

SHORT COMMUNICATION

HEART RATE AND GAS EXCHANGE IN FREELY DIVING
AMERICAN MINK (*MUSTELA VISON*)

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Several studies have shown that the diet of the North American mink can vary according to habitat, season and sex (Gerell, 1967; Akande, 1972; Day & Linn, 1972; Birks & Dunstone, 1985; Dunstone & Birks, 1987). It is clear that at times, particularly in autumn and winter, both male and female mink may obtain over 50% of their food (as fish and crustaceans) from an aquatic environment. Thus, mink will readily take to water and dive to capture prey despite the fact that they possess very few anatomical adaptations which enhance their ability to hunt underwater. Indeed, the unusually high resting metabolic rate of mustelids (Iversen, 1972) and the high energetic cost of transport during surface swimming (Williams, 1983) argue against the successful use of a diving foraging strategy. Brown & Lasiewski (1972) proposed that the adaptive advantage of the elongated body shape of mink (which is energetically expensive because of high rates of heat loss as a result of the high surface area to body volume ratio) lies in the increased ability to capture prey in confined spaces (e.g. lagomorphs in their burrows; Dunstone & Birks, 1987). Perhaps an enhanced ability to capture fish and crustaceans in underwater hides (e.g. Dunstone, 1978) compensates for their presumed locomotory inefficiency underwater.

The oxygen storage capacity of mink is no greater than that of the non-aquatic ferret *Mustela furo* (N. Dunstone, unpublished observations). Considering the requirement for a high level of metabolic heat production to balance high rates of heat loss, and the presumably high power output required for underwater propulsion (at least in dives which are not initiated by plunging into the water from above), this suggests that energetic constraints on diving behaviour may be particularly acute in the mink. Dunstone & O'Connor (1979*a,b*) concluded that oxygen storage capacity ultimately limits dive durations, though the greatest part (approximately 51%) of the variability in diving behaviour was due to factors related to the optimization of foraging activity.

No data are available for metabolic rate during involuntary or voluntary submersion, though heart rate has been monitored during involuntary submersion

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(Ploucha & Aulerich, 1982; West & Van Vliet, 1986) and during drowning while held underwater by a leg-hold trap (Gilbert & Gofton, 1982*a*). In both situations, a rapidly developing and intense bradycardia was found. There was also a less intense bradycardia in a single mink that performed voluntary head immersions (West & Van Vliet, 1986) and in unrestrained mink that were induced to dive (Gilbert & Gofton, 1982*b*). None of the dives in these studies is representative of normal foraging dives. To monitor physiological responses under more 'natural' conditions, heart rate and oxygen uptake (\dot{V}_{O_2}) were measured during diving activities in two unrestrained female American mink (body masses: 650 g and 1000 g) by the techniques of radiotelemetry and open-circuit respirometry described previously (Woakes & Butler, 1983; Butler & Woakes, 1984).

Heart rate and \dot{V}_{O_2} were recorded at the Department of Zoology and Comparative Physiology, University of Birmingham. For measurement of \dot{V}_{O_2} , the mink were introduced into a Perspex respirometer (40×40×35 cm) containing a wooden platform (40×15 cm) at water surface level to enable the mink to leave the water between dives. Air was drawn through the respirometer at a measured and constant rate of either 20 or 25 l min⁻¹. The respirometer was placed above a 40×40 cm access hole cut into a metal sheet which completely covered the surface of an indoor tank (1.63×1.0×1.7 m depth) at a depth of 3 cm. Thus, the mink resurfaced inside the respirometer between dives. For measurement of heart rate a single-channel PIM radiotransmitter (Butler & Woakes, 1982) was surgically implanted into an abdominal subcutaneous pouch with the animal under halothane anaesthesia. Bipolar loop electrodes were placed subcutaneously over the sternum. The radio signal encoding the electrocardiogram (ECG) was received and demodulated as described previously (Woakes & Butler, 1983). The mink were encouraged to dive for food (chopped fish) which was provided at a given depth in a submerged wooden container (15×7×7 cm) *via* a plastic pipe from the surface. Heart rate was measured during head dipping (in which only the head and thorax were submerged; Poole & Dunstone, 1976), shallow dives (in which the mink were exploring the underside of the surface barrier) and deep dives (in which the mink descended to a depth of >1 m to explore the floor of the tank or to obtain food), as well as during surface activity (grooming and 'escape' behaviour). Oxygen uptake was measured during periods of deep diving activity. Heart rates were also recorded at the Department of Zoology, University of Durham, where the mink were normally kept and where they were, therefore, fully familiar with their surroundings. Diving, surface activities and resting (sleeping) were monitored. Shallow dives occurred in an uncovered pool (2.8×1.6×0.3 m deep) and deep dives occurred in a covered tank (1.0×0.25×1.9 m deep). In the deeper tank, the mink entered the water through a hole (10 cm in diameter) in a metal plate which covered the surface of the water.

