

## CHANGES IN HEART RATE AND RESPIRATORY FREQUENCY DURING NATURAL BEHAVIOUR OF DUCKS, WITH PARTICULAR REFERENCE TO DIVING

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(Received 17 July 1978)

### SUMMARY

1. Heart rate and respiratory frequency were recorded from free-range pochards and tufted ducks by using an implantable radio-transmitter. Particular attention was paid to the changes associated with natural diving behaviour which occurred on an outside pond ( $4 \times 8 \times 0.65$  m depth).

2. Spontaneous dives, which occurred in the absence of any obvious external stimuli, often occurred in a series and there could be in excess of 40 dives in fairly quick succession. The first dive in a series was heralded by tachycardia and tachypnoea. Upon submersion there was transient bradycardia, but heart rate then increased over a period of 6-8 s until it was close to the value recorded when the bird was swimming on the pond before the dive. This rate was maintained throughout the dive. Upon surfacing, heart rate increased when lung ventilation commenced, and then decreased steadily until a few seconds before the next dive when it increased. The average duration of all spontaneous dives of a series was  $8.4 \pm 0.2$  (137) s for pochards and  $9.9 \pm 0.8$  (95) s for tufted ducks. The birds also dived in response to food being thrown onto the water (feeding dives). Changes in heart rate associated with these dives were similar to those described for the spontaneous dives. Heart rate did, however, tend to be higher during all stages of the feeding dives, and it often increased at the end of a dive before the bird started to ventilate its lungs.

3. When being chased with a net, the birds had extremely high values of heart rate and respiratory frequency. Immediately they dived to escape, heart rate fell to a rate which was similar to the rate recorded when the unstressed birds were swimming. This rate was maintained throughout the dive. Anticipatory increases in heart rate preceded lung ventilation at the end of the dives.

4. The birds showed a progressive reduction in heart rate when their heads were submerged under water in the laboratory. After 10 s submersion, heart rate was lower than the lowest heart rate recorded during any of the free-range dives.

## INTRODUCTION

When the head of a duck is placed under water, apnoea with progressive reductions in heart rate and cardiac output and selective vasoconstriction occur (Andersen, 1963; Johansen, 1964; Butler & Jones, 1968, 1971; Jones & Holeton, 1972). These responses to submersion of the head of ducks are similar to those that occur in seals during both natural and enforced dives (Elsner, 1969) and are often referred to collectively as the 'diving response'. This response enables the animal to conserve oxygen and to remain under water for periods of time longer than would otherwise be possible.

Compared with seals, the onset of the bradycardia, and the accompanying selective vasoconstriction, during head submersion of ducks are relatively slow, and their onset and maintenance can be explained largely in terms of a number of peripheral reflexes. Cessation of ventilation causes progressive hypercapnia and hypoxia which, via the carotid body chemoreceptors (Hollenberg & Uvnäs, 1963; Jones & Purves, 1970; Holm & Sørensen, 1972), elicit the progressive reduction in heart rate. Apnoea is maintained in the face of this increased chemoreceptor activity by the stimulation of receptors in the upper respiratory tract (Butler & Jones, 1968; Bamford & Jones, 1974; Blix, Rettedal & Stokkan, 1976). It has been suggested however, that peripheral reflexes such as these may not be the only factors involved during more natural dives (Butler & Jones, 1968) and that the gradually developed bradycardia seen during head submersion in the laboratory may be an artifact of the experimental conditions (Eliassen, 1960). One reason for the former suggestion is that under natural conditions the act of diving is volitional, also it must be added that during such dives the bird is active, usually searching for food.

The purpose of the present study was to monitor changes in heart rate and respiratory frequency in diving ducks using an implantable radio-transmitter (Woakes & Butler, 1975) during natural behaviour and in particular during diving. Some of the results from this investigation have been reported briefly elsewhere (Butler & Woakes, 1976*a, b*).

## MATERIALS AND METHODS

Data were obtained from two male and three female pochards (*Aythya ferina*) whose mass ranged from 0.68 to 0.8 kg, and from two male tufted ducks (*A. fuligula*) of mass 0.75 and 0.83 kg. The birds were obtained as young chicks from the Wildfowl Trust, Slimbridge, and were kept on an outside pond (4 × 8 × 0.65 m depth) on the campus of the University of Birmingham. The birds were pinioned, but they were able to roam freely within a perimeter fence which was 20 × 20 m and surrounded the pond. In addition to any natural supply of food, the birds were fed on growers' pellets and mixed corn (Heygates Ltd., Bugbrooke Mills).

Heart rate and respiratory frequency were obtained from free-range birds within the compound by way of an implantable radio-transmitter (Woakes & Butler, 1975). The transmitter contained a magnetic switch so that it was drawing current only when records were being made from the animal. The implantation procedure was performed after the birds had been given local injections of 2% (w/v) lignocaine hydrochloride with adrenaline 1:80000 (Xylocaine, Astra Hewlett Ltd., Watford).

The animal showed no signs of distress either during or after the operation. The transmitter and leads were sterilized in chlorhexidine (0.5% then 0.05%) before being implanted. The transmitter was placed in the abdominal cavity with the bipolar e.c.g. lead lying close to the heart. The other lead from the transmitter was guided beneath the skin up to the trachea and a thermistor at the end of this lead was placed into the lumen of the trachea (for details see Woakes & Butler, 1975). The wounds were sutured together and the bird was given an injection of ampicillin (15 mg, i.m. Penbritin, Beechams). The bird was kept indoors for 2–3 days after the operation and then placed outside in the compound. Only one bird was implanted with a transmitter at a time and it was accompanied in the compound by up to 8 diving ducks and 12 mallards.

Usually, within one week of the operation the bird was diving spontaneously and recordings of heart rate and respiratory frequency were made from 10 days after the operation. The bird was caught before a recording session in order to switch on the transmitter. The wounds from the operation were almost completely healed within a week of the operation, but it took another several weeks before the feathers had completely regrown. Ideally, it would have been better to wait until this time before the recordings were made. Unfortunately within 3 weeks of the operation the response time of the thermistor had invariably been reduced to an unacceptable level, generally as a result of it having been coated with tracheal secretions. Therefore, all of the recordings had to be made within 3 weeks of implanting the transmitter. As far as could be determined from the animal's behaviour, the presence of the transmitter caused the bird no distress nor did it cause it to behave abnormally except that it preened the area of the wound more than usual, particularly during the first 2 weeks after the operation. There was also a reduction in body mass during this period. On average, body mass at this time was 55 g less than at the time the transmitter was implanted. By the end of the third week, the mass of the birds had returned to within 10–15 g of the pre-operation level.

