Original Article

Hidden Markov analysis describes dive patterns in semiaquatic animals

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Existing methods of dive analysis, developed for fully aquatic animals, tend to focus on frequency of behaviors rather than transitions between them. They, therefore, do not account for the variability of behavior of semiaquatic animals, and the switching between terrestrial and aquatic environments. This is the first study to use hidden Markov models (HMM) to divide dives of a semiaquatic animal into clusters and thus identify the environmental predictors of transition between behavioral modes. We used 18 existing data sets of the dives of 14 American mink (*Neovison vison*) fitted with time-depth recorders in lowland England. Using HMM, we identified 3 behavioral states (1, temporal cluster of dives; 2, more loosely aggregated diving within aquatic activity; and 3, terminal dive of a cluster or a single, isolated dive). Based on the higher than expected proportion of dives in State 1, we conclude that mink tend to dive in clusters. We found no relationship between temperature and the proportion of dives in each state or between temperature and the rate of transition between states, meaning that in our study area, mink are apparently not adopting different diving strategies at different temperatures. Transition analysis between states has shown that there is no correlation between ambient temperature and the likelihood of mink switching from one state to another, that is, changing foraging modes. The variables provided good discrimination and grouped into consistent states well, indicating promise for further application of HMM and other state transition analyses in studies of semiaquatic animals. *Key words:* American mink, foraging strategy, hidden Markov model, mustelid, shallow diving, small bodied, time-depth recorder. *[Behav Ecol]*

INTRODUCTION

Diving has been studied extensively in fully aquatic mammals, birds, and reptiles (Putz et al. 1998; Halsey et al. 2007), usually in marine environments (Kooyman 2004; Rutz and Hays 2009). Such animals are anatomically and physiologically adapted to deep and protracted dives (Butler and Jones 1997; Williams et al. 2000) that are energy efficient (Handrich et al. 1997; Shepard et al. 2009; Mitani et al. 2010; Wilson et al. 2010). Recent technological advances allowed miniaturized time-depth recorders (TDRs) to be deployed on small-bodied animals that are physiologically or ecologically constrained to perform shallow dives. These include semiaquatic species such as platypus (Bethge et al. 2003), otter (Tinker et al. 2007), and American mink (Hays et al. 2007) as well as aquatic foraging seabirds such as the red-footed booby (Weimerskirch et al. 2006) and the Peruvian booby (Zavalaga et al. 2010).

The dives of many animals seem organized into temporal clusters with intermediate gaps—known as "bouts" (Boyd and Croxall 1992; Mori 1997; Staniland and Boyd 2003; Tremblay et al. 2003) or "movement steps" (Sims et al. 2008; Humphries et al. 2010; Hays et al. 2011). Clusters of behavior have been used to describe the foraging of both aquatic (Boyd et al. 1994; Edwards et al. 2007; Sims et al. 2008; Humphries et al. 2010; Hays et al. 2011) and terrestrial (Janssen et al. 1999; Johnson et al. 2002; Edwards et al. 2007; Reynolds 2009; Jansen et al. 2011) species. Recent debate has centered on the underlying distribution of the movement step lengths (Janssen et al. 1999; Johnson et al. 2006; Edwards et al. 2007; Sims et al. 2007; Edwards 2008; Reynolds and Rhodes 2009; Smouse et al. 2010) but has largely ignored what influences transitions between short and long step lengths (Hart et al. 2010). Moreover, step-length distribution models, developed for the more simply defined movement steps of fully aquatic or fully terrestrial species, may be inappropriate for the possible transition between aquatic and terrestrial habitats in semiaquatic animals. The behavior of semiaquatic species poses an uncertainty as to whether gaps between dives represent merely a pause within aquatic behavior or a behavioral switch to terrestrial activity. For example, a long pause between successive dives in a whale may represent resting or surface travel (Baird et al. 2002), but a long pause between successive dives in a mink may either represent resting or surface swimming, or movement onto land. Semiaquatic animals inhabit many of the ecologically sensitive and threatened habitats such as wetlands and rivers, yet are poorly studied because of the difficulty of following them in these habitat types. Thus, there is a need for models that classify behavior objectively and are not confounded by the transition between land and water to produce complete time budgets and to understand these animals' use of the environment. We use hidden Markov models (HMM) to discriminate between types of dives. We divide dives into clusters and attempt to identify the environmental predictors of transition between behavioral modes, building on a method previously used to describe transitions between behavioral units in diving penguins (Hart et al. 2010). We then use the temperature logger of a TDR on mink (*Neovison vison*)

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to infer the transition between land and water and validate our conclusions from HMM. We believe this is the first time HMM, or any analysis of transition between behaviors, has been used to analyze the foraging behavior of a semiaquatic animal. We illustrate the general approach to using HMM as an analytical method to answer questions about habitat use and the determinants of foraging patterns and rewards in semiaquatic animals.

