulated, it measures 50 mm × 10 mm × 7 mm and weighs 2 g (including battery and leads). The ducklings were given an intramuscular injection of 7.5 mg of Ampicillin (Penbritin, Beecham) at the time of the implantation.

After allowing them to recover for 2–5 days, the ducklings were placed individually on water in a glass tank (0.6 m × 0.6 m × 0.6 m deep) for two periods each day. During the first few sessions a grid, covering about half the area and suspended just above the water surface, was available for the ducklings to climb out of the water. This grid was removed when the ducklings were fully used to being on water for the whole of the experimental period. The ducklings dived for mixed corn (Heygates Ltd) which was thrown into the water. Each period lasted up to 2 h, and cardiac activity was continuously monitored. After each period on the tank they were taken back to their holding facility, so that no unmonitored dives could be made. The signal from the radiotransmitter was passed from a receiver (Sharp model FX-213 AU) to a purpose-built decoder (Woakes, 1980), which extracted the electrocardiogram (ECG). This was then stored on one channel of a stereo tape-recorder (Superscope CD-320) for later analysis. The other channel was used to record a spoken commentary of the birds' behaviour, particularly noting the moments of submergence and surfacing, so that these could be related to heart rate. Heart rates were also recorded from the ducklings when they were between 11 and 31 days old (mass between 100 and 385 g), during both day and night resting periods. Air temperature during recordings varied between 19 and 23°C and water temperature in the tank was 18–19°C.

Heart rates were determined, after a hard copy of the ECG had been obtained on a pen recorder (George Washington Ltd), at fixed times before, during and after a dive by measuring cardiac intervals. Mean values were obtained for each duckling, these mean values were averaged and the standard error (S.E.) of this final mean obtained. Where appropriate, variance-ratio test (F-test) and Student's *t*-test for small samples were used to test for significant difference between two means. A difference was considered to be significant when the probability that it was due to chance was less than 5% ($P < 0.05$). Correlation between mass and resting heart rates was tested using least-squares linear regression and 5% was taken as the fiducial limit of confidence.

Results

At the time the transmitter was implanted, the average age of the six ducklings was 11.5 ± 2.1 days and the average mass was 136 ± 29.2 g. Heart rate during day resting periods averaged 250.3 ± 20.6 beats min^{-1} , which is a significant 27% higher than during night resting periods when it was 197.4 ± 6.7 beats min^{-1} . Although the mass of the ducklings during the period that the recordings were made increased, there was no significant correlation between mass and resting heart rates during either day or night resting periods.

The average age of the ducklings was 14.5 ± 2.6 days and the average mass was 164 ± 35.9 g when they were first placed on deep water. They were invariably very active and hence had high heart rates. Their behaviour progressed from skimming the surface and dipping the beak, to head only submersion, to full dives, when they became completely submerged. The average response of the ducklings to *all* voluntary beak dipping and head submersion before first-ever whole-body dives were performed is given in Table 1. The duration of beak dips was always very short (fractions of a second) as were some of the head submersions. For those head submersions which could be timed, the average duration was 1.4 ± 0.2 s. Upon submersion of the beak or head there was invariably an immediate decrease in heart rate by an average of 31% from the elevated pre-submersion level of 370.6 ± 13.1 beats min^{-1} . During submersion, heart rate steadily increased and just before surfacing it was slightly above the value seen just before submersion. Upon surfacing, heart rate returned to the pre-submersion level. During head or beak submersion mean heart rate never fell below the mean daytime resting value (Table 1).

The first of the whole-body dives was performed at an average age of 15.7 ± 2.3 days, when the mass of the birds was 168 ± 35.7 g. The dives were only a few centimetres below the surface and, on average, of short duration (3.6 ± 1.6 s). Fig. 1 shows the cardiac response of individuals before, during and after these first-ever dives. Three ducklings exhibited a similar pattern and Fig. 1A shows one of these. Before the start of the dive there was a slight increase in heart rate, followed by a reduction immediately upon submergence. Lowest heart rate values were reached within 1 s of the start of the dive and were 57–60% of the values

