The effects of depth on the cardiac and behavioural responses of double-crested cormorants (*Phalacrocorax auritus*) during voluntary diving

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Summary

Heart rate and dive behaviour were monitored in double-crested cormorants (*Phalacrocorax auritus*) during shallow (1 m) and deep diving (12 m), after breathing different gas mixtures, to investigate the role of depth and the accompanying changes in blood gas levels in cardiac and behavioural control during voluntary diving. Pre-dive heart rate in both shallow- and deep-diving birds was approximately three times the resting heart rate (137.9±17.5 beats min^{-1}; mean ± S.D., N=5), falling abruptly upon submersion to around 200–250 beats min^{-1}. During shallow diving, the initial reduction in heart rate was followed by a secondary, more gradual decline, to around the resting level. In contrast, during deep diving, heart rate stabilised at 200–250 beats min^{-1}. In dives of similar duration, mean dive heart rate was significantly lower during shallow diving (163.2±14.0 beats min^{-1}) than during deep diving (216.4±7.7 beats min^{-1}), but in both cases was significantly above the resting value. The difference in cardiac response is probably due to an increase in arterial oxygen tension (Pa_{O_2}) during the descent phase of deep dives (compression hyperoxia). Exposure to a hyperoxic gas mixture before shallow diving

significantly increased mean dive heart rate, while exposure to a hypoxic gas mixture in both the shallow and deep dive tanks significantly reduced mean dive heart rate. In contrast, breathing hypercapnic gas before diving had no significant effect on dive heart rate. We suggest that the cardiac response to voluntary diving in double-crested cormorants is strongly influenced by changes in blood oxygen levels throughout the dive. Dive duration was unaffected by alterations in inspired gas composition, but surface interval duration decreased during hyperoxic gas exposure and increased during hypoxic gas exposure. The most efficient dive pattern (highest dive/pause ratio) was observed after hyperoxic exposure. Our study suggests that blood oxygen level is a powerful stimulus that facilitates the cardiac and behavioural adjustments during foraging that are important components of a strategy allowing double-crested cormorants to maximise the time spent under water and, hence, potential foraging time.

Key words: diving, double-crested cormorant, *Phalacrocorax auritus*, heart rate, behaviour, depth, carotid body chemoreceptor, blood gas, data logger, cardiac control mechanism.

Introduction

Cormorants and shags are foot-propelled pursuit divers (Ashmole, 1971), which were generally considered to perform shallow dives of short duration (Cooper, 1986; Johnsgard, 1993). Recent field studies using data loggers to monitor dive variables, however, have shown that some species are capable of extended and deep dives (e.g. South Georgian shags, *Phalacrocorax georgianus*, have been observed to dive for as long as 6.3 min and can reach a depth of 116 m) (Croxall et al., 1991; Wanless et al., 1992). The forces acting upon these divers when diving to depth are manifold and will limit the depth range that can be utilised. Oxygen stores are finite, and even their most economical use will limit dive duration and, hence, the dive depths that can be reached. Cardiovascular mechanisms that facilitate the economic utilisation of finite oxygen stores during diving might be of great importance to

active pursuit divers. Another important aspect is the pressure experienced when diving to depth. In addition to the problems related to the increased absorption of gases (e.g. nitrogen) into the tissues of divers that might cause problems during rapid ascent, the effects of hydrostatic compression on the physiological control systems that facilitate cardiovascular responses to changes in O_2 and CO_2 levels during these deep dives remain unclear.

Intravascular chemoreceptors (carotid bodies) that monitor changes in O_2 and CO_2 levels and pH in the arterial blood have been shown to be important in the cardiac responses to diving in both forcedly and voluntarily diving ducks. In freely diving tufted ducks (*Aythya fuligula*), the carotid bodies perform a role in maintaining and reinforcing the initial decline in heart rate during the later part of shallow dives

(Butler and Woakes, 1982a; Butler and Stephenson, 1988), although a role for other receptors cannot be excluded, especially when dives are long (Butler and Stephenson, 1988). Certainly, pressure changes during dives to depth will alter any chemoreceptor-driven response, while leaving the contribution from other receptors unaffected. During the descent phase of deep dives, overall pressure will increase by 1 atmosphere (101 kPa) for every 10 m of depth. This compression will increase alveolar oxygen tension ($P_{A_{O_2}}$) and may augment blood oxygenation at depth (Lanphier and Rahn, 1963). Markedly elevated arterial oxygen tensions ($P_{a_{O_2}}$) during the early descent phase of deep dives have been found during simulated dives to depth in Adélie (*Pygoscelis adeliae*) and gentoo (*P. papua*) penguins, in freely diving Weddell seals (*Leptonychotes weddelli*) and in breath-hold dives to depth in humans (Kooyman et al., 1973; Qvist et al., 1986; Qvist et al., 1993). This elevation in $P_{a_{O_2}}$ might have consequences for the development of the cardiac response during deep diving because it would inhibit the contribution of the chemoreceptors and, hence, delay the reinforcement of any initial decline in heart rate. However, alveolar CO_2 tension ($P_{A_{CO_2}}$) also increases during descent, so a higher $P_{a_{CO_2}}$ might counteract the effects of a high $P_{a_{O_2}}$.

Besides their effects on the cardiovascular performance of diving animals, blood gas levels are important regulators of ventilation. Adjustment of dive duration and the length of the subsequent surface interval are important behavioural components in the regulation of ventilation in diving animals. Hence, blood gas levels might play an important role in controlling dive behaviour, as has been shown for tufted ducks (Butler and Stephenson, 1988). The importance of blood gas levels in modulating the cardiac and behavioural responses to voluntary shallow and deep diving has never been investigated in cormorants. Forced submergence studies on double-crested cormorants revealed equivocal results. While Mangalam and Jones (1984) found that breathing different levels of O_2 and CO_2 before forced submergence had little effect on the bradycardia displayed during submergence, Jones and Larigakis (1988) reported significantly elevated heart rates during forced submergence after exposure to 100% O_2 before submersion.

Double-crested cormorants in British Columbia are opportunistic foragers, taking the majority of their prey in the littoral-benthic zone (Robertson, 1974). Although direct measurements of dive depth are not available, double-crested cormorants have been reported to dive in water ranging in depth from 1 to 20 m (Ross, 1974; Ainley et al., 1990; King et al., 1995). If double-crested cormorants forage predominantly on benthic prey, the maximum dive duration of 70 s (Munro, 1927) suggests that they are capable of submerging to even greater depths. Hence, double-crested cormorants are likely to experience the physiological effects of a substantial increase in ambient pressure during diving. The purpose of our study, therefore, was to investigate the effects of depth, especially as it affects blood gas levels, on cardiac and behavioural control during diving.

Materials and methods

Nine adult or sub-adult double-crested cormorants (*Phalacrocorax auritus* Lesson) (minimum age 2 years) with a mean mass of 2.36±0.17 kg (mean ± S.D., range 2.17–2.58 kg) were used in this study. The cormorants were captured as chicks (5–6 weeks of age) and housed communally in sheltered outdoor pens (8 m long×4 m wide×5 m high) with water tank access at the South Campus Animal Care Facility of the University of British Columbia (UBC), Vancouver. Birds were fed approximately 10% of their body mass daily with a mixed diet consisting of Pacific herring (*Clupea harengus*) and rainbow smelt (*Osmerus mordax*), supplemented with vitamin B1 tablets (thiamine hydrochloride; Stanley Pharmaceuticals Ltd, North Vancouver, British Columbia, Canada). All experimental procedures were approved by the UBC Animal Care Committee.

Training protocol

Within the first 3 months of capture, the cormorants were introduced into the shallow dive tank (9 m long×3 m wide×1 m deep). The surface of the shallow dive tank was progressively covered during the training sessions until only a small section at one end of the tank remained open. Birds submerged here, swam to the opposite end of the tank where chopped herring pieces had been placed, picked up a piece of fish and returned to the uncovered section to swallow their prey (Fig. 1A) ('shallow horizontal dives'). A few weeks later, the birds were rotated between the shallow dive tank and the outdoor holding pens. Five of the nine cormorants were introduced into the deep dive tank (13 m high×5 m in diameter), where they were trained to pick up chopped herring pieces from a feeding platform suspended within the water column (12 m water depth) (Fig. 1B) ('deep vertical dives'). Starting 3–4 weeks before data collection, birds were captured on a daily basis, equipped with a harness holding a dummy data logger and placed onto the shallow or deep dive tank. After one complete foraging bout, the birds were recaptured for removal of the harness and returned to their pens. A foraging bout was defined as the time from a bird's entrance into the water until it voluntarily stopped diving for at least 10 min. Water temperature in the tanks varied between approximately 6°C in winter and approximately 16°C in summer, which is close to the seasonal variation that would be experienced by wild double-crested cormorants on the south-west coast of British Columbia.