To explore the use of HMM in describing semiaquatic behavior, we used 18 existing data sets of the dives of 14 American mink in lowland England. The American mink is a small-bodied, semiaquatic North American mustelid, extremely adaptable and highly invasive in Europe, South America, and Asia (Macdonald and Harrington 2003; López-Giráldez et al. 2005; Peris et al. 2009). Mink's broad diet includes aquatic (crayfish, fish), semiaquatic (waterfowl, amphibians), and terrestrial prey (lagomorphs, rodents, birds) (Sargeant et al. 1973; Birks and Dunstone 1984; Birks and Dunstone 1985).

Mink are relatively poorly adapted to underwater foraging. Like most mustelids, they have a high surface area to body ratio (Brown and Lasiewski 1972), and their fur has comparatively low insulative properties (Fish et al. 2002), both of which mean that their rate of heat loss is high, particularly so when in the water. Further, swimming is an energetically expensive mode of transport for mink due to their inefficient propulsion mechanism (Williams 1983). Williams (1986) suggested that these constraints should limit mink swimming, especially in low temperatures. However, data loggers reveal that wild mink spend considerable amounts of time diving (Hays et al. 2007), with no difference in the number of dives performed between summer and winter (Harrington et al. 2012). Given the extremely short duration of individual mink dives (Harrington et al. 2012), it may be that temperature affects the clustering (or persistence) of diving rather than the number of dives per se; for example, we might predict that a period spent continually in the water was shorter in winter than in summer.

Tackling behavioral questions often requires detecting the decision points (Krebs and Davies 1987) and linking these to environmental variables. The need for principled approaches to identifying behaviors and transitions is heightened in semiaquatic animals because a transition from activity to inactivity on a TDR may not represent inactivity but in fact a return to land.

Tools to enable this would allow us to answer many of the questions routinely asked of terrestrial predators, such as what influences foraging success, how individuals avoid competition, and how animals cope with patchy or changing environments. We use HMM to separate these confounding behavioral units, validate the results using logged temperature in the TDR, and test whether changes in environmental temperature influence behavioral strategies in American mink.

MATERIALS AND METHODS

Data collection

The data set used in this study has previously been described by Harrington et al. (2012) in a study of single dives by American mink. CEFAS G5 TDR (31×8 mm; CEFAS Technology Ltd, Lowestoft, UK; Hays et al. 2007) was deployed on free-living American mink on the rivers Thames and Cherwell in the Upper Thames valley in Oxfordshire, UKingdom (approximate latitude, longitude: 51.62°N, 1.08°W) between January 2006 and January 2008. The site is described in Harrington et al. (2012). Using standard protocols, mink were captured in single-entry, wire mesh cage traps (Solway Feeders Ltd, Kirkcudbright, Scotland, UK) placed 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 dead rabbit or sardines for food and were checked once a day, early in the morning on the assumption that nocturnally active mink enter the traps at night. Findings from these loggers have revealed that mink may also be active in the day (Harrington et al. 2012), something of note for future studies.

Animals were anesthetized by qualified personnel under UK Home Office License, using isoflurane (IsoFlo: Schering-Plough Animal Health, Welwyn Garden City, Herefordshire, UK) delivered via a vaporizer attached to a portable oxygen cylinder (Mathews et al. 2002), induced in a wooden box (0.15×0.15×0.48 m) with a Perspex window (Yamaguchi et al. 2002) and maintained, during handling, via a face mask.

Mink were fitted with collars to which a TDR had been attached (further details in Harrington et al. 2012 and Hays et al. 2007). Initially, we attached TDRs to radiocollars (Wildlife Materials Ltd, Murphysboro, IL, USA). In later deployments, we attached TDRs to hand-sewn collars (ca. 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 (Hays et al. 2007). Weight (in air) of the radiocollar with the TDR was 18 g or less (<3% of the body weight of the smallest individual in this study). Animals were recaptured a week after TDR deployment (or as soon as possible after a week) and collars removed using the same procedures. Animal handling was completed within 10–30 min and mink recovered from anesthesia within 10–25 min. The TDR was recovered a week after deployment (or as soon as possible thereafter), and collars were removed using the same procedures; there were no cases of neck abrasion (or other injury) during these deployments.

Of 31 TDRs deployed on 24 mink (8 male; 16 female—all adults and subadults, i.e., adult sized), 20 were retrieved giving data for 16 individual mink (6 male; 10 female). 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, giving a total of 18 data sets due to repeated trapping of 3 individuals. Details of the data can be found in Harrington et al. (2012).