Table 1. Mean values \pm s.e. of measured variables in tufted ducklings

	Beak and head submersions			First-ever dives	Next 20 dives	Longer dives
Age (days)				15.7 \pm 2.3	17.7 \pm 2.1	19.0 \pm 2.4
Mass (g)				168.2 \pm 35.7	200.2 \pm 30.2	204.9 \pm 22.5
Duration (s)		1.4 \pm 0.2		3.6 \pm 1.6	3.0 \pm 0.5	10.9 \pm 1.0
Heart rate (beats min ⁻¹)						
Before submersion	-5 s			344.4 \pm 44.2 (5)	410.7 \pm 29.0	460.7 \pm 14.6 (3)
	-2 s	365.7 \pm 18.6		372.8 \pm 49.4	420.5 \pm 26.7	485.1 \pm 13.2
	-1 s	375.0 \pm 19.0		380.7 \pm 44.2	434.2 \pm 20.7	486.4 \pm 12.1
	-i	370.6 \pm 13.1		407.8 \pm 46.6	435.3 \pm 16.9	466.8 \pm 16.6
After submersion	+i	254.9 \pm 20.4		289.5 \pm 37.5	251.5 \pm 30.3	295.0 \pm 39.9
	+1 s			240.5 \pm 9.5 (2)	284.1 \pm 19.0	291.1 \pm 8.5
	+2 s				277.4 \pm 18.7 (4)	308.3 \pm 26.9
	+5 s					313.1 \pm 17.7 (3)
Halfway		296.2 \pm 25.9		290.5 \pm 38.4	288.6 \pm 15.4	320.4 \pm 4.2
Before surfacing	-5 s					316.7 \pm 9.9 (3)
	-2 s				281.5 \pm 10.0 (4)	329.4 \pm 20.0 (3)
	-1 s			241.5 \pm 111.5 (2)	303.7 \pm 19.2	327.8 \pm 34.0
	-i	407.9 \pm 20.8		354.2 \pm 35.4	387.8 \pm 23.7	396.1 \pm 33.7
After surfacing	+i	382.0 \pm 17.8		395.0 \pm 31.0	406.2 \pm 21.1	428.3 \pm 34.7
	+1 s	403.6 \pm 17.8		348.8 \pm 20.3 (5)	433.9 \pm 22.2	470.8 \pm 17.0
	+2 s	376.4 \pm 17.0		408.7 \pm 40.9	439.8 \pm 22.6	476.1 \pm 13.0
	+5 s			402.8 \pm 42.3 (5)	427.4 \pm 23.4	454.1 \pm 26.6

Number of ducklings contributing to the mean is six for beak and head submersions, first-ever and next 20 dives and four for the longer dives, except where otherwise indicated in parentheses.

i denotes measurement taken from cardiac interval immediately before (-i) or after (+i) submersion and surfacing.

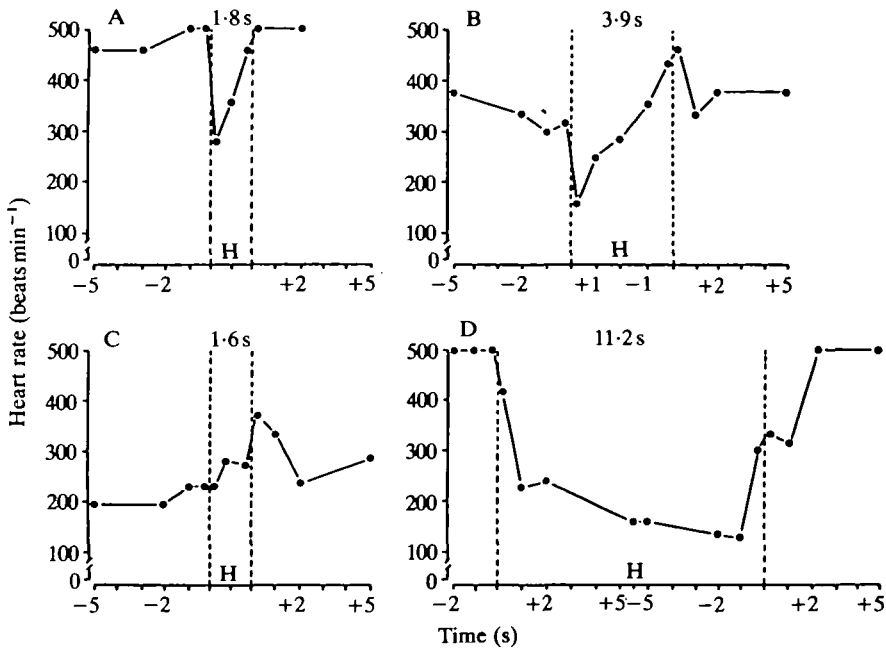


Fig. 1. Cardiac responses of four ducklings to first-ever dives (A,B, females; C,D, males). Dive durations are given between the two vertical dashed lines which indicate the moments of submergence and surfacing. Points closest to these lines are measurements taken from the cardiac intervals immediately before and after submergence and surfacing and H indicates the point halfway into the dive.