Instrumentation and experiments

To record heart rate, a purpose-built data-logging system was developed that included a submergence sensor (for details, see Andrews, 1998). The low-profile data logger (1 cm high×8 cm long×5 cm wide) was designed to minimise potential instrumentation effects on the birds (Bannasch et al., 1994; Andrews, 1998). Before experimental application, the data logger was glued onto a harness, made of rubber neoprene and Velcro straps, which was fitted onto the bird's back. Electrocardiogram (ECG) electrodes were implanted close to the heart under halothane anaesthesia (Fluothane, Wyeth-

Ayerst, Montreal, PQ, Canada). The ECG-lead assembly was tunnelled subcutaneously to an exit site on the midline of the dorsal surface (approximately 4 cm cranial to the caudal end of the synsacrum), where it was glued onto a small neoprene patch mounted on the bird's feathers with cyanoacrylate adhesive (Loctite Quick Set 404 industrial adhesive; Loctite Corporation, Rocky Hill, CT, USA; for details, see Andrews, 1998). The instrumental design was well tolerated by the birds and no changes in their swimming or diving behaviour were observed after instrumentation.

The birds were given at least 1 week to recover from surgery before the start of the experiments. Before a trial, a cormorant was caught in its holding pen, and the harness with data logger was placed on its back. The data logger's ECG electrode leads were connected to the implanted leads, and the sampling mode of the data logger was triggered. The handling time of the birds was kept to a minimum and usually did not exceed 5 min. The birds were immediately introduced into the shallow or deep dive tank, where they started diving spontaneously. To avoid disturbance, the trials were filmed using a video camera. At the end of a trial, which generally lasted 20–30 min, the birds were recaptured to unplug the ECG leads and remove the harness. The birds were released into their holding pens, and the data were downloaded from the data logger into a personal computer.

Blood gas levels (O_2 and CO_2) were manipulated before the onset of a dive bout by exposing the birds to different gas mixtures. On both the shallow and deep dive tank, a transparent polyvinylchloride (PVC) cage (0.8 m long×0.6 m wide×0.6 m high), covering the opening of the surface cover, was filled with the desired gas mixture from a gas bottle. The PVC cage was kept airtight by immersing its open bottom part; however, two small holes had to be introduced for a trapdoor that allowed some gas to escape. Gas samples were drawn continuously from the cage during the entire trial and analysed for their O_2 and CO_2 contents (Beckman O_2-analyser OM11 and Beckman CO_2-analyser LB-2; Beckman Instruments Inc., Schiller Park, IL, USA) to ensure that the desired mixture was maintained.

After the introduction of a bird into the cage, the gas flow was readjusted until the desired gas concentration stabilised. Water access was controlled through a trapdoor at the bottom of the cage. Birds were exposed to the stabilised gas mixture for 10 min before the trapdoor was opened and the dive bout started. During the trial, the gas flow into the cage was kept at a low but sufficient rate to keep the gas concentration stable. All birds were familiarised with the cage during training sessions. In the shallow dive tank, birds were exposed to the following gas mixtures: (i) normal air (control); (ii) hyperoxic air mixture (>80 % O_2); (iii) hypoxic air mixture (12 % O_2); (iv) hypercapnic/normoxic mixture (3 % CO_2 and air); or (v) hypoxic/hypercapnic mixture (12 % O_2 and 3 % CO_2). Preliminary trials in the shallow dive tank showed that hypercapnia had little effect on the cardiac response during voluntary diving. Hence, the hypercapnic trials were discontinued, so these data are available for the shallow dive

tank only. In the deep dive situation, birds were exposed to only normoxic (control) and hypoxic gas mixtures (here 8–9 % O_2). The lower oxygen concentration for the hypoxic mixture in the deep dive situation was chosen because, in preliminary trials, the compression experienced by the birds during descent and the accompanying increase in $P_{A_{O_2}}$, and therefore in $P_{a_{O_2}}$, appeared to prevent the chemoreceptor response at the level of hypoxia chosen for the shallow dive situation (12 % O_2).

All gas mixtures were administered at random. Although blood gas levels were not measured in this study, we are confident that the administration of the different gas mixtures used in this study for 10 min before diving produced the desired changes in blood gas levels. Mangalam and Jones (1984) elevated the $P_{a_{O_2}}$ of double-crested cormorants almost threefold (from 80 to 220 mmHg; from 10.7 to 29.3 kPa) by administering 50 % O_2 for 5 min prior to forced submergence. Breathing 12.8 % O_2 reduced $P_{a_{O_2}}$ to 70 mmHg (9.33 kPa).

Cormorants did not rest while on the water but dived continuously until leaving the water at the end of the foraging bout. Hence, resting heart rates were obtained from five birds while they were in their outdoor holding pens. Birds were equipped with the data logger and harness as described above but kept inside their holding pens. The birds perched immediately after release and returned to their routine shortly after the handler departed. Trials lasted for approximately 1 h and were carried out during daylight hours with post-absorptive birds that were awake and perched in an upright position.

Data analysis and statistics

To allow comparison between the different experimental situations and to reduce the influence of dive duration on the expression of the cardiac response to voluntary diving, only dives between 18 and 22 s in duration and only dives with an obvious foraging intention (i.e. birds swam to the feeding spot) were selected for analysis of heart rate. After training, the majority of dives by cormorants in the shallow and deep dive tanks fell into this category. Submergence and emergence times were determined from the record of the data logger's submergence sensor. Cardiac interbeat intervals were derived from the ECG trace after identifying the QRS peaks by eye. A mean value for the interbeat intervals of each dive was calculated and subsequently converted into heart rate (beats min^{-1}).

For each cormorant in each different treatment, six dives were analysed. A mean value for each bird was calculated from the six individual dives per treatment. For each treatment, a grand mean was calculated from the individual bird means. To compute heart rate profiles for the different experimental treatments, heart rate data were divided into 3 s intervals, starting 9 s before a dive and ending 9 s after its completion. Mean values for these intervals were calculated for all dives and used to generate grand means as described above. To investigate the effect of dive duration on the cardiac response during voluntary diving, all shallow dives performed by three individuals (dive duration 3–28 s) were included in a separate analysis.

Table 1. *Heart rates of double-crested cormorants during resting and voluntary diving in the shallow and deep dive tanks*

Bird	Resting	Pre-dive	Dive	Minimum	Post-dive
			Heart rate (beats min^{-1})		
Shallow diving					
1LR		375.8±10.0	152.1±9.3	71.3±6.5	392.3±13.4
LW		369.0±13.9	141.5±7.4	74.1±5.1	369.8±10.1
2G		366.1±40.0	162.0±4.4	82.2±8.5	435.4±14.5
1G	155.2±20.8	376.6±29.6	168.5±20.8	92.8±13.4	377.9±12.0
OG	142.3±38.3	393.2±4.6	155.8±6.0	89.1±13.5	398.0±7.6
OW	144.8±16.3	382.2±36.6	164.8±8.3	84.9±14.5	396.7±5.5
2P	108.7±14.9	404.2±5.5	187.0±9.4	123.7±28.2	405.6±6.4
RP	138.4±15.3	377.6±38.2	174.1±19.8	89.1±33.0	402.1±8.0
Grand mean	137.9±17.5	380.6±12.6*	163.2±14.0*,‡	88.4±16.1*,‡	397.2±19.6*
Deep diving					
1G		379.2±17.8	211.5±8.8	159.3±10.9	365.1±24.6
OG		377.7±5.3	213.4±10.7	175.6±15.6	377.3±5.2
OW		404.5±14.8	225.6±12.1	150.0±31.6	410.5±10.0
2P		395.5±7.9	223.7±14.4	166.7±7.5	401.5±6.1
RP		395.7±14.0	208.1±20.4	148.1±16.2	383.1±21.1
Grand mean		390.5±11.6*	216.4±7.7*,‡	159.9±11.5*,‡	387.5±18.4*

Values are presented as mean ± S.D.
A grand mean is the mean of the individual cormorant means.
Resting heart rates are the mean values taken over a 20 min session per bird.
Pre-dive and post-dive heart rates are mean values taken from 3 s intervals before and after diving, respectively.
Dive heart rates are mean values averaged over the entire dive duration.
Minimum instantaneous heart rates are the reciprocal of the single longest heart beat interval during each dive.
All heart rates related to diving are the mean values taken from dives lasting between 18 and 22 s (N=6 dives per cormorant).
*Significantly different from the resting heart rate values.
‡Significant difference between 'shallow diving' and 'deep diving'.

