Cardiovascular responses to diving and involuntary submergence in the rhinoceros auklet (*Cerorhinca monocerata* Pallas)

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Cardiovascular responses during diving behaviour were recorded via a cannulated carotid artery in five rhinoceros auklets. Heart rate and mean arterial blood pressure were unchanged from predive values during both escape and feeding dives. The responses to feeding dives and escape dives did not differ. Acidosis, accompanying elevated steady-state plasma lactate levels during escape diving activity, was partially compensated by lung ventilation between dives. The absence of progressive accumulation of lactate in the blood implies that an aerobic steady state was attained, despite the short intervals between dives (2.4 ± 0.4 s). Arterial blood oxygen tension was maintained at reduced levels (50–60 mmHg; 1 mmHg = 133.322 Pa) for up to 32 min of continuous escape diving activity. Immersion of restrained auklets or capture of diving auklets in a net provoked a rapid and intense bradycardia. Growth of hand-reared auklet nestlings peaked at a time corresponding to the natural fledging age for this species but the urge to leave the nest box was not triggered by reduced food availability, as has been suggested for wild semi-precocial alcids. Potential pitfalls in the maintenance and use of alcids in physiological research are discussed.

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Les fonctions cardiovasculaires au cours de la plongée ont été enregistrées par canulation de la carotide chez cinq Macareux rhinocéros. Le rythme cardiaque et la pression artérielle moyenne sont restés les mêmes avant et durant les plongées de fuite et les plongées de recherche de nourriture. Les valeurs étaient les mêmes au cours des deux types de plongée. L'acidose, reliée aux concentrations accrues du lactate plasmatique d'équilibre au cours des plongées de fuite, était partiellement compensée par une ventilation des poumons entre les plongées. L'absence d'une accumulation progressive du lactate dans le sang indique qu'il s'établissait un équilibre aérobique, en dépit des intervalles courts entre les plongées (2,4 ± 0,4 s). La tension artérielle de l'oxygène dans le sang restait faible (50–60 mmHg; 1 mmHg = 133.322 Pa) pendant les périodes d'activité de plongée de fuite qui pouvaient atteindre 32 min. L'immersion de macareux attachés ou la capture de macareux plongeurs dans un filet entraînait une bradycardie brusque et intense. La croissance d'oisillons gardés en élevage a atteint son climax au moment où les macareux en nature sont normalement prêts à s'envoler, mais la pulsion à quitter la boîte à nid n'était pas déclenchée par une nourriture moins abondante, comme on le croyait dans le cas des alcidés semi-précoces en nature. Les inconvénients qui peuvent être reliés au maintien en captivité et à l'utilisation d'alcidés en recherche physiologique sont examinés.

[Traduit par la rédaction]

Introduction

There is a substantial body of information concerning the physiological responses of ducks and penguins during unrestrained diving activities (Stephenson and Jones 1989; Kooyman 1989). However, there are currently no published data from the Alcidae (auks). Alcids are frequently considered the "northern hemisphere ecological counterparts" of the penguins (Wanless *et al.* 1988), presumably in the sense that both groups inhabit a marine environment, are carnivorous (fish and krill or other invertebrates being the primary prey items), and use their wings for underwater propulsion. However, these obvious similarities between the two taxonomic groups belie some important differences that may have significant physiological consequences. Conspicuous among these are the observations that penguins are "almost neutrally buoyant" (Butler and Woakes 1984) and possess anatomical adaptations that favour efficient underwater propulsion (Clark and Bemis 1979; Nachtigall and Bilo 1980; Hui 1988), whereas rhinoceros auklets have a relatively high positive buoyancy (Lovvorn and Jones 1991) and use wings whose design is a compromise for use in both aerial and underwater flight (Stettenheim 1959; Spring 1971; Pennycuick 1987; Johnsgard 1987). It would therefore seem likely, although this remains to be shown, that power output is greater in diving alcids than in diving penguins.

There are currently very few studies reporting simultaneous measurements of energetics and cardiovascular responses in diving birds. Comparisons between tufted ducks, *Aythya fuligula*, and Humboldt penguins, *Spheniscus humboldti*, reveal that voluntary dives are aerobic in both species and that circulatory adjustments are correlated with power requirements (Woakes and Butler 1983; Butler and Woakes 1984). Radiotelemetry measurements have shown that cardiovascular variables (heart rate and femoral artery blood flow) are little changed from resting values during voluntary dives, while blood circulation is increased between dives in penguins (Millard *et al.* 1973; Butler and Woakes 1984). In contrast, heart rate (Butler and Woakes 1979; Stephenson *et al.* 1986; Furilla and Jones 1986, 1987) and hind-limb blood flow (Stephenson and Jones 1992) are elevated during underwater exercise in diving ducks. Power input (Woakes and Butler 1983) and power output are higher in diving ducks than in diving penguins, mainly as a result of the high positive buoyancy of ducks (Stephenson

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et al. 1989; Lovvorn *et al.* 1991). Thus, if the power requirements of diving in alcids do differ from those in penguins and ducks as suggested above, it may be predicted that the cardiovascular responses will differ too.