All procedures were carried out under UK Home Office licenses PPL30/1826, PIL30/6530, and PIL30/6917 and were approved by Oxford University Zoology Department Ethical Review Committee. Mink were re-released for monitoring under section 16 of the Wildlife and Countryside Act 1981, Department for Environment, Food and Rural Affairs license WCA/06/4 and Natural England licenses NNR/2007/0024 and NNR/2007/0022.

Ambient air temperature measurements were obtained from the Radcliffe Meteorological Station (http://www.geog.ox.ac.uk/research/climate/rms/intro.html) situated in the center of Oxford, within 40 km of the study sites. Because water temperature tends to be more stable than air temperature, we used ambient air temperature as an indicator of environmental conditions.

Data analysis

TDRs recorded temperature at 5-s intervals and depth at 1-s intervals, over a period of 5–6 days. Individual dive data were extracted from the raw time series using MULTITRACE (Jensen Software Systems, Laboe, Germany), using a dive

threshold of 0.2 m (accuracy of TDRs ±0.05 m, Hays et al. 2007), as in Harrington et al. (2012). Further analysis—with the exception of HMM—was carried out in R 2.12.2 (R Development Core Team 2009).

HMM are a class of models in which the modeled system is assumed to be a Markov process with distinct states (Roberts et al. 2004) and where the transition from time step n to $n + 1$ is conditional on the state rather than previous states. HMM estimates the unknown (hidden) states and transition rates between states from the observed data. The HMM algorithm was applied in MATLAB 7.8 (The MathWorks™, www.themathworks.com), using HMMBOX, version 4.1, using variational Bayes (http://www.robots.ox.ac.uk/~parg/software.html), code previously developed to estimate the hidden states of navigation in homing pigeons (Guilford et al. 2004; Roberts et al. 2004) and used to identify states of diving in penguins (Hart et al. 2010). This method is a principled approach to identifying the number of behavioral states (where state is a statistically defined, distinct unit of behavior) and state membership of dives without ascribing a priori assumptions as to the purpose of a behavioral state. Even where classification may be simple to define, such as "on land" or "in water," the ability to classify behavior statistically and cross-validate with other metrics allows us to test the efficacy of statistical approaches to behavioral classification and to determine which transitions or boundaries are important to animal behavior (Mann et al. 2011).

Factors to be used in the HMM were chosen based on a principal components analysis (PCA) using the princomp function in package(stats). Four parameters (dive duration, dive temperature, dive depth, and dive interval, i.e., the length of pauses between dives) were investigated for correspondence (Figure 1). Dive interval and depth were used to define states because taken together these variables were nearly orthogonal and explained most of the variance.

The HMM was performed on depth and interval, seeking to identify between 2 and 5 states (the number of behavioral categories, irrespective of what these might be). We expected to find states corresponding to searching or travelling and foraging, plus also possibly a state for resting in water. Three states were identified in every data set, and occasionally a fourth state was found. Analysis was restricted to the 3-state model in accordance with occupancy guidelines described in Roberts et al. (2004).

One possible criticism of the HMM approach is that it is unnecessarily complex, when the pattern observed could be generated more simply using thresholds or a simpler clustering algorithm such as k-means (MacQueen 1967; Hartigan and Wong 1979) on the dive interval alone. We use HMM because the PCA showed 2 components of interest. However, we compare our results to k-means to highlight the difference between HMM using depth and interval, and k-means using dive interval. The k-means clustering was carried out within R 2.12.2.

Simulations to estimate expected transition rates between states given state frequencies were carried out using the Urn package (Altman 2007). The observed frequencies of different states were used to sample with replacement, which was simulated 1000 times for each mink. In all tests, $P = 0.05$ was accepted as significant. Tests were 2-tailed unless stated otherwise.

Linear regressions were run in R (using the *lm* function) to investigate the relationships between temperature and behavior. Individual was included as a blocking factor to remove the potentially confounding issue of individual strategies influencing results. We also examined the likelihood of switching between states at different temperatures to determine whether or not mink diving strategy is moderated by
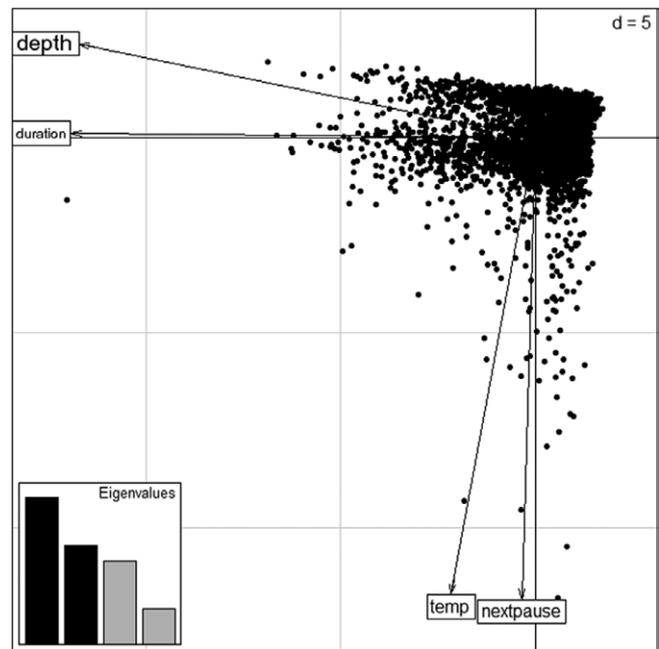