Three additional ducks had a single channel e.c.g. transmitter implanted. It was possible to leave these birds for several weeks to allow the down feathers around the wound to regrow completely and the contour feathers to regrow or be preened to cover the area. Feather regrowth and return to a normal body mass were completed within 6 weeks after implanting the transmitter, and at this time the changes in heart rate in association with spontaneous and induced escape dives were not significantly different from those recorded from animals with the respiration probe in place. These three birds were also used to record the changes in heart rate associated with submerging the head of the duck in water in the laboratory. This was done initially before implantation of the transmitter, using subcutaneous leads connected to conventional amplifiers and then 6 weeks after implantation of the transmitter, using radiotelemetry. The values of heart rate before, during or after head submersion obtained via telemetry were not significantly different from those obtained by the more conventional system.

When recording from free-range birds, the observer sat in a wooden hut which was situated inside the compound, some 3 m from the edge of the pond. The birds were not affected in any way by the presence of an observer inside the hut. Information from the bird was received by a Sony CRF 5090 receiver and was stored on one channel of a Teac A450 stereo cassette tape recorder. The other channel was used

both for marking the dives and for recording a commentary of the bird's behaviour for later correlation with the decoded physiological data. An attempt was made to gather information on heart rate and respiratory frequency associated with as wide a range of the bird's behaviour as possible. This included diving. Although the bird may have been searching for food during every natural dive, a distinction was made between those dives that occurred in response to food being thrown onto the pond, 'feeding' dives, and those that occurred on impulse, 'spontaneous' dives. As well as performing these natural dives, the bird was also induced to dive ('escape' dives) by chasing it with a net. When sufficient data had been collected outside and while the thermistor in the trachea was still responding satisfactorily, the animal was taken into the laboratory and its head was forcibly submerged in water for 10, 20 and 60 s (see Butler & Jones, 1968). Changes in heart rate and respiratory frequency associated with these 'dives' were recorded on tape via the implanted transmitter. When diving naturally, the birds changed their position very rapidly from the horizontal to the vertical. Inspection of the respiration subcarrier of the implanted transmitter indicated that a radio signal was being received continuously and that there was not a 'drop out', at the beginning of a dive, associated with this rapid change in position.

The tapes were played back through a purpose-built demodulator and hard copies of the e.c.g. and respiratory air flow were made by a 4-channel pen recorder (Devices Ltd.). Heart rate was determined by an instantaneous rate meter (Devices Ltd.). Values of heart rate and respiratory frequency were obtained from these traces and were stored in a computer (PDP 11/10, Digital Ltd.). Mean values of the variables were computed for the various types of activity displayed by the birds. For spontaneous dives on the pond, these mean values were obtained at 10, 5, 2 and 1 s before cessation of ventilation (as inferred from the trace of air flow through the trachea); 1, 2 and 5 s after cessation of ventilation; 2 and 1 s before commencement of ventilation at the end of a dive and 1, 2, 5 and 10 s after the duck started to ventilate. The maximum values of heart rate before and after a dive, as well as the minimum level during a dive were also noted. As these values invariably occurred within one second of the cessation or commencement of respiration, they are plotted on graphs at 0.5 s before or 0.5 s after cessation of ventilation at the start of a dive or 0.5 s after commencement of ventilation at the end of a dive. Cessation and commencement of ventilation were taken as indications of the beginning and end of the dive respectively.

Laboratory dives were analysed in a similar manner with the addition of an extra sample point 10 s into the dive. As these dives did not have associated with them extreme changes in heart rate upon submersion, the maximum heart rate just before and the minimum heart rate just after diving were not noted.

To obtain data on non-diving activity, periods were chosen where the bird showed the same type of behaviour continuously for 30 s. Heart rate and respiratory frequency were then sampled every 5 s within the 30 s period.

Mean values are given  $\pm$  S.E. of mean with the number of observations in parentheses. Students' *t*-test was used to test the significance of any difference between two mean values. The word 'significant' in the present report means significant at the 95% confidence level ( $P < 0.05$ ).

## RESULTS

*Non-diving behaviour*

The birds' behaviour was classified subjectively. For example, it was assumed that, when a duck was lying down with its head curled round onto its back or held under its wings, it was asleep. Also, there were no absolute divisions between fast and vigorous swimming so that there was, no doubt, some variability in these assessments from day to day. As far as pochards were concerned, heart rate was  $110 \pm 2.8$  (21) beats  $\text{min}^{-1}$  when they were drifting on the water, which was not significantly different from the value recorded when they were asleep on land ( $114 \pm 2.5$  (42) beats  $\text{min}^{-1}$ ). Respiratory frequency, however, was  $16.8 \pm 1.0$  (21) breaths  $\text{min}^{-1}$  when they were drifting on the water and this was significantly higher than the value recorded when they were asleep on land ( $10.9 \pm 0.6$  (42) breaths  $\text{min}^{-1}$ ). When the pochards were walking, heart rate was  $158 \pm 7.3$  (35) beats  $\text{min}^{-1}$  and respiratory frequency was  $25 \pm 1.5$  (35) breaths  $\text{min}^{-1}$ . These values were not significantly different from those recorded during periods of fast swimming when heart rate was  $160 \pm 3.2$  (84) beats  $\text{min}^{-1}$  and respiratory frequency was  $27 \pm 1.0$  (84) breaths  $\text{min}^{-1}$ . During vigorous swimming, however, heart rate was significantly higher at  $227 \pm 10.9$  (35) beats  $\text{min}^{-1}$ , whereas respiratory frequency did not show a significant change and was  $25 \pm 1.8$  (35) breaths  $\text{min}^{-1}$ . As the birds had been pinioned they could not fly properly, but the highest values of heart rate and respiratory frequency during non-diving activity were recorded in pochards when they attempted to fly and 'skated' across the surface of the pool with their wings flapping vigorously. Heart rate was  $425 \pm 10.3$  (35) beats  $\text{min}^{-1}$  and respiratory frequency was  $49.3 \pm 2.6$  (35) breaths  $\text{min}^{-1}$ . The next highest values of the two measured variables were recorded when the birds were feeding on land. Heart rate was  $360 \pm 14$  (28) beats  $\text{min}^{-1}$  and respiratory frequency was  $40 \pm 2.5$  (28) breaths  $\text{min}^{-1}$ . Fewer events were recorded from the two tufted ducks than from the pochards, but it was found that within the various categories of behaviour, heart rate was not significantly different between the two species.

There were wide ranges in heart rate and respiratory frequency during any one type of behaviour pattern and the total range for any variable was very large. For tufted ducks, respiratory frequency was as low as 3  $\text{min}^{-1}$  (drifting on water), or as high as 86  $\text{min}^{-1}$  (preening vigorously). For the pochards, the lowest recorded heart rate was 85 beats  $\text{min}^{-1}$  (drifting on water) whereas the highest recorded rate was 505 beats  $\text{min}^{-1}$  ('flying' across the pool). Some of the variability in the two measured variables could not be related to any behaviour of the animal. A pochard which was lying down with its head under its wing and was, presumably, asleep, showed sudden increases in both heart rate (100–280 beats  $\text{min}^{-1}$ ) and respiratory frequency (11–20 breaths  $\text{min}^{-1}$ ) for no apparent reason. Perhaps it was dreaming. A resting tufted duck showed a transient increase in heart rate from 105 to 250 beats  $\text{min}^{-1}$  when a human appeared within sight but did not approach the bird. This was followed by a larger rise in heart rate to 395 beats  $\text{min}^{-1}$  when the bird stretched one wing. In contrast, there was no change in heart rate in a pochard when it was approached by another pochard and made hissing noises at it.

