

## THE CONTRIBUTION OF NASAL RECEPTORS TO THE CARDIAC RESPONSE TO DIVING IN RESTRAINED AND UNRESTRAINED REDHEAD DUCKS (*AYTHYA AMERICANA*)

BY R. A. FURILLA AND DAVID R. JONES

*Department of Zoology, 6270 University Blvd, University of British Columbia,  
Vancouver, BC V6T 2A9, Canada*

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### SUMMARY

In restrained redhead ducks, forced submergence caused heart rate to fall from  $100 \pm 3$  beats  $\text{min}^{-1}$  (mean  $\pm$  S.E.M.,  $N = 12$ ) to a stable underwater rate of  $35 \pm 4$  beats  $\text{min}^{-1}$  ( $N = 12$ ) within 5 s after submergence. Bradycardia was unaffected by breathing oxygen before a dive, but was virtually eliminated by local anaesthesia of the narial region. In contrast, in a dabbling duck (*Anas platyrhynchos*) bradycardia in short dives was eliminated by breathing oxygen before a dive. In unrestrained diving, on a man-made pond, heart rate in redheads diving voluntarily ( $y$ ) was related to pre-dive heart rate ( $x$ ) by the equation  $y = 76 + 0.29 \pm 0.05x \pm 17$  ( $r^2 = 0.71$ ). Chasing, to induce submergence, had variable effects on this relationship. Local anaesthesia of the narial region inhibited voluntary diving but heart rates in chase-induced dives after nasal blockade were significantly higher, by 10–30%, than those obtained from untreated ducks in chase-induced dives. Breathing oxygen before voluntary dives had no apparent effect on heart rate after 2–5 s submergence. Voluntary head submersion by dabbling ducks caused no change in heart rate. We conclude that nasal receptors make only a minor contribution to cardiac responses in unrestrained dives, compared with forced dives, in diving ducks. Furthermore, these results show that little can be learned about cardiac responses in free diving ducks from studies of forced dives in dabblers or divers.

### INTRODUCTION

The cardiac response to diving shown by diving ducks submerging voluntarily is very different from that obtained by forcing the same ducks to dive in the laboratory (Butler & Woakes, 1979, 1982*a,b*). In voluntary diving, heart rate increases before the first dive in a series, and on or just before submersion there is a transient bradycardia. Heart rate then increases in the first few seconds of the dive to a steady rate, which is often quite similar to that obtained in ducks resting quietly on the surface (Butler & Woakes, 1979, 1982*a*). This contrasts with forced dives, in which heart rate falls progressively, usually to very low levels (Butler & Woakes, 1976, 1979, 1982*b*). The rapidity of the fall in heart rate, however, varies in divers and dabblers. In dabbling ducks, heart rate falls by 50% about 25–30 s after head

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submersion (Butler & Jones, 1968; Mangalam & Jones, 1984), while in divers heart rate usually falls much faster. Heart rate halves in pochards (*A. ferina*) and falls by 80 % of pre-dive levels in tufted ducks (*A. fuligula*) within 10 s of submersion (Butler & Woakes, 1979, 1982b).

These results suggest that the basic mechanisms initiating diving bradycardia in dabbling and diving ducks are different (Butler & Jones, 1982). Most of the bradycardia in response to forced submergence in dabbling ducks is prevented by denervating the carotid bodies (Jones & Purves, 1970; Lillo & Jones, 1982), yet this is not the case in divers (Butler & Woakes, 1982b). An 'immersion reflex' has been suggested to play an important role in divers, although its existence has never been unequivocally demonstrated in birds (Butler & Woakes, 1982a; Mangalam & Jones, 1984). On the other hand, 'immersion reflexes' have also been assumed to play a role in the development of bradycardia in forced-dived dabblers (Blix & Folkow, 1984), especially when pre-dive heart rate is high (Jones & Butler, 1982). Obviously, the mechanisms that predominate in causing bradycardia in diving and dabbling ducks need to be differentiated because, if these are different, it will certainly call into question the validity of using data from dabblers to explain observations in divers (Blix, 1985). A problem also exists as to how much the 'immersion reflexes' contribute to the response in free dives. Gabrielsen (1985) found only slight cardiac changes associated with voluntary head submersion in the dabbling duck (*Anas platyrhynchos*), while Butler & Woakes (1982a) have shown that in diving ducks, submerging voluntarily, the cardiac adjustment actually anticipates submergence. Hence, we decided to investigate the nature of 'immersion reflexes' principally in divers, but also in dabbling ducks, and have attempted to measure the contribution of these reflexes to the cardiac response in both restrained and free dives.