Data, which are presented separately for each animal (data for the 650 g mink are presented before those for the 1000 g mink in all instances), are expressed as mean ± s.e. with sample size (*N*) in parentheses. All gas volumes are corrected to STPD. Mean heart rates were measured from traces of ECG by using a BBC model B microcomputer and a GTCO digitizing pod (Digipod 5), employing a modified

version of the software developed by Woakes & Butler (1986). Mean diving (under all conditions) and head-dipping heart rates were measured for the entire duration of submergence. Mean surface activity, heart rates and mean resting heart rates were measured by analysing randomly chosen 20- to 30-s stretches of relevant ECG trace; the final means were calculated from several such measurements. 'Expiratory' resting heart rate was calculated from the longest cardiac interval coincident with expiration in sleeping mink (i.e. N represents the number of individual heart beats and the number of expirations). 'Hide-search' dives occurred when the mink voluntarily entered a series of pipes (approximately 15 cm i.d.) which were situated on the floor of the shallow pool at Durham. Mean heart rate under this condition was measured between the times of entrance and exit from the submerged pipes. Significance of differences between two mean values are quantified by Student's t -test (assuming unequal variances) and results are considered significant at the 95 % confidence level ($P < 0.05$). An attempt to resolve \dot{V}_{O_2} into submerged and surface phases by means of a multiple linear regression technique (see Woakes & Butler, 1983) was unsuccessful, though it was possible to obtain values for total diving activity (i.e. submerged and surface activities combined).

The values of \dot{V}_{O_2} recorded in this study [5.21 ± 0.45 ($N = 35$) and 7.87 ± 0.56 ($N = 45$) $\text{ml O}_2\text{g}^{-1}\text{h}^{-1}$] are close to or above the $\dot{V}_{O_{2\text{max}}}$ determined for surface-swimming mink (Williams, 1983). In view of the estimated 5- to 10-fold reduction in body drag during submerged swimming (Williams, 1983), the present values appear high. The probable reason for this is that the mink engaged in very variable amounts of surface activity, some of which was energetically very expensive. This surface activity contributed substantially to the total levels of \dot{V}_{O_2} during overall diving behaviour. It was observed that during deep diving activities the mink often propelled themselves into the water from the respirometer box using their hind limbs to produce thrust. They probably achieved greater velocities than would have been possible by swimming from the water surface to the bottom. The use of this type of dive (termed 'dive-chase' by Dunstone & O'Connor, 1979a) has been observed in hunting mink (Poole & Dunstone, 1976; Dunstone & O'Connor, 1979a) and may reduce energy expenditure during diving activities, since the fusiform body shape results in relatively low body drag while the efficiency of thrust production by all limbs during swimming is low due to their small surface area (Williams, 1983).

An obvious conclusion to be drawn from the results of this study is that heart rate in mink can be very variable under different conditions of voluntary submergence (Figs 1, 2). The highest heart rates observed during voluntary dives were recorded during shallow dives in the pool at Durham, the only situation in which the water was completely uncovered. Indeed, these shallow dives at Durham were the only ones in which mean dive heart rates [305.9 ± 18.0 ($N = 11$) and 210.6 ± 7.1 ($N = 22$) beats min^{-1}] did not fall below resting levels [200.0 ± 6.7 ($N = 13$) and 208.5 ± 5.5 ($N = 12$) beats min^{-1}]. At the other extreme, the lowest mean dive heart rates were recorded when the mink entered the submerged pipes [56.1 ± 6.5 ($N = 5$) and 82.7 ± 5.1 ($N = 22$) beats min^{-1}] and the bradycardia was maintained for the entire period for which the animals were inside the pipes.