Figure 1
PCA of dive duration, dive temperature, dive depth, and the length of pauses between dives to determine relationships between parameters.

ambient temperature. The ambient temperature used in the analysis was an average of mean daily temperatures for the period of TDR deployment for each mink.

RESULTS

HMM for identifying states

The HMM algorithm consistently identified 3 clear states in all individuals (Figure 2). Re-running the algorithm showed that most dives were consistently assigned, but that the last dive in the data set was not consistently assigned to the same state in successive iterations. The last dive was retained in these analyses, but is likely to have contributed to error. Future analyses may consider dropping the last dive. The 3 states appear to represent different types of behavior: State 1 is a temporal cluster of dives; State 2 is more loosely aggregated diving, which we have termed an aquatic foraging session; and State 3 is a terminal dive of a cluster/foraging session or a single, isolated dive (see Figure 3). This division is in line with the observations of temperature profiles for the dives at each state (Figure 3A,B). The TDR temperature between the dives in State 2 increases sharply enough to suggest that the animal is leaving the water between those lose dives; the temperature rise after dives in State 3 is dramatic enough to imply that a mink would go to a hiding place where it can warm up to a temperature close to that of its body, around 39–40 °C (Williams 1986).

Comparison with k-means

k-means described 3 states on the basis of interval length between dives. Most dives were classified as State 1, with very few in States 2 and 3 (for comparison with HMM, see Tables 1 and 2, and Supplementary Material). This meant that the behavior of animals that dived frequently was classified as a single, continuous "cluster" over several hours, and shorter movement step lengths were omitted. We, therefore, focus on the
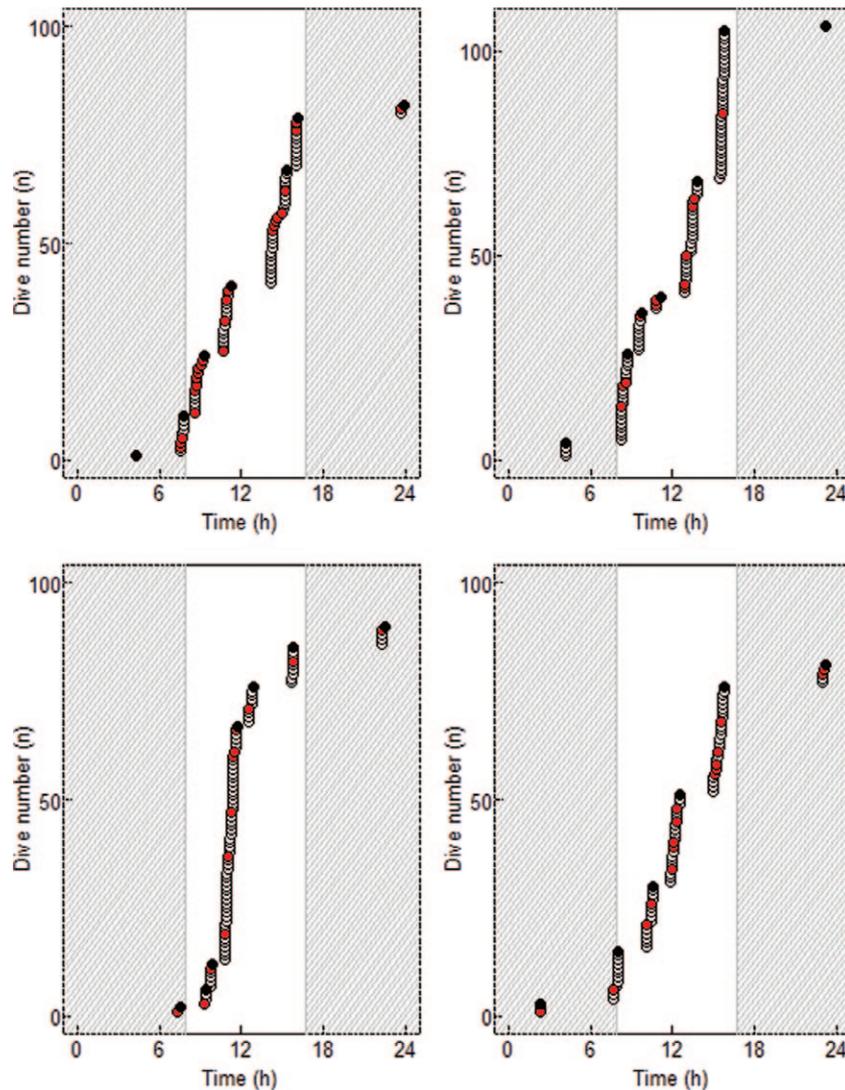
Figure 2
A modified version of Figure 6 from Hays et al. (2007) to illustrate the states identified by HMM with respect to the timing of individual dives. We present the same data set as Hays et al.; the graphs show dives of 1 mink on 4 separate days (mink 187a, graphs represent 24–27 January 2006, respectively, number of dives performed on each day was 82, 106, 90, and 81, respectively). White circles represent State 1, red circles represent State 2, and black circles represent State 3. Hours of darkness are shown by gray shading.