*Diving behaviour**Spontaneous dives*

These dives occurred in the absence of any noticeable external stimuli. They often occurred in a series and there could be in excess of 40 dives in fairly quick succession. Typically, the first dive in a series was heralded by increases in both heart rate and respiratory frequency. Immediately upon submersion there was an instantaneous reduction in heart rate to a level below that recorded while the animal was swimming (Fig. 1*a*). Heart rate then increased in a hyperbolic fashion during the early stages of the dive and eventually stabilized at a level which was between the values recorded during fast and vigorous swimming activity. The birds tended to breathe out upon submersion and there was often a further expiratory effort upon surfacing before the first large inspiration (Fig. 1*b*). An immediate increase in heart rate accompanied the commencement of lung ventilation. Both heart rate and respiratory frequency were relatively high upon surfacing but both then decreased steadily.

Sometimes no further dives occurred after the first one and, on average, it took  $14.8 \pm 1.7$  (6) s for heart rate and respiratory frequency to return to their pre-dive values in tufted ducks and  $10.8 \pm 0.9$  (13) s in the pochards. If no further dives occurred before full recovery of these variables, then the next dive that took place was designated the first dive of a series. When isolated dives did occur they often displayed unusual changes in heart rate. On occasions there was no obvious post-dive tachycardia (Fig. 1*c*) and more rarely there was no dramatic change in heart rate at all during the period of submersion (Fig. 1*d*).

The most common occurrence was for another dive to follow the first one before heart rate and respiratory frequency had fully recovered. The average time between first and second dives was  $12.6 \pm 2.2$  (18) s for tufted ducks and  $9.8 \pm 1.2$  (25) s for

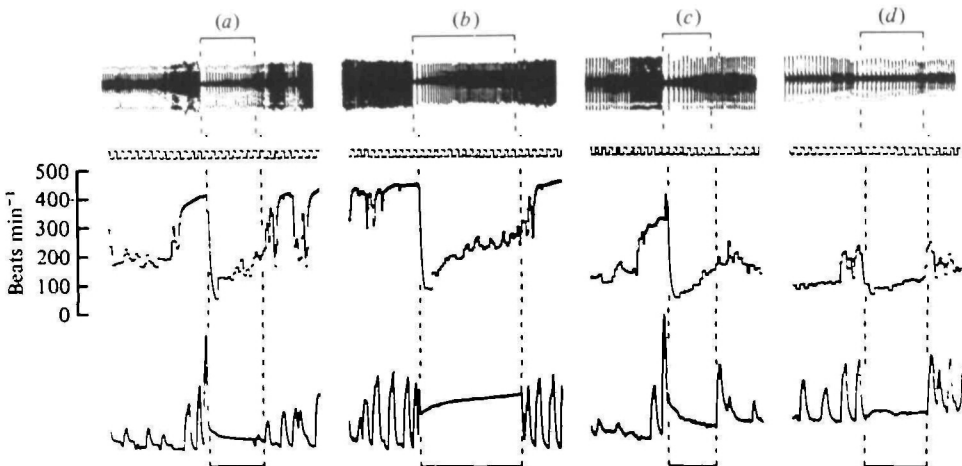


Fig. 1. Traces showing changes in heart rate and respiratory frequency associated with spontaneous dives. (a) First dive in a series and (b) sixth dive in same series, both performed by ♂ tufted duck (0.75 kg). Isolated dives performed by (c) ♂ tufted duck (0.65 kg) and by (d) ♀ pochard (0.7 kg). In each case the period of submersion is indicated by the dashed, vertical lines joined by horizontal bars. Traces in each set are from above downwards: e.c.g., time marker(s), instantaneous heart rate, air flow through the trachea (inspiration-up on trace).

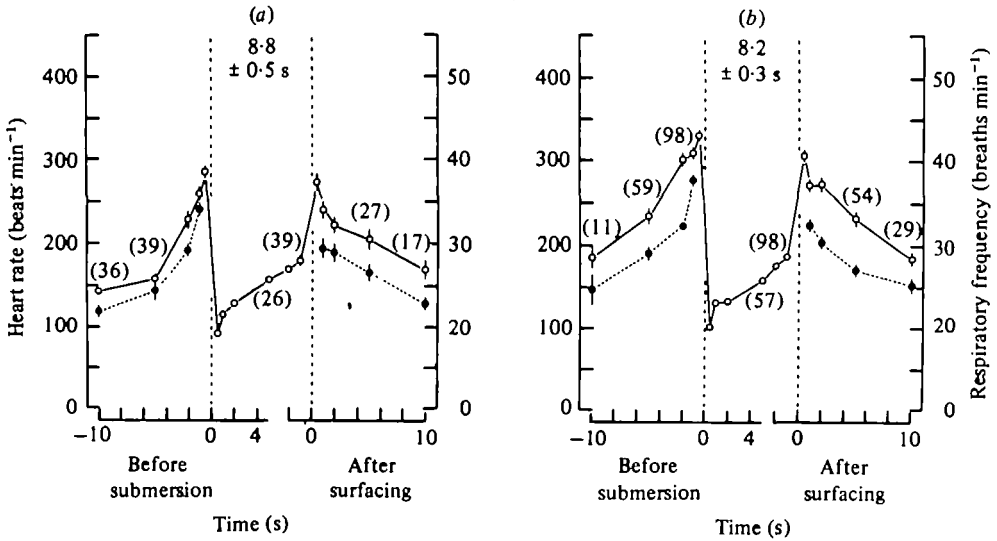


Fig. 2. Graphs showing mean values of heart rate (○) and respiratory frequency (●) in pochards before, during and after, (a) all recorded first spontaneous dives of a series, and (b) all recorded second and subsequent spontaneous dives of a series. The figure in parentheses above a set of points indicates the number of events contributing to those points and to each successive set of points without a number. Vertical lines associated with each point are  $\pm$  s.e. of mean. Where vertical lines are absent, the s.e. of mean is within the limits of the symbol. The mean duration of the dives  $\pm$  s.e. of mean is given between the vertical dotted lines on each graph which delimit the period of the dive.

pochards. Thus the anticipatory increases in heart rate and respiratory frequency which preceded the second (or subsequent) dives of a series were on top of already elevated rates (Fig. 1b). The average response for pochards can be visualized from Fig. 2 by continuing the 5 s post-dive values of the first dives (Fig. 2a) with the 5 s pre-dive values for the second and subsequent dives (Fig. 2b). Clearly, the shorter the duration between dives the less the reduction in heart rate and respiratory frequency, and vice versa. The changes in heart rate during the second and subsequent dives in a series were independent of the position of the dive in the series, so the data for these dives have been grouped together (Fig. 2b). In pochards the pattern of changes in heart rate and respiratory frequency in second and subsequent dives were similar to those of the first dive of a series (Fig. 2). This was also the case for the tufted ducks. For both species, however, the heart rates just before diving, immediately upon submersion and immediately upon surfacing were significantly higher for the second and subsequent dives in a series than they were for the first dives (Table 1). However, the lowest heart rate at the beginning of a dive did not vary significantly with respect to the position of the dive in a series.