To calculate resting heart rate, the instantaneous heart rate over the entire resting trial was plotted against time. Heart rate was elevated because of handling at the beginning of the trial but fell to a baseline value within 10 min. When heart rate had reached a stable level, a period of 20 min was chosen for the calculation of a single resting heart rate value. A mean value was calculated from all interbeat intervals during that selected period and converted into heart rate.

Dive behaviour was investigated by computing dive duration, surface interval duration and dive/pause ratios for five birds. For each cormorant in each different treatment (in both the shallow and deep dive tanks), ten dives and the subsequent surface intervals were selected at random from diving bouts in which birds performed at least three successive feeding dives. Only dives with a clear foraging intention (see above), lasting between 15 and 30 s and for which the subsequent surface interval did not mark the end of a dive bout were included in the analysis.

One-way repeated-measures analysis of variance (ANOVA) with Student–Newman–Keuls pairwise multiple comparisons was used for comparison among different treatments during shallow diving (air, hyperoxia, hypoxia, etc.) and among different phases of the dive (pre-dive, dive, post-dive). When single comparisons were made, as in comparing values obtained from the two treatments during deep diving (normoxia and hypoxia), Student's paired *t*-test was used. Significance was accepted at $P<0.05$. The average relationship between mean dive heart rate and dive duration that takes into account variability between subjects was determined using repeated-measures multiple linear regression, with each cormorant being assigned a unique index variable. All mean values are presented with the standard deviation (± S.D.).

Results

Cardiac responses to shallow and deep diving

The grand mean for resting heart rate from five birds was 137.9±17.5 beats min^{-1} (Table 1). Before the first shallow dive in a series, when birds floated quietly on the surface, heart rate was 200–250 beats min^{-1}, increasing just before submersion. Immediately upon submersion, heart rate dropped from a pre-dive rate of 380.6±12.6 beats min^{-1} to approximately 200–250 beats min^{-1} (Figs 2, 3). After the initial drop, heart rate continued to decline more gradually and reached a rate around or even below the resting level 10 s into the dive. Towards the end of the dive, heart rate increased in anticipation of surfacing, leading to a post-dive heart rate of 397.2±19.6 beats min^{-1} (Figs 2, 3). Mean dive heart rate during shallow diving
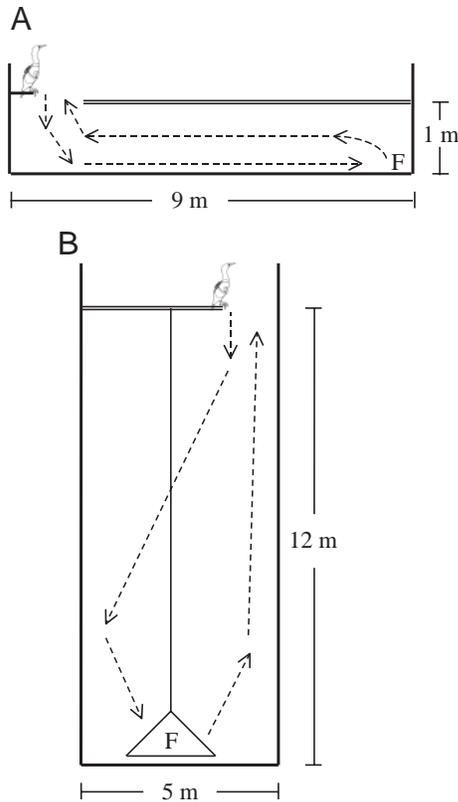
Fig. 1. Side view and dimensions of the shallow (A) and deep (B) dive tanks. 'F' indicates the feeding spot, where birds picked up chopped herring pieces. The approximate underwater routes taken by the birds are indicated by the dashed lines, with the arrowheads indicating the direction of locomotion.

$(163.2\pm14.0\,\mathrm{beats\,min^{-1}})$ was significantly above the resting heart rate (Table 1). Minimum heart rate during shallow diving $(88.4\pm16.1\,\mathrm{beats\,min^{-1}})$, however, was significantly below the resting value in all birds. The degree of the decline in heart rate during shallow diving was dependent on dive duration. Mean dive heart rate was higher during short dives than during long dives (Fig. 4).

When diving deeper than 1 m, cormorants displayed a strikingly different cardiac response (Figs 2, 3). Pre- and post-dive tachycardia were comparable with values in the shallow dive situation (Table 1), as was the initial drop in heart rate upon submersion (Fig. 2). During the dive, however, heart rate declined at a much slower rate compared with shallow diving (Figs 2, 3). The mean dive heart rate $(216.4\pm7.7\,\mathrm{beats\,min^{-1}})$ and the minimum heart rate during deep diving $(159.9\pm11.5\,\mathrm{beats\,min^{-1}})$ were significantly higher than the resting heart rate and significantly higher than the respective values during shallow diving (Table 1).

Cardiac responses to diving after breathing various gas mixtures

Manipulating the oxygen content of the inspired air before diving had marked effects on heart rate during diving (Fig. 5). Exposure to the hyperoxic gas mixture in the shallow dive tank increased the mean dive heart rate significantly (to $195.4\pm13.0\,\mathrm{beats\,min^{-1}}$) compared with the normoxic control situation $(174.3\pm13.4\,\mathrm{beats\,min^{-1}})$. Upon submersion, heart rate initially fell to a similar level as in the control situation, but did not decline appreciably during the rest of the dive (Fig. 6). Exposure to the hypoxic gas mixture reduced the mean dive heart rate significantly in both the shallow (to $154.0\pm11.5\,\mathrm{beats\,min^{-1}})$
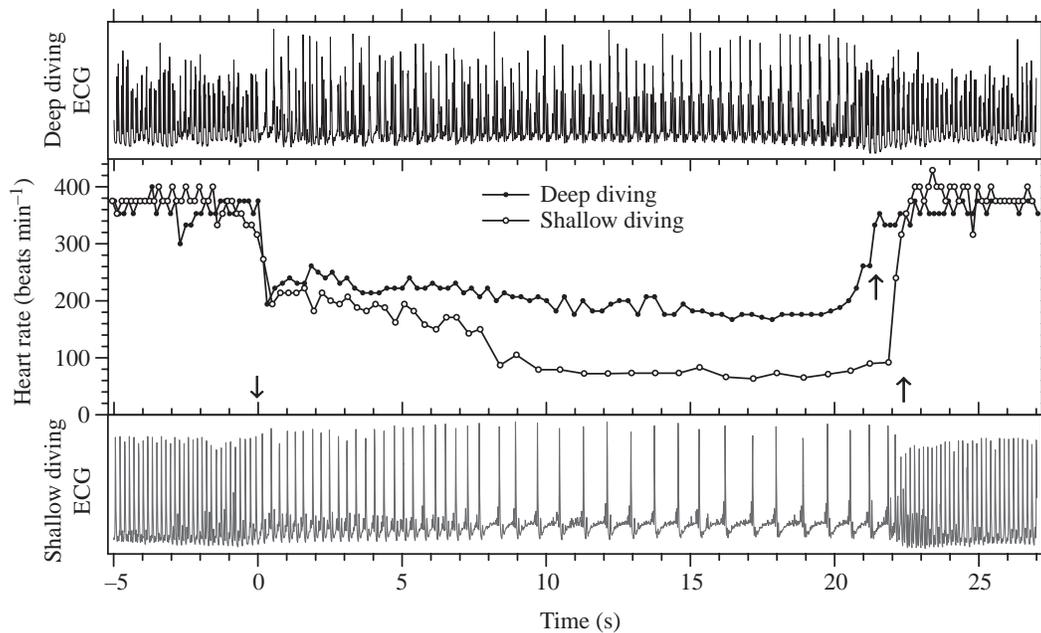

