The relationship between power output and heart rate in ducks diving voluntarily

Lowell T. McPhail *, David R. Jones

Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, BC V6T 1Z4, Canada

Abstract

Heart rate in response to natural and induced changes in power output was monitored in ducks diving voluntarily to a depth of 1.2 m. Adult lesser scaup (*Aythya affinis*) (3 female, 2 male), were trained to make shallow dives in an indoor tank (1.2 m depth) to obtain food. Heart rate was monitored using telemetry, and was determined for the following phases of a dive: predive, descent, feeding, ascent and postdive. Heart rate was found to be unaffected by changes in power output during the various dive phases. Power output by the ducks during a dive decreased when the duck's buoyancy was reduced 41% by injecting 0.10 kg mercury (Hg) into a bag implanted in the duck's peritoneal cavity. Calculated mechanical power output during the feeding phase of the dive was reduced 61% by the addition of Hg. Heart rate was recorded before adding Hg, with the Hg in place and after removing the Hg. No significant differences in diving heart rate were observed between ducks with or without Hg in the bag. However, leg beat frequency in the feeding phase of a dive was significantly reduced after filling the bag with Hg. We conclude that the level of power output in ducks diving to the shallow depth of 1.2 m has little influence on heart rate. © 1998 Elsevier Science Inc. All rights reserved.

Keywords: Aythya affinis; Buoyancy; Diving; Ducks; Power output; Telemetry; Heart rate

1. Introduction

Studies involving ducks and penguins have suggested that the differences in heart rate (f_H) seen during voluntary and forced dives may be attributable to the level of activity during the dive [11,20]. Level of activity is determined either by power input (P_I), usually measured as oxygen consumption, or by calculating the mechanical power output (P_O). The link between P_I and P_O is the aerobic efficiency and is equal to P_O/P_I. Mean oxygen consumption during a 13.5 s dive (4.6 l kg^{-1} h^{-1}; [15]) is only 21% higher than that measured for a tufted duck swimming at the surface at maximal sustainable speed (3.8 l kg^{-1} h^{-1}; [20]). Yet mean P_O during diving (1.74 W), and surface swimming (0.4 W)

differ by some four times, resulting in aerobic efficiencies of 12 and 3.7% for diving and swimming, respectively [15,18]. Because of such variations in aerobic efficiency, and the inability to measure oxygen consumption during the various phases of a voluntary dive (descent, feeding and ascent), we chose to use P_O as a measure of activity during the dive.

Buoyancy is the major factor contributing to power output during shallow diving in ducks [6,14,15,18,19]. Work against the buoyant force accounts for 62% of the power output during the descent phase with the remaining 38% from drag and inertial forces. During the feeding phase, 87% of the power output is used to overcome buoyancy, with the remaining 13% attributable to hindlimb drag [15]. Although the cardiac response to voluntary diving in ducks has been determined for the entire dive cycle [3–5], f_H has not been systematically investigated with respect to the different phases of a voluntary feeding dive.

---

* Corresponding author. Tel.: + 1 604 8224228; fax: + 1 604 8222416; e-mail: lmcphail@unixg.ubc.ca

Consequently, in the present study, the f_H response during diving in ducks (*Aythya affinis*) was investigated to determine the importance of power output in the control of f_H during these various phases. Ducks dived voluntarily and f_H was monitored using telemetry. The duck's buoyancy was decreased by the addition of 0.10 kg of mass to reduce their power output during dives. The additional mass was removed after 3 weeks. Leg beat frequency was determined during the feeding phase and power output calculated before adding the mass, with the mass, and again after removal of the mass. f_H was compared within the treatment conditions to determine the effect of power output on f_H during shallow diving in ducks.