Qualitatively, the changes in heart rate and respiratory frequency associated with dives of pochards (see Fig. 2) were similar to those of tufted ducks. There were however quantitative differences between the two species, particularly with respect to heart rate (Table 1) which increased to a significantly higher value in tufted ducks than it did in the pochards before a dive. On the other hand it fell to a significantly lower value at the beginning of a dive in the tufteds than it did in the pochards. Just

Table 1. *Mean values ± s.e. of mean for pochards and tufted ducks of dive duration and heart rate at specific times before, during and after spontaneous dives, feeding dives and induced escape dives*

(Values are given for the first dive in a series (1st) and for second and subsequent dives combined (2nd +). The number of events contributing to each mean value is given in parentheses)

	Spontaneous dives		Feeding dives		Escape dives	
	Pochards	Tufteds	Pochards	Tufteds	Pochards	Tufteds
Heart rate 5 s before submersion (beats min <sup>-1</sup> )	158 ± 6 (39) 235 ± 9 (59)	260 ± 18 (24) 364 ± 14 (48)	264 ± 33 (11) 420 ± 12 (24)	340 ± 50 (3) 398 ± 24 (10)	462 ± 5 (6) 465 (2)	522 ± 3 (4) 530 ± 10 (2)
Highest heart rate immediately before submersion (beats min <sup>-1</sup> )	285 ± 7 (39) 331 ± 6 (98)	395 ± 12 (24) 451 ± 6 (71)	341 ± 26 (10) 458 ± 4 (35)	457 ± 3 (3) 446 ± 10 (12)	482 ± 2 (6) 480 ± 3 (14)	532 ± 6 (4) 533 ± 3 (7)
Lowest heart rate immediately after submersion (beats min <sup>-1</sup> )	92 ± 3 (39) 102 ± 2 (98)	71 ± 4 (24) 81 ± 3 (71)	125 ± 14 (11) 159 ± 7 (35)	127 ± 16 (3) 107 ± 8 (12)	181 ± 22 (6) 154 ± 4 (12)	115 ± 24 (4) 88 ± 10 (7)
Heart rate 1 s before surfacing at end of dive (beats min <sup>-1</sup> )	181 ± 6 (39) 188 ± 4 (98)	199 ± 9 (24) 220 ± 5 (71)	212 ± 21 (11) 249 ± 12 (35)	222 ± 14 (3) 235 ± 12 (3)	257 ± 26 (6) 276 ± 15 (14)	267 ± 18 (4) 208 ± 12 (7)
Highest heart rate upon surfacing (beats min <sup>-1</sup> )	272 ± 10 (38) 307 ± 7 (97)	340 ± 20 (20) 406 ± 9 (65)	359 ± 32 (11) 459 ± 4 (35)	473 ± 6 (3) 403 ± 21 (12)	479 ± 5 (6) 479 ± 3 (14)	537 ± 4 (4) 536 ± 3 (7)
Duration of all dives (s)	8.4 ± 0.2 (137)	9.9 ± 0.8 (95)	10.9 ± 0.5 (46)	11.6 ± 1.1 (15)	9.6 ± 0.7 (20)	9.1 ± 0.9 (11)



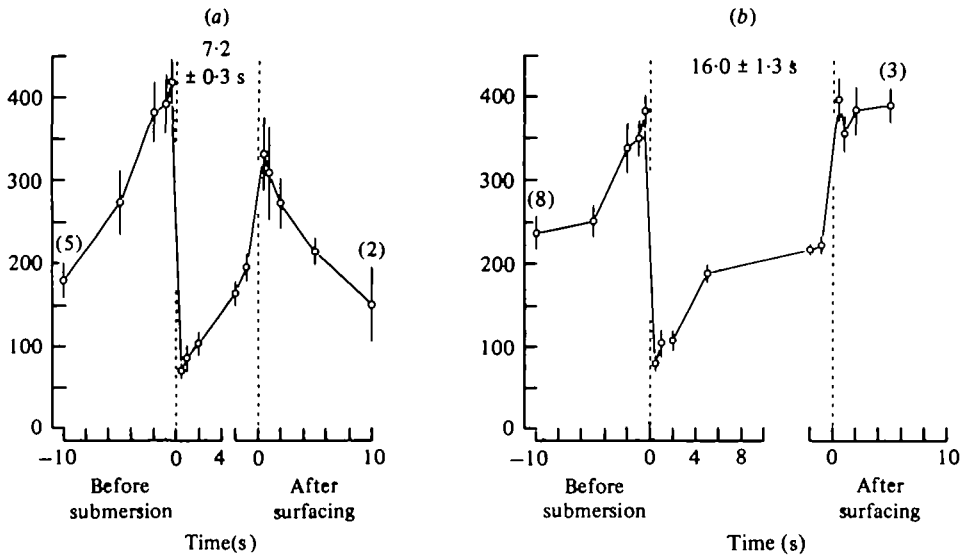


Fig. 3. Graphs showing mean values of heart rate in tufted ducks before, during and after, (a) all recorded first spontaneous dives of a series with a duration between 6 and 8 s, (b) all recorded first spontaneous dives of a series with a duration in excess of 12 s. For remainder of caption see Fig. 2.

before surfacing, and immediately upon surfacing, heart rate was significantly higher in the tufted ducks than in the pochards. Having reached its lowest level immediately upon submersion, heart rate increased almost linearly during the first 6–8 s of a dive, but from then on the rate of increase declined steadily. Thus during dives of short duration ( $< 8$  s) heart rate increased continuously during a dive (Fig. 3a), whereas during dives of longer duration a plateau was reached after the initial rise (Fig. 3b). This occurred in both species.