Fig. 2. Electrocardiogram (ECG) record and instantaneous heart rate during individual deep and shallow dives of one double-crested cormorant. Top, the ECG during a deep dive; bottom, the ECG during a shallow dive. Corresponding heart rates (beats min⁻¹) are shown in the centre. Submersion and emersion are indicated by the descending and ascending arrows, respectively.
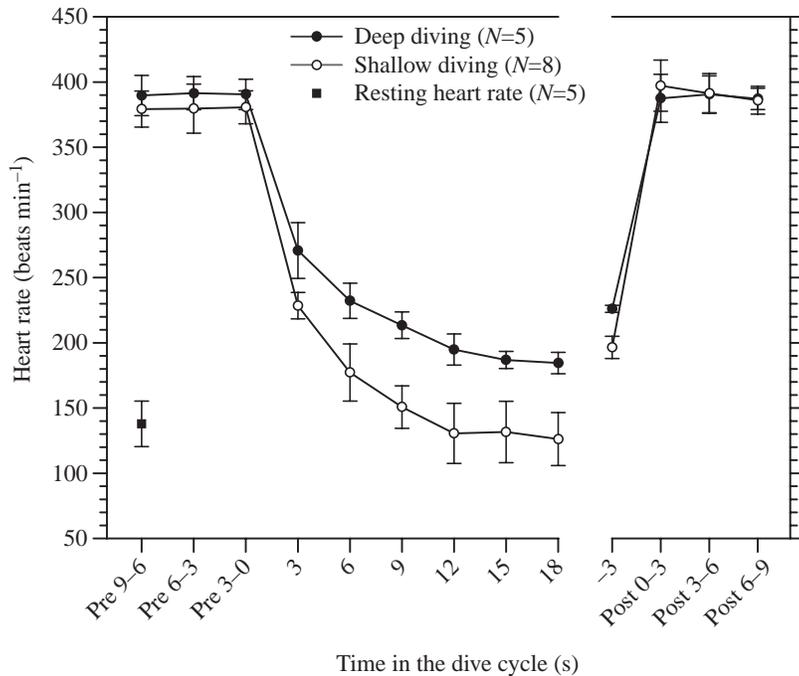
Fig. 3. Heart rate before, during and after deep and shallow diving. Values are means ± S.D. averaged over 3 s intervals from six dives per bird (all dives 18–22 s). N depicts the number of individuals used. '–3' refers to the last 3 s of the dive, preceding emergence. For comparison, resting heart rate is indicated.
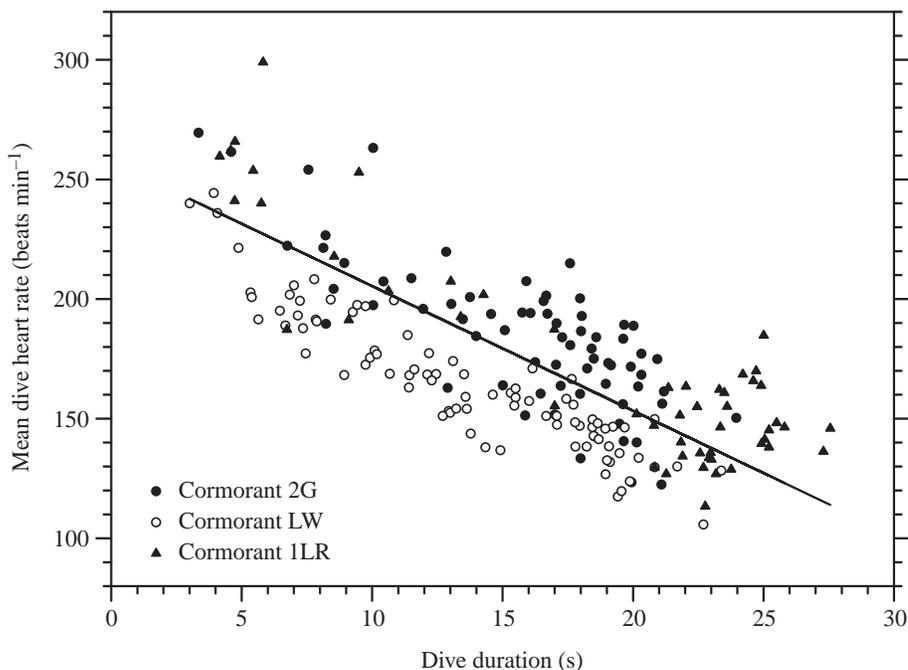

Fig. 4. Mean dive heart rate *versus* dive duration for three double-crested cormorants during shallow diving (N=208). Values for each cormorant demonstrated a significant negative relationship, with r^2 ranging from 0.60 to 0.84. The regression line is the average relationship for all cormorants and is described by y=257.48–5.21x, where y is mean dive heart rate and x is dive duration (r^2=0.761).

and the deep (to 153.3±17.1 beats min^{-1}) dive situation compared with normoxic dives (Fig. 5). The course of the heart rate response during diving after hypoxic exposure was almost identical in both situations, and heart rate stayed well below the control level throughout the dives (Figs 6, 7). Also, hypoxia reduced pre- and post-dive heart rates, with a more pronounced reduction in the deep dive situation, where the level of hypoxia was more severe. Inspiration of elevated levels of CO_2 before diving in the shallow dive tank had little effect on mean dive heart rate (Fig. 5) or the time course of the heart rate response. In the case of the hypercapnic hypoxic exposure, no further reduction in dive heart rate, beyond the response seen after hypoxic exposure alone, was detectable.

To ensure that diving inside the PVC cage *per se* had no effect on the cardiac responses before or during diving, mean pre-dive and dive heart rates of five birds (for which data from shallow and deep diving were available) diving inside the cage after exposure to air (control situation) were compared with dives made without the cage. In both dive regimes, diving with or without the cage had no effect on the mean pre-dive heart rate or the mean dive heart rate.

Dive behaviour

There was no significant difference in the mean dive duration of normoxic birds, whether diving in the shallow or the deep dive tank (20.43±0.83 s and 20.29±1.37 s respectively) (Fig. 8). The duration of the surface interval following a dive, however, was significantly different (shallow 9.08±1.45 s, deep 15.05±3.37 s), resulting in a higher dive/pause ratio during shallow diving (2.54±0.33 *versus* 1.48±0.38).

