CARDIAC RESPONSES TO DABBLING AND DIVING IN
THE MALLARD, ANAS PLATYRHYNCHOS

R. A. FURILLA2 AND DAVID R. JONES3

Department of Zoology, University of British Columbia, Vancouver, B.C. Canada V6T 2A9
(Accepted 12/22/86)

Mallards typically dabble for their food in shallow water. However, in the northern
climate, shallow ponds freeze in winter, and mallards may be forced to dive for food
in deep water. We have mimicked these feeding behaviors by confining mallards to
shallow (0.3 m deep) and deep (1.0 m) artificial ponds. Heart rate was monitored from
the ducks during these behaviors telemetrically. Dabbles lasted an average of 3.0 ± 1.0
s (±SD), with a maximum of 9 s, and heart rate changed little during head immersion.
Dives had a mean duration of 6.2 ± 2.1 s with a maximum of 11.6 s. Heart rate after
2-s submergence was nearly the same, at 250 beats·min⁻¹, regardless of predive heart
rate. In other words, if predive heart rate was low (<200 beats·min⁻¹), there was a
diving tachycardia; whereas, when predive heart rate was high (>300 beats·min⁻¹),
there was a noticeable diving bradycardia. This cardiac response to voluntary diving
was nearly eliminated by bilateral section of the vagal baroreceptor nerves. In true
diving ducks (Aythya sp.), heart rate after 2-s submergence is positively correlated with
heart rate in the immediate predive period, and this relation is unaffected by barore-
ceptor denervation. Obviously, mallards differ markedly from true diving ducks not
only in cardiac adjustments to diving but also in their control.

INTRODUCTION

Ducks are commonly divided into two
groups, divers and dabblers, but probably
all dabbling ducks dive when they are very
young, and even adult dabbling ducks dive
for food far more frequently than is gen-
erally acknowledged. Foraging dives by
mallards (Anas platyrhynchos), black ducks
(A. rubripes), African black ducks (A.
sparsa), pintails (A. acuta), Bahama pintails
(A. bahamensis), shovelers (Spatula cly-
peata), New Zealand brown ducks (A. auk-
landica chlorotis), gadwalls (A. strepera),
cape teal (A. capensis), gray teal (A. gibber-
ifrons), wood ducks (Aix sponsa), and
mandarin ducks (A. galericulata) have been
observed (Kutz 1940; Dean 1950; Mylne
1954; Chapman, King, and Webb 1959;
Kear and Johnsgard 1968; Bourget and
Chapdelaine 1982). Dives may be made to
depths greater than 3 m (Kutz 1940). Mean
dive times are approximately 5 s (Dean
1950; Bourget and Chapdelaine 1982), with
maximum dive times of 10 s (Chapman et
al. 1959; Bourget and Chapdelaine 1982).
Bourget and Chapdelaine (1982) suggested
that dabbling ducks spending the winter in
northerly regions may be forced to dive for
food because shallow water is more likely
to be frozen over during cold spells.

The heart rate response to forcible sub-
mergence of a restrained dabbling duck is
characterized by a gradual slowing of the
heart and an increase in peripheral resis-
tance (Butler and Jones 1982). This re-
sponse is virtually eliminated by sectioning
the carotid body nerve (Jones and Purves
1970), indicating that it is brought on by
the progressive hypoxemia and hypercap-
nemia associated with the breath-hold dive.
In contrast, in diving ducks such as the red-
head (Aythya americana), bradycardia de-
velops immediately on submergence and is
inhibited by spraying a local anesthetic over
the external and internal nares (Furilla and
Jones 1986). Hence nasal receptors, which
contribute only to apnea in dabbling ducks
(Bamford and Jones 1974), have an im-
portant cardiovascular influence in diving
ducks.

Although ducks can withstand many
minutes of forced submergence, in nature
most voluntary dabbles and dives are extremely short. Dabbles seldom exceed 5-s duration, and dives are usually less than 20 s. Voluntary head submersion by dabbling ducks causes little or no change in heart rate (Furilla and Jones 1986). This is not surprising, given that the periods of submersion are too short to cause sufficient changes in blood gas tensions to stimulate systemic chemoreceptors. On the other hand, heart rate changes would be expected in divers submerging voluntarily as soon as the nasal receptors contact water. While this appears to be the case, close correlation of heart rates broadcast from ducks by telemetry with cine films of diving behavior shows that, some seconds before the dive, both breathing and heart rates increase, and heart rate then falls just before rather than actually on submersion (Butler and Woakes 1979, 1982; Woakes and Butler 1983). The first cardiac interval in voluntary dives is usually the longest, and heart rate then rises to stabilize in the range of 100–200 beats·min⁻¹ within 2–5-s submersion (Furilla and Jones 1987). This is very different from the response in forced dives, when heart rate falls to about 20 beats·min⁻¹ in a similar time period (Furilla and Jones 1986).