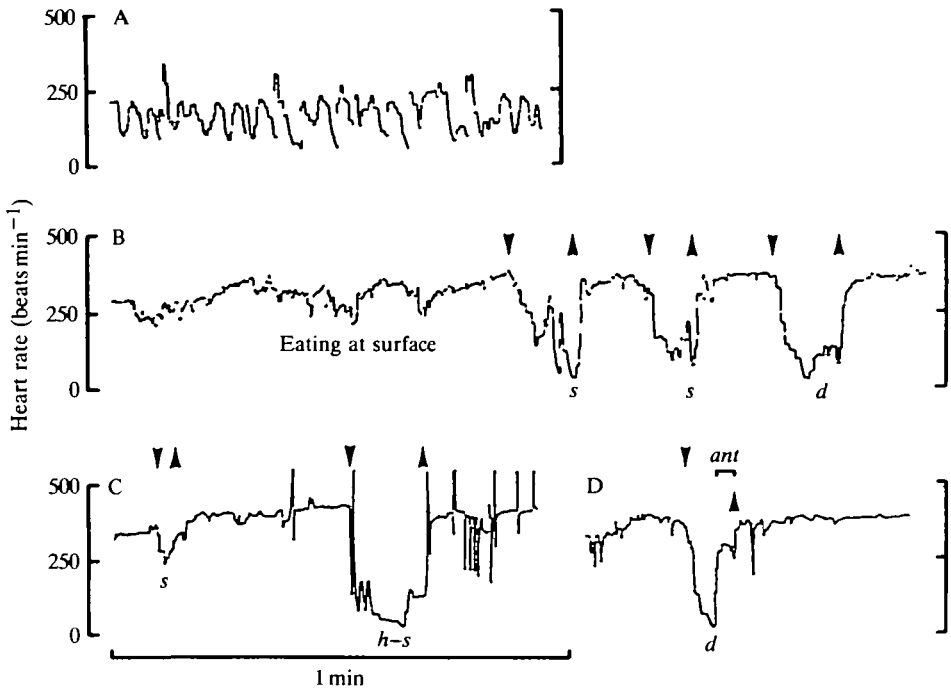


Fig. 1. Traces of instantaneous heart rate recorded from a 650 g female mink at rest (A), while eating and during shallow and deep dives in an indoor tank at the University of Birmingham (B), during shallow and hide-search dives at the University of Durham (C), and during a deep dive at Durham (D). *s*, shallow dives; *d*, deep dives; *h-s*, hide-search dive, i.e. when the animal was inside a confined space; *ant*, anticipatory increase in heart rate as mink ascends to the surface at the end of a deep dive at Durham. Downward pointing and upward pointing arrowheads indicate points of submersion and surfacing, respectively.

This variability of the heart rate response strongly suggests that psychological factors can have a potent effect on physiological responses in mink. For example, despite the fact that the mink were allowed to become fully accustomed to being inside a Perspex respirometer box while at Durham, transportation to Birmingham and the novel surroundings of the laboratory and diving tank appeared to unsettle the animals to such an extent that their behaviour and physiology were markedly affected (Figs 1, 2). A third mink refused to dive in the tank at Birmingham and, in the two that would dive, mean heart rates during submersion were significantly lower (by between 60 and 180 beats min^{-1}) in the tank at Birmingham than in the more familiar tanks at Durham (Fig. 2). The dives in both locations were to similar depths and of similar duration, so it seems unlikely that depth and duration are causative factors in the differences between heart rate responses. Furthermore, analysis of data collected at Birmingham (where all dives were performed in one tank) revealed that mean heart rate was unaffected by dive depth (see Fig. 2) and was not correlated with dive duration ($r^2 = 0.099$).