Manipulation of the breathing gases had no significant effect on the dive duration of birds in any of the trials (Fig. 8). Surface interval duration and the resulting dive/pause ratio, however, were strongly and significantly affected after different gas exposures (Fig. 8). Hyperoxia in the shallow dive tank reduced the time spent at the surface between dives, thereby increasing the proportion of the dive cycle spent under water. This was reflected in the highest dive/pause ratio observed in this study (4.02±0.57). Hypoxia produced the opposite effects, increasing the surface interval duration and, hence, reducing the dive/pause ratio, especially in the deep
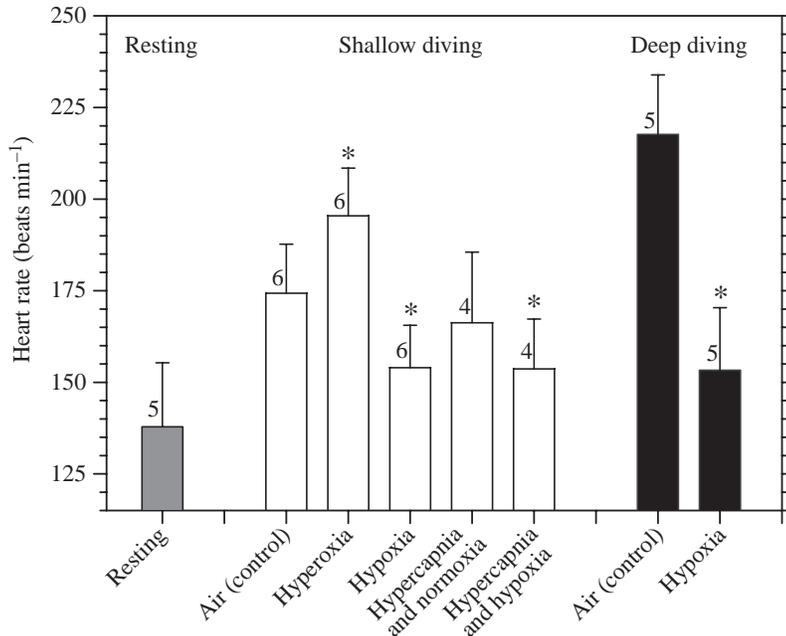
Fig. 5. Heart rate during resting, shallow and deep diving and after exposure to different levels of O_2 and CO_2. Values are means + s.D. from six dives per bird (all dives 18–22 s); the values above of the columns indicate the number of individuals used; resting heart rate was calculated from a 20 min section of ECG recording per bird. For the gas mixtures used, see Materials and methods. *Significantly different from the respective control values (air).
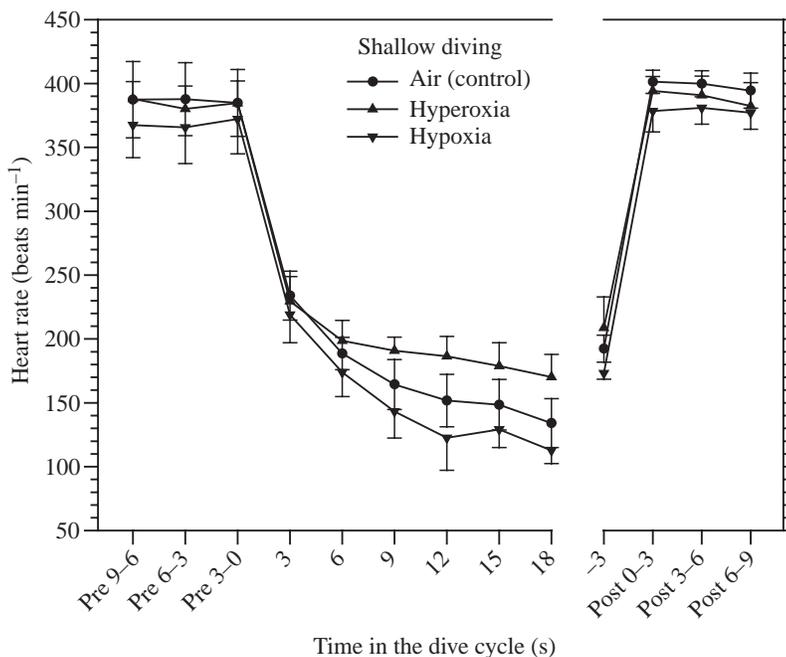

Fig. 6. Heart rate before, during and after shallow diving following exposure to different ambient oxygen levels. Values are means ± s.D. averaged over 3 s intervals from six dives per bird (all dives 18–22 s; *N*=6 birds). '–3' refers to the last 3 s of the dive, preceding emergence. For gas mixtures used, see Materials and methods.

dive situation. Exposure to elevated levels of CO_2 in the shallow dive tank increased the post-dive surface interval compared with the control situation. This increase was especially remarkable in the hypercapnic/normoxic exposure since changes in the hypercapnic/hypoxic exposure were of the same magnitude as in hypoxic exposure alone.

Discussion

Cardiac responses

Our study shows that double-crested cormorants, like many other diving vertebrates, undergo marked cardiac changes during their daily foraging activities. The resting heart rate of our cormorants was similar to the predicted resting rate for a 2.36 kg bird (127.9 beats min^{-1}) on the basis of allometry (Calder, 1968) and the 'basal' heart rate of double-crested cormorants recorded at night (100–120 beats min^{-1}) (Kanwisher et al., 1981). The cardiac responses observed in voluntarily shallow- and deep-diving cormorants in the present study consisted of a marked decrease in heart rate during diving compared with pre-dive heart rate (57.0±3.0 % decline in shallow dives; 44.4±1.6 % decline in deep dives). When compared with the resting heart rate, however, the cardiac changes associated with voluntary diving should perhaps be described as a pre- and post-dive tachycardia rather than a diving bradycardia. Heart rate rarely fell below the resting level during shallow diving and never during deep diving (Fig. 3) (Table 1). Stephenson et al. (Stephenson et al., 1986) defined 'bradycardia' as a reduction in heart rate below the value that is 'normal' for a given level of activity and suggested that surface swimming is probably the closest approximation to diving exercise, at least in ducks. Although heart rate during surface swimming was not systematically recorded in our study, occasional recordings revealed a heart rate in the range of 200–250 beats min^{-1}, i.e. similar to the heart rate of double-crested cormorants during 'moderate activity' reported by Kanwisher et al. (1981). Hence, the cardiac responses of double-crested cormorants during deep diving do not seem to comprise a bradycardia. During shallow diving, however, a bradycardia is evoked. However, the cardiac decline during both voluntary shallow and deep diving was less drastic than the extreme bradycardia observed during forced submergence (Mangalam and Jones, 1984; Jones and Larigakis, 1988). This difference in cardiac response to voluntary diving and forced submergence is already present during the first ever submergence of double-crested cormorant chicks (Enstipp et al., 1999).

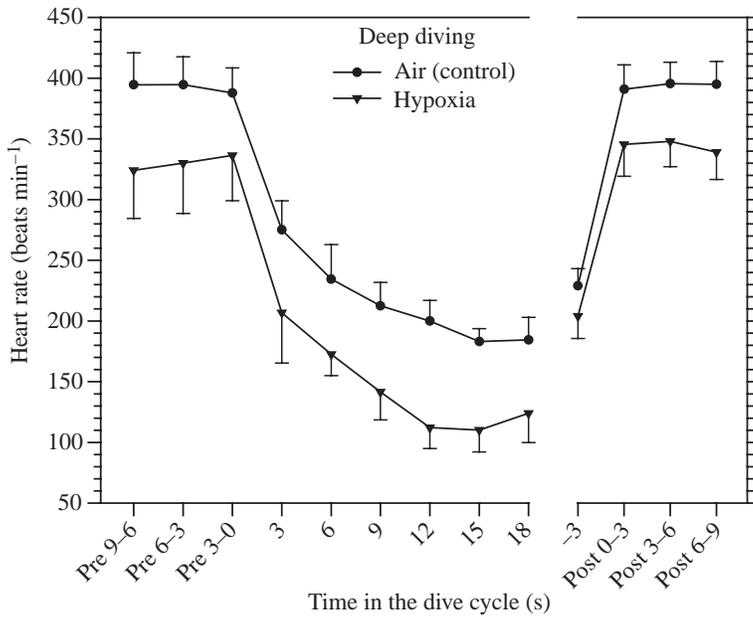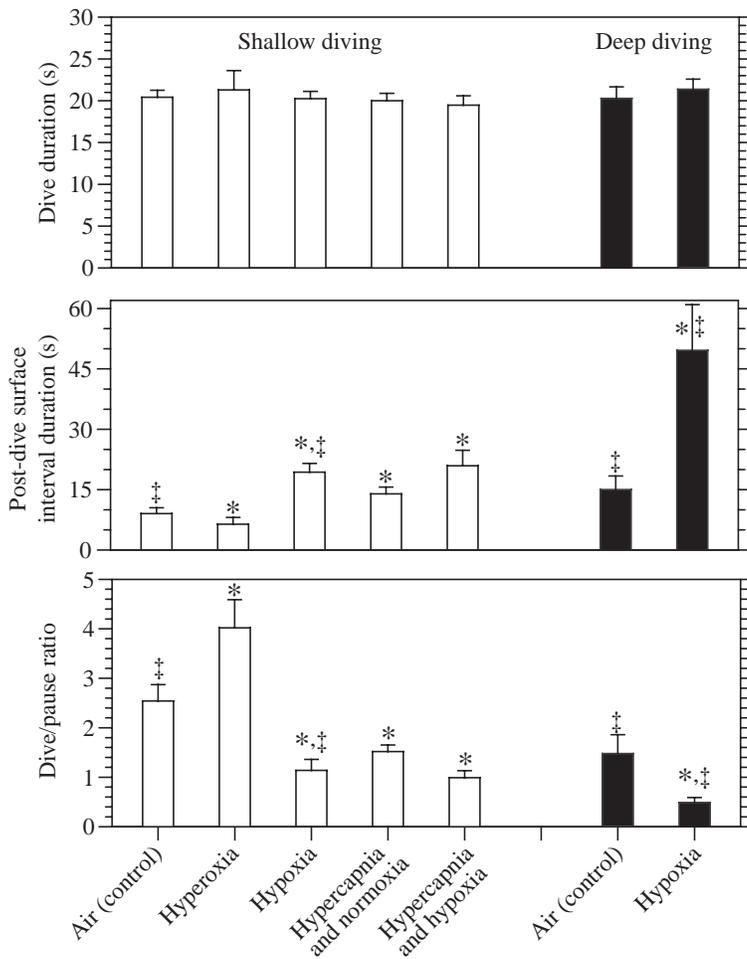The cardiac responses of double-crested

