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Dive performance in a small-bodied, semi-aquatic mammal in the wild

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Aquatic foraging is a fundamental component of the behavior of a number of small mammals, yet comprehensive observations of diving are often difficult to obtain under natural circumstances. Semiaquatic mammals, having evolved to exploit prey in both aquatic and terrestrial environments, are generally not as well adapted for diving (or for life in the water) as are fully aquatic species. Because dive ability also tends to increase with body size, small, semiaquatic mammals are presumed to have fairly limited dive ability. Nevertheless, diving plays an important role in food acquisition for many such species. We used time–depth recorders (TDRs) to measure and describe the dive performance of 9 female and 5 male free-living American mink (*Neovison vison*; body mass approximately 1 kg) on lowland rivers in the southern United Kingdom. We recorded dives up to 2.96 m deep (maximum depth $\bar{X}$ = 1.82 m) and up to 57.9 s in duration (maximum duration $\bar{X}$ = 37.2 s). Dive duration was approximately 40% of that predicted by allometry for all air-breathing diving vertebrates (as might be expected for a small, semiaquatic animal) but was twice as long as previously measured for mink in captivity. Mink performed up to 189 dives per day ($\bar{X}$ = 35.7 dives/day), mostly during daylight, and spent a maximum of 38.4 minutes diving per day ($\bar{X}$ = 7.6 min/day). Some individuals maintained particularly high diving rates over the coldest months, suggesting that the benefits of aquatic foraging in winter outweigh the costs of heat loss. We observed a number of very shallow dives (depth approximately 0.3 m) of particularly long duration (up to 30 s). The function of these dives is currently unknown, but possibilities include searching for prey, travelling, or avoidance of threats. There is only 1 other study of which we are aware that presents detailed measurements of dive performance in a small, shallow-diving, semiaquatic mammal.

Key words: aquatic foraging, data logger, mink, mustelid, *Neovison*, time–depth recorder, TDR

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Aquatic air-breathing vertebrates exhibit several physiological, morphological, and behavioral adaptations for diving (Boyd 1997; Butler and Jones 1997; Fish 1993). The ability to tolerate prolonged periods of diving (and maintain aerobic metabolism) depends on oxygen stores and the rate of oxygen consumption (Boyd 1997; McNab 2002). Thus, diving animals often have large oxygen stores (relative to their mass) and use a variety of oxygen-conserving mechanisms during diving (e.g., bradycardia, hypometabolism, and decreased peripheral blood flow—Kooyman 1989). In addition, semiaquatic mammals are well insulated to reduce heat loss (Estes 1989), possess hydrodynamic body shapes for efficient swimming and modified limbs to increase propulsion (Fish 1993), and use methods such as gliding further to reduce swimming effort and the energetic cost of the dive (Williams et al. 2000).

Semiaquatic mammals, having evolved to exploit prey in both aquatic and terrestrial environments, are generally not as well adapted for diving (or for life in the water) as are fully aquatic species (Dunstone 1998; Fish 2000; Williams 1998); they are usually inefficient swimmers (Williams 1999) and are generally considered to be relatively poor divers (Fish 2000). Because dive ability also tends to increase with body size (Halsey et al. 2006; Schreer and Kovacs 1997), smaller

mammals are expected to be poorer divers than larger mammals, and thus semiaquatic mammals that are also small in size are presumed to have fairly limited dive ability. However, there are very few studies on the diving ability of this group; studies of natural dives by semiaquatic mammals in the wild have until recently been limited to observational studies of animals on the water's surface (e.g., platypus [*Ornithorhynchus anatinus*—Kruuk 1993], Eurasian otter [*Lutra lutra*—Kruuk 2006], and Cape clawless otter [*Aonyx capensis*—Somers 2000]). There is only 1 other detailed data set of which we are aware on diving in free-living, small, semiaquatic mammals (platypus—Bethge et al. 2003).

Because semiaquatic mammals forage on land and in water, we cannot fully understand their foraging strategies without a better understanding of their capabilities in terms of hunting (fishing) in the water. American mink (*Neovison vison*) occur in a range of wetland habitats in both freshwater and seawater, are highly sexually dimorphic (males are larger than females), and consume a wide variety of prey including mammals, birds, fish, amphibians, crustaceans, and aquatic insects (Dunstone 1993). The diet of mink, in general, varies in response to prey availability, and their relative consumption of terrestrial and aquatic prey varies among habitats (Macdonald and Strachan 1999), seasons (Sidorovich 2000), and in the presence of intraguild competitors (e.g., otters—Bonesi et al. 2004; Clode and Macdonald 1995; Harrington et al. 2009). Early studies of dive ability in captive mink suggested that hunting of aquatic prey is constrained by oxygen limitations, and that the time that mink can spend underwater may be restricted to only a few seconds (Dunstone and O'Connor 1979a, 1979b; Poole and Dunstone 1976). Measurements of diving made in captivity, however, are limited by tank size and depth, and may underestimate true diving ability.

Until recently it was not possible to study diving in free-living mink in any detail. Radiotracking is generally used to assess activity periods and activity rates of mink (Dunstone 1993) but for animals that hold home ranges along narrow strips of riverbank the method is insufficiently precise to allow partitioning of activity between the water and the riverbank (Harrington and Macdonald 2008). Time–depth recorders (TDRs) that record depth and temperature at frequent intervals were developed in the 1970s but were initially large and imprecise, and consequently could only be used on large, deep-diving animals (e.g., fur seals—Kooyman et al. 1976). Recent development of small, powerful TDRs, however, means that detailed measurements of diving in small-bodied species are now possible (Hays et al. 2007).

We used data loggers to measure and describe the dive performance of free-living mink on lowland rivers in the southern United Kingdom. Although mink are presumed to be relatively poor divers compared to fully aquatic species, dietary studies suggest that diving plays an important role in food acquisition for this species, particularly when aquatic resources are abundant or accessible, or terrestrial prey are scarce, or both. In the present study we explore sex-based differences in dive performance, and examine seasonal changes in the extent of diving in American mink. We compare dive performance in the wild with that described previously from captive studies (Dunstone 1993 and references therein), with dive performance in other semiaquatic mammals as published in the literature, and with allometric predictions of dive ability. Herein we describe dive performance at the level of individual dives. Sequential behavior analyses will be presented separately elsewhere.

Materials and Methods

Study area.—The study was carried out on 2 lowland rivers in the southern United Kingdom: the River Cherwell and the River Thames, in the Upper Thames Valley, Oxfordshire (latitude and longitude: 51.62°N, 1.08°W), between January 2006 and January 2008. Both rivers are slow-flowing, between 5 and 20 m wide, and up to approximately 3 m deep. Both rivers are fringed with willow trees (*Salix fragilis*), and vegetation predominated by nettles (*Urtica dioica*), brambles (*Rubus fruticosus*), blackthorns (*Prunus spinosa*), and hawthorns (*Crataegus monogyna*), and are bordered on either side by a mixed agricultural landscape (predominantly grazed pasture). The climate is temperate, with summer temperatures that vary between a minimum of 12–14°C and a maximum of 20–27°C and winter temperatures that vary between a minimum of 0–5°C and a maximum of 6–10°C; there were 0–12 days of frost per month during November–March (Oxford weather station: www.metoffice.gov.uk/climate/uk/stationdata).