Despite their obvious adaptation to an aquatic lifestyle, penguins are intolerant of forced submergence compared with ducks (Scholander 1940; Kooyman 1975). Scholander (1940) concluded that "the problem as regards penguins resembles more that pointed out already by Bohr in regard to *Uria* [an alcid], namely, how they can withstand repeated submersions with only a few or a single respiration between each dive." This pattern of diving behaviour (many short dives in series, each separated by a brief pause at the water surface) is in fact usually observed in foraging penguins, alcids, and ducks (Dewar 1924; Scholander 1940; Eliassen 1960; Kooyman *et al.* 1971; Millard *et al.* 1973; Kooyman 1975; Butler and Woakes 1984; Wanless *et al.* 1988; Naito *et al.* 1990). On the basis of field observations of diving behaviour of four alcid species, and physiological measurements made during short forced submergences in these birds, Eliassen (1960, 1963) suggested that freely diving alcids may also not utilize an oxygen-conserving cardiovascular response during voluntary dives. The present study was designed to address that hypothesis by observation of cardiovascular responses to restrained and unrestrained dives in the rhinoceros auklet.

Methods

All experimental procedures used in this study conformed to the principles laid down by the Canadian Council on Animal Care.

Acquisition and maintenance of animals

Ten auklet nestlings were obtained from Pine Island (50°58′N, 127°41′W) in July 1989 and shipped by road to the Department of Zoology, University of British Columbia. Pine Island is located near the British Columbian coast, off the northern tip of Vancouver Island (see Bertram *et al.* 1991 for a map and topographical information). The sex of the birds was not determined. The age of the nestlings on the date of acquisition was estimated from body weight, using the mean of the composite growth curves for Pine Island rhinoceros auklets published by Bertram *et al.* (1991). Body weight of the captive auklets was regularly measured to the nearest gram using a triple beam balance (Ohaus Scale Corp., Union, N.J.).

Nestlings were kept in an indoor aviary in cardboard nest boxes large enough to allow the birds to flap their wings. Air temperature inside the boxes was 20–23°C. The floor of each box was covered with newspaper and coarse sawdust, which was changed once or twice per day. The boxes themselves were changed at approximately weekly intervals.

The date of release from the nest boxes (fledging) was dependent upon experimental protocol (see later). (In the rhinoceros auklet, downy plumage is replaced by feathers at approximately the time of nest departure and "fledging" is used to indicate the latter in this paper.) Most of the birds were initially released onto an outdoor tank (2 m in diameter × 1.2 m deep) enclosed by netting to prevent access by predators and escape of the auklets. A wooden shelf (1 × 0.15 m), fitted with a sloping ramp descending into the water, was attached to the tank to allow the auklets access to dry land. The shelf was coated with artificial turf to prevent damage to and infection of the feet. As a result of excessive handling, the plumage was not water resistant so the auklets were returned to indoor mesh cages for 2 weeks and were subsequently transferred to a sheltered outdoor pen (5 × 3 m). The floor of the pen was covered with artificial turf and contained a shallow circular tank (1.5 m in diameter × 0.1 m deep) in which the birds were fed and could swim and preen. Heat lamps were provided in one sheltered corner of the pen to prevent hypothermia in waterlogged birds, a problem that gradually disappeared, particularly following the spring moult. Before and during diving experiments, the auklets were kept on a larger outdoor pool (5.5 × 3 m) with a sloping floor (maximum depth 1.7 m). All tanks were filled with continuously flowing dechlorinated fresh water, which drained from the surface into standpipes, thereby helping to prevent the accumulation of a layer of surface-active materials (Swennen 1978).

Auklets were initially fed herring slices but these were replaced after 5 months by whole defrosted "jack" herring (maximum length 5 in., 1 in. = 25.4 mm). The diet was supplemented with a thrice-weekly dose of thiamine hydrochloride (vitamin B_1; approximately 10–30 mg per bird) to avoid the risk of thiamine deficiency caused by the presence of thiaminase in herring (Geraci 1972). The auklets were also occasionally fed live salmon (length about 3–5 in.). Frozen salmon were found to be unsuitable because, unlike herring, they disintegrated into a semiliquid consistency after thawing.

Resting heart rate of nestlings

Seven auklet nestlings were each fitted with an externally mounted FM ECG radio transmitter (Narco Biosystems, Downsview, Ont.). Fully encapsulated radio transmitters weighed approximately 10 g, with approximate dimensions 5 × 2 × 1 cm. Sterile, insulated bipolar electrodes (CZ1322 multifilament copper biomed wire; Cooner Wire Co., Chatsworth, Calif.) were placed in close proximity to the base and apex of the heart via angiocath needles (20 gauge) inserted into the interclavicular and posterior thoracic or abdominal air sacs, respectively. The outer sheath of the angiocath was modified to include a lateral hole that opened to the tip via a longitudinal slit. After insertion of the angiocath into the air sac through the skin, the hypodermic needle was withdrawn and the wire electrode was threaded through the lateral hole in the angiocath sheath and advanced approximately 3–6 cm in the direction of the heart. The sheath was then withdrawn in such a way that the wire passed through the slit and was retained within the air sac. Using a 20-gauge needle, the electrodes were led under the skin and exited at the nape of the neck where the birds could not peck at them. The wire was sutured to the skin and the wound was liberally coated with antibiotic powder (Cicatrin; Burroughs Wellcome Inc., Kirkland, Que.). A single intramuscular injection of ampicillin (50 mg · kg^{-1} Penbritin; Ayerst Laboratories, Montréal, Que.) was given at the time of electrode implantation.

