

SHORT COMMUNICATION  
THE EFFECT OF BREATHING OXYGEN AND AIR ON  
DIVING BRADYCARDIA IN CORMORANTS  
(*PHALACROCORAX AURITUS*)

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Cardiovascular chemoreceptors are crucial for the development of forced diving responses in dabbling ducks such as the mallard (*Anas platyrhynchos*). Denervation of the peripheral chemoreceptors or allowing the duck to breath 100 % oxygen before a forced dive eliminates or considerably delays the onset of noticeable bradycardia (Jones & Purves, 1970; Mangalam & Jones, 1984). These procedures have no effect on the level of bradycardia established after 10 s or so underwater in diving ducks or cormorants in forced dives (Butler & Woakes, 1982; Mangalam & Jones, 1984; Furilla & Jones, 1986). The afferent neural pathway for the dive response is unclear in cormorants, but in diving ducks it is the stimulation of nasal receptors with water that causes dive bradycardia (Furilla & Jones, 1986). When forced dives are prolonged, then peripheral chemoreceptors appear to affect heart rate in diving ducks. Heart rate is elevated in ducks (*Aythya fuligula*) in which the carotid body has been denervated, compared with intact ducks, after 50 s or so of forced submergence (Butler & Woakes, 1982). The purpose of the present study was to investigate whether chemoreflexes also influence heart rate in cormorants in forced dives of up to 120 s duration.

Experiments were performed on seven young (about 5-month-old) double-crested cormorants (*Phalacrocorax auritus*) caught on Mandarte Island, British Columbia some 2–3 months before the start of the experiments. The masses of the animals ranged from 2.2 to 2.6 kg and they were kept in a simulated 'natural' environment at the UBC Animal Care facility. Animals were unconfined and were allowed to dive on a freshwater pond. They were fed daily with fish supplemented with vitamin B<sub>1</sub>.

All dives were performed on restrained cormorants. Each bird was strapped to a table, ventral side down, by means of tapes. Care was taken to keep the tapes loose enough so that breathing was not impaired. The feet were tied back and the head held in a brace by rubber tubing. The open end of a plastic bag was stretched around the top of a funnel and the brace, holding the head, was inserted into the funnel through a hole in the base of the bag. The funnel could be filled, through

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the spout, from the cold-water tap (8°C). Between dives, either air or 100% oxygen was passed through the funnel and bag at a rate of 5 l min<sup>-1</sup>.

The electrocardiogram (ECG) was recorded between electrodes located near the heart and on the lower abdomen. Breathing was measured by an impedance converter with electrodes placed at the base of the neck and near the tail. ECG and respiration were recorded on a Harvard chart recorder.

A cormorant's head was held in the dive position in the funnel for at least 1 h before any dives started. A dive was initiated by simultaneously stopping the gas flow and starting the water flow; the water filled the funnel and submerged the bird's head within 3 s. The dive was terminated by removing the hose and draining the funnel. Each dive lasted from 1.5 to 2 min, and at least 10 min rest was allowed between dives. The bird's head was not raised throughout the course of the experiment, including the rest periods. Air and oxygen were administered randomly; when the gas was changed, the bird breathed the new gas for at least 10 min before the next dive. Heart and breathing rates were recorded before, during and after all dives.

When referring to values of variables in a group of animals, the values are given as means  $\pm$  S.E. of  $n$  observations on  $N$  animals. Between-group comparisons were made by comparing means at each time interval using a one-way analysis of variance (UBC ANOVAR) and Bartlett's chi-square test. Within-group comparisons, i.e. comparing mean heart rates at two different times, were made using a one-way ANOVA and the Tukey test (or 'honestly significant difference test'). In all comparisons 5% ( $P < 0.05$ ) was taken as the fiducial limit of significance.

The mean resting heart rates of cormorants breathing oxygen and air were not significantly different. At the start of forced diving, mean heart rates fell rapidly in both groups and were significantly below their respective pre-dive values after 5 s of submergence. Even at this time, the mean heart rate of cormorants that breathed oxygen before diving was significantly higher than that of birds that breathed air before diving. A significant difference between the mean heart rates of cormorants that breathed air or oxygen before diving was maintained for the rest of the dive (Fig. 1). After 10 s submergence, mean heart rates stabilized in both groups. No further significant changes in mean heart rates occurred, with dive time, in either group (Fig. 1). Minimum diving heart rate in cormorants that breathed oxygen before diving was  $83.4 \pm 6.9$  beats min<sup>-1</sup> and birds that breathed air had a minimum rate of  $53 \pm 2.9$  beats min<sup>-1</sup>.