2. Materials and methods

Three female and two male adult diving ducks (*A. affinis*) were used in these experiments. The ducks were raised and housed at the South Campus Animal Care Center of the University of British Columbia. Ducks were kept together in a pen 1.6 m l × 0.6 m h × 0.9 m w, with free access to a tank of water 2.5 m l × 1.25 m h × 0.8 m w. Most of the surface of the tank (1.3 × 0.8 m) was covered by wire mesh except the end nearest to the pen which restricted the ducks to diving from and resurfacing at the same place. The tank was divided into two channels by an 'L' shaped plastic mesh placed vertically, from top to bottom, under the wire mesh. The plastic divider ran half way across the width of the tank and then ran down the long axis of the tank, stopping 25 cm from the end opposite the open water surface. The divider required the ducks to follow a 'U' shaped path in order to obtain food placed at the end of the 'U'. Wheat (Buckerfield's, Abbotsford, BC) was placed at the bottom of the tank to encourage diving. During the training period, the wheat was slowly moved from directly under the open area of the water surface to the end of the 'U' shaped path. Goose and duck pellets (Buckerfield's) were provided in limited amounts in the pen to supplement the bird's diet.

Electrocardiogram (ECG) transmitters (Narco Proprietary Design, Downsview, ON) were embedded in an epoxy encapsulate (Sealtronic epoxy encapsulate, Industrial formulators of Canada, Burnaby, BC). The transmitters were equipped with a 3.5 V button tab battery (Biotelemetrics, Boca Raton, FA) and a miniature magnetic reed switch (Biotelemetrics) enabling the transmitter to be turned on or off after implantation in the duck. The battery and switch were then covered with a mixture of paraffin and beeswax and the entire device coated with silicone (G.E. RVT 118, Mississauga ON). The transmitter leads consisted of 18 guage hypodermic needles shaped into a loop and pressed onto the end of stainless steel biomedical wire (Cooner Wire Co.,

Chatsworth, CA). Connections between the wire and the loop were sealed with silicone (G.E.). An implantable 7.5 ml PVC bag was made from a 25 ml IV bag (Baxter Corporation, Toronto, ON) by cutting down the sides and heat sealing them together. A 5 cm piece of tubing (#7 Bolab Incorporated, Lake Havase City, AZ) was sealed into one end of the bag and the bag was covered in silicone.

For surgical anesthesia, ducks were ventilated with 98% oxygen and 2% halothane (Fluothane, Wyeth-Ayerst, Montreal PQ). Exposed skin at the site of incision (the midline of the ventral abdominal wall, just below the caudal end of the sternum) was cleaned with Betadine (Purdue Fredrick, Pickering, ON). The transmitter was implanted in the peritoneal cavity and sutured to the abdominal wall. The two transmitter lead were pushed rostrally through a small hole made in the oblique septum and were placed one on each side of the heart. The bag was also implanted in the peritoneal cavity with the end of the tubing extending through the abdominal wall to lie just below the skin. Following surgery, an antibiotic powder (Cicatrin, Burroughs Wellcome, Kirkland, PQ) was applied to the incision and 2 ml kg^{-1} of Tribrissen antibiotic (Coopers Agropharm Ajax, ON) was injected into the pectoral muscle.

Experiments were started 1–2 weeks after surgery when the animals were diving normally. The transmitter was turned on by passing a magnet over the ventral surface of the duck. The control phase consisted of gathering ECG from dives over several days after which buoyancy was measured. A small area of skin was cleaned with Betadine and an incision made through the skin under local anesthetic, (Xylocaine, 0.3 ml 2% lidocaine hydrochloride, Astra Pharm, Mississauga, ON) to allow access to the tube attached to the PVC bag. The tube was brought out through the skin and the bag was filled using a needle and syringe with 0.1 kg (∼7.5 ml) of mercury (Hg). The tube was sealed, the wound closed, antibiotic powder was applied to the incision and the ducks were returned to the tank. After 3 weeks of diving, buoyancy was remeasured and the Hg was removed by cleaning a small area of skin with Betadine, making a small incision, exposing the tube and withdrawing the Hg. Again the tube was sealed, the wound closed, antibiotic powder applied to the incision and the ducks were returned to the tank.