A small "backpack," fashioned out of Velcro, was attached to the nestlings and the trailing ends of the electrode wires were held securely between two opposing pieces of Velcro. Attempts to attach the Velcro to the feathers by means of glue (Heath 1987) were not successful so an adjustable soft elastic strap was constructed that passed around each wing and across the breast. The elastic was quickly preened under the feathers and was tolerated extremely well by the birds, and no instances of skin abrasion were noted. After the nestlings had been observed for 2 days for signs of distress or discomfort, a radio transmitter was soldered to the electrodes. The radio signal was monitored using a communication receiver (IC-R7000, ICOM, Osaka, Japan).

The nest boxes were placed on partly inflated rubber balloons connected via PE 190 tubing to a Statham pressure transducer, the amplified output of which was recorded on a Harvard Student oscillograph. Even very minor movements by the nestlings (e.g., preening) could be detected as pressure oscillations. ECG signals were recorded when the nestlings had been completely inactive for at least 5 min. Readings were taken at night (12:00–03:00) and during daylight hours (08:30–15:00).

For comparison, heart rate and mean arterial blood pressure were later measured in five adult auklets resting quietly while sitting alone in nest boxes during daylight hours.

Forced submergence

In two fledgling auklets (body weights 290 and 361 g), the implanted ECG electrodes were soldered to a shielded cable and the connection was sealed with fast-drying epoxy glue. The ECG signal was amplified using Gould Universal and isolated preamplifiers and recorded on a Techni-Rite two-channel chart recorder. The birds

were held by hand with wings folded against the body and fully immersed in water for 10–15 s. Immediately after emersion the birds were released and allowed to swim on the water surface. Each auklet was subjected to two forced immersions with several minutes of recovery between them. Experiments were discontinued when it became apparent that rhinoceros auklets evoke the expected bradycardia, as reported previously for other alcid species during forced submergence (Eliassen 1960).

After completion of the above procedures, the ECG electrodes were removed from the auklet fledglings and they were allowed several months to recover in a sheltered outdoor pen (described above).

Feeding, escape, and trapped dives

After they had regained waterproof plumage and diving activities had resumed, five adult auklets (age approximately 14 months; body weight 569 ± 14 g) were fitted with a PVC cannula (i.d. 0.58 mm, o.d. 0.99 mm; Bolab Inc., Lake Havasu City, Ariz.) in one carotid artery. The cannula was pretreated with TD-MAC heparin complex (Polysciences Inc., Warrington, Pa) to inhibit blood clotting, and it was flushed daily using heparinised sterile saline (100 USP units heparin · mL^{-1}; Allen and Hanburys, Toronto, Ont.). Each auklet was restrained in a supine position and the skin on both ventral and dorsal sides of the neck was anaesthetised by subcutaneous injection of 1% lidocaine hydrochloride (Xylocaine; Astra Pharmaceuticals Canada Ltd., Mississauga, Ont.). The cannula was advanced approximately 2–3 cm into the carotid artery, toward the heart, until its tip lay in the brachiocephalic artery. The cannula was filled with heparinised saline and the distal end was sealed by a flame, then tied to the skin where it exited the dorsal surface of the neck. The incision in the ventral skin of the neck was kept as small as possible and feathers were deflected rather than plucked. Care was taken at all times to avoid undue damage to the plumage. The auklets were subsequently given daily injections (10 mg · kg^{-1}, i.m.) of ampicillin into the leg musculature.

Arterial blood pressure and heart rate were measured by connecting the carotid cannula via a 3 m long extension tube (PE 160) to a P10EZ miniature pressure transducer (Gould Inc., Valley View, Ohio), which in most experiments was fixed to a wooden rod at water-surface level. In some experiments, pulse pressure was unacceptably low owing to partial blockage of the cannula so only mean arterial blood pressure was obtained. In other measurements, the length of the cannula was shortened by attaching the pressure transducer to the end of a 1 m long rod that was used manually to guide the cannula around the pool behind the diving auklet, in which case only heart rate was obtained, since transducer height was not constant.

Diving behaviour was recorded using a VCR and camera (JVC Canada Inc., Scarborough, Ont.). The output of the pressure transducer was recorded on one audio channel of the video tape by means of an FM recording adapter (model 2D; A. R. Vetter Co., Rebersberg, Pa.) so that behaviour and cardiovascular responses could be directly correlated during analysis. Dives were classified as feeding dives, in which the auklets picked up and ate fish lying on the floor of the pond; escape dives, in which experimenter movements inadvertently or deliberately caused the auklet to dive; and trapped dives, in which the auklet was pursued and captured with a hand-held net and held underwater for up to 35 s before being released from the net. Each bird was subjected to only one trapped dive.