Potential competitors for mink in the area include otters, polecats (*Mustela putorius*), foxes (*Vulpes vulpes*), and stoats (*M. erminea*). Prey species of mink present include rabbits (*Oryctolagus cuniculus*), small mammals, birds, fish, and crayfish (*Pacifastacus lenusculus*).

Animal handling and TDR deployment.—Mink were captured in single-entry, wire-mesh cage traps (Solway Feeders Ltd., Kirkcudbright, Scotland, United Kingdom) set on floating rafts secured to the riverbank (Reynolds et al. 2004). Traps were set within a wooden tunnel fixed to the raft and thus were protected from the weather; there was no evidence of disturbance of traps by otters. Traps were provisioned with hay for insulation and rabbit or sardines for food, and were checked once per day, early in the morning. Under anesthesia (see methods in Harrington et al. [2008] and Hays et al. [2007]), captured mink were implanted with a passive integrated transponder tag (MID Fingerprint, Weymouth, United Kingdom) for individual identification (if they had not previously had a tag implanted as part of a longer-term study of mink ecology) and fitted with a collar to which a CEFAS G5 TDR (31 × 8 mm; CEFAS Technology Ltd., Lowestoft, United Kingdom) had been attached. Initially, we attached TDRs to radiocollars (Wildlife Materials Ltd., Murphysboro, Illinois). In later deployments, we attached TDRs to hand-sewn collars (approximately 1 cm wide, made of 3 layers of pure wool material, sewn with cotton thread), designed to deteriorate and fall off naturally if animals were not recaptured. TDRs were protected within semiflexible,

9-mm-diameter plastic tubing and attached to collars using monofilament line, glue, and tape (see Hays et al. 2007). Animals were weighed at their 1st capture. Procedures were usually completed within 10–30 min and animals recovered from anesthesia within 10–25 min. Mass (in air) of the collar with the TDR was 18 g or less (<3% of the body mass of the smallest individual in this study). Animals were recaptured 1 week after TDR deployment (or as soon as possible after 1 week) and collars were removed using the same procedures. There were no cases of neck abrasion (or other injury) due to the collars used over this short time interval.

All procedures were carried out under United Kingdom Home Office licenses PPL30/1826, PIL30/6530, and PIL30/6917; were approved by Oxford University Zoology Department Ethical Review Committee; and met guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). Mink were rereleased for monitoring under section 16 of the Wildlife and Countryside Act 1981, Department for Environment, Food and Rural Affairs licence WCA/06/4 and Natural England licenses NNR/2007/0024 and NNR/2007/0022.

Dive analysis.—Time–depth recorders were set to record depth at 1-s intervals and temperature at 5-s intervals, over a period of 5–6 days (the total period being limited by battery life). We used MULTITRACE (Jensen Software Systems, Laboe, Germany) to extract dive parameters, with a dive threshold of 0.2 m to exclude surface swimming and fluctuations in the water's surface due to wave action (precision of TDRs 0.05 m—Hays et al. 2007). All dives were viewed, and the surface baseline corrected manually for each dive, before accepting parameter values. For each dive, we recorded dive depth (m) and dive duration (s).

Comparative data from captive mink in the laboratory were taken from Dunstone (1993) in which maximum dive duration was 30 s, mean dive duration was 9.9 s, and ''most'' dives were less than 10 s in duration. Predicted maximum dive depth and duration were calculated using the following equations from Schreer and Kovacs (1997) for diving, air-breathing vertebrates:

$$\text{maximum depth(m)} = 36.31 M_b^{0.33} \quad (1)$$

and

$$\text{maximum duration(s)} = \left(1.62 M_b^{0.37}\right) * 60, \quad (2)$$

where M_b is body mass (kg).

We also calculated, for each individual mink, the number of dives per day, the time spent diving per day (min; both calculated only for days in which we recorded at least 1 dive), the hourly ''dive rate'' (the average number of dives performed per hour) and ''dive effort'' (min; the average time spent diving per hour; both calculated for all hours within which we recorded at least 1 dive, i.e., this is the average number of dives per hour during an hour of ''active diving''—hours in which mink did not dive were excluded—where hour was defined by clock time, i.e., the number of dives between 1100 and 1200 h), and the time of day that diving occurred. Mink in the Upper Thames River area during this study were predominantly active during daytime (Harrington et al. 2009); therefore, to allow direct comparisons between seasons, we also calculated an approximate hourly ''average dive rate'' and ''average dive effort,'' as the number of dives per hour, or the time spent diving per hour, averaged over all daylight hours (http://www.halesowenweather.co.uk/sunrise_sunset_times.htm).

Statistical analysis.—Most dive parameters were positively skewed within individual, thus we used the median to represent the central tendency of an individual's diving ability; for overall summaries we used means, weighted by either the number of dives, number of hours, or number of days, of individual median values. Dive parameters were compared among individuals, and between sexes and among seasons (defined by mean monthly temperatures during the study: summer—August and September, autumn—October, and winter—November–March) using analysis of variance (ANOVA) and mixed-factor general linear models (GLMs), respectively. Data were transformed prior to analysis to correct for the skewed distribution of the data as necessary to meet the assumptions of parametric analysis (transformations given in the text). Where appropriate, an individual was included in the model as a random factor, nested within sex or season (fixed factors), to account for repeated measurements on single individuals. Nonparametric tests were used for untransformed data and were as specified in the text.

Statistical analyses were carried out in MINITAB, except for the analysis of the relationship between dive duration and dive depth that was carried out in R (R Development Core Team 2008) using the package car (Fox 2009). Statistical significance was accepted at $P < 0.05$; all tests were 2-tailed unless otherwise stated.

RESULTS

Of 31 TDRs deployed on 24 mink (8 males and 16 females), 20 were retrieved, providing data for 16 individual mink (6 males and 10 females; Table 1). Mean body masses of study animals were: for females, 710 g ($SD = 80$ g); for males, 1,410 g ($SD = 220$ g); all animals were adult or subadult. In total, we recorded 3,750 dives. There was considerable variation in the total number of dives performed by individual mink, ranging from 5 to 789 dives over the 5–6 days recorded by the data logger (median number of dives = 103, $n = 20$ data sets). One data logger failed prematurely and only recorded for 2 days. Two individuals for which we recorded fewer than 20 dives were excluded from further analysis.