Fig. 7. Heart rate before, during and after deep diving following exposure to different ambient oxygen levels. Values are means ± S.D. averaged over 3 s intervals from six dives per bird (all dives 18–22 s; $N=5$ birds). '–3' refers to the last 3 s of the dive, preceding emergence. For gas mixtures used, see Materials and methods.

cormorants during deep diving were comparable with the moderate heart rate changes displayed by diving ducks and Humboldt and Adélie penguins during shallow diving (Stephenson et al., 1986; Furilla and Jones, 1986, 1987; Butler and Woakes, 1976, 1979, 1984; Culik, 1992). They were also similar to heart rates reported for two freely diving double-crested cormorants (Kanwisher et al., 1981).

The greater cardiac response during shallow diving, compared with deep diving, closely resembled the response shown by tufted ducks making 'extended' horizontal dives in a covered 2.8 m deep tank (Stephenson et al., 1986). In these dives, averaging 41.4 s, the heart rate of ducks declined steadily after approximately 7.5 s, reaching sub-resting levels after approximately 27.5 s. These tufted ducks, like our cormorants during shallow diving, had to swim actively towards and away from the feeding spot, while cormorants during vertical deep diving returned to the surface more or less passively. Hence, it is conceivable that the energetic costs of shallow horizontal dives might be increased, compared with deep, vertical dives. First, passive surfacing from deep vertical dives will reduce locomotor effort and save energy during these dives. Second, buoyancy during deep vertical diving will be reduced, compared with shallow horizontal diving, further decreasing energy expenditure (Lovvorn and Jones, 1994). In lesser scaups (*Aythya affinis*) performing shallow (1.5 m) but vertical dives, buoyancy is the dominant factor determining dive costs (Stephenson, 1994). Loss of air from the plumage layer and compression of the buoyant air spaces due to hydrostatic pressure decrease buoyancy at depth in these lesser scaups by 32 % compared with the surface (Stephenson, 1994). Third, swimming close to the surface during shallow horizontal diving (as observed in our cormorants) will increase drag and add to the energetic cost of these dives (Hertel, 1969). Hence, ducks and cormorants performing shallow horizontal dives face an energetically challenging situation. If oxygen is used up at a faster rate during shallow horizontal diving than during deep vertical diving, Pa_{O_2} would be depleted more rapidly and evoke a stronger cardiac response *via* intravascular chemoreceptors during these shallow dives.

The difference in the heart rate response to shallow and deep diving might be further accounted for by the effects of pressure changes associated with deep diving

Fig. 8. Dive behaviour associated with shallow (open columns) and deep (filled columns) diving and after exposure to different levels of O_2 ($N=5$ birds) and CO_2 ($N=4$ birds). Values are means + S.D. from 10 dive cycles per bird. *Significantly different from the respective control (air) values. ‡A significant difference between 'shallow diving' and 'deep diving'.

on the cardio-pulmonary system. Birds diving to depth will experience a compression hyperoxia during descent (Lanphier and Rahn, 1963; Kooyman et al., 1973; Qvist et al., 1986). If Pa_{O_2} stays elevated during this phase of the dive (Qvist et al., 1993), any chemoreceptor-mediated reinforcement of the initial reduction in heart rate will be delayed as a consequence. Although the compression hyperoxia during descent will be accompanied by an increase in Pa_{CO_2}, this seems to have little effect on the cardiac response expressed (see below). Energetic savings, due to the reduced locomotor effort during the bottom (reduced buoyancy at depth) and ascent (passive surfacing) phases of deep-diving cormorants, will help to maintain a relatively high Pa_{O_2}, further delaying any chemoreceptor contribution to the cardiac response. Hence, heart rate stayed well above the resting level during these relatively short dives (18–22 s). It is conceivable that in longer dives heart rate will fall more drastically, because Pa_{O_2} will drop, provoking a chemoreceptor-driven cardiac inhibition. In fact, marked cardiac responses were observed in much longer (range 140–287 s) and deeper (range 35–101 m) dives of South Georgian shags diving at sea (Bevan et al., 1997). In these dives, heart rate fell to a level near the resting value in the early phase (after approximately 30 s) and reached sub-resting levels later in the dive. In contrast to this deep-diving scenario, shallow-diving birds will not experience a compression hyperoxia; hence, Pa_{O_2} will decrease early in the dive (especially if shallow horizontal diving is, in fact, associated with increased energetic costs), enhancing any chemoreceptor-mediated cardiac inhibition.

During the ascent phase of deep dives, PA_{O_2} will fall rapidly (Lanphier and Rahn, 1963), potentially reversing the direction of oxygen transport (Olszowka and Rahn, 1987). Accordingly, there should be a drop in Pa_{O_2}, which would increase the chemoreceptor drive and, in turn, reduce heart rate. In the present study, however, heart rate did not decrease further during ascent and actually increased just before birds reached the surface. Obviously, other neurological inputs must override the chemoreceptor contribution during this phase of deep dives. In addition to possible influences of higher brain centres, anticipating the return to the surface, re-expansion of the respiratory system might activate pulmonary stretch receptors, which would in turn increase heart rate (Harrison, 1960; Kooyman, 1989). Increasing heart rate in anticipation of surfacing seems to be a usual feature of the cardiac response to voluntary diving in birds and mammals (Butler and Jones, 1997). For ringed seals (*Phoca hispida*), it has been shown that visual orientation is important in facilitating the anticipatory increase in heart rate during ascent (Elsner et al., 1989), which stresses the influence of components of the central nervous system above the reflex level.

In the only other laboratory study in which the heart rate of diving birds was recorded during dives of greatly varying depth (de Leeuw et al., 1998), tufted ducks showed no relationship between heart rate at different phases of the dive cycle and dive depth. Heart rate during diving was similar whether diving to 1.5 m (averaging 12.7 s) or to 5.5 m (averaging 26.5 s). In other words, compression hyperoxia did not seem to affect heart rate during diving. Since dive duration increased considerably with depth, however, this effect might have been masked by the effects of dive duration on heart rate. Descending to 5.5 m will take longer and, hence, will require more oxygen than descending to 1.5 m. As a consequence, the greater drop in Pa_{O_2} due to the longer time required to reach the bottom in deep dives might counteract the effects of an increased Pa_{O_2}, due to compression hyperoxia, on heart rate.

Taken together, the following findings seem to suggest that intravascular chemoreceptors are important in mediating the cardiac responses during voluntary diving in double-crested cormorants. First, the secondary, more gradual, decline in heart rate observed a few seconds after initiation of a shallow dive (Fig. 2) might reflect an increase in chemoreceptor discharge frequency caused by a reduction in Pa_{O_2}. Second, the significant linear relationship between mean dive heart rate and dive duration found for three birds during shallow diving (Fig. 4) suggests that a gradual mechanism facilitates the reduction in heart rate, again pointing at chemoreceptors. Third, in deep dives, during which Pa_{O_2} will be elevated initially as a result of hydrostatic compression, heart rate stayed relatively stable throughout the dive or declined at a much slower rate compared with shallow dives.

Alteration of inspired gas composition

The results obtained from experimental manipulation of the oxygen content in the inspired air before diving further emphasise the importance of intravascular chemoreceptors for cardiac control during voluntary diving in double-crested cormorants. Our findings are in agreement with results reported for voluntarily diving tufted and redhead (*Aythya americana*) ducks. In tufted ducks, chronic bilateral denervation of the carotid bodies had no effect on the immediate reduction in heart rate upon submersion (Butler and Woakes, 1982b). Heart rate was, however, significantly elevated towards the end of spontaneous dives. Similarly, Furilla and Jones (1986) found that altering the level of O_2 breathed by redhead ducks before voluntary submersion had no effect on heart rate early in the dive (after 2–5 s of submergence). Dive duration, however, was positively correlated with the level of oxygen in the inspired air. Although Butler and Stephenson (1988) found that the heart rate of tufted ducks during diving was unaffected by the inspired gas composition in control and carotid-body-denervated ducks, dive heart rate was increased in carotid-body-denervated ducks irrespective of the gas mixture breathed beforehand. From these studies, it was generally concluded that carotid body chemoreceptors might play only a minor role in the control of cardiac responses to diving, at least under the circumstances investigated (short and shallow vertical dives).