Blood samples (1 mL) were withdrawn from birds at rest in nest boxes, during inactive periods at the water surface, and during escape dives. Cardiovascular variables were not measured simultaneously and PE 50 tubing was used as the extension (instead of PE 190 used above) to reduce dead space. It was not possible to identify the precise timing of a diving blood sample, because the cannula was long and each blood sample was usually withdrawn over the course of more than one dive. In the latter situation, actual withdrawal only occurred when the auklets were submerged. The samples were analysed for blood gases and pH using an IL micro 13 analyser. Haematocrit of each sample was measured in duplicate by microcentrifugation. Plasma from the remainder of each blood sample was deproteinised using two parts 8% perchloric acid, then stored at −80°C until analysis for lactate content using a standard enzymatic assay (L (+) lactate diagnostic kit; Sigma Chemical Co., St. Louis, Mo.).

Data analysis

Data are presented as means ± SEM. When more than one observation (n) was made in an animal for any given condition, a mean value was obtained and a grand mean derived from these individual means is reported (i.e., N = number of animals). This was done to avoid bias resulting from unequal contributions from each bird. The summary statistics therefore describe the variation occurring between birds. By comparing standard deviations in all cases where $n > 2$, it was found that within-bird variability was less than between-birds variability so only the latter is reported.

Statistical analyses were performed using Systat software (Systat Inc., Evanston, Ill.). Independent and paired t-tests and repeated-measures analysis of variance were performed as required, and differences are considered significant at the 95% confidence level ($P < 0.05$).

Results

Nestling behaviour and growth rate

According to body weight (289 ± 10 g, N = 10) and the estimate of age derived from it (45 ± 2 days, N = 10), the auklet nestlings were close to fledging age at the time of acquisition. The nestlings were initially inactive for much of the time, particularly during daylight hours, but became progressively more restless (as indicated by direct observation and by the pressure-sensitive activity recordings) as they grew older. They were consistently more active at night. The nestlings were also very eager to accept fish at first but their appetite diminished in parallel with their increased restlessness as they approached their natural fledging age of approximately 45–60 days (Wilson and Manuwal 1986; Ydenberg 1989). Indeed, all nestlings had to be force-fed at least part of their daily meal after they were about 70 days old. As a result, all of the auklets underwent a biphasic growth pattern wherein body weight increased to a peak (341 ± 7 g at 63 ± 2 days of age) and then declined gradually until the birds were allowed to leave the nest boxes (288 ± 8 g at 90 ± 3 days of age). The auklets were detained within their nest boxes until resting heart rate measurements had been completed. Two nestlings and three fledglings died of hypothermia or respiratory infections (aspergillosis). After fledging, the five healthy birds quickly regained their appetites and body weight increased progressively to 544 ± 23 g (N = 5) within 3 months.

Cardiovascular variables in inactive nestling and adult auklets

The heart rate of inactive auklet nestlings (age approximately 86 ± 2 days) during daylight hours was 132 ± 5 beats · min^{-1} (N = 7), while at night it was significantly higher at 168 ± 9 beats · min^{-1} (N = 7). By comparison, the heart rate of cannulated adult auklets (age approximately 14 months) resting quietly within closed boxes was 177 ± 12 beats · min^{-1} (N = 5).

Forced submergence

The effect of involuntary whole body immersion on heart rate is illustrated in Fig. 1. Forced submergence lasted 11.8 ± 0.6 s (n = 4 from two animals). Heart rate decreased to 50% of the pre-immersion rate within 2 s and continued to fall to 11% of the pre-immersion rate by 10 s.

The heart rates of these birds were 324 and 190 beats · min^{-1} when they were sitting in nest boxes following electrode attachment. However, we do not consider that the birds

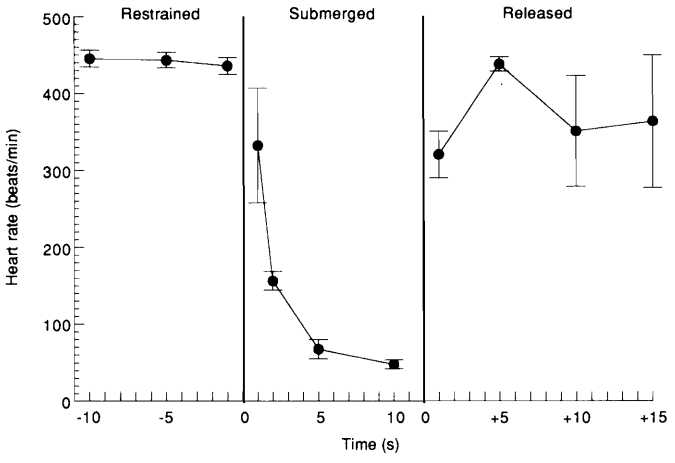

FIG. 1. Mean (± SEM) heart rates of two young rhinoceros auklets before, during, and following brief involuntary submergence. Each animal was submerged twice with several minutes of recovery between each trial (i.e., $n = 4$). Vertical lines demarcate the times of immersion and emersion.