Bouyancy was measured by the volumetric displacement method [8,9,18]. After recording the mass of the duck on a balance (EK-1200A, A and D Engineering Milpitas, CA), the duck was secured to a Plexiglas form with an aluminium bar attached to it. The feet, wings and bill tip were taped to the form in a posture similar to that of the duck during diving. After exhalation, the duck was lowered head first into a water filled plastic tube (17 cm id × 56 cm tall) for ≈5 s. Water displace-

ment was measured using a glass pipette that was hydraulically connected in parallel with the large plastic tube. The volume of the plexiglass form and bar was then subtracted from the measurement to yield the volume of the water displaced by the duck. The difference between the mass of the duck and the mass of the water displaced by the duck was multiplied by gravitational acceleration (9.8 m s^{-2}) to yield buoyancy in Newtons.

During diving sessions, the ECG signal was monitored using an FM receiver (Model 555, Sony, Canada). The ECG signal was modulated using an FM recording adaptor (A.R. Vetter, Rebersberg, PA) to enable the signal to be recorded on the audio channel of a video recorder. A camera (Panasonic, Secausus, NJ) was used to record the duck's diving behavior on the video channel. The video tapes were replayed, the ECG signal was demodulated and interbeat intervals calculated on an IBM-compatible computer using Labtech Notebook software (Laboratory Technologies, Wilmongton, MA). The interbeat intervals were subsequently converted into beats min^{-1}. An event marker connected to the computer allowed correlation of diving activity on the video channel with heart rate on the audio channel during review of the video tape.

Each dive was divided into five stages: predive, descent, feeding, ascent, and postdive. Only dives lasting > 15 s and < 20 s were analysed to reduce possible variations in f_H caused by dive length [17]. Six such dives from each duck in each condition (pre Hg, Hg, post Hg) were chosen at random and analysed. Mean f_H for each dive stage was then calculated for each duck ($n = 5$). For the predive stage, the mean f_H of the 5 s immediately preceding the dive was used. For descent, feeding and ascent, the time interval analysed varied with each dive. Postdive f_H was obtained by analysing the first 5 s following surfacing. Routine f_H was the mean f_H during three 1 min periods for each treatment condition when the duck was quietly paddling on the water surface. f_H determined for six dives was then averaged to give a mean for each of the three conditions: preHg, Hg and postHg. Means for all five ducks ($n = 5$) were averaged to give a group mean $\pm$ SEM.

Mechanical work (J) done per leg-beat cycle during the feeding (bottom) phase of a dive was calculated using equations in Stephenson [15]. However, calculation of the respiratory system and plumage volume (V_{r+p}; ℓBTPS) for the added mass condition involved modification of the term (M_b/p_{t+f}) in Stephenson's [15] equation No. 7:

$$(V_{r+p}) = V_{tot} - (M_b/p_{t+f}) \qquad (1)$$

where V_{tot} is the total volume of the duck, M_b is the mass of the duck (kg), and p_{t+f} is the air-free tissue density of a feathered bird (1.04×10^3 kg m^{-3} [14]). In the case of the additional mass condition, (M_b/p_{t+f}) was calculated as follows
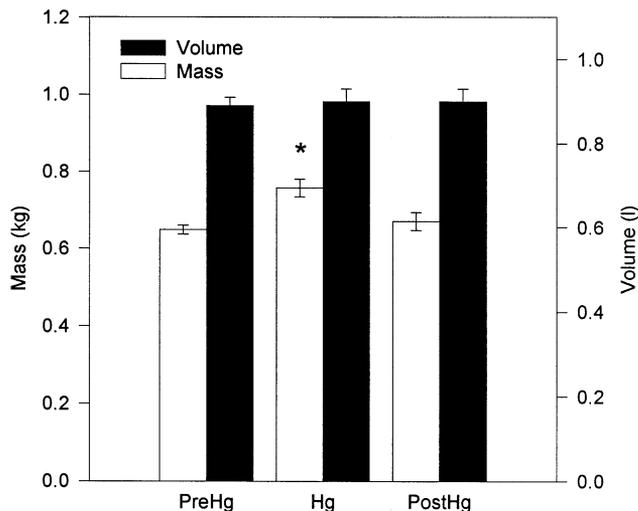

Fig. 1. Mean mass and volume ($\pm$ SEM, $n = 5$) of ducks before, during and after the addition of 0.10 kg of Hg to the ducks. * Indicates values significantly different from the preHg condition.