HMM results as the inclusion of depth and the application of an algorithm that does not use simple thresholds appears more biologically meaningful, particularly for a semiaquatic animal where short breaks may be an important feature of diving.

Sequential nature of diving

There was a higher frequency of State 1 than would be expected if all dives followed a common pattern—that is, if all 3 states were equally likely—demonstrating that mink dive in clusters (Figure 4). Mean proportion of State 1 is 0.656 (median: 0.690, range: 0.400–0.878, $N = 18$), of State 2 is 0.188 (median: 0.184, range: 0.051–0.394, $N = 18$), and of State 3 is 0.157 (median: 0.113, range: 0.281–0.480, $N = 18$).

Temperature dependence

We found no relationship between the ambient air temperature and the proportion of dives in each state (Figure 5A) (linear regression, State 1: $F_{1,3} = 3.4372$, $P = 0.1608$, $N = 18$;

State 2: $F_{1,3} = 0.7246$, $P = 0.4572$, $N = 18$; State 3: $F_{1,3} = 0.7995$, $P = 0.4371$, $N = 18$). There was also no difference among mean ambient temperatures for each state (in °C): State 1 = 13.42, State 2 = 15.39, and State 3 = 16.510, or TDR temperatures: mean temperature of State 1 = 13.35, State 2 = 15.52, and State 3 = 16.82 (Figure 5B).

The likelihood of switching between states (or the probability of a mink persisting at one behavior) was not correlated with ambient temperature for any sequence of states (see Table 3). After correcting for multiple measurements of the same individual, the transition from State 2 to State 3 appeared to be correlated with ambient temperature (slope = 0.006231, $F_{1,3} = 15.5508$, $P = 0.02907$); however, after a Holm–Bonferroni correction, this result turned out to also be not significant ($P = 0.26163$).

DISCUSSION

The diving behavior of American mink is hugely variable among individuals and over time (Harrington et al. 2012)
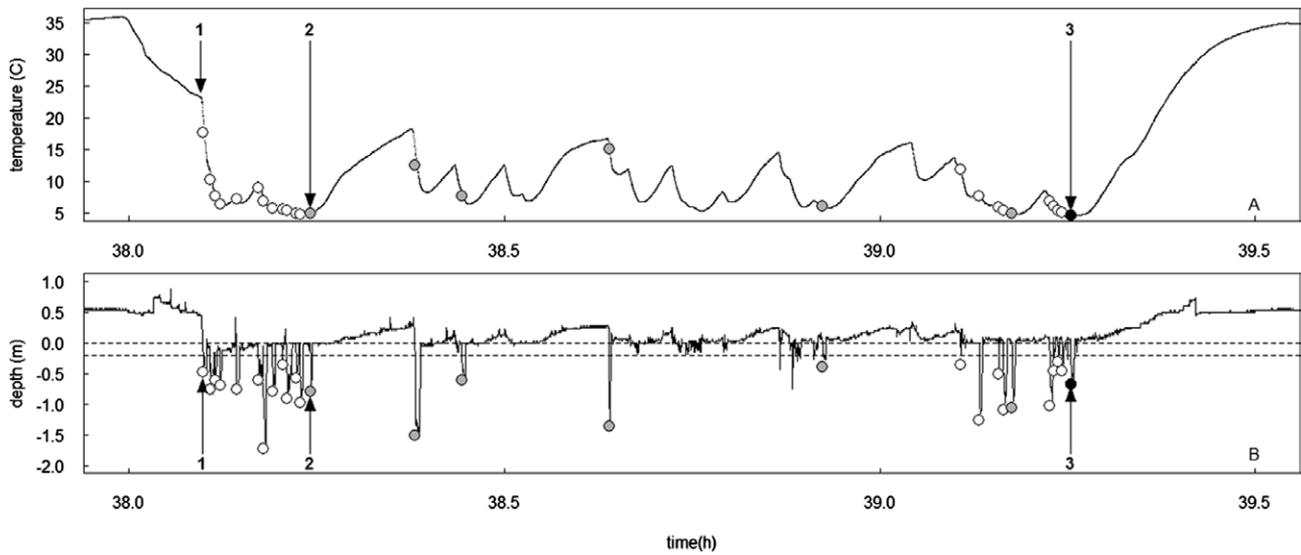
Figure 3