#### MATERIALS AND METHODS

Six redhead ducks (*Aythya americana*) of both sexes were used to test the role of nasal receptors in the initiation of the diving response. Heart rate was monitored using needle electrodes placed subcutaneously on the left side of the abdomen and the right shoulder. The ducks were forcibly submerged by gently lowering the head into a container of water. This manoeuvre was done carefully to prevent the animals struggling on submersion. Each duck was submerged three times, and a mean heart rate response was calculated for that animal. Xylocaine (Lidocaine USP, Astra Pharmaceuticals Canada Ltd, Mississauga, Ontario) in aerosol form was administered into the nares for local anaesthesia of nasal receptors. To minimize the possibility of anaesthetizing the glottis, loosely packed cotton wool was placed over the glottis to shield it from the spray. A slip of the cotton protruded out of the corner of the mouth, and the beak was taped closed to prevent the duck swallowing the cotton. Fifteen minutes after Xylocaine application the cotton wool was removed and another 5 min allowed before the first of a series of three dives on each animal was performed. Two hours later, after recovery from the application of Xylocaine, the birds were again tested for a diving response.

Another six redhead ducks were tested to determine the effect of high arterial oxygen tension on the initiation of the diving response. A plastic bag was placed over the duck's head, and either air or 100% oxygen was passed through the bag for at least 3 min before the animal was submerged. As above, three dives per animal for each condition were recorded. These data were compared with heart rates in forced dives by one Pekin duck (*A. platyrhynchos*) performed after breathing air or oxygen before the dive.

Heart rate was determined from the cardiac interval taken at 1, 2, 5, 10 and 15 s in the dive. Dive duration was varied to minimize the effect of conditioning (Gabbott & Jones, 1985), but all dives lasted at least 15 s. The data were analysed using analysis of variance, and significance was set at  $P < 0.05$ . All values from this series of experiments are given as means  $\pm$  S.E.M. and  $N$  is the number of animals contributing to the mean.

To test the response to voluntary diving, ECG transmitters (FM-1100-E3 & E2, Narco Scientific Ltd, Downsview, Ontario) were implanted in the peritoneal cavity of three dabbling ducks (two mallards and one Pekin) and five diving ducks (two male, three female, redhead). Bipolar loop electrodes were placed on the pericardium, and the peritoneal cavity was closed with surgical silk. All surgery was performed under local anaesthesia. Following the surgery, 125 mg of Ampicillin was administered and the birds were allowed 1 day to recover before being placed on the pond. The dabbling ducks were placed on a pond 20 cm deep while the diving ducks were placed on a pond deep enough to allow them to dive for food. This pond was man-made and had a surface area of  $3 \times 5.5$  m. The bottom of the pond sloped so that the depth of the water ranged from 0.3 to 1.7 m. A platform ( $2.0 \times 1.5$  m) and a Plexiglas enclosure ( $1.0 \times 1.5 \times 0.8$  m high) were placed at the shallow end of the pond. The enclosure had a vertically sliding door to seal it sufficiently so that oxygen levels in the enclosure could be altered. The surface of the water outside the enclosure was covered with netting stretched over wooden frames. Each frame was  $1 \text{ m}^2$ . The frames floated on the water and were to prevent the birds from surfacing anywhere but within the enclosure. However, the birds could lift the netting to take a breath if it became necessary. At the corner of the pond farthest from the enclosure was a feeding station with a chute through which food could be dropped into a receptacle at the bottom. Nitrogen or oxygen was infused ( $20 \text{ l min}^{-1}$ ) into one side of the enclosure and exited from the opposite side. A fan was mounted inside the box to mix the air. Gas from the box was led to a Beckman  $F_3$  paramagnetic oxygen analyser which was calibrated with precision gas mixtures. The 50% level of oxygen was estimated from flow rate and enclosure volume and should not be taken as precise. The value does, however, represent a high concentration of inspired oxygen.