Dive depth and duration.—Median dive depth for individual mink varied between 0.30 and 0.86 m (overall weighted mean of median depth = 0.45 m, $n = 14$ individuals). Maximum dive depth varied between 0.76 and 2.96 m (maximum depth $\bar{X} = 1.82$ m, $n = 14$; Fig. 1a). Dive depth was extremely variable within individuals (coefficient of variation [CV] = 0.44–0.86) and differed significantly among individuals (ANOVA, inverse transformed depth: $F_{13,3,726} = 49.42$, $P < 0.001$). There was no difference, however, in dive depth between the sexes (GLM: $F_{1,12} = 0.59$, $P = 0.456$) or seasons (GLM: $F_{2,11} = 0.21$, $P = 0.813$).

Table 1.—Time–depth recorder deployments on American mink (*Neovison vison*). Note that repeat deployments were made on some individuals. F = female; M = male.

Animal	Sex	Body mass (kg)[a]	River	Month and year equipped	Length of deployment	No. dives recorded
M39	F	0.78	Cherwell	January 2006	5.4	497
				August 2006	6.3	238
M16	F	0.73	Thames	February 2006	6	5[b]
M36	F	0.62	Cherwell	February 2006	5.5	789
M43	F	0.6	Cherwell	March 2006	4.7	99
M23	F	0.79	Cherwell	March 2006	0.8[c]	67
M04	F	0.69	Thames	August 2006	5	190
M110	F	0.85	Cherwell	August 2007	1.7[d]	75
M117	F	0.66	Thames	October 2007	6.6	376
M121	F	0.72	Thames	November 2007	6.6	368
M123	F	0.67	Cherwell	December 2007	5.3	144
M47	M	1.28	Thames	February 2006	5.5	5[b]
M18	M	1.5	Cherwell	August 2007	6.5	107
M113	M	1.73	Cherwell	August 2007	6.3	22
M115	M	1.12	Thames	September 2007	5.8	407
M116	M	1.32	Cherwell	October 2007	6	189
				November 2007	6.3	56
				January 2008	6.6	27
M42	M	1.52	Cherwell	October 2007	6.2	66
				October 2007	5.7	23

[a] Recorded to the nearest 10 g.
[b] These 2 individuals were excluded from statistical analysis.
[c] Data logger recorded for full 5 days; dives recorded on only 1 of those days.
[d] Data logger failed prematurely and only recorded for 2 days.

Median dive duration varied between 7.4 and 18.0 s (overall weighted mean of median duration = 10.9 s, $n = 13$ individuals, duration data missing for 1 individual). Maximum dive duration varied between 25.0 and 57.9 s (maximum duration $\bar{X} = 37.2$ s, $n = 3$; Fig. 1b). As for dive depth, dive duration was extremely variable within individuals ($CV = 0.41–0.75$), and differed significantly among individuals (ANOVA, square-root transformed [duration − 1]: $F_{12,3,620} = 53.33$, $P < 0.001$) but not between the sexes (GLM: $F_{1,11} = 0.57$, $P = 0.464$) or seasons (GLM: $F_{2,11} = 0.15$, $P = 0.861$). Nine of 13 wild mink in our study exceeded Dunstone's mean dive duration of 9.9 s (Wilcoxon, 1-tailed tests, $W = 1{,}745–219{,}650$, all $P < 0.003$, $n = 67–735$ dives per individual), and all but 2 individuals exceeded the maximum dive duration of 30 s. For all individuals combined, both mean and maximum dive duration were significantly greater than expected based on Dunstone's captive studies (Wilcoxon, 1-tailed tests, $W = 88$ and 85, $P = 0.002$ and 0.003, respectively, $n = 13$ for both). However, long-duration dives were not common: per individual, the percentage of dives exceeding 30 s in duration ranged between less than 1% and 18% (on average [weighted mean] 2.7% dives >30 s, $n = 13$ individuals). Between 18% and 59% of dives, per individual, were less than 10 s in duration (weighted mean = 41.1% dives <10 s).

Dive duration increased significantly and nonlinearly with dive depth such that there was a diminishing increase in dive duration with increasing depth (estimated slope of the relationship between [log] dive duration and [log] dive depth, for all individuals pooled = 0.59, 95% confidence interval [95% *CI*] = 0.569, 0.618; Fig. 2a). The slope of the log-log relationship was not affected by outliers, and was relatively consistent among individuals (see Appendix I), although R^2 was low for both individual relationships and the pooled data (individuals: $R^2 = 0.08–0.59$; pooled data: $R^2 = 0.38$). The ratio of dive duration to dive depth (the duration of a dive in relation to its depth) declined significantly, and nonlinearly, with increasing depth (estimated slope of the relationship between [log] duration : depth and [log] depth, for all individuals pooled = −0.41, 95% *CI* = −0.433, −0.384; Figs. 2b and 2c). Low duration : depth ratios were recorded over the range of dive depths observed, and, at depths greater than approximately 0.5 m, duration : depth remained low and relatively constant (Fig. 2c). At shallow depths, however, we recorded a range of duration : depth ratios with some extremely high values depicting shallow dives of relatively long duration (Fig. 2c). The range in duration : depth ratios at shallow depths was not due to observer error in assessing the duration of shallow dives. There was no relationship between the difference in 2 independent readings of dive duration and dive depth (tested for 1 data set, dives analyzed by 2 observers, $n = 94$ dives).

Allometric comparisons.—Allometry predicts that the average female mink in our study would be able to dive up to 32.3 m, and the average male up to 40.7 m. The actual maximum dive depths recorded (above) were 6% and 4% of predicted values for females and males, respectively. Similarly, the average female in the study was predicted to be able to dive for up to 85.5 s, and the average male up to 110.8 s. Actual maximum dive durations recorded were 44% and 34% of predicted values for females and males, respectively.

Daily and hourly dive performance.—The number of dives per day, and the time spent diving per day, differed significantly among individuals (ANOVA, square-root–transformed variables: number of dives per day: $F_{12,77} = 13.8$, $P < 0.001$; time spent diving per day: $F_{11,73} = 8.19$, $P < 0.001$) and was highly variable within individuals: 1 individual (M115) dived between