A diving profile of mink M39a in January. Graph A shows TDR temperature and graph B shows depth profiles over time. The positive offset in the depth records at the start and end of the trace reflects baseline drift caused by the massive temperature change; these start and end sections really represent a value of "0 m." Using the HMM, we have assigned 1 of 3 categories to each dive: State 1 (white circles)—a temporal cluster of dives; State 2 (gray circles)—more loosely aggregated diving, which we have termed an aquatic foraging session; and State 3 (black circles)—a terminal dive of a cluster/foraging session, or a single, isolated dive. An example of a cluster can be seen between points 1 and 2, and an aquatic foraging session between points 1 and 3. Within a foraging session, temperatures fluctuate between 5 and 17 °C, indicating that the animal may have been continually moving between aquatic and terrestrial environments (i.e., between the river and the riverbank). After State 3 dives, the temperature rises close to the mink's body temperature, suggesting that the animal is inactive in a shelter location.

due to the possibility of switching from aquatic to terrestrial foraging. HMM identified 3 states in the diving of this semiaquatic species. State 1 is a temporal cluster of dives, characterized by continual diving. State 2 is more loosely aggregated diving, forming a part of an aquatic activity mode, which may include events such as jumping out onto the bank or quick runs to the burrow. State 3 is a terminal dive of a cluster or a single, isolated dive, possibly reflecting a switch from an aquatic mode to a terrestrial one. The variables—dive depth and dive interval—provided good discrimination and grouped into consistent states well, despite the possibility of diving behaviors in semiaquatic animals being so similar (i.e., constrained by depth and other factors) as to be intractable.

HMM, unlike frequency-based methods, are able objectively to identify distinct transitions and the time at which they occur. The method not only allows the examination of patterns within diving behavior, but takes into account the switch to terrestrial mode, and potentially a change of strategy, that

Table 1

The numbers of dives of each state calculated by HMM and k-means

Method	Number of dives in each state		
	State 1	State 2	State 3
HMM	2656	715	343
k-means	3508	139	67

Table 2

Breakdown of dives assigned to each state by HMM and k-means

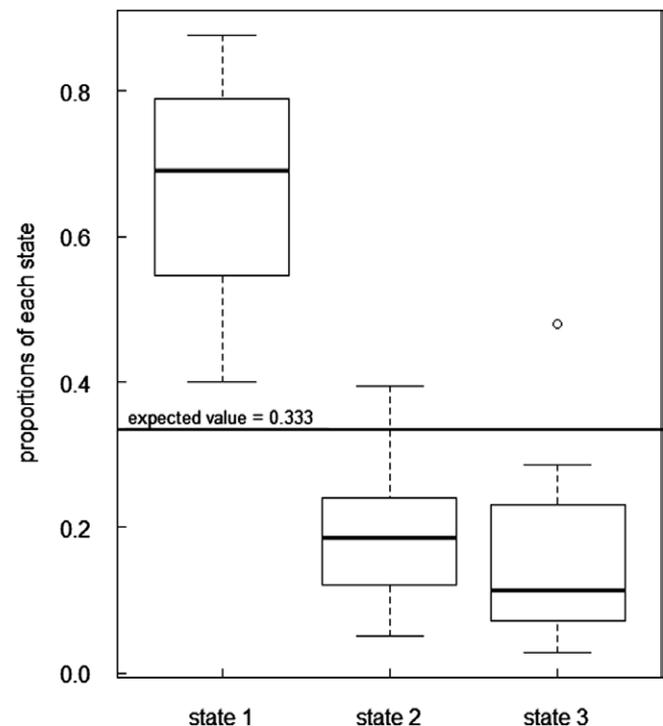|	HMM		
	State 1	State 2	State 3
k-means			
State 1	2655	709	144
State 2	0	6	133
State 3	1	0	66