Most voluntary dives occurred in the period after food was delivered into the feeding chute. To reduce the sympathetic contribution to the increase in heart rate before a voluntary dive,  $1.5 \text{ mg kg}^{-1}$  of propranolol was injected into the muscles of three redhead ducks, and the animals were returned to the pond immediately. Xylocaine blockage of the nasal area was performed as described for restrained animals, and a short, forced dive was done to confirm the efficacy of the blockade

before the animals were put back onto the pond. Ducks were reluctant to dive after their nasal area had been blocked with Xylocaine. So few voluntary dives were obtained that we had to resort to chasing the birds to make them submerge (Butler & Woakes, 1979). Usually we did this by banging on the lid of the enclosure with a stick or wagging a net at them.

Heart rate data were received on an FM-1100-7 biotelemetry receiver (E & M Instrument Co. Inc., Houston, Texas, USA), stored on magnetic tape and displayed on a pen recorder. For unrestrained dives, pre-dive heart rate was determined from the last second before the dive, and dive heart rate was taken from the point at which the heart rate stabilized, but not later than 5 s after submergence. Data were analysed by plotting the relationship between pre-dive heart rate and the mean heart rate which occurred in the first 2–5 s of diving, and performing a linear regression on the data. The significance of any difference (at  $P < 0.05$ ) between data from chase-induced dives by untreated and Xylocaine-blocked ducks was assessed from the statistics for linear regressions on both sets of data. In this series of experiments,  $n$  is the number of observations and  $N$  is the number of animals.

## RESULTS

### *Effect of anaesthetization of the nares, or breathing oxygen, on the cardiac response to submergence in restrained ducks*

Heart rate of restrained redhead ducks in the laboratory was between 90 and 110 beats  $\text{min}^{-1}$  ( $100 \pm 3$  beats  $\text{min}^{-1}$ ;  $N = 12$ ). On submergence, heart rate fell rapidly and progressively to a stable rate of  $35 \pm 4$  beats  $\text{min}^{-1}$  ( $N = 12$ ) within 5 s (Fig. 1A,B). The cardiac response to forced diving in dabbling and diving ducks is compared in Fig. 2. Bradycardia developed slowly in the dabbler, *Anas platyrhynchos*, and was prevented by allowing the duck to breath oxygen before the dive (Fig. 2A). These observations have been noted by others, most recently by Mangalam & Jones (1984). In contrast in the diver, *Aythya americana*, bradycardia occurred rapidly (Fig. 2B) and was unaffected by breathing oxygen before the dive (Fig. 1A). Application of Xylocaine to the narial region virtually eliminated diving bradycardia in redhead ducks (Figs 1B, 2B). After Xylocaine, heart rate fell to only 80% of the pre-dive rate 15 s after submersion (Fig. 1B).

### *Effect of anaesthetization of the nares, or breathing oxygen, on the cardiac response to voluntary submergence in unrestrained ducks*

As reported previously by Butler & Woakes (1979), we also found that heart rate rose before the first dive in a series, to at least 300 beats  $\text{min}^{-1}$ , and continued to increase in the brief recovery periods between dives so that after five or 10 dives, pre-dive heart rate approached 500 beats  $\text{min}^{-1}$ . Heart rate fell markedly on or just before submergence and then rose to a stable rate which was obtained after 2–5 s under water (Fig. 3A). In contrast, dabbling ducks (*Anas platyrhynchos*) showed little change in heart rate before or during voluntary head submergence (Fig. 3C). This confirmed the recently reported observation of Gabrielsen (1985).