It has been suggested that the predive hyperventilation and tachycardia are correlates of the high aerobic energy demands in voluntary dives in that these maneuvers serve to flush CO₂ from and load O₂ into the blood and pulmonary oxygen stores (Butler 1985). Butler (1985) has suggested that the high heart rates in voluntary dives are the expression of a balance between the cardiovascular responses to forced diving and to exercise in air, with the balance being tipped toward the exercise response. Consequently, what cardiac adjustments to diving would be expected in dabbling ducks that have been trained to make voluntary dives? This study was undertaken to investigate the nature of these cardiac adjustments in the dabbling duck (A. platyrhynchos) and the underlying mechanisms bringing about these adjustments.

MATERIAL AND METHODS

Two male mallards and one female Pekin duck (Anas platyrhynchos) were used to record the cardiac response to voluntary dabbling. Five mallards (two male and three female) were used in the voluntary diving observations. Heart rate was obtained telemetrically using EKG transmitters (Narco Biosystems, Downsview, Ont.). The transmitter was sterilized with benzalkonium chloride (Zephrin, 1:750, Winthrop Laboratories, Aurora, Ont.). A midline incision was made in the skin and body wall over the abdomen after anesthetizing the area by injection of Xylocaine. Bipolar loop electrodes were placed on the pericardium, and the transmitter was placed in the peritoneal cavity. The peritoneal cavity was then closed with surgical silk. After surgery, 125 mg of Ampicillin (Penbritin, Ayerst Laboratory, Montreal) was administered i.m., and the birds were allowed 1 day to recover before being placed on the pond.

For dabbling, the ducks were placed in a 0.8 (w) × 2.8 (e)-m fiberglass tank with water 0.3 m deep and a 0.8 × 0.8-m platform at one end. Only those dabbles lasting longer than 3 s were used in data analysis. This was done to ensure that the heart rate was not changing at the 2-s mark as the result of any activity associated with surfacing. The EKG signal was received on a Narco FM-Biotelemetry receiver, stored on magnetic tape, and simultaneously displayed on a pen recorder. On playback, heart rates were obtained either by measuring the cardiac intervals by hand or electronically by using a cardiotachometer.

For diving, the mallards were placed singly in a 0.8 (w) × 1.8 (e)-m fiberglass tank with water 1.0 m deep and with a 0.8 × 0.4-m platform at one end. Food was scattered on the surface and quickly sank. For the first week, the birds ate only that food that could be reached before it sank. If the bird did not dive after 1 wk, a small amount of food was placed on the platform daily. The amount of food was kept small to maintain the health of the animal while preserving the hunger drive. The duck was removed from the tank if diving had not begun by the end of the second week. The ducks’ behavior was recorded on a Canon VR-40 VHS video recorder using a JVC GX-N4 camera. Once diving had begun, an EKG transmitter was implanted, and the signal was placed on one of the audio tracks of the video recorder. The videotape was reviewed at high speed. When a dive was
observed, the tape was played at normal speed, and the audio signal was displayed on a pen recorder. Heart rate was obtained from the EKG using a cardiotachometer. Only those dives lasting longer than 4 s were used in data analysis so that heart rate at 2 s of the dive was unaffected by the activity of surfacing. The transmitters were removed after data collection.

A β-blocker with a long half-life was used to test the effect of sympathetic influences on the predive and dive heart rates. Nadolol (Corgard, Squibb Montreal), a nonselective β-blocker with a half-life of 24 h was used in preference to propanolol, which has a half-life of only 2 h (Gilman, Goodman, and Gilman 1980). Nadolol was administered orally to one mallard—4 mg on the first day followed by 2 mg daily for 2 additional days. This treatment was repeated using the same protocol about one week later. The β-blockade was judged to be effective because predive heart rate was usually less than 300 beats·min⁻¹.