In the tufted ducks, there was a linear relationship between heart rate 10 s before submersion and the duration of the first dive in a series (heart rate =  $99.62 + 10.88 \times$  (dive length),  $r = 0.82$ ). For both species of duck, the magnitude of the post-dive tachycardia seen upon surfacing at the end of a first dive in a series was related to the duration of the dive (Fig. 4). There was no such relationship between respiratory frequency upon surfacing and dive length. Respiratory frequency 10 s before the first dive of a series was similar for both species of duck, but at 1 s before the first dive it was significantly higher in the tufted ducks than in the pochards (Table 2). Upon surfacing, respiratory frequency was similar for both species of duck (Table 2). The mean duration of all spontaneous dives was significantly longer for tufted ducks (Table 1). The dives varied in duration from 3.6 to 23.5 s for tufted ducks and from 3.0 to 16.3 s for pochards. The mean interval between all dives was  $8.9 \pm 0.5$  (98) s for pochards and  $11.5 \pm 0.9$  (70) s for tufted ducks. In other words the mean dive length was similar to the mean time between dives. There was, however, no relationship between the duration of a dive and the time from the last dive, nor between the duration of a dive and the time to the next dive. During spontaneous dives the birds did not seem to travel far under water, as they often surfaced within 0.5–1 m of the place where they submerged.

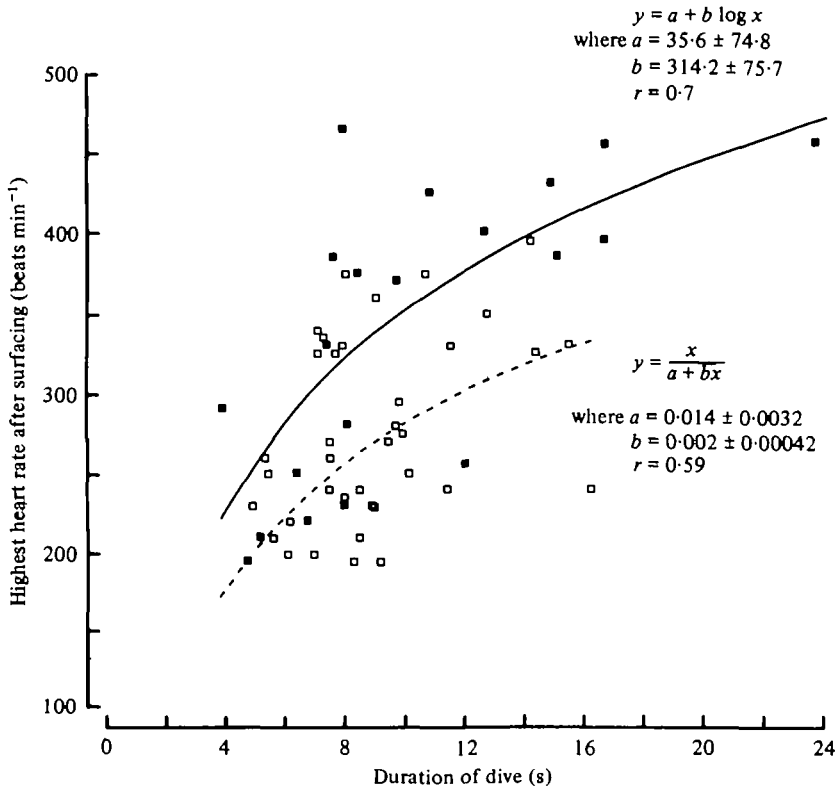


Fig. 4. Graphs to show the relationship between the highest heart rate recorded upon surfacing after the first spontaneous dives of a series and the duration of the dive in pochards ( $\square$ ) and tufted ducks ( $\blacksquare$ ). The line of best fit is drawn through the points. The equation describing each line and the correlation coefficient ( $r$ ) are given with each line.

Sometimes a bird would upend itself in the water and 'dabble' at the edge of the pond in a fashion similar to that displayed by mallard ducks. Several 'dabbles' often occurred in a series and there were no consistently large changes in heart rate associated with each period of head submersion, even when the head was under water for 6 s or more (Fig. 5a). Also, the birds would periodically go through the initial motions of a spontaneous dive to the point of placing the head under water, but then instead of the rest of the body being submerged, the head would come to the surface. Several of these 'head ducking' manoeuvres would often occur in a series and although heart rate was somewhat irregular during such a series (Fig. 5b), there were not the large changes in heart rate which accompanied a complete dive.

#### Feeding dives

These dives occurred in response to food pellets being thrown into the water, and the changes in heart rate and respiratory frequency were qualitatively similar to those seen during the spontaneous dives. One characteristic quantitative difference was that heart rate was often higher during feeding dives (Table 1). For the pochards, heart rate just before the dive was always higher for feeding dives than for spon-

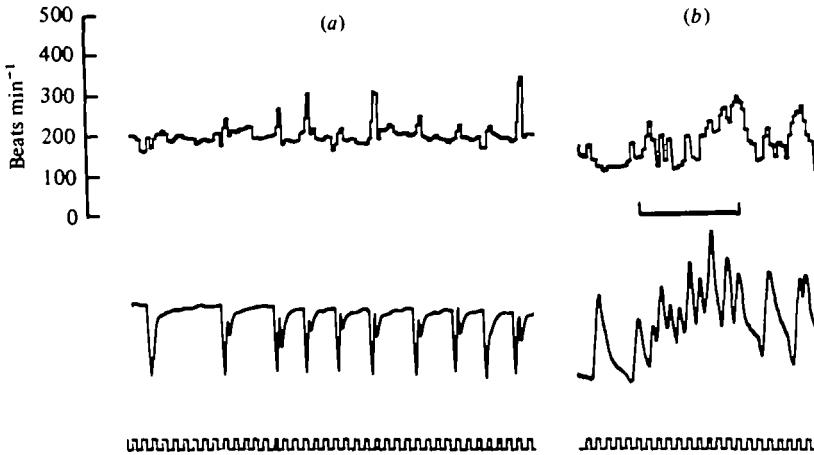


Fig. 5. Traces from ♂ tufted duck (0.75 kg) showing changes in heart rate associated with: (a) 'dabbling' under water, (b) 'head ducking'. In (a) the bird upended itself like a mallard duck during the periods of apnoea indicated on the air flow trace. In (b) the bird went through the initial manoeuvres of a dive to the point of ducking its head under water, but instead of submerging itself completely it then removed its head from the water. This procedure was repeated several times during the period indicated by the black bar. Traces in each set are from above downwards: instantaneous heart rate, air flow through the trachea (inspiration-up on trace), time marker(s).

taneous dives. This was also the case for the tufted ducks as far as the first dive in a series was concerned, but not so for second and subsequent dives. For both species of duck, the heart rate immediately upon submersion was always significantly lower during spontaneous dives than during feeding dives (Table 1). For pochards, heart rate associated with all stages of the second and subsequent feeding dives was significantly higher than during the first feeding dive of a series. This was not the case for tufted ducks (Table 1). There were no consistent differences in respiratory frequency associated with spontaneous or feeding dives for either species of duck (Table 2).