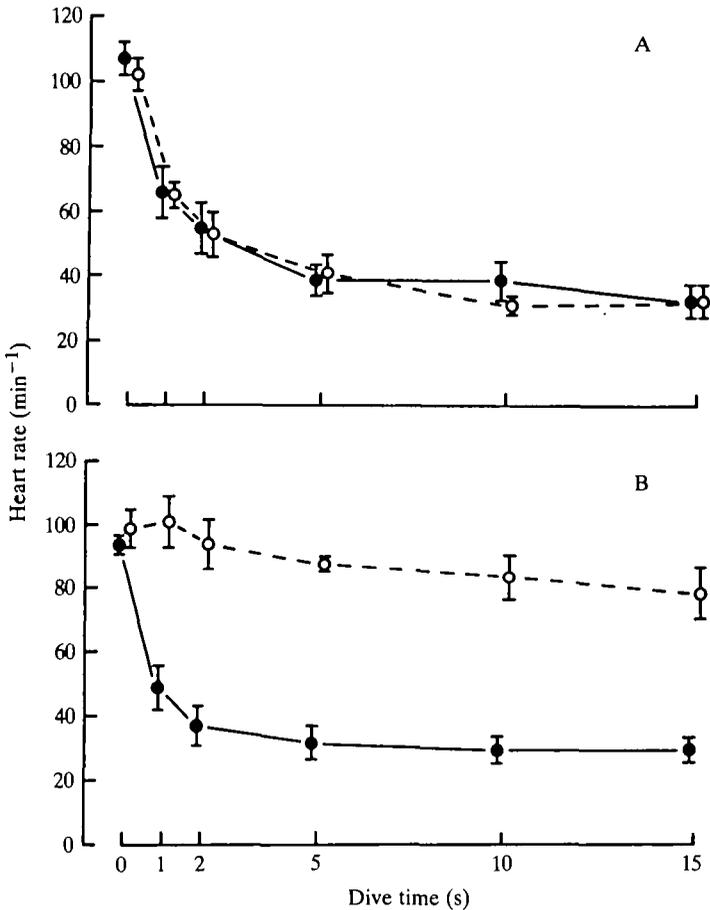


Fig. 1. Heart rate response to submersion in diving ducks (mean  $\pm$  1 S.E.M.). (A) Response of animals breathing oxygen (○) or air (●) before submersion,  $N = 6$ . (B) Response of animals after nasal anaesthetization (○) compared with untreated animals (●). These animals were breathing room air before submersion,  $N = 6$ .

Heart rate, during the first 2–5 s of diving, in voluntary dives was positively correlated ( $r^2 = 0.71$ ) with pre-dive rate, and  $\beta$ -blockade with propranolol did not appear to affect the relationship (Fig. 4A). In chase-induced dives, the length of the first cardiac interval was highly variable (Fig. 3B). In contrast, in voluntary diving the cardiac interval occurring on or just before submersion was nearly always the longest (Fig. 3A). In one duck, chasing had no apparent effect on dive heart rates compared with those in voluntary dives. In another duck, however, chasing caused a more pronounced fall in heart rate than in voluntary dives. Dive heart rates after chasing were some 10% below those in voluntary dives and this difference was significant. The regression lines describing the relationship between dive and pre-dive heart rates in chased-induced dives, in three ducks, were compared with those obtained from the same animals after blockade of the nasal area with Xylocaine (Fig. 4B). In all three cases, the elevations but not the slopes of these regression lines

were significantly different, with the heart rates from Xylocaine-treated ducks being above those from untreated animals (Fig. 4B). In the duck shown in Fig. 4B, dive heart rate was elevated after Xylocaine blockade by 15–30%, depending on the pre-dive heart rate. In contrast, in another duck the elevation in dive heart rate was 10%, regardless of pre-dive heart rate. The third duck showed an elevation in heart rate of 20–25% over a much more restricted range of pre-dive heart rates. A few voluntary dives were obtained from two of the ducks, after nasal blockade, and these indicated a similar degree of elevation in dive heart rate, compared with voluntary dives before nasal blockade, to that obtained in chase-induced dives.