Four mallards were used to study the effect of baroreceptor denervation on the cardiac response to voluntary diving. All surgery was performed under general anesthesia (20 mg·kg⁻¹ sodium pentobarbital, Somnotol, MTC Pharmaceuticals, Mississauga, Ont.). Entry to the thoracic cavity was gained through the interclavicular air sac. In three ducks the left baroreceptor nerve was sectioned approximately 1.5 cm distally from the nodose ganglion, and the right nerve was sectioned near the pulmonary vein at a point where the nerve turns ventrally and medially toward the heart. After denervation, the air sac was closed with surgical silk and the skin was sutured over the repaired air sac. The ducks were allowed 1 wk to recover and then placed on the diving tank. When diving resumed, the EKG transmitter was implanted, using the same procedure as for intact ducks. In one duck, the nerves were exposed during initial surgery and a loop of thread was placed around each nerve. One end of each thread was anchored to the skin high in the neck after the wound was closed. After heart rate data were collected for this condition (sham operated), the duck was again anesthetized, and the threads were slowly pulled through the wound sectioning the nerves. Hence, the duck acted as its own control for baroreceptor denervation. The duck was returned to the tank on the following day, and data collection started when diving resumed. Chronic barodenervation is usually accompanied by high heart rates (Jones et al. 1983), and Nadolol was used to reduce predive heart rates in this group.

The effectiveness of denervation was tested by injecting 25 µg of phenylephrine into the brachial vein while monitoring blood pressure from the brachial artery and noting the presence or absence of a fall in heart rate. At the end of observations, the animals were killed with a lethal dose of sodium pentobarbital and baroreceptor nerve section checked postmortem. One of the four mallards underwent a bradycardia following administration of the vasoconstrictive drug. The postmortem inspection revealed that only the left baroreceptor nerve was sectioned.

Predive heart rate was determined 1 s before submergence, and dive heart rate was determined 2 s after submergence. The data are shown as least-squares regressions with the 95% confidence limits of the slope and the standard error of estimate (Zar 1984). The slopes were tested for significance (P < .05) against slopes of either 0 or 1, using the t-statistic.

RESULTS

When dabbling voluntarily, heart rate did not change noticeably, although the slope of the regression line is significantly different from one (figs. 1, 2A). Large changes in heart rate were rare, and these were not always related to the moments of submersion or emersion. The mean duration of submersion was 3.0 ± 1.0 (SD) s with a maximum of 9 s; however, the large majority of dabbles were less than 3 s and were therefore not used in this analysis.

The time required to dive to the bottom of the tank and return to the surface was approximately 2 s. Dive time increased during the first week of diving from 2 s to 6 s, and the combined mean of all ducks after the first week was 6.2 ± 2.1 s with a maximum dive time of 11.6 s.

When voluntarily diving, the ducks showed little or no anticipatory increase in heart rate before the dive even if the predive heart rate was low (fig. 2B). The heart rate was lowest before the first of a series of dives and increased progressively between subsequent dives. Predive heart rates ranged
from 150 to 500 beats·min⁻¹ (fig. 3A). In one duck, the mean dive time was 7.7 ± 1.2 s, the dive:pause ratio was one, and predive heart rate rapidly increased to 500 beats·min⁻¹ during a series of dives. The duck represented by the data in figure 4 (solid circles) had a low dive:pause ratio (<1). The heart rate of this duck was usually above 400 beats·min⁻¹ immediately after a long dive (>9 s), but the duck rested at the surface for more than 10 s, during which heart rate decreased. Consequently, the rate before the next dive was never higher than 350 beats·min⁻¹.

The heart rate at 2 s into the dive was nearly the same regardless of the predive rate. The combined data from three mallards (50 dives each) show that dive heart rate was about 250 beats·min⁻¹ (fig. 3A). When the data for each animal were analyzed separately, the regression lines of two of the three ducks were not significantly different from zero, but the regression line for the third duck was significantly different from zero. The regression lines, for individual ducks or all ducks together, cross the line of identity, indicating that the heart rate increased in dives when predive heart rate

**Fig. 1.**—The relationship between presubmergence and submerged heart rate during voluntary dabbling when the head was underwater for over 3 s. The broken line represents the regression of these data. In this and all other figures, the line passing through the origin represents the line of identity.

**Fig. 2.**—EKG and cardiotachometer traces from mallards. **A,** dabbling; **B,** diving. The broken line at 250 beats·min⁻¹ represents the typical heart rate at 2 s into dives. There is no typical heart rate for dabbles.
was low while it decreased in dives when predive heart rate was high (figs. 2B, 3A, 4).