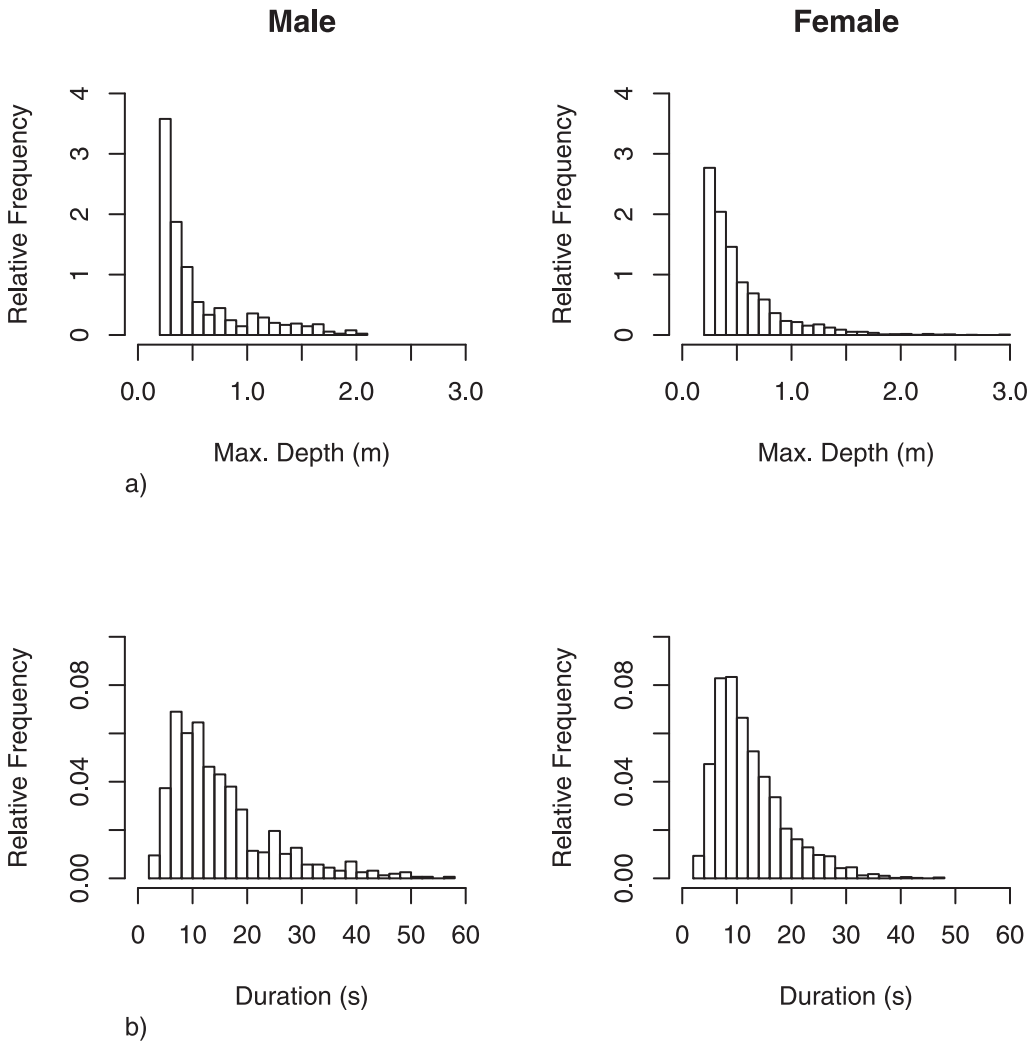
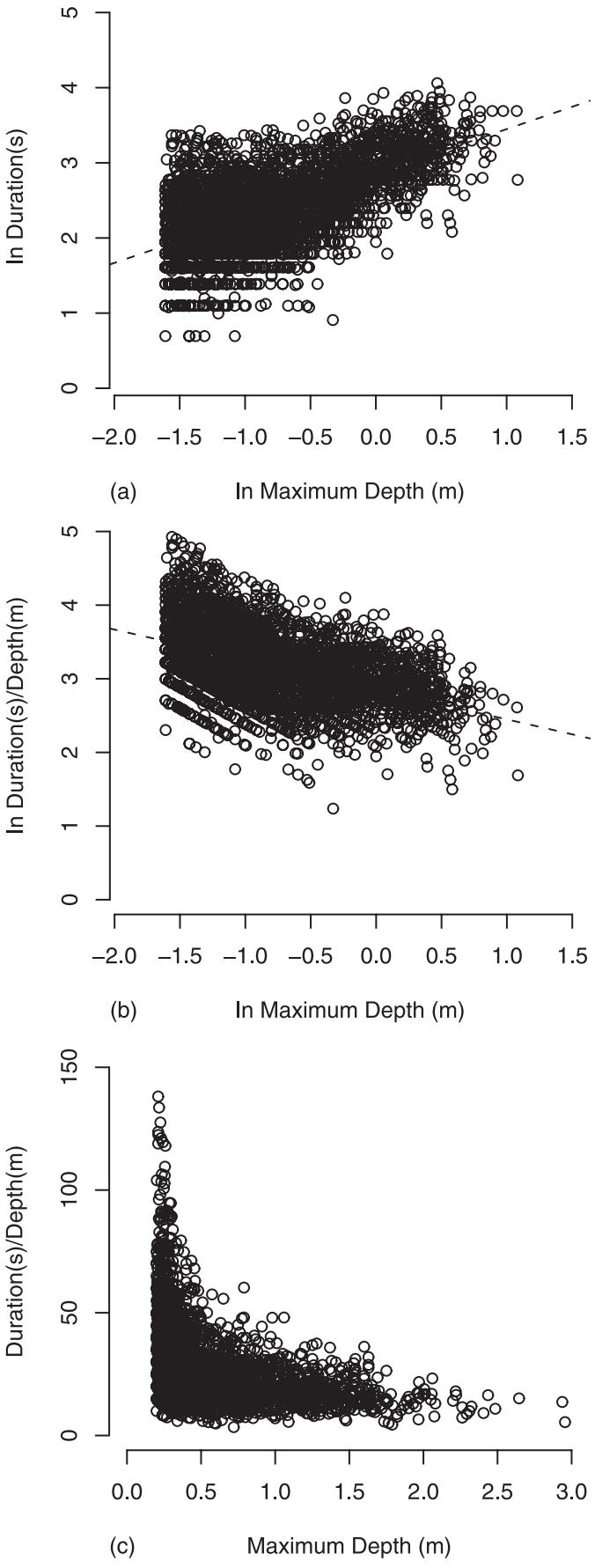


Fig. 1.—Distribution of a) depth and b) duration of dives, for all American mink (*Neovison vison*) with >20 recorded dives. $n = 14$ individuals (5 males and 9 females); $n = 897$ dives (males), $n = 2{,}843$ dives (females).

5 and 143 times per day and spent between 1 and 27 min per day diving. The overall mean number of dives (weighted mean of individual medians, $n = 2$–18 days per individual) was 35.7 dives/day and overall (weighted) mean of median time spent diving per day was 7.6 min; maxima recorded were 189 dives/day and 38.4 min spent diving per day. Females dived significantly more per day (in terms of both total number of dives and total time spent diving) than did males, over all seasons combined (GLM: number of dives per day: $F_{1,11} = 7.17$, $P = 0.021$; time spent diving per day: $F_{1,10} = 6.39$, $P = 0.030$; Table 2). However, there was no difference between sexes in summer (number of dives per day: $F_{1,4} = 0.53$, $P = 0.498$; time spent diving per day: $F_{1,4} = 0.10$, $P = 0.762$; Table 2). We were unable to test specifically for sex differences in winter because of the low number of males sampled in winter. There was no statistically significant seasonal effect for males and females combined (GLM: number of dives per day: $F_{2,11} = 0.74$, $P = 0.483$; time spent diving per day: $F_{2,11} = 0.50$, $P = 0.617$). There appeared to be a tendency for some females to dive more, and to spend more time diving, in winter than in summer (Table 2) but the difference was not statistically significant (number of dives per day: $F_{2,6} = 0.520$, $P = 0.622$; time spent diving per day: $F_{2,6} = 0.47$, $P = 0.645$).