The average duration of feeding dives was significantly greater than for spontaneous dives in pochards, but not in the tufted ducks (Table 1). In a number of feeding dives there was a clear indication of heart rate increasing at the end of a dive before lung ventilation commenced (Fig. 6*a, b*). It is also clear from the respiration traces in Fig. 6 that the birds breathed out several times during a feeding dive. These expirations may have been related to the feeding manoeuvres themselves.

#### *Escape dives*

These dives were induced by chasing the animal with a pond net. The birds were clearly highly stressed as their heart rates were consistently high whilst being chased, and these rates were the highest recorded for either species of bird. There was, therefore, no further rise in the heart rate before submersion (Fig. 7). There were no consistent differences in heart rate between first escape dives and second and subsequent dives of a series for either species (Table 1). The tufted ducks again displayed significantly higher heart rates than the pochards before submersion and yet upon submersion, heart rate fell to significantly lower values in the tufteds than in the pochards (Table 1). At its greatest extreme during second and subsequent dives in

Table 2. Mean values  $\pm$  S.E. of mean of respiratory frequency for pochards and tufted ducks at various times before and after spontaneous dives, feeding dives and induced escape dives

(Values are given for the first dive in a series (1st) and for second and subsequent dives combined (2nd+). The number of events contributing to each mean value is given in parentheses.)

	Spontaneous dives		Feeding dives		Escape dives	
	Pochards	Tufteds	Pochards	Tufteds	Pochards	Tufteds
Respiratory frequency 10 s before submersion ( $\text{min}^{-1}$ )	1st 23.6 $\pm$ 1.3 (32)	21 $\pm$ 2 (23)	23.9 $\pm$ 2.2 (11)	17.8 $\pm$ 6.2 (3)	60.3 $\pm$ 10.0 (6)	64.2 $\pm$ 13 (4)
	2nd+ 29.4 $\pm$ 3.5 (11)	22.5 $\pm$ 2.9 (13)	21.3 $\pm$ 6.7 (2)	21.4 $\pm$ 4.1 (5)	57 (1)	43 (1)
Respiratory frequency 1 s before submersion ( $\text{min}^{-1}$ )	1st 48.2 $\pm$ 1.5 (39)	57 $\pm$ 4 (24)	43.3 $\pm$ 3.4 (11)	68 $\pm$ 6.7 (3)	98.7 $\pm$ 13.9 (6)	79 $\pm$ 9.7 (4)
	2nd+ 55.6 $\pm$ 1.2 (98)	63.6 $\pm$ 2.3 (71)	71.5 $\pm$ 3.7 (35)	56.7 $\pm$ 4.4 (12)	102.8 $\pm$ 7.8 (14)	80.7 $\pm$ 6.1 (7)
Respiratory frequency 1 s after surfacing ( $\text{min}^{-1}$ )	1st 38.9 $\pm$ 2.2 (38)	39.4 $\pm$ 3.5 (24)	38.6 $\pm$ 4.1 (11)	38.5 $\pm$ 5.2 (3)	82.2 $\pm$ 8 (6)	64.2 $\pm$ 1.7 (4)
	2nd+ 44.9 $\pm$ 1.4 (98)	38.8 $\pm$ 1.6 (66)	54.5 $\pm$ 3.3 (35)	34.7 $\pm$ 6.6 (12)	91.1 $\pm$ 6 (14)	69.9 $\pm$ 4.5 (7)
Respiratory frequency 5 s after surfacing ( $\text{min}^{-1}$ )	1st 33.1 $\pm$ 2.2 (27)	26.9 $\pm$ 2.7 (13)	34.6 $\pm$ 4.5 (8)	31.1 $\pm$ 4.9 (2)	70.5 $\pm$ 16.9 (3)	60.7 $\pm$ 5.3 (3)
	2nd+ 34.1 $\pm$ 1.4 (54)	29.6 $\pm$ 1.3 (33)	42.7 $\pm$ 2.5 (28)	24 $\pm$ 3.4 (11)	65.4 $\pm$ 7.1 (5)	54.3 $\pm$ 5.7 (3)

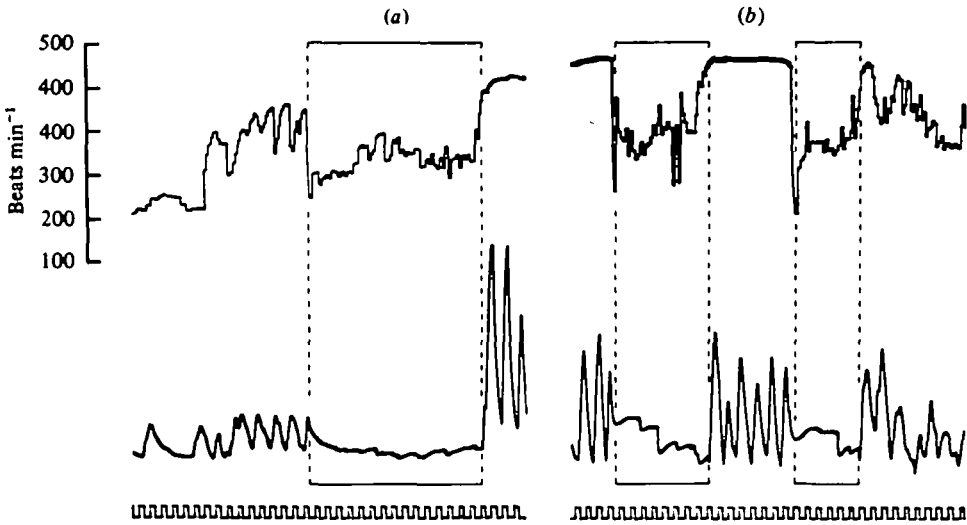


Fig. 6. Traces from ♀ pochard (0.73 kg) showing changes in heart rate and respiratory frequency associated with feeding dives. (a) First dive in a series, (b) last two (14th and 15th) dives in the same series. In each case the period of submersion is indicated by dashed, vertical lines joined by horizontal bars. In each set the traces are from above downwards: instantaneous heart rate, air flow through the trachea (inspiration-up on trace), time marker(s).

the tufteds, heart rate decreased on average by almost 460 beats  $\text{min}^{-1}$ . Within a second of submersion, heart rate had increased above the low, initial value, and then rapidly decreased again. This new level was maintained throughout the duration of the dive until just before surfacing (Figs. 7, 8). Thus, there was not the gradual increase in heart rate during the first 6–8 s of a dive as was seen in spontaneous and feeding dives. There was, however, quite often a definite increase in heart rate just before lung ventilation commenced at the end of a dive. This is clearly seen in Fig. 8. During the dive shown, the heart rate began to increase approximately 5.5 s after the duck had submerged. By 7 s after submersion, heart rate was about 500 beats  $\text{min}^{-1}$  and the bird had just begun to breathe out but saw the net above the water and submerged again. The heart rate fell immediately upon re-submersion. A similar anticipatory increase in heart rate was apparent just before the bird did eventually surface and ventilate its lungs completely. On average, for the escape dives, heart rate began to increase  $0.9 \pm 0.09$  (19) s before surfacing in pochards and  $0.92 \pm 0.14$  (11) s before surfacing in tufted ducks.