Changing the level of oxygen in the air breathed before diving affected voluntary dive duration (Fig. 5A) but had no effect on heart rate after 2–5 s submergence (Fig. 5B). Dive duration increased as the concentration of oxygen in the inspired air increased. The increase appeared to be linear at oxygen levels between 10 and 15% with a correlation coefficient ( $r^2$ ) of 0.98 (Fig. 5A). At oxygen levels below 10% all diving ceased even if food was withheld for 1 day before the trial. At oxygen levels above 15% dive time increased more slowly with an increase in oxygen concentration (Fig. 5A). However, no correlation occurred between the dive heart rate and the level of oxygen breathed before the dive. Dive heart rates after breathing 50%

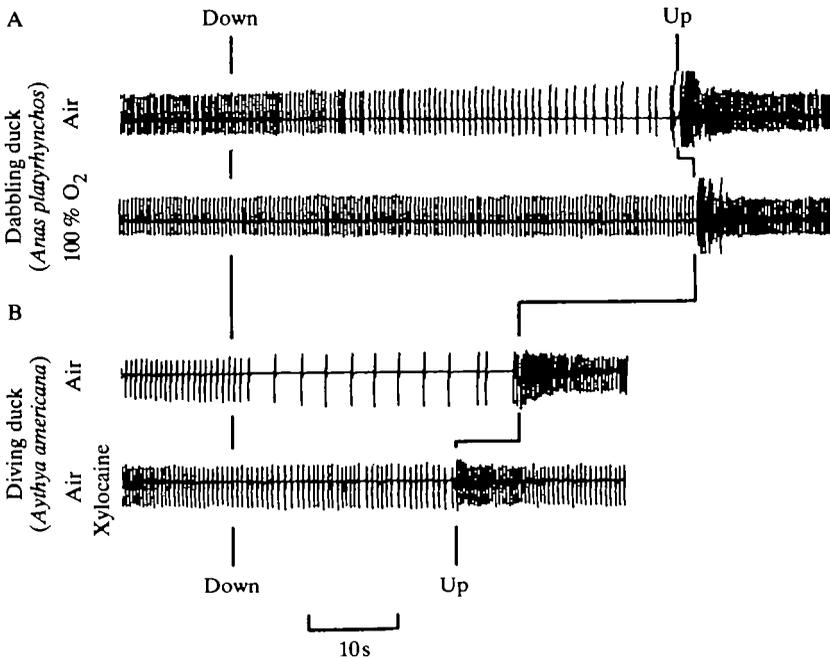


Fig. 2. Traces showing heart rates of restrained ducks before, during, and after forced submergence. (A) A dabbling duck having breathed air (upper trace) and oxygen (lower trace) before submergence. (B) A diving duck having breathed air before submergence (upper trace). The lower trace shows the cardiac response to submergence after the application of Xylocaine to the nares. 'Down' refers to the time at which the beak entered the water and 'up' refers to the time when the animal surfaced.