Similarly, the number of dives per hour, and the time spent diving per hour, differed significantly among individuals (ANOVA: number of dives per hour [inverse transformed]: $F_{13,462} = 8.47$, $P < 0.001$; time spent diving per hour [square-root transformed]: $F_{12,435} = 11.13$, $P < 0.001$) and was variable within individuals: 1 individual dived between 1 and 70 times/h. The overall mean number of dives (weighted mean of individual medians, $n = 3$–98 h per individual) was 6.0 dives/h and overall (weighted) mean of median time spent diving per hour was 1.4 min; maxima recorded were 70 dives/h and 11.2 min spent diving per hour. As for daily diving, females dived significantly more per hour (in terms of both total number of dives and total time spent diving) than did males over all seasons combined (GLM: number of dives per hour: $F_{1,12} = 12.39$, $P = 0.003$; time spent diving per hour: $F_{1,11} = 8.59$, $P = 0.012$; Table 2) but not in summer alone (number of dives per hour: $F_{1,4} = 1.69$, $P = 0.245$; time spent



diving per hour: $F_{1,4} = 0.34$, $P = 0.592$; Table 2). There was no statistically significant seasonal effect for females and males combined (GLM: number of dives per hour: $F_{2,13} = 0.53$, $P = 0.599$; time spent diving per hour: $F_{2,12} = 2.36$, $P = 0.135$) or for females alone (number of dives per hour: $F_{2,7} = 0.43$, $P = 0.665$; time spent diving per hour: $F_{2,6} = 2.59$, $P = 0.146$; Table 2). Mostly, dives occurred at a rate of 1 or 2 dives/min; the maximum we recorded was 7 dives/min.

Diving occurred mostly during daylight (83% of all dives were recorded during daylight hours) with the number of hours over which diving occurred increasing in summer in accordance with an increase in the number of hours of daylight (Fig. 3). Accordingly, although there was no statistically significant difference in the total number of dives per day (or the total amount of time spent diving per day) among seasons (above), the average dive rate (number of dives per hour of daylight) increased from an overall median of 1.5 dives per daylight hours in summer ($n = 7$ individuals) to 4.4 dives per daylight hours in winter ($n = 7$ individuals; Mann–Whitney: $W = 69$, $P = 0.0407$). The average dive effort (time spent diving per daylight hour) appeared to show a similar increase from 20.4 s/h diving in summer to 45.0 s/h diving in winter but this trend was not statistically significant (Mann–Whitney: $W = 54$, $P = 0.520$).

Discussion

Aquatic foraging is a fundamental component of the behavior of a number of semiaquatic small mammals (e.g., Dunstone 1993; Kruuk 1993, 2006; MacArthur 1992), yet comprehensive observations of diving are often difficult to obtain under natural circumstances. Our results provide the 1st quantitative information on the natural dive performance of mink, and how this varies between seasons and sexes. Examination of our data shows that individual variation in dive activity is high, with some individuals making many dives each day, whereas others did not dive at all. Of those mink that did dive regularly, examination of the data shows that, contrary to expectations of nocturnality, diving activity was largely confined to daylight hours. Furthermore, diving activity (at least in some females) was proportionally more important in winter than summer, suggesting that mink are sufficiently successful aquatic predators that the acquisition of energy outweighs the costs of heat loss.

←

Fig. 2.—The relationship between a) dive duration and dive depth of American mink (*Neovison vison*) for all individuals pooled (ln duration [s] = 2.85 + 0.59(ln depth) [m]; $F_{1,3,631} = 2267$, R^2 [adjusted] = 0.38, $P < 0.001$); b) dive duration : dive depth and dive depth for all individuals pooled (ln duration [m]: depth (s) = 2.85 − 0.41(ln depth) [m]; $F_{1,3,609} = 1{,}072$, R^2 [adjusted] = 0.23, $P < 0.001$); c) dive duration : dive depth and dive depth for all individuals pooled (untransformed data). $n = 14$ individuals (5 males and 9 females).

Table 2.—Daily and hourly dive performance in female and male American mink (*Neovison vison*) on a lowland river in the southern United Kingdom. *n* = number of individuals (number of days per individual = 2–18 [some individuals had 2 or 3 separate data-logger deployments]; number of hours per individual = 3–98). F = female; M = male; S = summer; W = winter.

Parameter	Sex	Season	*n*	Median values; overall mean[a] (range)	Maximum values; mean[a] (range)
No. dives/day	F	S	3[b]	28.5 (25.5–31.5)	64.3 (40–71)
		W	5	71.9 (17.0–175.0)	110.3 (58–189)
	M	Combined[c]	5	12.4 (1.0–70.0)	41.9 (12–143)
Time spent diving/day (min)	F	S	3	5.6 (4.2–7.3)	14.3 (9.1–17.3)
		W	5	15.3 (3.2–27.3)	24.5 (12.4–38.4)
	M	Combined	4[d]	2.6 (0.1–8.5)	13.6 (2.9–26.8)
No. dives/h	F	S	3	4.9 (4–7.5)	19.1 (17–22)
		W	6	10.5 (4–26)	40.4 (25–70)
	M	Combined	5	3.7 (1.0–10.5)	15.6 (3–33)
Time spent diving/h (min)	F	S	3	1.0 (0.8–1.9)	4.4 (3.5–4.1)
		W	6	2.2 (0.9–5.0)	8.0 (5.0–11.6)
	M	Combined	4[c]	0.9 (0.2–2.0)	3.8 (1.5–7.0)

[a] Weighted by the number of days or hours per individual.
[b] One female dived on only 1 day so was excluded from analysis of daily data.
[c] Male data are not presented separately by season because there was only 1 male in winter.
[d] Dive duration data missing for 1 male.

In general, our data corroborated a general tendency for short-duration, shallow dives, as found in earlier captive studies (Dunstone 1993; Poole and Dunstone 1976) but also showed that wild animals in their natural environment are capable of dives of much longer duration (up to 60 s) than predicted by captive studies (the maximum recorded previously for mink was 30 s). Nevertheless, as might be expected, dive performance of mink was poorer than predicted by allometry, presumably reflecting the limited physiological and morphological adaptations for diving in this small, semiaquatic species. Other small, semiaquatic species, however, dive relatively well (e.g., the platypus—Bethge et al. 2003; Kruuk 1993), and some even better than would be predicted by allometry (e.g., the star-nosed mole [*Condylura cristata*]—McIntyre et al. 2002; Table 3); therefore, poor dive performance does not appear to be a general phenomenon among these species. However, there have been very few detailed studies on diving in small mammals, so general conclusions are difficult to draw.