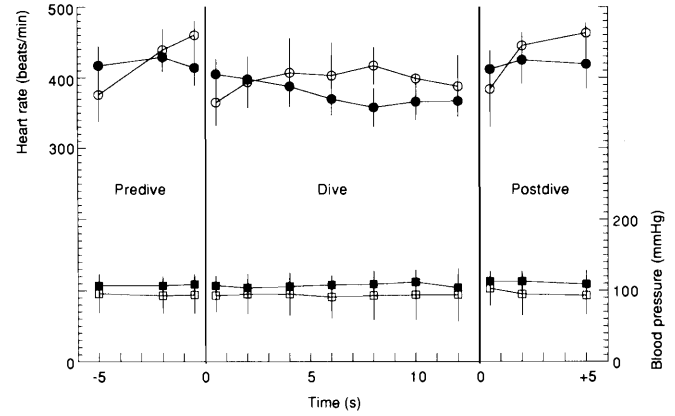

FIG. 2. Heart rate (○, ●) and mean arterial blood pressure (□, ■) at specific times before, during, and following feeding dives (○, □) and escape dives (●, ■). Values are given as the mean ± SEM (± range is given in cases where $N = 2$). In escape dive data, $N = 5$ (except for 6 data points where $N = 4$ and 1 datum where $N = 3$). In all feeding-dive data, $N = 3$ (heart rate) or $N = 2$ (blood pressure).

were in a "resting" state under those conditions since they were clearly agitated by the handling and the presence of the newly attached wires.

Diving responses

Recordings were made during a total of eight feeding dives by three auklets ($n = 3, 3, 2$). Feeding dive duration was 13.7 ± 1.4 s ($N = 3$; range 7.1–20.3 s) and each auklet performed at least one dive of duration >12 s. Each feeding dive was followed by a long (>1 min) pause at the water surface. In all cases only one fish was picked up and it was swallowed after the bird had resurfaced. Prior to cannulation, auklets were commonly observed to consume more than one fish per dive, swallowing them without resurfacing. Escape dive duration was 9.0 ± 1.3 s ($N = 5$; range 1.2–17.2 s) and interdive interval was 2.4 ± 0.4 s ($N = 5$).

Heart rate was elevated to over twice the resting value during diving activity. The cardiovascular responses to feeding dives were not significantly different from those during escape

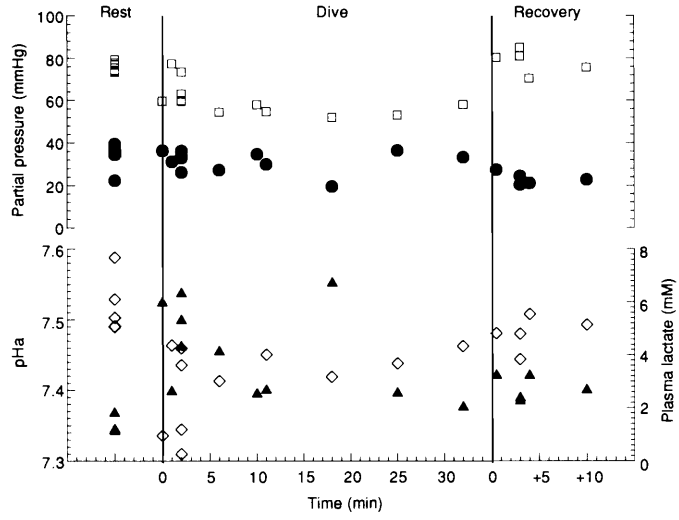

FIG. 3. Partial pressures of oxygen (□) and carbon dioxide (●), pH (◇), and lactate concentration (▲) of arterial blood. Blood samples were obtained from five adult auklets resting quietly in a closed nest box, and from three auklets during bouts of escape diving activity and the subsequent recovery period. Most diving samples were obtained over the course of more than one dive but blood withdrawal only took place while the birds were submerged.

dives and are illustrated in Fig. 2. Univariate repeated-measures ANOVA revealed that neither heart rate nor mean arterial blood pressure changed significantly from predive levels during feeding and escape dives. Mean heart rate was also calculated over the entire durations of dives and interdive intervals. During escape diving activity, heart rate decreased from 422 ± 21 beats · min^{-1} at the surface to 378 ± 17 beats · min^{-1} ($N = 5$) while submerged (paired t-test, $P = 0.054$). Similarly, heart rate averaged over the 5-s periods immediately preceding and following feeding dives was 432 ± 16 beats · min^{-1} and decreased to an average of 397 ± 20 beats · min^{-1} ($N = 3$) during submersion (paired t-test, $P > 0.1$). Mean arterial blood pressure during escape diving activity (108.2 ± 13.6 mmHg (1 mmHg = 133.322 Pa); $N = 5$) was 17% higher than resting levels (92.0 ± 3.4 mmHg; $N = 5$), a difference that was not statistically significant. Mean arterial blood pressure during feeding dives averaged 93.3 mmHg ($N = 2$).

