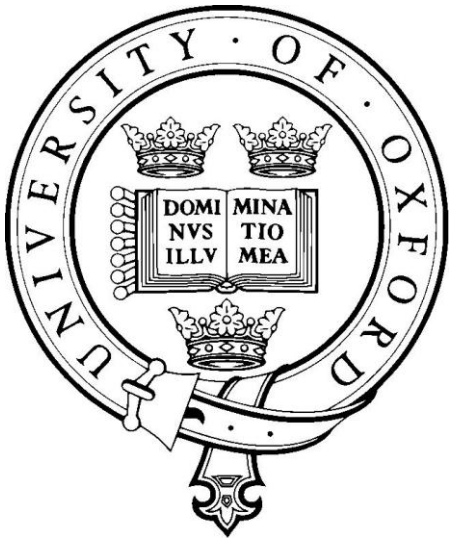
Diving behaviour and activity patterns of the invasive American mink, *Neovison vison*

A thesis submitted for the degree of

Doctor of Philosophy



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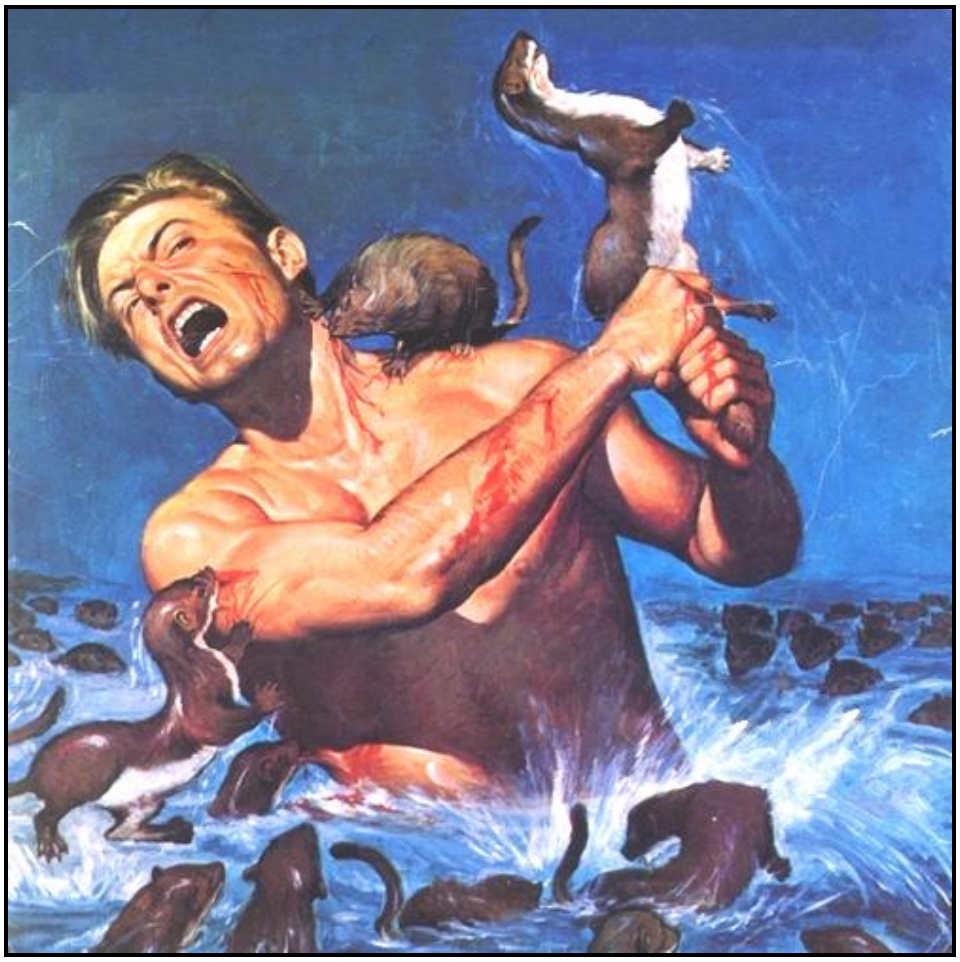

Image: “Man’s Life” magazine cover, September 1956

“Mink diving behaviour… this should be easy.”

Dr Tom Hart, 2009

“This son of the seaworld and the skyworld keeps to secretive places and avoids others, though sometimes you may see him basking in the sun on a rock in the river wearing that beautiful fur robe – Mink, Made-Like-The-Sun.”

Barry McWilliams, based on a Kwakiutl legend

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Abstract

Semi-aquatic mammals have evolved to forage in both aquatic and terrestrial environments, and they generally lack locomotor specialisation for either. Having relatively unspecialised adaptations, some semi-aquatic species are generalist foragers, and their activity and diving patterns provide insight into constraints on their foraging behaviour.

The recent miniaturisation and improved accuracy of logging devices allow remote data collection from small (<1kg), shallow-diving species. The development of analytical methods has lagged behind technological advances (and techniques developed for fully aquatic animals do not account for the variability of behaviour typical of semi-aquatic animals and their switching between terrestrial and aquatic environments). I applied and developed novel analytical techniques to identify activities and diving patterns of a semi-aquatic mustelid, the American mink (*Neovison vison*), fitted with Time-Depth Recorders (TDRs). Using a hidden Markov model (HMM) algorithm allowed me to classify dives into three states to identify clustering, and describe sequential diving patterns by mink. TDRs were used to determine active/inactive periods on the basis of rapid TDR temperature changes, and this method was validated empirically. Having developed this methodology, I applied it to 18 datasets collected from 14 mink in lowland England. Terrestrial activity of mink was positively related to ambient temperature (across both sexes), however aquatic activity, especially diving, appeared to be more influenced by daylight than by temperature. Mink showed intersexual differences, with males being more nocturnal and more active on land, and females more diurnal, and more persistent in diving. There was considerable variability between sexes and individuals. This is the first study to use HMM to classify the dives of a semi-aquatic animal, and the first to use TDR temperature records to identify mammalian activity patterns. These methods will be generally applicable to animals that make rapid transitions between environments and have thus far been difficult to study.