(M_b/p_{t+f})

$$= (M_b - 0.1 \text{ kg Hg}/p_{t+f}) + (0.1 \text{ kg Hg}/p\text{Hg}) \qquad (2)$$

where pHg is the density of Hg (13.6×10^3 kg m^{-3}). Leg beat frequency was determined by counting leg beats during frame by frame advancement of the video tape. The average frequency of leg beats (Hz) during the feeding phase was multiplied by the work done per leg beat cycle to obtain power output (W) during feeding.

For statistical analysis of the data, one way analysis of variance (ANOVA) for repeated measures was used. Multiple comparison procedures (Student–Newman–Keuls Method) were performed. All statistics were cal-
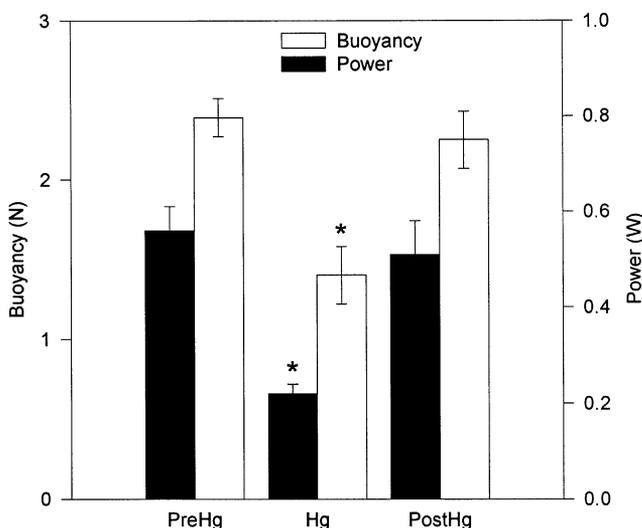

Fig. 2. Effect on power in the feeding phase and surface buoyancy of the addition of 0.10 kg of Hg to the ducks ($\pm$ SEM, $n = 5$). * Indicates values significantly different from the preHg condition.

Table 1
Dive times and leg beat frequency during diving

Condition	Descent (s)	Feeding (s)	Ascent (s)	Sum (s)	Total (s)	Leg beat frequency (Hz)
PreHg	4.7 ± 0.3	8.6 ± 0.8	4.3 ± 0.4	9.1 ± 0.3	17.6 ± 0.3	3.39 ± 0.09
Hg	4.8 ± 0.2	8.5 ± 0.5	4.4 ± 0.2	9.1 ± 0.3	17.8 ± 0.3	$3.01 \pm 0.09*$
PostHg	4.7 ± 0.2	7.9 ± 0.8	4.6 ± 0.4	8.7 ± 0.4	17.2 ± 0.4	3.33 ± 0.06

Time (s) for the descent, feeding, ascent phases, sum (sum of the descent to the mid-point of feeding phase), total dive time and leg beat frequency (Hz) ($\pm$ SEM, $n = 5$), during the feeding phase before, during and after addition of the Hg to the bag.
* Indicates that this value is significantly different from the preHg condition, prior to addition of the mass and the resultant decrease in power output.

culated with SigmaStat software (Jandel Scientific, San Rafael, CA) with $P < 0.05$ considered a significant difference.

3. Results

The addition of 0.10 kg of Hg to the bag significantly increased the mass of the ducks to 0.757 ± 0.023 kg on average, an increase of 17% over the preHg value of 0.648 ± 0.012 kg (Fig. 1). Removal of Hg for the postHg condition reduced the average mass to 0.670 ± 0.023 kg, not significantly different from the preHg condition.