Blood gas tensions, pH, and lactate concentration during sustained escape diving activity are illustrated in Fig. 3. P_{aO_2} decreased to approximately 50–60 mmHg after less than 3 min of continuous escape diving activity. This low P_{aO_2} was maintained for 32 min of diving activity in one auklet. In contrast, P_{aCO_2} was unchanged from resting levels throughout the dive series. Arterial blood pH (pHa) decreased by approximately 0.1 pH unit from resting levels (7.52 ± 0.02 units, $N = 5$) during diving activities. Plasma lactate concentration increased from a resting value of 1.27 ± 0.13 mM ($N = 5$) to 2–8 mM during diving. Resting haematocrit, measured before diving blood samples were taken, was 37.0 ± 0.9% ($N = 5$). Haematocrits of blood samples taken during diving activity averaged 25.2 ± 0.8% ($n = 32$ from three animals).

It can be seen in Fig. 4 that trapping the auklets under water elicited a pronounced bradycardia. Heart rate was elevated to levels similar to those seen during escape and feeding dives during the chase phase of the trapped dives (compare Fig. 4 with Fig. 2). Only when the birds became entangled in the net

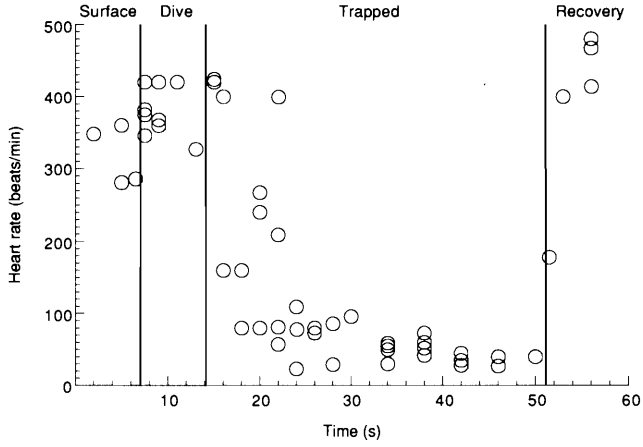

FIG. 4. Heart rate values recorded before, during, and after trapped escape dives in five rhinoceros auklets. While sitting quietly at the water surface, the birds were stimulated to dive by approach of a hand-held net and they were actively chased (dive) and captured (trapped) while underwater. Once trapped, they were held submerged for up to 35 s then released (recovery).

did heart rate begin to decrease. Upon capture, the submerged auklets struggled violently and heart rate decreased rapidly to <50 beats $\cdot$ min^{-1}, a value similar to that observed during restrained forced submergence (compare Fig. 4 with Fig. 1). Mean arterial blood pressure was not recorded due to uncertainty about the position of the pressure transducer in relation to the bird during trapped dives.

Discussion

This study has confirmed that rhinoceros auklets do not invoke an oxygen-conserving cardiovascular response during unrestrained dives. It has also confirmed the prediction that heart rate responses to unrestrained dives in the rhinoceros auklet are qualitatively and quantitatively different from those of diving penguins and ducks. In penguins, there was a slight tachycardia between dives and heart rate returned approximately to resting values during dives (Millard *et al.* 1973; Butler and Woakes 1984). Auklets also showed very little change in heart rate upon immersion but, unlike penguins, a tachycardia of over twice the resting levels was maintained. The predive heart rate of rhinoceros auklets was quantitatively similar to that in ducks but, unlike ducks, there was no significant reduction in heart rate upon diving. In diving ducks, heart rate decreased substantially by an amount that was dependent upon the predive heart rate, but it nevertheless remained significantly above resting levels during submergence (Butler and Woakes 1979; Furilla and Jones 1987). Rhinoceros auklets, like redhead ducks, *Aythya americana* (Stephenson and Jones 1992), showed no change in mean arterial blood pressure during dives.

The differences in heart rate responses to voluntary dives in unrestrained penguins and ducks have been attributed to differences in the power requirements of underwater swimming in the two groups (Butler and Woakes 1984). The buoyant force of the diving rhinoceros auklet is unknown, but our own observations confirmed those of Sanford and Harris (1967), who found that a common murre, *Uria aalge*, was forced to swim downward in order to remain submerged, suggesting that the buoyancy of alcids is relatively high compared with that of penguins. In support of this suggestion, Lovvorn and Jones (1991) found that the buoyant force of restrained rhinoceros auklets was similar to that of restrained ducks. Added to this are the increased drag associated with the trailing cannula and the likely high costs of acceleration associated with the observed nonsteady propulsive style of the rhinoceros auklets used in this study. It seems likely that power requirements of diving of the rhinoceros auklets in the present study were higher than those of the penguins studied by Millard *et al.* (1973) and Butler and Woakes (1984) and this may at least partially explain the occurrence of the higher heart rate in the auklets. It would be interesting to compare these data with observations in vigorously exercising penguins.