One clear limitation to understanding the full extent of diving ability from field studies is the depth of water available (Halsey et al. 2006; Schreer and Kovacs 1997). Diving in both aquatic and semiaquatic animals is not only determined by physiology, ecology also plays an important role. For example, the walrus (*Odobenus rosmarus*), despite being 1 of the largest of the pinnipeds, makes particularly shallow and short dives relative to other smaller pinnipeds; however, it feeds in vast areas of relatively shallow water where prey is abundant and there is no need to dive deep or long to satisfy its feeding requirements (Gjertz et al. 2001). Similarly, belugas (*Delphinapterus leucas*) in Hudson Bay dive in shallow coastal waters although they are capable of much deeper dives (Martin et al. 2001). It is likely that dive parameters recorded in our study at least partly reflect mink ecology (and specifically the ecology of mink inhabiting a lowland river); however, in the absence of further data, it is not possible to separate these effects from physiological limitations. Dive depth was clearly limited by the depth of the river (maximum river depth was 3 m, approximately equal to the maximum dive depth of 2.96 m), and therefore, it is possible that mink are capable of much deeper (and perhaps longer) dives than shown here. In Argentina, we have measured mink dives up to 5 m, and Hatler (1976) infers from observations of coastal mink and their consumption of bottom-dwelling crab species, that mink might be capable of diving to 7.4 m. These coastal mink dived for up to 48 s (Hatler 1976), comparable to our maximum duration of 60 s. There are no other studies of diving in free-living mink of which we are aware. Eurasian otters (which are also semiaquatic but much larger than mink; mass = 5–14 kg) also tend to dive in shallow waters and for short durations (Kruuk 2006): maximum dive durations recorded for Eurasian otters are approximately 40–50% of predicted values, based on allometry, which is comparable to our results for mink (Table 3).

Dive duration and dive depth are positively correlated across taxa, that is, deeper dives take longer to perform (Halsey et al. 2006). Accordingly, and as expected, we found a significant positive (but nonlinear) relationship between the duration and depth of dives of mink. However, although most shallow dives by mink were also of short duration, some shallow dives were relatively long in duration (Fig. 2c), and were comparable in duration to dives of much deeper depths (Fig. 2a). Several large animals that dive to shallow depths for ecological reasons make use of the physiological advantage that their size confers by diving for longer periods and, thus, increasing their foraging efficiency (Halsey et al. 2006). This strategy also could be utilized by small divers when the depth of the dive is sufficiently shallow that they are able to dive for longer than is necessary to reach that depth and return to the surface. Mink, however, are ''single-prey loaders'' that must surface, and leave the water, to consume their prey (Dunstone 1993) and, therefore, are unable to obtain more than 1 prey item per dive regardless of the duration of the dive, suggesting that long-duration, shallow dives in mink have an alternative purpose (see also Dunstone 1998). One possibility is that long,

TABLE 3.—Predicted and observed maximum dive durations for small (<15 kg), semiaquatic mammals (defined here as animals that forage for both aquatic and terrestrial prey). Predicted values are based on allometric equations in Schreer and Kovacs (1997; see text for details). Observed values are from the literature.

Species common name	Scientific name	Body mass (kg)	Predicted maximum dive duration (s)	Observed maximum dive duration[a] (s)	% predicted value	Source
Eurasian otter[b]	*Lutra lutra*	7	200	96	48	Kruuk 2006
American mink[c]	*Neovison vison*	1	97	30	31	Dunstone 1993
American mink[b]				48	49	Hatler 1976
American mink[d]				60	62	This study
North American river otter[c]	*Lutra canadensis*	11	236	88	37	Ben-David et al. 2000
Cape clawless otter[b]	*Aonyx capensis*	13	251	approximately 48 (marine)	19	Somers 2000
				26 (freshwater)	10	Somers 2000
Spotted-necked otter[b]	*Lutra maculicollis* (sometimes classified as *Hydrictis maculicollis*)	4	162	21	13	Kruuk 2006
				20	12	Rowe-Rowe and Somers 1998
				40	25	Rowe-Rowe and Somers 1998
Marine otter[b]	*Lontra felina*	4.5	170	64	38	Kruuk 2006
Star-nosed mole[c]	*Condylura cristata*	0.05	32	19	59	McIntyre et al. 2002
				120[e]	375	
				47	146	McIntyre et al. 2002
American water shrew[c]	*Sorex palustris*	0.013	19	37.9[e]	199	McIntyre et al. 2002
Muskrat[c]	*Ondatra zibethicus*	0.7	85	96 (under ice)	113	MacArthur 1992
				86 (exploratory)	101	MacArthur et al. 2001
				224 (alarm)	264	
Platypus[b]	*Ornithorhynchus anatinus*	1.8	121	75	62	Kruuk 1993
Platypus[c]				660 (inactive)	545	Evans et al. 1994
Platypus[d]				138 (inactive)	114	Bethge et al. 2003
Eurasian water shrew[c]	*Neomys fodiens*	0.012	19	16	84	Churchfield 1998
				24	126	Vogel et al. 1998
				4	21	Mendes-Soares and Rychlik 2009
Mediterranean water shrew[c]	*Neomys anomalus*	0.015	21	2.3	11	Mendes-Soares and Rychlik 2009
Australian water rat[c]	*Hydromys chrysogaster*	0.8	89	36	40	Petzold 1995

[a] These are absolute maximum durations recorded.
[b] Focal observations of wild animals.
[c] Captive animals observed in the laboratory.
[d] Data-logger data from wild animals.
[e] Forced dives.

shallow dives represent a ''search strategy'' whereby mink scan for prey while swimming beneath the surface of the water (comparable to the ''dive searches'' described by Dunstone [1993]). Observations of mink behavior, in the laboratory and in the wild, suggest that mink optimize underwater pursuit time by locating aquatic prey from outside the water, or by dipping their head in the water, before diving (Melquist et al. 1981; Poole and Dunstone 1976). ''Search dives'' may serve a similar purpose. An alternative possibility is that long, shallow dives are ''travelling dives'' that help to reduce energy expenditure when swimming. To minimize surface wave generation during swimming, and hence minimize drag (and energetic cost), animals need to swim at a depth of at least 2.5–3 times their body thickness (Hertel 1966; see also Fish 1993). Sea otters (*Enhydra lutris*) are able to reduce the energetic cost of swimming by 41% by swimming submerged rather than on the surface at the same speed (Williams 1989) and, although mink are inefficient swimmers (Dunstone 1998), Williams (1983) calculated that mink would achieve a 7- to 10-fold reduction in energy costs by swimming underwater. Distinct foraging and travelling dives have been found in other species (e.g., blue whales [*Balaeontoptera musculus*] and fin whales [*B. physalus*—Croll et al. 2001] and dugongs [*Dugong dugon*—Chilvers et al. 2004]); animals that undertake long-distance migrations appear to minimize their cost of transport by swimming at shallow depths (e.g., green turtles [*Chelonia mydas*]—Hays et al. 2001). Travelling dives may, therefore, offer an economical means of transport for mink (see Schmidt-Nielsen 1972). We are not able to estimate the distances travelled during a long, shallow dive; however, based on the measurement of Williams (1983) of swimming speed at 0.5 m/s, the maximum dive duration of 60–70 s we recorded accords well with the measurement of Petersen (1966) of mink swimming underwater for 30–35 m. We have, however, observed mink swimming both beneath and on the surface of the water, so mink clearly do not always take the least-costly