Using the values for mass and volume from Fig. 1, surface buoyancy in Newtons (N) was calculated (Fig. 2). Buoyancy decreased significantly from a preHg level of 2.39 ± 0.12 to 1.4 ± 0.18 N after addition of 0.10 kg of Hg, a reduction of 41%. Following removal of the Hg (postHg condition), buoyancy returned to the preHg level of 2.25 ± 0.18 N. Addition of Hg resulted in a significant reduction in leg beat frequency during the feeding phase from 3.39 ± 0.08 Hz in the preHg condition to 3.01 ± 0.09 Hz in the Hg condition (Table 1). After removal of the Hg, the leg beat frequency increased to 3.33 ± 0.06 Hz, a rate not significantly different from the preHg condition (Table 1). Average mechanical power output (W) during the feeding phase of the dive showed a similar trend to that of buoyancy (Fig. 2). Power output fell significantly with the addition of Hg, from a preHg level of 0.56 ± 0.05 to 0.22 ± 0.02, a reduction of 61%. Upon removal of the Hg, postHg power output in the feeding phase increased to 0.51 ± 0.07 W.

Dive cycles were divided into five phases (Fig. 3). Phase one was the predive phase consisting of the 5 s immediately before the duck submerged below the water surface. This phase was characterized by an increase in f_H over routine f_H. The descent phase (phase two) began with the duck starting to submerge and continued until the duck reached the feeding zone. The feeding phase was the phase during which the duck was actively feeding at the bottom. The ascent phase started when the duck stopped feeding and began its return to

the surface, ending when the duck's head broke the surface of the water. The postdive phase was the 5 s immediately following the end of the ascent phase when the duck was at the surface. Times for the different dive phases, the total dive time as well as the sum of the descent phase to the mid-point of the feeding phase are shown in Table 1. The mean total dive time during the preHg condition was 17.6 ± 0.3 s, and the sum of the descent to the mid-point of the feeding phase was 9.1 ± 0.3 s (Table 1). The 'sum' was used to correct buoyancy for time submerged in the calculation of power output in the feeding phase. No significant difference in duration of any of the dive phases was seen after addition of Hg.

A typical dive profile for f_H and its corresponding ECG trace is shown in Fig. 3. The average f_H in beats min^{-1} for ducks paddling quietly on the water (routine) and during the five phases of the dive cycle are shown in Fig. 4. Mean f_H was significantly different among the three dive phases (descent, feeding and ascent), and this difference was unaffected by addition or removal of the Hg from the bag. There was no significant change in routine f_H during the different power output conditions; routine f_H remained near the preHg value of 187 ± 12 beats min^{-1}. f_H did not change significantly with the artificial increase in mass and calculated 61% reduction in power output during the feeding phase. In the preHg condition f_H was 210 ± 6 beats min^{-1} during the feeding phase and was not affected significantly by the reduction of power output in the Hg condition ($f_H = 192 \pm 7$ beats min^{-1}). f_H in the feeding phase during the postHg condition was 190 ± 19 beats min^{-1} following return of mass and calculated power output to preHg levels.

4. Discussion

The present study has presented no evidence that changes in power output play any role in modulating f_H in ducks during a voluntary dive to shallow depths. Adding 0.10 kg mass to the ducks caused a 41% reduction in buoyancy, which resulted in a 61% reduction in calculated power output during the feeding
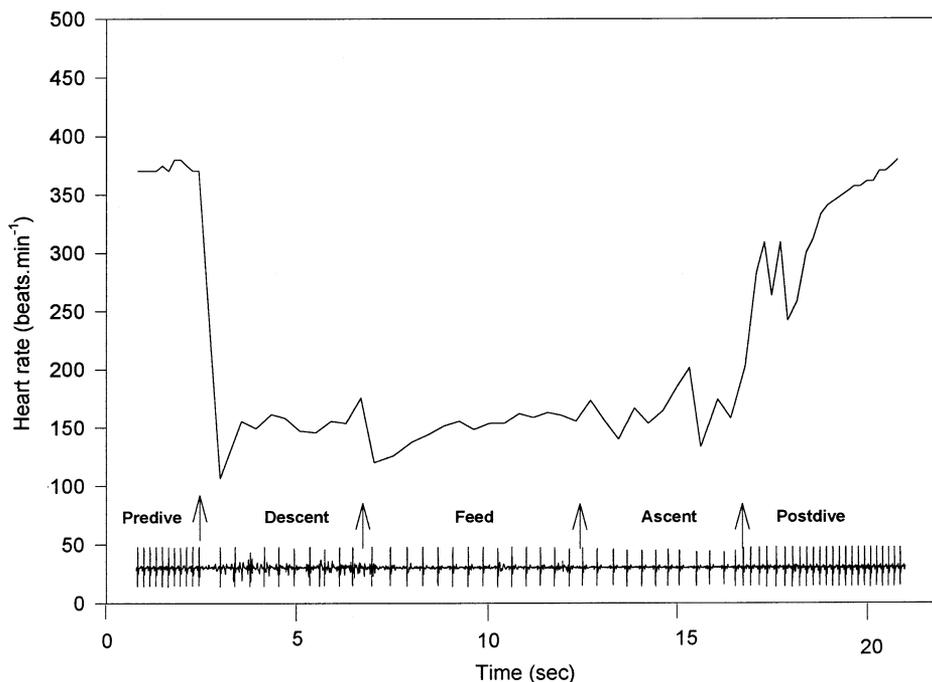
Fig. 3. Heart rate during the control condition for one duck before, during and after a voluntary dive. Lower trace is the ECG. Upper trace is the heart rate. Arrows indicate starting points for the various phases of a dive: predive, descent, feeding, ascent and postdive.