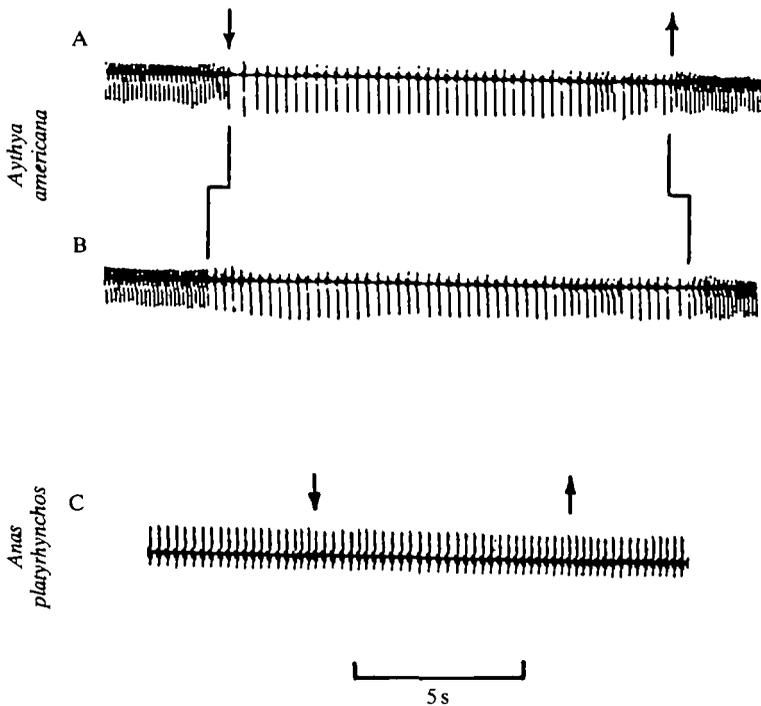


Fig. 3. ECG trace obtained from unrestrained ducks submerging voluntarily. (A) A diving duck diving voluntarily, (B) a chase-induced dive and (C) a dabbling duck dabbling voluntarily. The downward pointing arrow indicates the approximate time at which the beak entered the water, and the arrow pointing up indicates the approximate time the animal surfaced.

oxygen were in the same range as those obtained after breathing air or 13–16% oxygen (Fig. 5B).

#### DISCUSSION

The present results have shown that redhead ducks differ from mallards or Pekin ducks in the mechanism by which bradycardia is initiated during enforced submersion. Mallards and Pekin ducks show a gradual slowing of the heart, with the lowest rates being reached after 30 s or so of submergence (Butler & Jones, 1968). Mangalam & Jones (1984) and Jones, Milsom & Gabbott (1982) showed that breathing 100% oxygen before a dive greatly reduced the cardiac response to enforced submergence of the Pekin duck, and this was confirmed in the present study. When pre-dive heart rate is lower than 150–190 beats  $\text{min}^{-1}$ , virtually all of the bradycardia in dabblers during forced dives results from stimulation of peripheral arterial chemoreceptors (Jones & Purves, 1970; Jones *et al.* 1982). In our divers, however, heart rate fell immediately on forcible submergence, and giving the duck 100% oxygen to breathe before submergence had no effect on the bradycardia in the first 15 s of the dive. This was not unexpected because Butler & Woakes

(1982*b*) had shown that carotid body denervation did not alter the onset of bradycardia in tufted ducks.

Anaesthetization of the narial region in our diving ducks completely eliminated diving bradycardia in forced dives, performed with care. Diving mammals, such as seals and muskrats, also show a rapid heart rate response to forced diving which is eliminated by neurotomy or anaesthesia of the facial and/or narial region (Dykes, 1974; Drummond & Jones, 1979). Hence, it appears that rapid bradycardia in forced dives is likely to be associated with a 'nasal reflex' (Jones, 1981). Nevertheless, an immersion reflex has been claimed to exist in dabbling ducks, which is more obvious