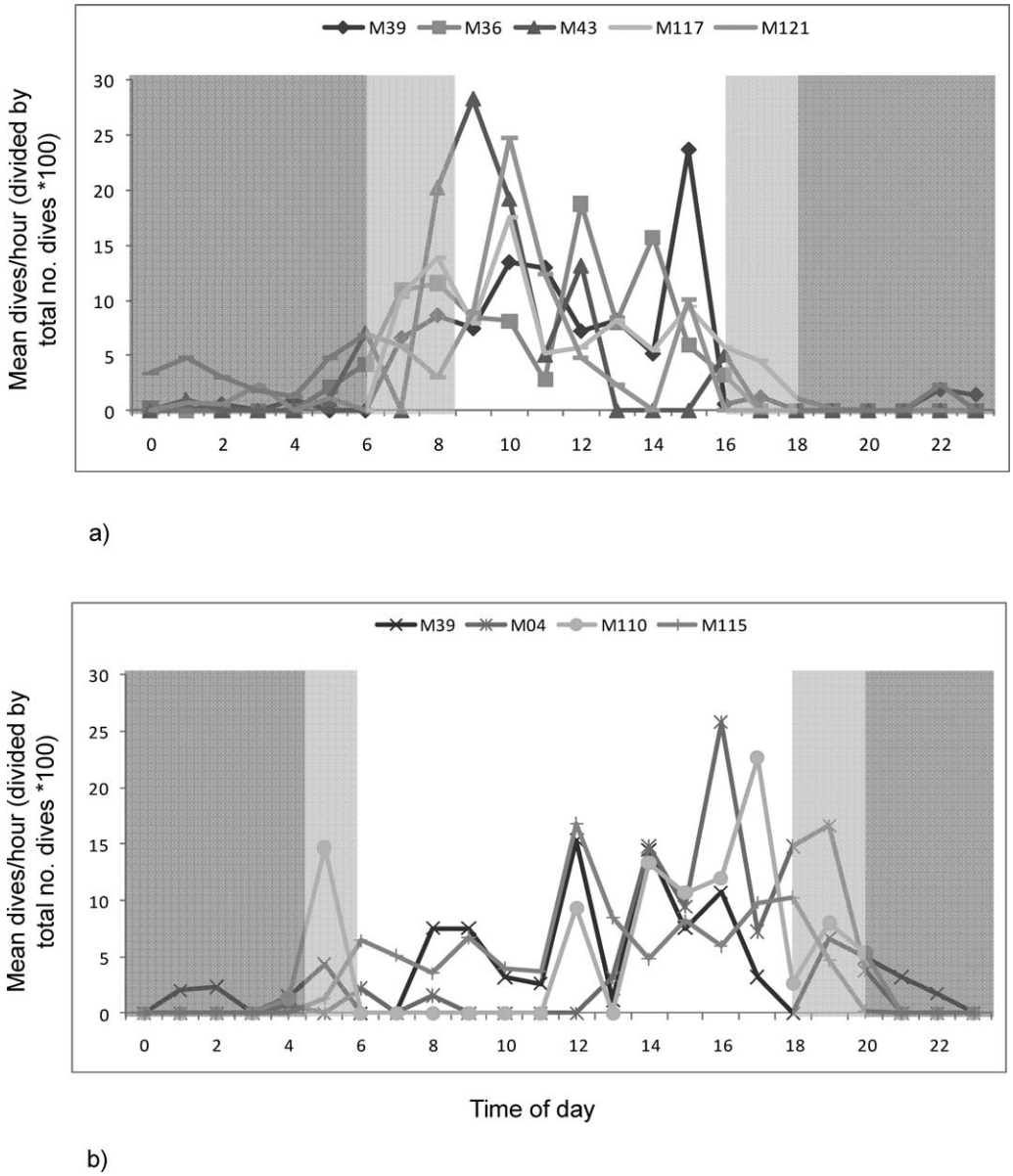


Fig. 3.—Diel dive patterns of American mink (*Neovison vison*). Data are the mean number of dives per hour as a percentage of the total number of dives in a) winter and b) summer. Light gray blocks show dawn and dusk; dark gray blocks show hours of dark. Only individuals that dived at least 5 times per hour are included.

option. A 3rd possibility is that shallow dives are an escape tactic, to avoid terrestrial predators or perceived threats.

Diel diving patterns of mink through the year appeared to correlate with daylight hours (Fig. 3), suggesting that mink prefer to dive in daylight and are able to exploit a longer ''active period'' in summer. The fact that dives occurred predominantly during daylight hours was surprising, because mink are generally presumed to be nocturnal (Dunstone 1993; but see Harrington et al. 2009; Hays et al. 2007). Two possible explanations for daytime diving in a nocturnal species are related to the availability of their prey and foraging efficiency and the avoidance of competitors. It is widely accepted that the diel patterns of foraging by divers are finely tuned to the local conditions, such as the diel availability of their prey (e.g., Hays 2003) and it might be expected that mink will fine tune their diving to maximize prey acquisition. Underwater visual acuity in mink is poor, but is optimal in high light levels (Dunstone and Sinclair 1978) and, thus, aquatic foraging efficiency in mink could be predicted to be maximized during the day (see also Dunstone 1993). However, competition and risk of predation also may influence habitat utilization and temporal activity patterns by divers (e.g., Heithaus et al. 2007). Adaptation of foraging behavior in response to predators is common among terrestrial mammals (e.g., Fenn and Macdonald 1995) and there is evidence to suggest that mink avoid otters (larger and dominant competitors) by shifting their activity periods (Harrington et al. 2009). Under this scenario, daytime would be the ''safest'' time for aquatic foraging. Further studies under different competitor scenarios are required to distinguish between these 2 hypotheses.