phase when power output is directed to overcoming the buoyant force. The significant reduction in leg beat frequency during the feeding phase in the reduced buoyancy condition indicated that less power output was required to keep the duck at the bottom. However, f_H during the feeding phase remained unchanged from the control condition despite reduced buoyancy and power output. Routine f_H values also remained unchanged after addition of Hg indicating that the absence of a reduction in f_H in the feeding phase due to decreased power output was not compensated by a temporary increase in f_H due to treatment condition.

Other evidence leads us to believe that the level of activity during diving in ducks has little affect on f_H because of the lack of correlation between f_H and power output during different phases of a dive. In tufted ducks, halving surface swimming velocity from 0.79 to 0.4 m s^{-1} causes a reduction in oxygen consumption of $\approx 70\%$, while f_H falls 47% [20]. However, there is no clear relationship between changes in power output and f_H in ducks diving voluntarily. The descent phase of a dive requires the most power output (3.63 ± 0.38 W) of the three diving phases (descent, feeding and ascent) [10,15], yet f_H is at its lowest during this phase (Fig. 4). f_H increases during the feeding phase (Fig. 4) despite an $\approx 58\%$ decline in power output to 1.51 ± 0.10 W from the descent phase [15]. Furthermore, the ascent phase, which is virtually passive as the duck floats to the surface [18], is associated with the highest f_H of the dive (Fig. 4).

The inverse relation between P_O and f_H is also reflected in the relation between P_T and f_H. Oxygen consumption (P_T) during dives of 15–20 s duration falls consistently throughout the dive [20], yet f_H increases. Bevan et al. [1] pooled data with those from an earlier study by Woakes and Butler [20] to statistically substantiate the relation between P_T and dive time. Unfortunately, these two data sets are quite different. In Woakes and Butler [20], ducks performed dives to a depth of 1.7 m compared with 0.6 m for ducks in Bevan et al. [1]. Nevertheless, both studies indicate a trend of decreasing rate of oxygen consumption with dive time despite the different duration of descent time. Obviously, even though the descent phase is much more energetically costly compared with the other phases of the dive, any reduction in oxygen consumption during long dives cannot be a reflection of the decreasing proportion of the descent phase relative to the rest of the dive. However, if dives are extended then f_H falls along with the decline in P_T.