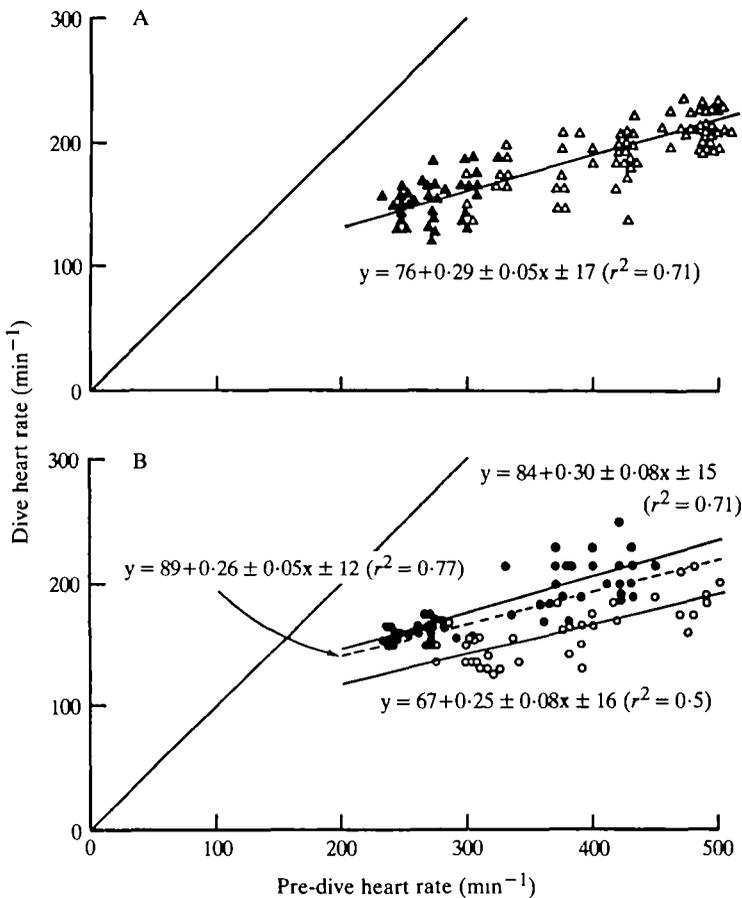


Fig. 4. Relationship between pre-dive and dive heart rate in dives by unrestrained ducks. The line passing through the origin represents equal pre-dive and dive heart rates. (A) Combined data from five ducks diving voluntarily: ▲, β-blocked with propranolol; △, untreated. (B) Data from chase-induced dives by a single female redhead: ●, after local anaesthesia of the nares; ○, untreated. Data for propranolol-blocked dives for this duck are not identified by use of a separate symbol but are included in the regression analysis. The broken line is the regression line for voluntary dives by this animal with no nasal blockade. The regression equations include the 95% confidence limits of the slope and the standard error of estimate.

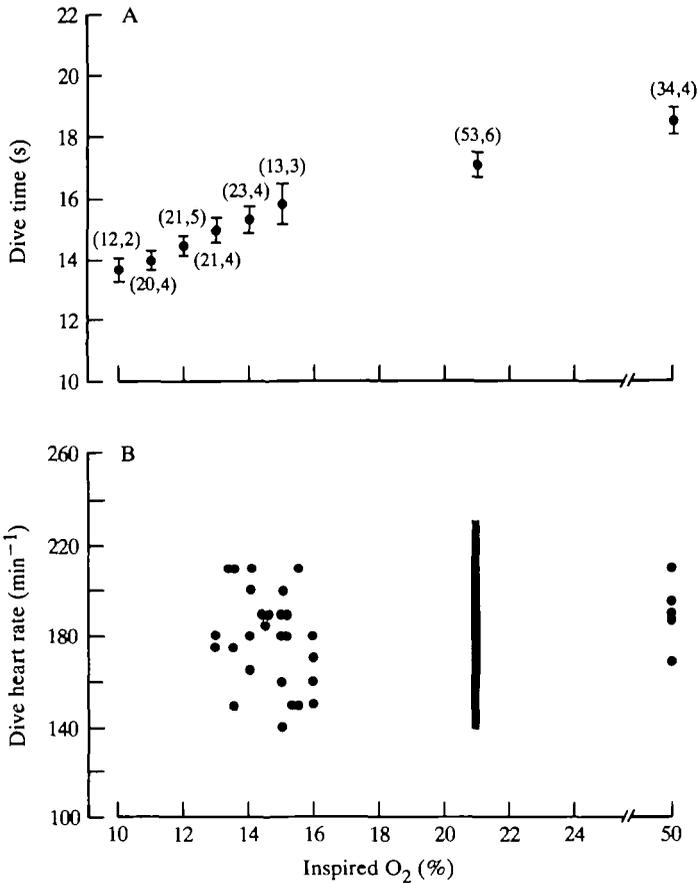


Fig. 5. (A) Relationship between inspired oxygen and dive time in voluntary dives. The numbers in parentheses above or below the points are  $n$  and  $N$ . (B) The range of heart rates obtained between 2 and 5 s into voluntary dives when the animals breathed air, low or high oxygen concentrations before diving. The bar at 21 % oxygen represents the range of heart rates of 42 dives from five ducks with the greatest density of points occurring at 190 beats  $\text{min}^{-1}$ .