That mink spend as long diving, and make as many dives, in winter as in summer (and dive at a higher average rate over daylight hours), despite colder winter temperatures, suggests that there are substantial energetic benefits to be gained by aquatic foraging at this time (or that the benefits outweigh the presumed costs). All semiaquatic mammals have poor insulation relative to fully aquatic species (Dunstone 1998), and long, thin-shaped mustelids have a particularly high rate of heat loss (Brown and Lasiewski 1972; King and Powell 2007) that is increased when wet (Williams 1986; but see Korhonen and Niemelä 2002). Several terrestrial mustelid species are known to reduce their activity in winter (e.g., American marten [*Martes americana*—Buskirk et al. 1988] and black-footed ferret [*Mustela nigripes*—Richardson et al. 1987]); both star-nosed moles (McIntyre et al. 2002) and muskrats (*Ondatra zibethicus*—MacArthur 1984) make shorter and less-frequent dives in cold water. However, no reduction in diving occurred in mink in the southern United Kingdom during the winter, no difference in dive duration was detected among seasons, and, remarkably, dive rate (averaged over a shorter number of daylight hours) was, on average, higher in winter than in summer. Several authors have noted an increase in fish consumption by mink in winter (e.g., Gerell 1968; Sidorovich 2000) and suggested that this is due to the slower swimming speed, and hence increased susceptibility to capture, of fish in winter—a case of endothermic predators exploiting their ectothermic prey. In other taxa, animals can operate in physiologically challenging conditions if the reward is high. For example, cormorants (which have very poor insulation) survive in the high arctic even when the amount of time they can spend in the water is limited to less than 10 min daily, simply because their feeding rate in these very restricted periods is so high (Gremillet et al. 2001). Likewise, for mink, diving in winter may be physiologically challenging but the reward may be very high.

Of course, season encompasses differences in both temperature and day length and it is not possible in this study to fully separate these effects (given the correlation between these 2 factors, and the relatively narrow range of temperatures experienced in the southern United Kingdom for any given day length). Further detailed analysis of the fine-scale effects of temperature on diving behavior, perhaps on a daily basis, as well as studies of diving in other parts of the world where daylight–temperature scenarios differ, are warranted.

Higher diving rates, and diving effort, in female mink than in male mink is consistent with 1 study showing that coastal females consume more fish than do males (Birks and Dunstone 1985) and conforms with theories of intersexual niche partitioning (see Thom et al. 2004). However, an intersexual difference in dive behavior was not apparent in summer in this study, and our results are inconclusive. Many apparently specialized species are in fact composed of individual specialists (Bolnick et al. 2002, 2003); that this possibility applies to mink is tentatively supported by the exceptionally high diving rates shown by only 3 (of 16) individuals in this study (2 females in winter and 1 male in summer; Table 1) and by dietary studies showing that some individual mink specialize on a particular prey type (Sidorovich et al. 2001). However, this is a question for the future because our sampling regime was not designed to distinguish between individual specialists and a generalist that may temporarily be exploiting a patchy resource (see Bolnick et al. 2002).

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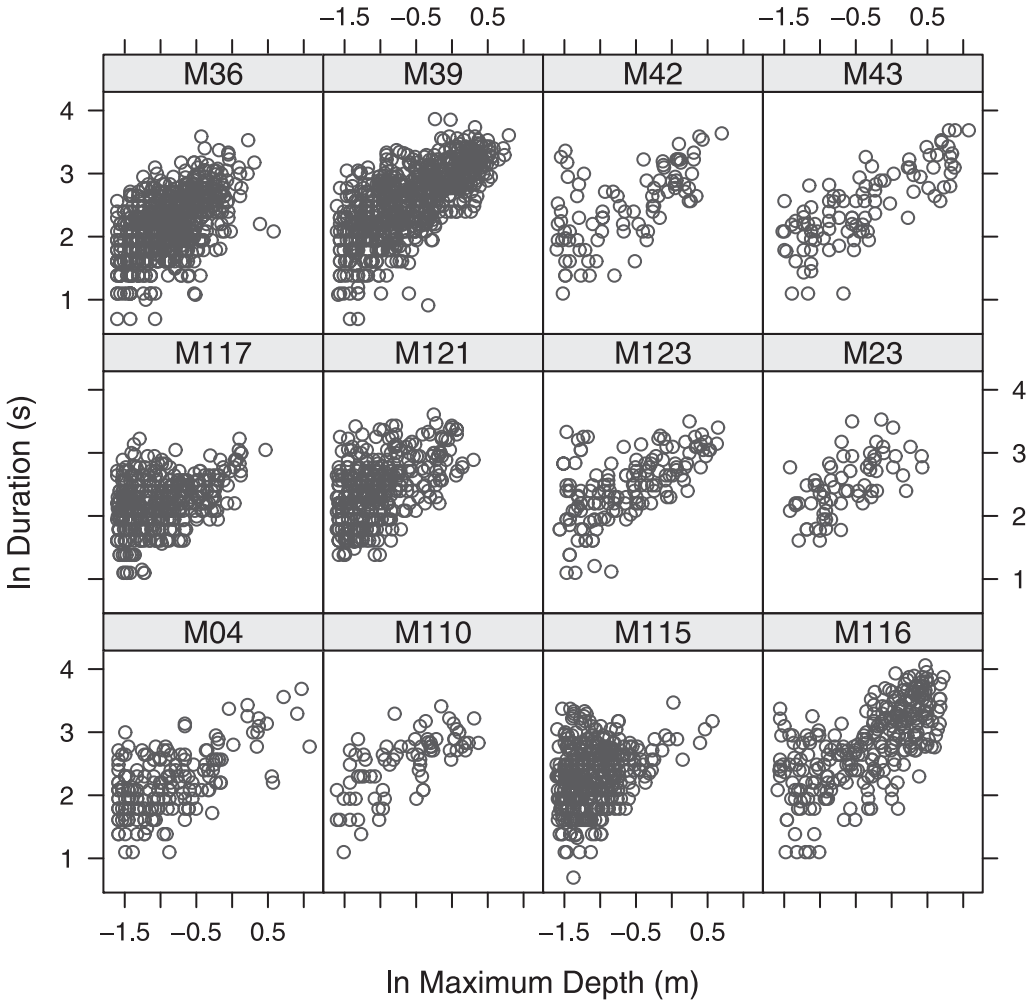
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Appendix Ia.—The relationship between dive duration and maximum depth for all individuals with >50 dives. The increase in log duration with log depth was significant ($P < 0.001$) for all individuals, and the slope of the relationships was significantly different from 1 ($P < 0.001$) in all cases, indicating nonlinear relationships between dive duration and maximum depth. Regression coefficients and *t*-test statistics are given in Appendix Ib below.

Appendix Ib

Individual log-log regression values (for 12 individuals with >50 data points).

Animal	Intercept	Slope	R^2 (adjusted)	*t*-test (slope = 1) (*t*, *d.f.*)
M04	2.62	0.49	0.34	−10.47, 188
M110	2.89	0.58	0.44	−5.56, 73
M115	2.72	0.39	0.08	−9.90, 405
M116	3.03	0.63	0.43	−8.70, 270
M117	2.55	0.35	0.14	−15.21, 374
M121	3.02	0.60	0.28	−7.98, 366
M123	2.78	0.50	0.35	−8.72, 142
M23	2.86	0.60	0.36	−4.22, 65
M36	2.73	0.62	0.30	−11.12, 787
M39	2.93	0.65	0.48	−13.92, 733
M42	2.84	0.55	0.38	−6.08, 87
M43	2.73	0.61	0.59	−7.67, 97
$\bar{X}$	2.81	0.55	0.35	—
Overall, for pooled data	2.85	0.59	0.38	—