Another factor that may have contributed to the high diving heart rate in rhinoceros auklets was the fact that they appeared agitated as a result of the capture and handling required to attach the cannula extension. After release, most surface time was spent preening (rather than "head dipping" in search of food as was common in the noninstrumented birds), but this was not directed especially at the cannula. Voluntary feeding dives were rare after the cannula extension was attached and it was difficult to know whether those dives were inadvertently triggered by a movement made by the investigators. Nevertheless, on eight occasions three of the auklets picked up and ate fish lying on the floor of the pond. The cardiovascular responses to these feeding dives were not significantly different from those during deliberately induced escape dives in which no feeding attempts were made. This concurs with observations made in diving ducks in which heart rate responses to feeding and escape dives were similar (Butler and Woakes 1979; Stephenson and Jones 1992).

It has been shown in tufted ducks that cannulation of the brachial artery can cause elevated heart rates during surface swimming (Woakes and Butler 1986) so it is possible that the diving heart rates observed in the present study are artificially high. However, heart rate of cannulated redhead ducks during escape dives (Stephenson and Jones 1992) was similar to that of noncannulated ducks (Butler and Woakes 1979; Furilla and Jones 1987). Furthermore, the pronounced bradycardia evoked during trapped dives confirms that the auklets had not lost the capacity to reduce heart rate after cannulation. Attempts were made to record heart rate by radiotelemetry to check for possible effects of cannulation. However, the radio signal was lost upon immersion of the externally mounted devices and the transmitters were too large to implant into these small birds.

In the present study the auklets were capable of sustained escape diving activity in which approximately 80% of the time was spent submerged. The fact that a steady state was achieved in terms of blood gases and acid–base state is testimony to the remarkable ability of these birds to recover rapidly between dives, as suggested previously (Scholander 1940; Eliassen 1960). Nevertheless, the birds achieved incomplete respiratory compensation for the acidosis accompanying elevated plasma lactate levels (constant P_{CO_2} and reduced P_{O_2}), indicating that the observed acidosis was of combined metabolic and respiratory origin. The sustained elevation of plasma lactate concentration may have been caused by high exercise levels rather than restricted oxygen delivery, since this condition is also found in tufted ducks swimming vigorously at the water surface under fully aerobic conditions (Woakes and Butler 1986). Oxygen delivery to the tissues during dives may have been assisted by the acidosis via a Bohr effect. Alcids possess relatively high concentrations of myoglobin in the

flight muscles (Davis and Guderley 1987), which will also serve to facilitate oxygen delivery to the muscle mitochondria during dives. Given the heart rate responses observed in the present study, it seems likely that the locomotor muscles of auklets are continuously perfused during dives, in which case the myoglobin would cause the muscles to act as a sink for blood oxygen rather than as an oxygen store. Davis and Guderley (1987) concluded from their study of the comparative biochemistry of pectoral and supracoracoideus muscles in two alcid species and two nonaquatic species that alcids do not rely extensively on anaerobic glycolysis during diving. Lack of a continuous accumulation of lactate in the blood also supports the notion that dives are predominantly aerobic in the rhinoceros auklet.

Scholander (1940) showed that penguins were unable to survive forced submersion for as long as domestic ducks and attributed this to differences in the efficacy of the cardiovascular oxygen-conserving response, although the intensity of the bradycardia in the gentoo penguin, *Pygoscelis papua*, and Adelie penguin, *Pygoscelis adeliae*, was recently shown to be little different from that in ducks (Kooyman and Ponganis 1990). The cardiac response of rhinoceros auklets to involuntary submergence was qualitatively similar to that of other alcid species (Eliassen 1960), although a greater decrease in heart rate was observed in the present study. Bradycardia was rapid in onset and was maintained until emersion in rhinoceros auklets.

Capture of the auklets in a net while diving also evoked a rapid and profound bradycardia. This was very similar to the response seen in diving ducks that were trapped at the end of voluntary feeding dives (Stephenson *et al.* 1986; Furilla and Jones 1987). An interesting point of difference between auklets and ducks, however, relates to the observations that trapping during escape dives (rather than voluntary dives) greatly increased the variability of the heart rate and blood flow responses in ducks (Stephenson 1987; Stephenson and Jones 1992). The auklets were trapped during escape dives but the response was not very variable (Fig. 4). A bradycardia was also observed by Butler and Woakes (1984) in Humboldt penguins prevented from resurfacing during voluntary dives. Bradycardia was, however, much slower in onset and less intense in penguins than in auklets and ducks. Penguins were inactive during the trapped phase of the dive, unlike the situation in ducks and auklets, indicating that any relationship between exercise intensity and heart rate during submersion (Woakes and Butler 1983; Butler and Woakes 1984) is restricted to voluntary feeding dives. The auklets were engaged in vigorous muscular activity during both escape dives and trapped dives yet there was a tachycardia in the former and a bradycardia in the latter. A similar observation was made in ducks (Stephenson *et al.* 1986). If exercise is effective in causing an increase in heart rate during voluntary feeding dives, this effect is clearly susceptible to modulation by other as yet unidentified factors and can be completely abolished when access to air is prevented.