A naturally occurring change in buoyancy might contribute to the reduction in energetic requirements in extended dives. Stephenson et al. [17] trained ducks to make extended dives for food and f_H started to decline at a mean rate of 5.63 ± 0.2 beats min^{-1} s^{-1} starting, on average, 7.5 s into the dive and continuing to decline until ≈ 7 s before resurfacing. So despite the duck exercising at a high level during its horizontal swim to the food source (descent phase lasting ≈ 18 s), f_H progressively declined. Air is lost from the plumage during the descent and feeding phases at a rate of 7.8
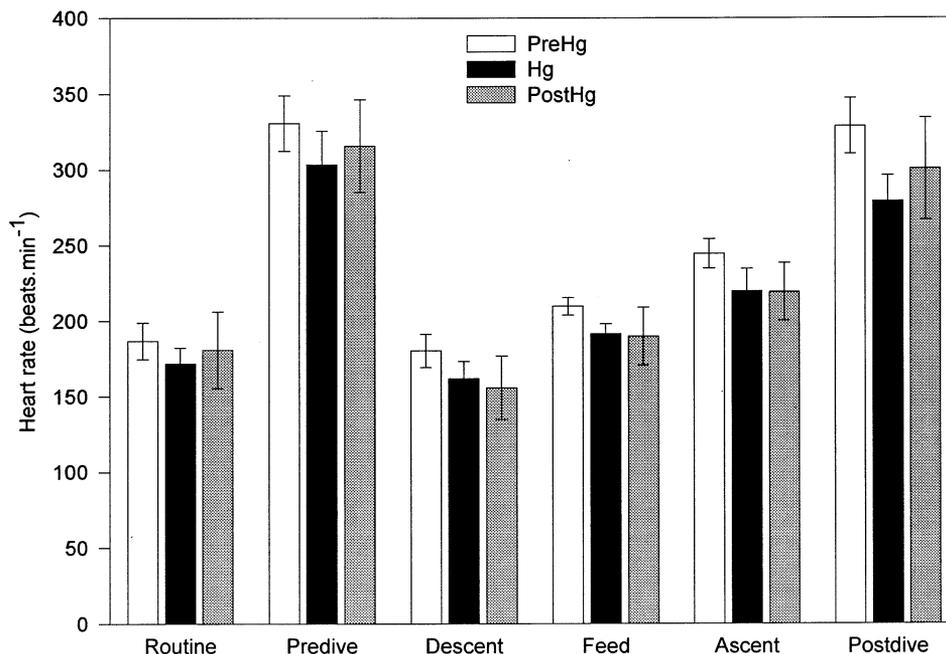
Fig. 4. Effect of the reduction in buoyancy on mean heart rate during five phases of dives as well as on routine heart rate ($\pm$ SEM, $n = 5$).

ml s^{-1} [15]. Plumage air volume is estimated at 184 ml [16], so during long dives, if air loss is linear, all the air would be gone within 24 s. Since air was lost from the plumage in our experiments, then the buoyancy change occurring naturally is similar to that experienced by ducks in the present experiments after the addition of Hg. Yet f_H continues to decline during the descent and feeding phases in dives over 34 s [1,17]. The reduction in f_H at the end of extended dives is substantially reduced after bilateral denervation of the carotid body chemoreceptors [2,5]. Therefore, part of the reduction in f_H during the later stages of extended dives is due to the inhibitory effect of the chemoreceptors, although the effect, if any, of a reduction in activity on f_H due to dive phase or a reduction in buoyancy from air escaping from the plumage remains to be established.

If a duck is prevented from surfacing near the end of a voluntary dive then there is an immediate reduction in f_H similar to that seen during forced dives, even though the duck continues to swim underwater [7,17]. Signore and Jones [12] also showed that when they forced unrestrained muskrats to dive in a cage, f_H was significantly lower than in voluntary dives, despite the fact that the animals continued to swim extremely actively in the cage. Diving f_H is indeed affected by increasing exercise in muskrats, but the effect was significant only for the highest water velocities against which the muskrats were forced to swim when compared with still water [13]. Nevertheless, based on our present findings, in combination with other observations, we are confident that during shallow diving the level of power output is not the predominant factor in

the control of f_H. Although the rate of oxygen extraction from the blood plays a role in the control of f_H during longer dives via the chemoreceptors, a f_H response to exercise similar to that seen in ducks swimming at the surface does not seem to occur during voluntary diving.