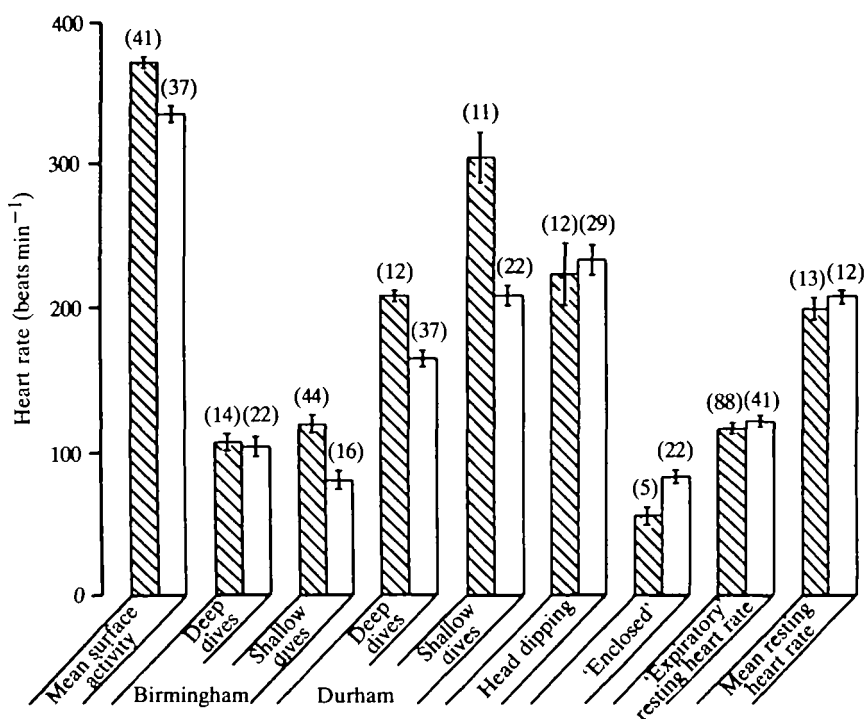


Fig. 2. Mean (\pm S.E.) heart rates in two female mink (body masses 650 g, hatched bars, and 1000 g, open bars) during unrestrained diving activities in indoor tanks located at the University of Birmingham and the University of Durham. Resting heart rates were recorded when the mink were apparently sleeping, and 'expiratory' values were obtained by averaging the long cardiac intervals which were visually correlated with expiration during sleep. 'Hide-search' heart rate represents the mean value (\pm S.E.) for the period in which the animals were inside a confined space during submersion. Sample size (N) is presented in parentheses above each column.

Another observation which indicates that 'psychogenic influences' may affect heart rate is that a pronounced anticipatory increase in heart rate often occurred before the mink broke the surface at the end of deep dives performed at Durham (Fig. 1), though this was not observed during dives of similar depth and duration at Birmingham. This anticipatory increase in heart rate, which has also been observed in diving ducks (Butler & Woakes, 1979) and in Weddell seals (Guppy *et al.* 1986), obviously occurred in the absence of lung inflation since the animals were still underwater.

Heart rate fell from elevated levels during surface activities to slightly above mean resting levels [i.e. 224.3 ± 22.5 ($N = 12$) and 233.7 ± 11.0 ($N = 29$) beats min^{-1}] in both animals upon voluntary head submersion [head dipping; mean durations 2.7 ± 0.5 ($N = 12$) and 3.2 ± 0.2 ($N = 29$)], a much higher rate than that recently reported for a single mink by West & Van Vliet (1986). It is possible that the mink used by the latter authors was exhibiting an extreme response induced by stress, in a

similar way to one mink (1000g animal) in the present study, in which it was observed that heart rate was significantly lower during the first exploratory head submersions in the tank at Birmingham than during subsequent head-dipping activity. Mean heart rate for the first five voluntary head submersions of this animal was 63.7 ± 8.89 beats min^{-1} and the lowest heart rate of 38.4 beats min^{-1} was recorded for the very first submersion. Instances of reductions in heart rate in response to loud noises (perhaps fear bradycardia; see Smith, Sims & Vich, 1981) were noted in mink engaged in non-aquatic exploratory or hunting activity at the University of Durham. This suggests that a nervous mechanism exists to invoke a fear-induced reduction in heart rate, although whether this same mechanism is operative during dives and head dipping remains to be seen.