Baroreceptor denervation altered the relationship between predive and dive heart rate (fig. 3B). The regression line now approaches, although is significantly different from, the line of identity (fig. 3B). The duck that had only one baroreceptor nerve sectioned (fig. 4) gave a response between that of intact ducks and those ducks whose baroreceptor nerves were sectioned bilaterally (fig. 3B).

DISCUSSION

When diving ducks (*Aythya* sp.) dive voluntarily, there is always a fall in heart rate, and the dive heart rate is positively correlated with the predive rate (Furilla and Jones 1986). This fall in heart rate appears to result from a constant increase of vagal output regardless of the predive heart rate, while the variability of predive and dive heart rates is probably set by the amount of cardiac sympathetic activity present during each dive (Furilla and Jones 1987). In contrast, mallards appear to be regulating heart rate during the early stages of the dive, with the regulated rate being approximately 250 beats · min⁻¹. The adjustment in heart rate must be vagally mediated because the cardiac sympathetic nerves are incapable of bringing about rapid changes in heart rate (Furilla and Jones 1987). Consequently, in dives, not only is the amount of change of vagal activity variable, but the direction of change depends on the predive rate.

The heart rate response to voluntary dabbling shown by the mallard is puzzling. There is no doubt that chemoreceptors are responsible for the cardiovascular adjustments to forced diving (Jones and Purves 1970; Lillo and Jones 1982), so it is not surprising that little or no cardiac adjustment occurred during short periods of head submersion. However, Furilla and Jones (1986) showed that, when the duck’s heart rate was high just before a forced dive, heart rate fell rapidly to approximately 146 beats · min⁻¹. Evidence from voluntarily dabbling geese (Kanwisher, Gabrielsen, and Kanwisher 1981) and Pekin ducks (Gabrielsen 1985) also indicates changes in heart rate to approximately 150 beats · min⁻¹ on submersion, with heart rates of 200–300 beats · min⁻¹ during the short breathing period. Although observations from this study reveal some changes in heart rate during dabbles, heart rate did not fall to 150 beats · min⁻¹ with any regularity. In fact, figure 2A shows that the presence of a bradycardia was unpredictable, while the rate of fall of cardiac frequency was variable.

As with mallards, penguins show no anticipatory tachycardia, but, unlike mallards, penguins show little or no cardiac adjustments to voluntary submergence (Butler and Woakes 1984). Penguins are almost neutrally buoyant, while dabbling ducks are far more buoyant than diving ducks (Den-
Fig. 4.—The relationship between predive and dive heart rate from one mallard before (solid circles), and after denervation of the left baroreceptor nerve (solid triangles). The regression equations for heart rate data before and after unilateral barodenervation are given below and above the regression lines, respectively. These data are from the same bird and are not included in the previous figure.

ner [1946] in King 1966) and must work harder to dive. In fact, two of the five ducks used in the present study seemed unable to submerge fully without the aid of the wings but, once underwater, they switched to leg propulsion. Consequently, a predive tachycardia would be expected in mallards if the predive tachycardia seen in diving ducks is in anticipation of a high level of exercise during submersion.

The cardiac response to voluntary diving in mallards is greatly reduced by bilaterally sectioning the baroreceptor nerves, but not by unilateral section. This contrasts with diving ducks, such as the redhead (Aythya americana), in which barodenervation has no effect on the cardiac response to voluntary submersion (Furilla and Jones 1987). Information concerning heart rate is undoubtedly carried in duck baroreceptor nerves (Jones 1973), but whether ducks—or any animals—use this information to regulate heart rate, rather than arterial blood pressure, is unknown. It is unfortunate that our knowledge of the adjustments to submersion is limited to heart rate because if arterial pressure is being maintained during the dive, it may be that the system is responding to, and correcting for, changes in pressure brought about by alterations in total peripheral resistance. Since mallards are leg-propelled divers, the change in total resistance may be largely the result of modifications in hind limb perfusion. There is no evidence, however, for or against arterial pressure being maintained, and, if it is not, heart rate itself is the likely regulated variable. Other factors must be involved, however, because the slope of the regression after baroreceptor denervation is markedly different (0.58 ± 0.08) from 1. Even so, it is clear from this and other studies of voluntary dabbling and diving in birds that few generalizations can be made regarding not only the cardiovascular adjustments to submersion but also their control.