Buoyancy and its changes during the course of a dive will greatly influence power output. Stephenson [15] monitored the change in air pressure in a closed system caused by the exit and return of a duck before and after a dive to determine the change in body volume of a duck during a voluntary dive. A comparison of these volumes with volumes obtained by the water displacement method shows that measurement of body volume using the water displacement method could underestimate volume by 25%. Stephenson's [15] method of determining body volume in ducks, however, appears to have a long response time and therefore may not register predive exhalation and pilosuppression, which would result in an overestimation of body volume. In addition, air is lost from the plumage during diving which could further impact on buoyancy during the dive. Stephenson [15] assumes that the loss of air from the plumage is linear at 7.8 ml s^{-1} which may not be the actual situation during dives. In fact, if the majority of air from the plumage is lost within the first seconds of a dive and the water displacement method gives a more accurate representation of body volume, calculated power output levels during a dive would be substantially reduced. In this case, power output during diving would be similar to power output during surface swimming, thus eliminating any difference in aerobic

efficiencies between surface and subsurface modes of propulsion.

References

[1] Bevan RM, Keijer E, Butler PJ. A method for controlling the feeding behaviour of aquatic birds: heart rate and oxygen consumption during dives of different duration. J Exp Biol 1992;162:91–106.

[2] Butler PJ, Stephenson R. Chemoreceptor control of heart rate and behaviour during diving in the tufted duck (*Aythya fuligula*). J Physiol Lond 1988;397:63–80.

[3] Butler PJ, Woakes AJ. Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. J Exp Biol 1979;79:283–300.

[4] Butler PJ, Woakes AJ. Telemetry of physiological variables from diving and flying birds. Symp Zool Soc Lond 1982;49:107–28.

[5] Butler PJ, Woakes AJ. Control of heart rate by carotid body chemoreceptors during diving in tufted ducks. J Appl Physiol Respir Environ Exerc Physiol 1982;53:1405–10.

[6] Dehner EW. An analysis of buoyancy in surface feeding and diving ducks. PhD thesis. Department of Zoology, Cornell University, 1946.

[7] Furilla RA, Jones DR. The relationship between dive and pre-dive heart rates in restrained and free dives by diving ducks. J Exp Biol 1987;127:333–48.

[8] Lovvorn JR, Jones DR. Effects of body size, fat and changes in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can J Zool 1991;69:2879–87.

[9] Lovvorn JR, Jones DR. Body mass, volume, and buoyancy of some aquatic birds, and their relation to locomotor strategies. Can J Zool 1991;69:2888–92.

[10] Lovvorn JR, Jones DR, Blake RW. Mechanics of underwater locomotion in diving ducks: Drag, buoyancy and acceleration in a size gradient of species. J Exp Biol 1991;159:89–108.

[11] Millard RW, Johansen K, Milsom WK. Radiotelemetry of cardiovasular responses to exercise and diving in penguin. Comp Biochem Physiol 1973;46A:227–40.

[12] Signore PE, Jones DR. Effect of pharmacological blockade on cardiovascular responses to voluntary and forced diving in muskrats. J Exp Biol 1995;198:2307–15.

[13] Signore PE, Jones DR. Autonomic nervous control of heart rate in muskrats during exercise in air and under water. J Exp Biol 1996;199:1563–8.

[14] Stephenson R. The contributions of body tissues, respiratory system and plumage to buoyancy in waterfowl. Can J Zool 1993;71:1521–9.

[15] Stephenson R. Diving energetics in lesser scaup (*Aythya affinis*, Eyton). J Exp Biol 1994;190:155–78.

[16] Stephenson R. Respiratory and plumage gas volumes in unre-strained diving ducks (*Aythya affinis*). Respir Physiol 1995;100:129–37.

[17] Stephenson R, Butler PJ, Woakes AJ. Diving behaviour and heart rate in tufted ducks (*Aythya fuligula*). J Exp Biol 1986;126:341–59.

[18] Stephenson R, Lovvorn JR, Heieis MRA, Jones DR, Blake RW. A hydromechanical estimate of the power requirements of diving and surface swimming in the lesser scaup (*Aythya affinis*). J Exp Biol 1989;147:507–19.

[19] Wilson RP, Hustler K, Ryan PG, Burger AE, Nöldeke EC. Diving birds in cold water: Do Archimedes and Boyle determine energetic costs. Am Nat 1992;140:179–200.

[20] Woakes AJ, Butler PJ. Swimming and diving in tufted ducks, *Aythya fuligula*, with particular reference to heart rate and gas exchange. J Exp Biol 1983;107:311–21.