Figure 4

Proportion of State 1, State 2, and State 3 throughout all data sets. The expected value if all dives follow a common pattern is 0.333.
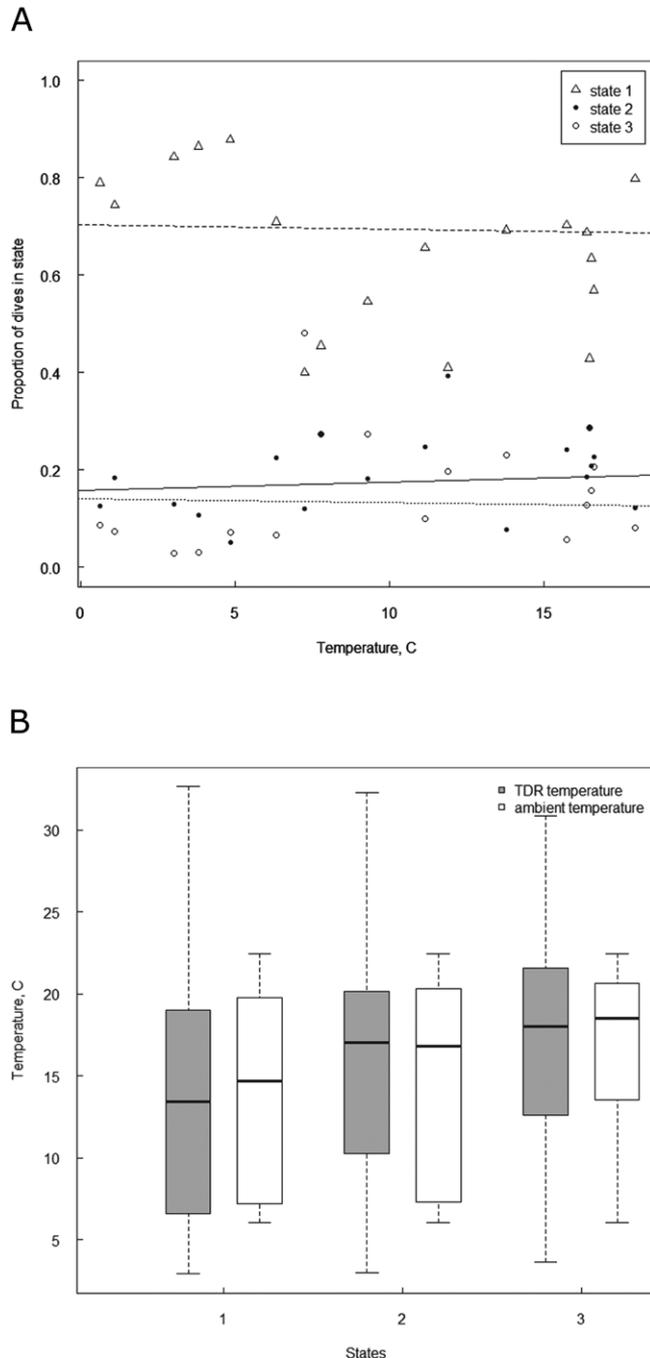
A

B

Figure 5
Links between TDR temperature and behavioural states. A shows the
relationship between ambient air temperature and the proportion
of dives in each state; each mink data set is represented by 3 states.
B shows the cumulative ranges of ambient air temperatures (from
weather station) and TDR temperatures (measured on mink, and thus
affected by its body heat) at different behavioural states for all animals.

is, allows investigation of the effect of potential predictors of
switching. This is thus the first step to describing the activity
patterns and types of a free-living semiaquatic mammal. The
next stage, describing terrestrial activity patterns, would
require an analysis of gaps between terminal dives (State
3) and the beginning of the next dive or dive cluster, ideally
using inputs from temperature sensors, triaxial accelerators,
or other devices. Using HMMs, it is possible to determine
the beginning and end points for the terrestrial behaviors,

Table 3

**The *P* values of correlations between ambient temperatures and the
likelihood of switching between states at time *t* and *t* + 1**

	State *t* + 1		
	1	2	3
State *t*			
3	0.1592	0.2203	0.6218
2	0.1722	0.7026	0.0291*
1	0.1823	0.3611	0.1134

*$P < 0.05$.

to look at rapid changes between environments, and to see
the patterns within diving behavior. We hope this technique
will allow us to address how animals balance expenditure
and rates of reward between 2 very different environments,
as well as posing questions about foraging that are routine in
terrestrial and fully aquatic animals.