In the present study, however, alteration of the oxygen content in the inspired air before diving produced strong and significant effects on the heart rate response during shallow (horizontal) and deep (vertical) diving. It might be argued that, because dive duration in the duck studies was short, a full

chemoreceptor response could not develop. However, the differences in heart rate response of cormorants to alteration of inspired gas composition were established early during shallow diving (Fig. 6). In the case of hypoxic exposure before deep diving, the difference was established even before submersion (Fig. 7). Butler and Stephenson (1988) found that in an experimental set-up in which tufted ducks performed 'extended' horizontal dives – an almost identical situation to our cormorants performing shallow dives – the bradycardia during diving was significantly slowed following carotid body denervation. Hence, they concluded that, under these circumstances, carotid body chemoreceptors might become more important.

Exposure to hypoxia effectively reduced pre- and post-dive heart rates of double-crested cormorants, although this effect was significant only for the deep diving situation, where the level of hypoxia was more severe. This is unlike the situation in tufted ducks, where hypoxic exposure significantly elevated pre- and post-dive heart rates in both control and carotid-body-denervated birds (Butler and Stephenson, 1988). It seems, however, that, although breathing gas with a lowered oxygen content causes a consistent increase in pulmonary ventilation, the cardiovascular effects are variable, depending on species and the degree of arterial hypoxaemia and hypocapnia (Daly, 1997).

Hypercapnia had no significant effect on the diving heart rate of double-crested cormorants (Fig. 5), which is similar to the situation found in Pekin (*Anas platyrhynchos*) and tufted ducks. Jones et al. (1982) reported that CO_2 contributed little (approximately 20%) to the bradycardia accounted for by the carotid bodies in forcibly submerged Pekin ducks, while the strongest contribution came from O_2 (approximately 65%). Similarly, Butler and Stephenson (1988) found that hypercapnia had no effect on the diving heart rate of voluntarily diving tufted ducks. While their ducks showed a significant reduction in pre- and post-dive heart rates after hypercapnic exposure, this was not the case in our cormorants. This difference might be due to the stronger degree of hypercapnic exposure in the tufted duck study.

Dive behaviour

The dive patterns observed during voluntary shallow diving in the present study are very similar to dive patterns reported for double-crested cormorants foraging in the wild. Ross (1974) observed double-crested cormorants diving in water 1.5–7.9 m deep. Dive and surface interval duration were 25.1 and 10.3 s, respectively, resulting in a dive/pause ratio (which is generally used as an index of dive efficiency) of 2.43. While the dive durations of our cormorants during shallow and deep diving are longer than those reported for double-crested cormorants foraging in shallow catfish ponds (King et al., 1995), they are much shorter than the maximum dive duration (70 s) reported for this species (Munro, 1927). A wide range of dive/pause ratios (between 1.95 and 4.36) was reported by Cooper (1986) in his review of the diving patterns of 19 *Phalacrocorax* species. In the majority of *Phalacrocorax*

species, however, dive duration during foraging typically exceeds the subsequent surface interval by a factor of 2–3 (Ross, 1974; Cooper, 1986; Ainley et al., 1990), except for very low dive/pause ratios (0.3–0.4) reported for South Georgian shags diving to great depth (maximum 116 m) (Croxall et al., 1991).

Dive durations in the present study did not differ during shallow and deep diving (Fig. 8). Why the birds increased the subsequent surface interval in the deep dive situation compared with the shallow dive situation is not easily explained. Since the birds were foraging on the same prey items (herring pieces), it is unlikely that increased surface times in the deep dive tank were associated with longer prey handling times. Considering the less dramatic cardiac changes associated with the deep diving situation, one could speculate about the functional significance of a dive bradycardia in facilitating efficient dive patterns. The rapid decline in heart rate observed during shallow diving presumably reflects the conservation of oxygen. If birds use less of their total oxygen store during the dive, they will be able to replenish these stores faster once ventilation resumes at the surface. A shorter post-dive surface interval would increase the proportion of the dive cycle spent under water and, hence, dive efficiency.

Alteration of inspired gas composition

Alteration of inspired gas composition (and hence blood gas tensions) had no effect on dive duration, which might be due to limitations of our experimental arrangement. Birds in both tanks did not have to chase prey under water but merely picked up a single herring piece and returned to the surface. Hence, the actual 'bottom time' was relatively short, and dive duration was dictated by the transit time. Since only dives with an obvious foraging intention (i.e. birds swam to the feeding spot) were included in the analysis, it is not surprising to find that dive duration stayed constant irrespective of the composition of the breathing gas administered. With the dive duration being dictated by the experimental arrangement, birds were left only with the possibility of adjusting the duration of the subsequent surface interval. The adjustment of surface interval duration in accordance with the gas mixture administered (Fig. 8) clearly illustrates the importance of blood gas levels (O_2 and CO_2) in controlling the dive behaviour of double-crested cormorants.

This is similar to the situation reported for redhead and tufted ducks (Furilla and Jones, 1986; Butler and Stephenson, 1988). The diving ducks in these studies, being stationary feeders that ingest food under water, could alter their food intake by adjusting dive duration (unlike the cormorants in our study). Accordingly, the dive duration of voluntarily diving redhead ducks increased as the level of O_2 in the inspired air increased (Furilla and Jones, 1986). In tufted ducks, dive duration decreased after hypoxic and after hypercapnic exposure, while hypercapnia increased the surface interval duration as well (Butler and Stephenson, 1988). The dive efficiencies of double-crested cormorants in the present study follow the same general trend as those for tufted ducks: hypoxia and hypercapnia both decrease dive efficiency, while

hyperoxia increases efficiency. The variance in dive/pause ratios in our study is probably explained by a change in recovery time in accordance with the O_2 concentration in the inspired air. Refuelling O_2 stores in a hypoxic environment will take longer than in a normoxic environment, necessitating longer surface intervals. Refuelling in a hyperoxic environment should be accelerated, decreasing surface interval duration. This might explain the short surface interval duration (resulting in the highest dive/pause ratio) after hyperoxic exposure in the shallow dive tank. Elevated heart rates during these dives (compared with the control) should lead to a greater O_2 depletion, which would necessitate longer surface intervals to refuel O_2 stores. The high O_2 concentration in the inspired air, however, might allow for faster refuelling of the O_2 stores, effectively reducing surface interval duration.

Butler and Stephenson (1988) suggested that surface interval duration is controlled primarily by CO_2 concentration and that O_2 concentration is the primary determinant of dive duration. Such a clear distinction is not possible in the present study because, given the experimental arrangement, the birds did not adjust their dive duration. Diving activity of ducks ceases at a 'critical' O_2 or CO_2 concentration in the inspired air (Furilla and Jones, 1986; Butler and Stephenson, 1988). Similarly, when the O_2 concentration in the inspired air fell below 8 %, our cormorants would not dive. The change in dive behaviour after hypoxic exposure in the deep dive situation was impressive. Surface interval duration increased by a factor of 4, resulting in a dive/pause ratio comparable with that of South Georgian shags performing much longer and deeper dives.

In conclusion, our study suggests that blood oxygen level is an important stimulus that allows double-crested cormorants to adjust their cardiac and behavioural system in accordance with the physiological restraints imposed during foraging. We propose that carotid body chemoreceptors, sensing arterial oxygen tensions, are the most likely mechanism facilitating the observed cardiac and behavioural responses. It is possible that these cardiac and behavioural adjustments to diving enable double-crested cormorants to maximise the time spent under water and, hence, potential foraging time.

References

Ainley, D. G., Strong, C. S., Penniman, T. M. and Boekelheide, R. J. (1990). The feeding ecology of Farallon seabirds. In *Seabirds of the Farallon Islands* (ed. D. G. Ainley and R. J. Boekelheide), pp. 51–127. Stanford, CA: Stanford University Press.