Mink have been observed to explore confined spaces in search of prey organisms underwater, as well as during terrestrial hunting activities (Dunstone, 1978; Dunstone & O'Connor, 1979a; Birks & Dunstone, 1985). A pronounced bradycardia during such dives suggests that in this situation the mink invoke physiological adjustments (i.e. an oxygen-conserving response) that will result in an increased breath-hold endurance time. The duration of dives during which the animals entered submerged pipes [11.9 ± 1.43 ($N = 5$) and 7.0 ± 0.44 ($N = 22$) s] was greater than the duration of normal shallow dives [3.3 ± 0.34 ($N = 11$) and 4.6 ± 0.29 ($N = 22$) s] in the same tank, a finding which corroborates the results of Dunstone (1978). Since live fish were not provided as prey, all dives consisted only of the search phase of foraging dives and it would be interesting to know whether the physiological adjustments (more intense bradycardia) enable total duration of dives in which live prey are located (i.e. both search and pursuit phases) to be extended in hide-search dives, compared with shallow dives. Also, since giving-up time is inversely related to fish encounter rate in mink (Dunstone & O'Connor, 1979a), it would be interesting to determine whether the physiological adjustments during hide-search dives are affected by fish encounter rate. In other words, is the occurrence of a bradycardia an adopted mechanism whereby breath-hold endurance capacity can be extended under situations where food availability is low (i.e. analogous to 'extended' dives in the tufted duck; Stephenson, Butler & Woakes, 1986) or is it an effect of being in an enclosed space while submerged and therefore being unable to obtain easy access to the water surface (i.e. analogous to 'enclosed' dives in the tufted duck; Stephenson *et al.* 1986)?

The results of this study suggest that, as in the tufted duck, both mechanisms may operate in mink under the appropriate circumstances. The occurrence of very low heart rates during dives in the tank at Birmingham (approximately 80–120 beats min^{-1}), where the mink were not familiar with their surroundings, and upon entrance to a confined space during hide-search dives, is supportive of the latter suggestion (enclosed dive analogy). In favour of the former suggestion (extended dive analogy) is the observation that when the mink are in familiar surroundings (Durham) dive depth may affect mean diving heart rate, with lower rates occurring during deeper dives. However, owing to differences in the physical structure of the

two tanks at Durham, we do not know to what extent, if any, psychogenic influences affected these results. The question as to the effect of dive depth can only be resolved by comparing the cardiac responses to shallow and deep dives in an uncovered tank or pond in unstressed and equally motivated (hungry) animals.

West & Van Vliet (1986) demonstrated that the rapidly developing bradycardia which occurred during tracheal water flow in anaesthetized mink was mainly a reflex effect of stimulation of upper airway receptors and lung deflation. Peripheral arterial chemoreceptor stimulation had a relatively weak effect on heart rate. The results of the present study indirectly indicate that heart rate may also be strongly affected by lung ventilation in unanaesthetized mink. Resting heart rates, which were recorded while the mink were apparently asleep in their normal boxes at Durham, were characterized by pronounced oscillations (with an amplitude of approximately $100 \text{ beats min}^{-1}$), which were visually correlated with the respiratory cycle (i.e. probably sinus arrhythmia; see Fig. 1). These oscillations in heart rate were not present in awake, active mink, despite the elevated levels of lung ventilation associated with exercise during surface activities between dives. Rather, heart rate was remarkably constant at between 350 and $375 \text{ beats min}^{-1}$ in both animals (Figs 1, 2). Interestingly, while eating, when ventilation was presumably less regular and interrupted periodically by swallowing, heart rate was more variable, between 200 and $350 \text{ beats min}^{-1}$ (Fig. 1).

The mink were sometimes observed to exhale while underwater at the start of deep dives and it is notable that heart rates during such dives at Birmingham [107.7 ± 6.7 ($N = 14$) and 104.4 ± 6.1 ($N = 22$) beats min^{-1}] reached levels which were similar to those during normal resting expiration [117.5 ± 3.4 ($N = 88$) and 122.0 ± 4.5 ($N = 41$) beats min^{-1}]. This has also been observed in hooded and harbor seals (Päsche & Krog, 1980) and Humboldt penguins (Butler & Woakes, 1984). It would be interesting to know whether the mink also exhaled during shallow dives (if not this may explain why heart rate remained higher during these dives at Durham) and upon entrance to the confined space during hide-search dives. The occurrence of expiration may provide a mechanism by which the cardiac response can be controlled during different types of dives. Whether the fear bradycardia described above is associated with hypoventilation or apnoea is not known.

The results of this pilot study raise many interesting questions relating to mechanisms of cardiovascular control, energetics of aquatic locomotion and the physiological basis of behavioural strategies used by mink when hunting in an aquatic environment. In support of comments made by Farrell & Wood (1968), it is clear that if future experiments are to yield meaningful information, the mink must be housed permanently at the site of measurement so that they can become fully accustomed to the experimental set-up, thus eliminating any physiological consequences of new surroundings or disturbances. Ideally, the results of laboratory studies should be compared with those obtained by telemetry from wild mink in natural conditions.

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