Nestling activity increased at night and this was associated with a significantly higher resting heart rate compared with that during the daytime. This is probably related to the nocturnal provisioning habits of the adult breeding rhinoceros auklet (Richardson 1961; Wilson and Manuwal 1986; Bertram *et al.* 1991) and is in contrast to the situation in tufted ducklings (Keijer *et al.* 1988), which are normally more active during daylight hours (Hill and Ellis 1984). The behaviour of the auklet nestlings suggested that the urge to leave the nest was not dependent upon an external cue such as reduced food availability caused by changes in provisioning by the "parent." Auklet nestling activity increased considerably after the natural fledging age and food appetite decreased considerably. The latter effect was so marked that it became difficult to maintain the body weight of the nestlings and force-feeding was required in all birds. Voluntary feeding began immediately following release of the birds from the nest boxes. It is clear that auklet nestlings are not content to remain in the secure environment of the nest indefinitely, even when food is available *ad libitum*. These observations do not exclude the possibility that the timing of the urge to leave the nest burrow has evolved in response to selective pressures that include growth–mortality trade-offs for the nestlings and provisioning risks for the adults (Gaston and Nettleship 1981; Ydenberg 1989). However, the data do not support the hypothesis that on an individual basis the recession in nestling body mass is a direct result of reduced provisioning rates: it is an effect of reduced appetite, the proximate cause of which is unknown. These results confirm similar observations in the Atlantic puffin, *Fratercula arctica* (Harris 1976, 1978). Indeed, it is possible that the reduction in food delivery to burrows by adult rhinoceros auklets (Bertram *et al.* 1991) is a response to lack of interest on the part of the nestlings (Harris 1978).

We have succeeded in recording cardiovascular adjustments during active dives in rhinoceros auklets despite numerous problems with their care and maintenance. In addition to the auklets reported in the foregoing sections of this paper, we acquired and raised another group of six nestlings in 1987, all of which died before physiological experiments were conducted. We therefore feel that a brief discussion of the pitfalls that were encountered is justified, since it may be of use to others planning to undertake similar work.

Taking the two groups of auklets together (i.e., a total of 16 birds), hypothermia claimed the lives of 4 fledglings. Excessive handling of the nestlings was the primary problem, since it resulted in significant damage to the feather structure and thereby destroyed the water-repellent properties of the plumage. Upon entering the water, the birds rapidly became waterlogged and refused to dive. We found it best to allow the fledglings to enter the water voluntarily from a sloping "beach" and to provide sufficient heat lamps over dry areas to prevent hypothermia. It is our belief that more fledglings would have succumbed to hypothermia had these precautions not been taken. Two of the deaths noted above occurred in young adult birds with good plumage condition. In these cases, an overnight interruption of water flow in the diving tank had allowed a film to settle on the water surface and it is likely that this altered the surface tension, allowing penetration of water into the feathers (Swennen 1978). We concur with Swennen (1977, 1978) that the water flow must be continuous, that the pond surface must be continuously agitated and (or) drained away, and that uneaten food and faeces must be removed regularly.

Lesions on the plantar surface of the foot ("bumblefoot") arose in some of the auklets in 1987 and this problem was subsequently avoided by providing artificial turf on all dry surfaces. Upon postmortem examination it was also found that all of the auklets were infected to some extent with aspergillosis. Lesions were visible in the respiratory and digestive systems. We suspect that this was contracted during their stay in the indoor aviary, where they came into close proximity to Pekin

ducks and we suggest that seabirds and waterfowl are kept separately whenever possible. None of the auklets used in diving studies exhibited any clinical signs of the disease, which include dyspnea, wheezing, lethargy, and emaciation (Harrison and Harrison 1986) and were considered healthy at the time of experiments.

Predation by raccoons claimed two auklet fledglings. It is likely that the raccoons were attracted by the fish odour, since they ignored ducks housed in adjacent (and more accessible) pens. A final problem that deserves mention pertains to the effects of surgery on the auklets. There were signs of infection at the site of cannula implantation after approximately 3–8 days, despite the application of ampicillin and use of sterile materials. Experiments on individual auklets were discontinued when infection became apparent but it is nevertheless possible that the physiological responses reported herein were modified by the effects of low-level infection. It is suggested that the use of salt water rather than fresh water in the diving tank may help prevent this problem. Alcids are clearly more susceptible to infection than ducks.

Despite technical limitations, the results of this study add further support to the idea that cardiovascular responses of diving birds differ considerably depending upon whether or not the animals have free access to the water surface. In alcids, as in ducks and penguins, unrestrained (voluntary and escape) dives are mainly aerobic with cardiovascular adjustments appropriate for delivery of oxygen to working muscles, whereas oxygen-conserving mechanisms are evoked during both active and inactive forced submergence.

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