Heart rate increased rapidly after surfacing and a tachycardia occurred which in cormorants that breathed oxygen before diving was significantly lower than that in air-breathing birds (Fig. 1). Heart rate usually returned to the pre-dive rate within 1–3 min of surfacing.

These results clearly show that, as early as 5 s in a forced dive, blood oxygen levels influence bradycardia: heart rate was significantly elevated in birds that had breathed oxygen before diving compared with those breathing air before diving. The bradycardia established after 10 s of submergence was not reinforced as the dive was prolonged, regardless of the gas breathed before the dive. The effect of

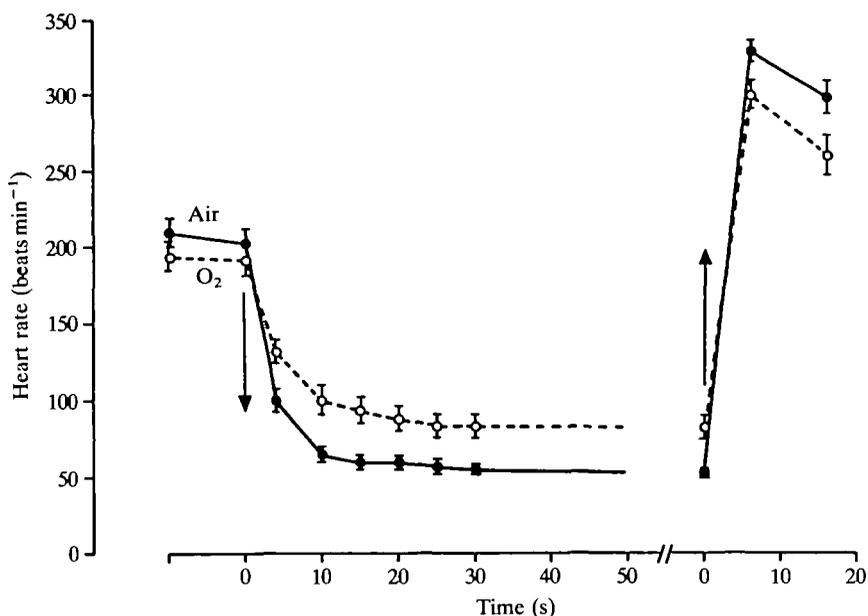


Fig. 1. The effect of breathing air (●;  $n = 22$ ,  $N = 7$ ) and oxygen (○;  $n = 16$ ,  $N = 7$ ) before diving on the heart rate response to forced diving in cormorants. Dives commenced at the downward-pointing arrow and ended at the upward-pointing arrow. Dives lasted from 90 to 120 s. Values are means  $\pm$  s.e.

arterial chemoreceptor stimulation would be expected to be progressive, yet the difference in heart rates between dives after breathing air or oxygen was established very early in the dive and was maintained, unchanged, throughout the dive. Similar diving heart rate profiles were obtained previously by Mangalam & Jones (1984) in that heart rates were constant from 30 to 120 s during forced dives, even after breathing hypoxic and hypercapnic gases before diving. It can be argued that chemoreceptors are active when the cormorant is breathing air and that this level of chemoreceptor activity reinforces a bradycardia set in train by mechanisms unknown. However, it seems likely that arterial chemoreceptors will be stimulated to at least a similar degree as in birds breathing air by the marked increase in blood carbon dioxide in dives after breathing oxygen (Mangalam & Jones, 1984), yet this increased chemoreceptor activity does not influence the bradycardia. Bradycardia is reduced in cormorants that breath oxygen before a dive, but the mechanism of this reduction is as likely to be through some unknown chemosensory effect as through the activities of arterial chemoreceptors.

These observations have thrown no light on the mechanism which initiates bradycardia during forced diving in cormorants. Stimulation of naso- or chemo-receptors, which do the job in Anseriformes, is unlikely. Cormorants lack any form of functional external nares and possess chemosensory mechanisms that, to say the least, must be unconventional. Cormorants are deep divers in nature and

would perhaps not experience hypoxaemia in dives until the ascent. Consequently, this could be reflected even in forced dives with respect to mechanisms initiating and controlling bradycardia. In fact, a difference in controlling mechanisms between Anatidae and Phalacrocoracidae would not be unexpected in view of the extreme phylogenetic distance between these groups of birds (Sibley & Ahlquist, 1987).

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