Andrews, R. D. (1998). Instrumentation for the remote monitoring of physiological and behavioral variables. *J. Appl. Physiol.* **85**, 1974–1981.

Ashmole, N. P. (1971). Sea bird ecology and the marine environment. In *Avian Biology*, vol. 1 (ed. D. S. Farner and J. R. King), pp. 223–286. New York, London: Academic Press.

Bannasch, R., Wilson, R. P. and Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. Exp. Biol.* **194**, 83–96.

Bevan, R. M., Boyd, I. L., Butler, P. J., Reid, K., Woakes, A. J. and Croxall, J. P. (1997). Heart rates and abdominal temperatures of free-ranging South Georgian shags, *Phalacrocorax georgianus. J. Exp. Biol.* **200**, 661–675.

Butler, P. J. and Jones, D. R. (1997). Physiology of diving in birds and mammals. *Physiol. Rev.* **77**, 837–899.

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

Butler, P. J. and Woakes, A. J. (1976). Changes in heart rate and respiratory frequency associated with spontaneous submersion of ducks. In *Biotelemetry III* (ed. T. B. Fryer, H. A. Miller and H. Sandler), pp. 215–218. New York, San Francisco, London: Academic Press.

Butler, P. J. and Woakes, A. J. (1979). Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *J. Exp. Biol.* **79**, 283–300.

Butler, P. J. and Woakes, A. J. (1982a). Control of heart rate by carotid body chemoreceptors during diving in tufted ducks. *J. Appl. Physiol.* **53**, R1405–R1410.

Butler, P. J. and Woakes, A. J. (1982b). Telemetry of physiological variables from diving and flying birds. *Symp. Zool. Soc. Lond.* **49**, 107–128.

Butler, P. J. and Woakes, A. J. (1984). Heart rate and aerobic metabolism in Humboldt penguins, *Spheniscus humboldti*, during voluntary dives. *J. Exp. Biol.* **108**, 419–428.

Calder, W. A. (1968). Respiratory and heart rates of birds at rest. *Condor* **70**, 358–365.

Cooper, J. (1986). Diving patterns of cormorants Phalacrocoracidae. *Ibis* **128**, 562–570.

Croxall, J. P., Naito, Y., Kato, A., Rothery, P. and Briggs, D. R. (1991). Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps. J. Zool., Lond.* **225**, 177–199.

Culik, B. (1992). Diving heart rates in Adélie penguins (*Pygoscelis adeliae*). *Comp. Biochem. Physiol.* **102A**, 487–490.

Daly, M. de B. (1997). *Peripheral Arterial Chemoreceptors and Respiratory–Cardiovascular Integration*. Monographs of the Physiological Society no. 46. Oxford: Clarendon Press. 739pp.

De Leeuw, J. J., Butler, P. J., Woakes, A. J. and Zegwaard, F. (1998). Body cooling and its energetic implications for feeding and diving of tufted ducks. *Physiol. Zool.* **71**, 720–730.

Elsner, R., Wartzok, D., Sonafrank, N. B. and Kelly, B. P. (1989). Behavioral and physiological reactions of arctic seals during under-ice pilotage. *Can. J. Zool.* **67**, 2506–2513.

Enstipp, M. R., Andrews, R. D. and Jones, R. D. (1999). Cardiac responses to first ever submergence in double-crested cormorant chicks (*Phalacrocorax auritus*). *Comp. Biochem. Physiol.* **124A**, 523–530.

Furilla, R. A. and Jones, D. R. (1986). The contribution of nasal receptors to the cardiac response to diving in restrained and unrestrained redhead ducks (*Aythya americana*). *J. Exp. Biol.* **121**, 227–238.

Furilla, R. A. and Jones, D. R. (1987). The relationship between dive and pre-dive heart rates in restrained and free dives by diving ducks. *J. Exp. Biol.* **127**, 333–348.

Harrison, R. J. (1960). Experiments with diving seals. *Nature* **188**, 1068–1070.

Hertel, H. (1969). Hydrodynamics of swimming and wave-riding dolphins. In *The Biology of Marine Mammals* (ed. H. T. Andersen), pp. 31–63. New York: Academic Press.

Johnsgard, P. A. (1993). *Cormorants, Darters and Pelicans of the World*. Washington, London: Smithsonian Institution Press. 445pp.

Jones, D. R. and Larigakis, S. (1988). The effect of breathing oxygen and air on diving bradycardia in cormorants (*Phalacrocorax auritus*). *J. Exp. Biol.* **136**, 499–502.

Jones, D. R., Milsom, W. K. and Gabbott, G. R. J. (1982). Role of central

and peripheral chemoreceptors in diving responses of ducks. *Am. J. Physiol.* **243**, R537–R545.

Kanwisher, J. W., Gabrielsen, G. and Kanwisher, N. (1981). Free and forced diving in birds. *Science* **211**, 717–719.

King, D. T., Glahn, J. F. and Andrews, K. J. (1995). Daily activity budgets and movements of winter roosting double-crested cormorants determined by biotelemetry in the Delta region of Mississippi. In *The Double-Crested Cormorant: Biology, Conservation and Management* (ed. D. N. Nettleship and D. C. Duffy). *Col. Waterbirds* **18 (special publication 1)**, 152–157.

Kooyman, G. L. (1989). *Diverse Divers: Physiology and Behavior.* Berlin, Heidelberg: Springer Verlag. 200pp.

Kooyman, G. L., Schroeder, J. P., Greene, D. G. and Smith, V. A. (1973). Gas exchange in penguins during simulated dives to 30 and 68 m. *Am. J. Physiol.* **225**, 1467–1471.

Lanphier, E. H. and Rahn, H. (1963). Alveolar gas exchange during breath-hold diving. *J. Appl. Physiol.* **18**, 471–477.

Lovvorn, J. R. and Jones, D. R. (1994). Biomechanical conflicts between adaptations for diving and aerial flight in estuarine birds. *Estuaries* **17**, 62–75.

Mangalam, H. J. and Jones, D. R. (1984). The effects of breathing different levels of O_2 and CO_2 on the diving responses of ducks (*Anas platyrhynchos*) and cormorants (*Phalacrocorax auritus*). *J. Comp. Physiol. B* **154**, 243–247.

Munro, J. A. (1927). Observations on the double-crested cormorant (*Phalacrocorax auritus*) on Lake Manitoba. *Can. Field-Nat.* **41**, 102–108.

Olszowka, A. J. and Rahn, H. (1987). Breath-hold diving. In *Hypoxia and Cold* (ed. J. R. Sutton, C. S. Houston and G. Coates), pp. 417–428. New York: Praeger.

Qvist, J., Hill, R. D., Schneider, R. C., Falke, K. J., Liggins, G. C., Guppy, M., Elliott, R. L., Hochachka, P. W. and Zapol, W. M. (1986). Hemoglobin concentrations and blood gas tensions of free-diving Weddell seals. *J. Appl. Physiol.* **61**, 1560–1569.

Qvist, J., Hurford, W. E., Park, Y. S., Radermacher, P., Falke, K. J., Ahn, D. W., Guyton, G. P., Stanek, K. S., Hong, S. K., Weber, R. E. and Zapol, W. M. (1993). Arterial blood gas tensions during breath-hold diving in the Korean ama. *J. Appl. Physiol.* **75**, 285–293.

Robertson, I. (1974). The food of nesting double-crested and pelagic cormorants at Mandarte Island, British Columbia, with notes on feeding ecology. *Condor* **76**, 346–348.

Ross, R. K. (1974). A comparison of the feeding and nesting requirements of the great cormorant (*Phalacrocorax carbo* L.) and double-crested cormorant (*P. auritus* Lesson) in Nova Scotia. *Proc. N.S. Inst. Sci.* **27**, 114–132.

Stephenson, R. (1994). Diving energetics in lesser scaup (*Athyta affinis*, Eyton). *J. Exp. Biol.* **190**, 155–178.

Stephenson, R., Butler, P. J. and Woakes, A. J. (1986). Diving behaviour and heart rate in tufted ducks (*Aythya fuligula*). *J. Exp. Biol.* **126**, 341–359.

Wanless, S., Harris, M. P. and Morris, J. A. (1992). Diving behaviour and diet of the blue-eyed shag at South Georgia. *Polar Biol.* **12**, 713–719.