the higher the pre-dive heart rate (Andersen, 1963*a,b,c*; Feigl & Folkow, 1963; Folkow, Nilsson & Yonce, 1967; Rey, 1971; Butler & Jones, 1982; Blix & Folkow, 1984; Blix, 1985). However, Jones *et al.* (1982) suggested that any initial rapid heart rate decline in dabblers may not necessarily mirror a similar change in cardiac output. In fact, cardiac output is most likely to be unchanged in this period. Furthermore, they also showed that there was a strong relationship between any change in heart rate in the first few seconds of submergence ( $y$ ) and the pre-dive heart rate ( $x$ ). The relationship was expressed by the formula  $y = x - 188$  for pre-dive heart rates above 188 beats  $\text{min}^{-1}$ , so if pre-dive heart rate was below 188 beats  $\text{min}^{-1}$  there was no change in heart rate early in the dive. As an adjunct to the present experiments we have analysed more data than were used in those experiments, now covering a much wider range of pre-dive heart rates, and find the relationship is altered somewhat. The present regression equation is  $y = 1.01x - 146$  for pre-dive

heart rates above  $146 \text{ beats min}^{-1}$ , which explains why no trace of an 'immersion reflex' was observed when we forced our present Pekin duck to dive because pre-dive heart rate was always less than  $146 \text{ beats min}^{-1}$ . This or a similar relationship also appears to apply to the Canada goose during voluntary dabbles (Kanwisher, Gabrielsen & Kanwisher, 1981). Heart rate fell rapidly, from rates in the range of  $230\text{--}290 \text{ beats min}^{-1}$  before submergence, to a rate in the range of  $140\text{--}150 \text{ beats min}^{-1}$  upon submersion. Therefore, when heart rates are very high, the potential exists for rapid cardiac adjustments on submergence even though a specific 'immersion reflex' may not have been shown to exist.

Our dabblers, submerging their heads voluntarily, had low pre-dive heart rates and it is not surprising that there were no changes in heart rate since arterial chemoreceptors predominate in causing the dive response. Obviously, the short submersions were not sufficient to reduce blood oxygen or elevate blood carbon dioxide enough to stimulate them. In contrast, diving ducks showed marked changes in heart rate during every voluntary and chase-induced dive even after breathing air with 50% oxygen in the pre-dive period. This confirms the observation of Butler & Woakes (1982*b*) that after carotid body denervation heart slowing in voluntary dives by tufted ducks was little changed from that of intact animals in the early part of submergence. That is not to say that in longer dives information from carotid bodies is ignored. Tufted ducks, with their carotid bodies denervated, have a mean dive duration 3 s longer than intact ducks, and a maximum dive time 6 s greater than that of intact animals (Butler & Woakes, 1982*b*). Furthermore, heart rate at the end of a dive is higher in ducks with denervated carotid bodies than in intact ducks (Butler & Woakes, 1982*b*).

In free dives, unlike the situation in restrained dives, nasal blockade with Xylocaine did not have a great effect on heart rate after 2–5 s submergence. Stimulation of nasal receptors in free diving would appear to cause between 10 and 30% of the heart rate adjustment. Heart rate fell lower in chase-induced than voluntary dives in two of the three ducks investigated, but our results suggest that the contribution from nasal receptors is similar in both voluntary and chase-induced submersions. Furthermore, the heart rate data obtained in voluntary dives after breathing oxygen confirm that chemoreceptors do not make an important contribution to heart rate adjustments up to 5 s after submergence. Consequently, on present evidence, it appears that nasal receptors and chemoreceptors combined only account for a fairly minor component of the initial cardiac responses to voluntary submersion.

There is no doubt that in free dives, another input (or group of inputs) predominates in causing the cardiac responses and it is not displayed in forced dives. This is supported by claims of 'anticipation' of the dive response. Butler & Woakes' (1976) original claim for 'anticipation' was compromised somewhat by their earlier statement that 'the initial bradycardia occurs just as the animal dives and not before' (Woakes & Butler, 1975). However, more recent data, linking ciné films of submersion behaviour to telemetric recordings of heart rate, have shown conclusively that lengthening of the cardiac interval occurs before the nasal area contacts the water

(Butler & Woakes, 1982a). Obviously, the neural control of the cardiac response in free diving animals is a matter of considerable complexity and we can learn little about it from studies of restrained dives made by diving ducks, let alone dabblers.

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