Sequential nature of diving

Based on the proportion of dives in each state, we conclude
that mink tend to dive in clusters, that is, in successions of
consecutive dives, rather than in single, widely spaced dives;
this is reflected by the higher than expected proportion of
dives in State 1. If State 1 represents foraging for fish or crus-
tacea such as crayfish (which we think is likely), then the
motivation to search for these relatively high-value prey items
is reflected by persistence in a single behavior, something
previously found in captive mink (Cooper and Mason 2000;
Warburton and Mason 2003). Because mink are single-prey
loaders (Dunstone 1993) and need to go to shore to process
food, a successful hunt would be reflected in the breaking of
an observed cluster of dives.
By their nature, semiaquatic animals are likely to have more
modes of foraging activity than fully aquatic or terrestrial
species, so studying semiaquatic animals remains problematic
when trying to build a time or energy budget. In marine
species, foraging is always linked to diving (though not
necessarily vice versa), and because they tend to forage far off
shore it is straightforward to separate groups of dives from
periods of resting on the sea surface and from a return to land.
These distinctions can be less clear for semiaquatic animals,
which may undertake short commutes to land. Moreover,
semiaquatic species may use the water to travel (Williams 1989)
or as an escape tactic (Strachan and Jefferies 1993) as well as for
foraging, and may dive to reach burrows (Muller-Schwarze and
Sun 2003); thus foraging in these species is not always associated
with diving and dives do not always represent foraging.

Temperature dependence

Ambient temperature does not seem to affect mink diving
behavior within the range typical of our study area. We found
no relationship between ambient temperature and the pro-
portion of dives in each state or between temperature and the
rate of transition between states, meaning that, in our study
area, in lowland England, mink are apparently not adopting
different diving strategies at different temperatures or in dif-
ferent seasons. This is surprising given that, even though they
occur in very cold countries, mink seem to be poorly adapted
to withstanding low temperatures in water (Brown and
Lasiewski 1972; Fish et al. 2002) and is not in accordance with
our prediction that as temperature declines, clusters of dives
would shorten. The analysis of transitions between states has

shown that there is no correlation between ambient air temperature and the likelihood of mink switching from one state to another, that is, changing foraging modes. This means that if mink are diving, they are just as likely to continue to dive at low temperatures as at high ones, which confirms the findings of Harrington et al. (2012), who showed that mink dive as much in winter as they do in summer. These observations could indicate that factors such as seasonal prey availability and ease of capture play a more important role than temperature in governing mink diving behavior (Harrington et al. 2012), though naturally temperature will influence the availability of poikilothermic prey. However, there was an overall lack of consistency in foraging strategies among individuals, leading us to suggest that individual strategies may be important to success in this generalist species. Techniques such as this that work across a wide range of habitats could be important to investigate how specialist versus generalist predators hunt in the same environment.

Limitations of behavioral analysis

Although we can pinpoint transition points between aquatic and terrestrial activity at specific points of time, we still lack a clear understanding of mink activity patterns on land. The terrestrial behavior of semiaquatic animals has been studied through other means—for example, radiotelemetry (Niemimaa 1995; Garin et al. 2002; Marcelli et al. 2003; Peters et al. 2009; Zschille et al. 2010), GPS loggers (Durner et al. 2011), or direct observations (Garcia et al. 2009)—but until terrestrial and aquatic modes of behavior are coupled in a single study, there are too many unknown factors to build a full activity budget (e.g., if the mink is not in water, we cannot precisely tell whether it is active or inactive on land). Ultimately, this is important to understand how animals make decisions over where and how long to forage for, and how they weight their preference for habitats based on foraging success or predictability. Ideally, TDRs would be coupled with GPS loggers; however, at this point in time, simultaneous deployment of both devices on a small-bodied animal seems unfeasible from the welfare perspective.

Analysis of the detailed temperature record obtained from the TDR, or the use of additional sensors (such as in triaxial accelerometers), may allow us to distinguish among, and more fully describe, further modes of behavior in future; in so doing, HMM will be a valuable analytical tool for examining the effect of many potential variables on behaviors and switches between different behavioral states. More sophisticated loggers, coupling TDRs with GPS, or adding other recording inputs (such as fast-acting wet or dry switches) are required to determine the nature of the pauses within aquatic foraging sessions; they may also help establish the type and function of dives (Gleiss et al. 2011)—for example, foraging, travelling, or escape. Nonetheless, currently we believe that HMM are a useful tool for describing the behavioral strategies of other semiaquatic species and investigating the factors that influence them. Future use of HMM also shows promise as this robust statistical method is capable of incorporating and distinguishing between additional behavioral states from more complex data sets.

CONCLUSIONS

We have demonstrated the use of HMM as a valid method for analyzing the diving behavior of semiaquatic animals, particularly the transition between land and water. HMM has now been applied to fully (Hart et al. 2010) and semiaquatic animals. HMM should be easier to apply to terrestrial animals, for which behavioral observations could validate behavioral states. We were able to identify behavioral patterns and show that mink dive in clusters of successive dives, something that has already proved useful in explaining habitat use in other diving animals (Heath et al. 2010). We have also shown how HMM can be utilized to test specific hypotheses regarding behavioral patterns and the factors that influence them.

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