In the tufted ducks respiratory frequency, like heart rate, was consistently high when the birds were above water and being chased. In the pochards, however, especially for the first dives of a series when there was sufficient recording time before a dive, respiratory frequency still showed a significant further progressive increase before submersion (Table 2). The average duration of the escape dives was not significantly different from that of the spontaneous dives, for both species (Table 2). A feature of escape dives was that the animals would often surface several metres from the place of submersion.

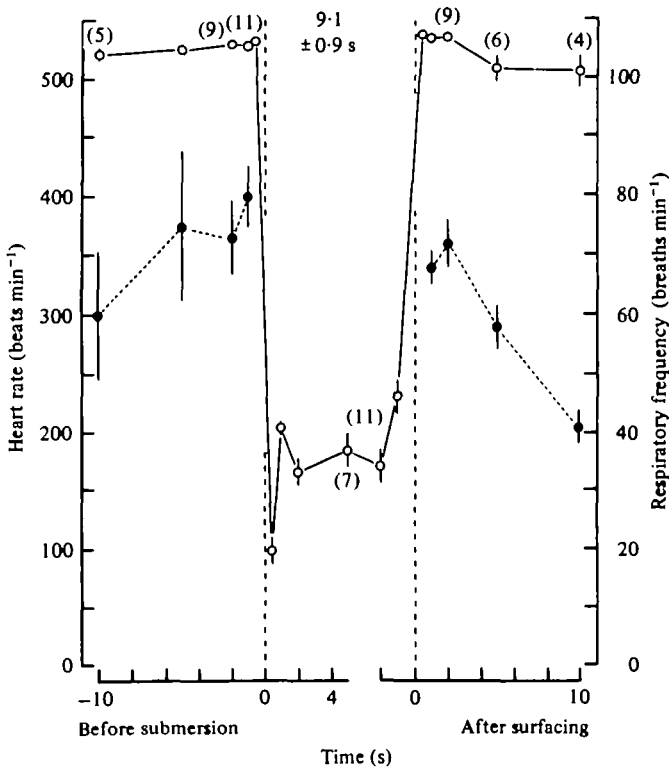


Fig. 7. Graph showing mean values of heart rate (○) and respiratory frequency (●) before, during and after all recorded induced escape dives of a series for tufted ducks. For remainder of caption see Fig. 2.

### Laboratory 'dives'

When the ducks were lightly restrained ventral side down in the laboratory, heart rate, at  $115 \pm 4$  (7) beats  $\text{min}^{-1}$ , was similar in the pochards to those values recorded in the free range animals when they were asleep on land or drifting on the water. In the tufteds, resting heart rate in the laboratory was  $110 \pm 1$  (3) beats  $\text{min}^{-1}$ .

The changes in heart rate and respiratory frequency associated with head submersion in the laboratory were completely different from those seen in association with natural dives for both species of birds. There were no significant increases in either of the variables just before head submersion, neither was there an immediate reduction in heart rate upon submersion. Instead, heart rate decreased progressively, during the first 10 s when it reached a level that was maintained for at least the next 10 s. This heart rate was  $54 \pm 10$  (7) beats  $\text{min}^{-1}$  for pochards and  $22 \pm 1$  (3) beats  $\text{min}^{-1}$  for tufteds. These values are significantly lower on average than the mean lowest rate recorded during any of the natural dives. For 'dives' of 60 s duration, heart rate eventually reached a value of  $25 \pm 2$  (3) beats  $\text{min}^{-1}$  in the pochards which is significantly lower than the value at the end of the 'dives' of 10 s or 20 s duration. In the tufted ducks, heart rate at the end of the 60 s 'dives' was not significantly lower than it was at the end of the 20 s 'dives'. The increases in heart rate upon

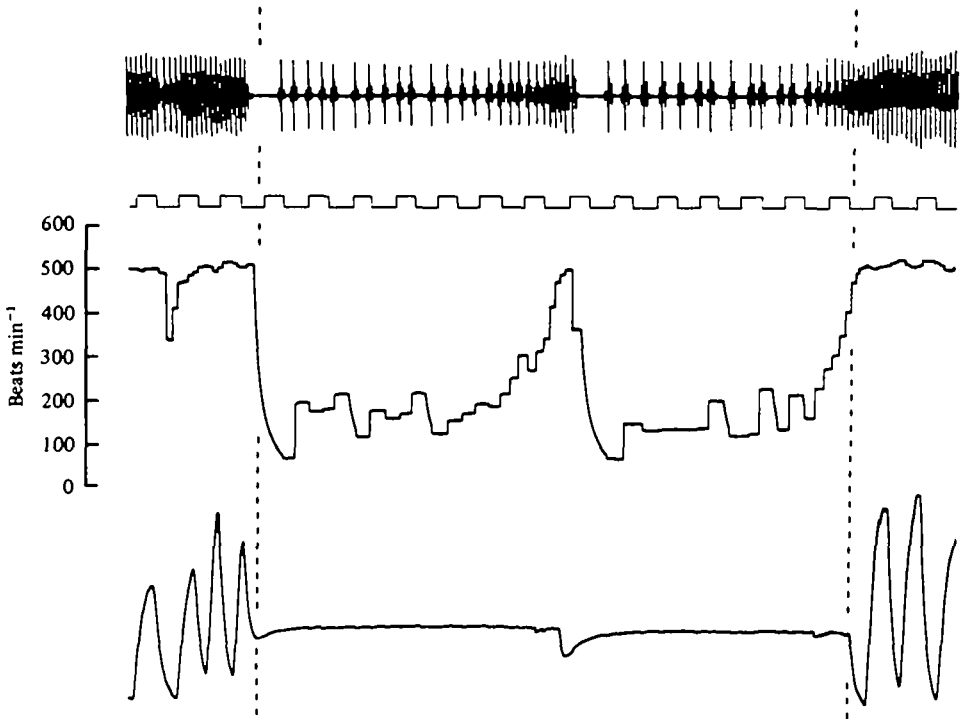


Fig. 8. Trace from ♂ tufted duck (0.75 kg) showing changes in heart rate and respiratory frequency associated with an induced escape dive. The period of submersion is between the vertical dashed line. The traces are from above downwards: e.c.g., time marker(s) instantaneous heat rate, air flow through the trachea (inspiration-up on trace).

emersion of the head into air was greater for longer periods of submersion in the pochard (not enough 'dives' were performed for a similar comparison in the tufted ducks), and this post 'dive' tachycardia was significantly greater in the tufted ducks than in the pochards for 'dives' of equal duration.