immediately before submergence. Heart rate then increased during the remainder of the dive. Upon surfacing, there was a further increase in heart rate. The cardiac response of the duckling illustrated in Fig. 1B differed from that shown in Fig. 1A in that there was a decrease in heart rate before the onset of the dive. During the dive, however, heart rate showed a similar pattern to that described above (Fig. 1A), with a 50% reduction in heart rate immediately upon submergence and an increasing heart rate during the remainder of the dive. This gave a heart rate at the end of the dive above the level seen just before submergence. Heart rate after surfacing immediately dropped to a level similar to that before the dive. In one duckling (Fig. 1C) there was no reduction in heart rate. In fact, it increased both before and during submersion. The fourth type of response is illustrated in Fig. 1D. The first-ever dive performed by this duckling was very long (11.2s) compared with those of the other ducklings. Heart rate was at a constant level of 500 beats min⁻¹ before the dive. Upon submergence there was an immediate decrease in heart rate which, within 1 s, was reduced to 46% of pre-dive level. Heart rate then continued to fall progressively during the dive until 1 s before surfacing when, having fallen to 26% of the pre-dive level, it increased. Upon surfacing, heart rate increased further and reached its pre-dive level 2 s after surfacing.

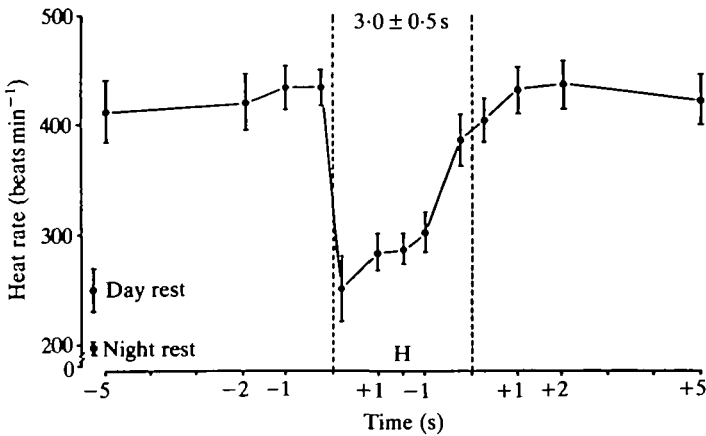


Fig. 2. Average heart rates for the six ducklings at specific times before, during and after 20 dives per duckling performed after the first-ever dive. Error bars indicate \pm s.e. of the mean. The mean duration \pm s.e. of the dives is given between the vertical dashed lines which delimit the mean period of the dives. Mean heart rates (\pm s.e.) during day and night resting periods are given at the bottom left-hand corner. Points closest to the dashed lines are measurements taken from the cardiac intervals immediately before and after submergence and surfacing and H indicates the point halfway into the dive.

The average response of the six ducklings to the first-ever whole-body dives is given in Table 1. In the period before submersion there was a slight increase in heart rate. Upon submersion there was an immediate 29% reduction in heart rate, with a further decrease, until 1s after submersion a lowest level was reached representing a 41% reduction from the level immediately before the dive. Heart rate then increased during the first half of the dive. The decrease that followed, to the level reached 1s before surfacing, is due to the very low heart rate at this point of the duckling in Fig. 1D. In the other duckling contributing to this point (Fig. 1B), heart rate was above the level seen halfway into the dive. Upon surfacing heart rate had increased to a level similar to that before the start of the dive.

For the next 20 dives of each duckling, which were performed at an average age of 17.7 ± 2.1 days and mass 200.2 ± 30.2 g and lasted 3.0 ± 0.5 s, there was much less variation in the cardiac response. Table 1 and Fig. 2 show the average response for the six ducklings. Before the onset of the dives there was no significant increase in heart rate. Upon submergence there was an immediate 42% reduction in heart rate to a level which was similar to that during day resting periods. Heart rate then increased during the remainder of the dive, particularly during the last second before surfacing, to above resting level. Upon surfacing, heart rate was similar to the pre-dive level.

Occasionally, some of the ducklings performed dives of longer duration. The average cardiac response of four birds (mean age 19.0 ± 2.4 days; mean mass

204.9 ± 22.5 g) before, during and after 20 of these dives, lasting an average of 10.9 ± 1.0 s, is given in Table 1. As with the shorter dives (Fig. 2) there was no significant pre-dive increase in heart rate. Immediately after submergence, heart rate dropped to 61 % of its value 1 s before the start of the dives (i.e. a 39 % reduction), which was not significantly different from the level measured during day resting periods. Heart rate then increased during the first part of the dive, until it reached a plateau value of 324.6 ± 4.0 beats min⁻¹ (average of heart rates 5, 2 and 1 s before the end of the dive), which was a significant 30 % above the value measured during day resting periods. During the last second before the end of the dive, heart rate started to increase as the ducklings began to rise to the surface. Heart rate 1 s after surfacing was similar to the pre-dive level. During all types of whole-body dives, mean heart rate never fell below the mean daytime resting value (Table 1).

Discussion

Heart rate recorded in this study from unrestrained tufted ducklings during day resting periods was about 40 % lower than those reported for restrained domestic ducklings of up to 1 month old (Rey, 1971) and 1-week-old mallard ducklings (West, 1981). Compared with that in resting adult tufted ducks, in which radiotransmitters were also used to record heart rates from unrestrained birds (Butler & Woakes, 1979; Woakes & Butler, 1983; Stephenson *et al.* 1986), resting heart rate in the ducklings was about twice as high. Butler & Woakes (1979) and Stephenson *et al.* (1986) recorded the changes in heart rate associated with voluntary head submersion in adult tufted ducks. The latter authors found that heart rate changes during such behaviour were qualitatively similar to those seen during voluntary whole-body diving; the same applies to the results found in the present study for beak and head submersions performed before whole-body diving occurred (Table 1). This is in contrast to the results found for dabbling ducks, where voluntary head submersion did not cause substantial changes in heart rate (Furilla & Jones, 1986, 1987a).

From Fig. 1, it is clear that there was a large variation between ducklings in the cardiac response to the first whole-body dive. In particular the ducklings illustrated in Fig. 1C and D showed a response which was very different from that of the others (Fig. 1A). For the duckling in Fig. 1C, pre-dive heart rate was only 52 % of that recorded from the other five ducklings and there was no decrease in heart rate upon submersion. It may be that the cardiac response upon voluntary submersion is determined by heart rate before the dive (cf. Jones *et al.* 1982, studying involuntary submersion in white Pekin ducks). The duckling in Fig. 1D performed a first-ever dive which was more than five times longer than the average duration for the other five ducklings (2.1 ± 0.5 s). Although the duckling made this dive without any restrictions on resurfacing, it is very interesting to note that the heart rate response closely resembles that of adult tufted ducks being temporarily unable to surface from what had started as a normal feeding dive, and that of adult tufted ducks performing dives in which the horizontal distance to food was

extended (Stephenson *et al.* 1986). Thus, the psychological state of the duckling may account for the observed cardiac response, in which case it would appear that higher regions of the central nervous system can modify the cardiac response to submergence, a point that was also noted by Stephenson *et al.* (1986) and Furilla & Jones (1987*b*) for adult ducks.

The average initial cardiac responses to beak and head submersions (performed before any dives), first-ever dives (Table 1), the following 20 dives (Table 1; Fig. 2) and the longer dives (Table 1) were very similar to that seen in adult tufted ducks upon voluntary submersion (Butler & Woakes, 1979, 1982*b*; Stephenson *et al.* 1986). Levels of heart rate in the ducklings 5 s before any submersion were 50–150 beats min^{-1} higher than those in adult ducks (about 300 beats min^{-1}). This can be attributed to the fact that the ducklings were always very active whilst on the surface of the water. Thus, the substantial pre-dive cardiac acceleration seen in adults, particularly before the first dive of a series, was not apparent in the ducklings. Heart rates immediately before the onset of the dives in the ducklings were about the same or slightly higher than in the adults (about 400 beats min^{-1}). West (1981) reported a highest value for heart rate in newly hatched restrained mallard ducklings of 485 beats min^{-1} and the highest values observed in this study were 500 beats min^{-1} . Lowest heart rates immediately after submersion for both juvenile and adult ducks are about the same as the daytime resting heart rate. For the ducklings this represents a reduction of 40–50 %, whereas in adult ducks it is a reduction of about 75 % from the pre-dive level. As in adult ducks, heart rates during the second half of the dives are above resting levels and increase sharply during the last second of the dive, in anticipation of surfacing. Post-dive heart rates in both adult and juvenile ducklings return to the immediate pre-dive level, and decrease slightly to levels similar to those 5 s before the onset of the dives.

Obviously, the ducklings could not be deprived of drinking water, but they were prevented from immersing their beaks before they were allowed access to deep water. Bearing this in mind, the present study has shown that the initial cardiac response to voluntary head submersion in ducklings is not modified from the first immersion of the beak to the subsequent whole-body dives and is qualitatively similar to that seen in voluntarily diving adults. In fact, the essential features of the cardiac response to voluntary diving were present from the time that the ducklings were first put on to water. There is, therefore, no evidence to support the idea that this response results from the habituation of the classical bradycardia seen during involuntary dives.

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