#### DISCUSSION

The significance of the present observations depends to a large extent on any effects that the presence of the telemetry system may have had on the animals' behaviour and physiology. Apart from the preening of the feathers around the area where the transmitter was inserted during the first 2 weeks following the operation, there were no signs of differences in behaviour after implantation of the transmitter. This is in contrast with earlier experiments involving transmitters in a backpack which was held in place by a harness. In this case, the birds pecked at the straps of the harness, in most cases until the straps eventually broke (Butler & Woakes, 1976*b*). The duration of the natural dives was similar to what would be expected on the basis of the relationship between the depth of water and dive length (Dewar, 1924). The observations on the three additional birds (see Materials and Methods), indicate that the thermistor in the trachea and the subcutaneous leads to it, the implanted

transmitter, the areas denuded of feathers and the slight loss of body mass during the first two weeks after the operation, did not appear to affect the cardiac response of the birds to natural diving. Unfortunately it was not possible to do similar checks on the effect of the thermistor probe on respiratory activity, although Butler, West & Jones (1977) found that a similarly placed thermocouple had no noticeable effect on lung ventilation of pigeons in the short term.

The two species of diving duck studied show essentially similar cardiac responses to natural diving and these are substantially different from those seen during head submersion in the laboratory. There are probably psychological and physiological factors involved in these differences. The tachypnoea and tachycardia which precede spontaneous dives may be taken as indications that the birds anticipate their diving behaviour. These anticipatory adjustments may serve to load the animal with oxygen by increasing the oxygen tension in the air sacs and in the venous blood. The slight exhalation upon diving may serve to reduce the buoyancy of the animal which in terms of its energy budget may more than offset the loss of oxygen in the exhaled air. The instantaneous reduction in heart rate upon submersion, which may precede cessation of ventilation (Butler & Woakes, 1976*b*), is more than likely elicited by higher centres of the brain. It is extremely unlikely that the hypothalamic area (area A) which was electrically stimulated by Folkow & Rubinstein (1965) is involved in this response as these authors described a slight initial decrease in heart rate followed by a progressively more intense bradycardia. There was no instantaneous reduction in heart rate associated with 'dabbling' or 'head ducking' manoeuvres, so that it was not likely to be the result of a postural reflex or of sudden changes in pressure in some part of the cardiovascular system. Also, the absence of a dramatic reduction in heart rate during these two manoeuvres and the fact that heart rate did not decline so rapidly during head submersion in the laboratory as it did during natural dives would suggest that unlike the situation in seals (Daly, Elsner & Angell-James, 1977), stimulation of branches of the trigeminal nerve does not make any significant contribution to the instantaneous bradycardia at the beginning of natural dives. There was no reduction in the initial bradycardia upon submersion during the later spontaneous dives in the series; there was thus no habituation of the initial cardiac response to diving. This argues against the idea that the response to natural dives is similar to the orienting reflex (Goodman & Weinberger, 1970).

The significance of the early, large reduction in heart rate is unclear. There was no relationship between the duration of submersion and this initial bradycardia, which was followed by a gradual increase in heart rate during the first 6–8 s of spontaneous and feeding dives. The rate of increase in heart rate declined markedly after the first 6–8 s of a spontaneous dive and it is tempting to propose that in deeper water, where the duration of dives would be longer (Dewar, 1924), the picture would be similar, with the stable heart rate merely continuing until the animal surfaced. From the present observations there is no evidence to support the notion that dive length in ducks is related to the heart rate established early in the dive (cf. Jones *et al.* 1973). Nevertheless it is conceivable that the initial bradycardia and subsequent progressive increase in heart rate may be related to the time taken to reach the bottom of the body of water and to the effort involved in this activity as these will both



increase as the depth of water increases, and as the former is thought to be more or less constant for a given depth (Dewar, 1924). The intensity of the bradycardia at the beginning of the dive and the level of the steady heart rate during the later stages of submersion, both seem to be related to the pre-dive heart rate. The presentation of food caused large increases in heart rate when the birds were on water as it did when they were on land, and a heart rate was consistently higher throughout all stages of the feeding dives compared with the spontaneous dives.

The main physiological difference between natural dives and head submersion in the laboratory, is the fact that the birds were active during the former. The settled heart rate during all dives was not substantially different from that recorded when the birds were swimming relatively quickly on the surface of the water. It has been stated that the bradycardia associated with natural submersion in seals 'probably also reflects the initiation of the redistribution in blood flow' (Jones *et al.* 1973). Whether or not the obverse is true in ducks, i.e. that the absence of a reduction in heart rate below that seen during swimming may be indicative of a lack of redistribution of blood, remains to be seen. For spontaneous dives up to a duration of 25 s at least, the classical idea of selective redistribution of blood accompanying bradycardia and reduction in cardiac output must be viewed with caution. On the other hand, the high values of heart rate and respiratory frequency when the birds were being chased, were no doubt indicative of high values of cardiac output as the birds swam and flapped their wings in efforts to escape. Upon submersion the immediate reduction in heart rate was dramatic, and during these dives this bradycardia was doubtless accompanied by a reduction in cardiac output and may well have reflected a redistribution of blood flow, away from the then inactive flight muscles.

Millard, Johansen & Milson (1973) reported that penguins, like seals (Jones *et al.* 1973), showed anticipatory increases in heart rate before the first ventilatory effort upon emersion. The only time that this was consistently seen in the ducks used in the present observations, was at the end of escape dives, although it was apparent at the end of some feeding dives. Ducks do, then, show all of the cardiac responses to natural submersion that have been described in seals. They anticipate the dive, and the cardiac slowing may precede cessation of lung ventilation, there is an instantaneous reduction in heart rate and under certain circumstances there is a clear increase in heart rate before ventilation begins upon surfacing. Heart rate does not, however, stabilize at the low values that have been recorded in free diving seals (Elsner, 1969; Jones *et al.* 1973) and there may not be in ducks, therefore, the massive reduction in cardiac output that accompanies the bradycardia in seals (Elsner, 1969). Perhaps this is not surprising, as seals stay under water for much longer periods of time than ducks.

The carotid bodies are responsible for approximately 85% of the reduction in heart rate that is seen in ducks during head submersion in the laboratory (Jones & Purves, 1970). It would be interesting to see whether these sense organs are at all responsible for reducing heart rate during natural dives. If there are any substantial changes in blood gas tensions during the longer spontaneous dives, towards the end of a series of dives or during escape dives, then asphyxic stimulation of the carotid bodies may play an important role in maintaining some degree of cardio-inhibition

during the later stages of these dives (cf. Daly *et al.* 1977). If asphyxic stimulation of the carotid bodies does occur, then central inhibition of the respiratory drive from such stimulation via receptors in the upper respiratory tract (Butler & Jones, 1968; Bamford & Jones, 1974; Blix *et al.* 1976) may also be important.

This work was supported by the Science Research Council. The authors wish to express their thanks to the Wildfowl Trust, Slimbridge, for supplying the animals.

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