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Contents

Chapter 1

General Introduction

Semi-aquatic mammals have evolved to function in both aquatic and terrestrial environments, without locomotor specialisation in either. They represent the transitional forms which gave rise to highly evolved aquatic mammals (Fish and Baudinette 1999); and their transitional lifestyle incurs costs 2.4-5.1 times higher than those of locomotor specialists (Williams 1999). Yet the diving and behavioural transitions of semi-aquatic generalists have not been investigated much in the wild, and little is known of the constraints on their foraging behaviour.

Studies of aquatic and marine behavioural ecology have traditionally lagged behind terrestrial ones because of the difficulty in collecting data from animals foraging remotely from the researcher. However, recent decades have seen a huge increase both in the pace of development of technologies for studying animal behaviour, and in the number of studies using it (Ropert-Coudert and Wilson 2005). In particular, the different bio-logging and molecular approaches have illuminated the ecology and behaviour of hitherto difficult to study animals (Rutz and Hays 2009).

Despite the recent progress, many of the approaches that work well on terrestrial species do not work in the aquatic environment and vice versa, leaving important gaps in our knowledge of semi-aquatic species. Small semi-aquatic animals such as the American mink (*Neovison vison*, Schreber 1777) have thus only been studied in either a terrestrial or aquatic setting. Recent miniaturisation of bio-logging devices means that loggers such as Time-Depth Recorders (TDRs) are now within the load capability of mink. For the first time, this permits research of their complete time budget, the transitions between the terrestrial and aquatic environments, and details of their diving behaviour. Driven by these technological developments is the urgent need to develop appropriate analytical methods to study small-bodied, semi-aquatic

animals. In my thesis I employ novel analytical methods to study the behavioural ecology of an invasive alien species, the American mink, in Oxfordshire, UK.

1.1 The American mink

The American mink is a small-bodied, solitary, semi-aquatic mustelid. It has an elongated body of 30-50 cm in length, with relatively short limbs, and weighs between 500 and 2000g depending on sex, habitat, and time of year (Dunstone 1993). Mink are naturally found throughout North America: in Canada and most of the United States, excluding Arizona and the more xeric parts of California, Nevada, New Mexico, Texas and Utah (Lariviere 1999). Outside of the USA and Canada, they are considered an invasive alien species in Europe, South America and Asia (Macdonald and Harrington 2003; López-Giráldez, Gómez-Moliner et al. 2005; Peris, Sanguinetti et al. 2009).

Mink are members of the Mustelidae family (suborder Caniformia, order Carnivora). Until a few years ago they were classified as *Mustela vison*, having initially been considered closely related to the European mink, *Mustela lutreola*, because of their similar morphological traits and mode of life (Heptner, Nasimovich et al. 1988; Kurose, Abramov et al. 2008). However, recent molecular evidence points to a more distant relationship (Harding and Smith, 2009); and currently the American mink has been placed in its own genus; *Neovison*, on the basis of biochemical, cytogenetic, and molecular differences, as well as morphological characteristics such as bacular structure (Koepfli, Deere et al. 2008; Kurose, Abramov et al. 2008).

Genetic evidence suggests that the predecessors of the American mustelids crossed into the New World from Siberia during the late Miocene eight to ten million years ago (Harding and Smith 2009). Even though mink were not common among

Pleistocene fauna, their records extend back as far as the Irvingtonian (Kurtén and Anderson 1980; Humphrey and Setzer 1989; Seal, Thorne et al. 1989). Fossil occurrence – about 20 – corresponds to the species' natural range, i.e. most of North America excluding the desert regions (Kurtén and Anderson 1980). The Pleistocene American mink did not differ much in size and morphology from modern animals, although an increase in size has been apparent from the Irvingtonian through to the Illinoian and Wisconsinan periods (Kurtén and Anderson 1980).

1.1.1 Introduction into Europe and the UK

The rich, soft coat of the American mink has made it popular with the clothing industry for centuries. Mink were first trapped for pelts and were later widely domesticated for the fur industry. The first fur farms were established in Canada in the 1800s (Bowman, Kidd et al. 2007), and the trend soon followed in other parts of the world. The American mink was introduced to Europe in the early 1920s (Macdonald and Harrington 2003), with the first farms established in Germany between 1925 and 1930 (Kuscha 2011), in 1927 in Norway (Bevanger and Henriksen 1995), in 1929 in the UK (Dunstone 1993), in late 1920s in Sweden (Bonesi and Palazon 2007) and others following later, with farms in Ireland opening in 1951 (Smal 1988), and in Poland in 1953 (Lisiecki and Sławoń 1980). In 1933, American mink were released in multiple regions of the Soviet Union to establish a population of game animals (Heptner, Nasimovich et al. 1988). Mink from these introductions subsequently colonised a large part of Russia, as well as Eastern (Belarus, Ukraine, Poland) and northern (Finland, Norway) Europe (Bonesi and Palazon 2007).

There have been multiple documented escapes and releases from fur farms (Bonesi and Palazon 2007). Escaped mink have produced viable populations in very

different environments. Currently mink are invasive aliens in at least 28 European countries (Bonesi and Palazon 2007), including Fennoscandinavia (Kauhala 1996), Denmark (Hammershøj, Thomsen et al. 2004), the UK (Harrington and Macdonald 2008), Ireland (Smal 1988), Poland (Brzeziński and Marzec 2003), Spain (Garcia, Mateos et al. 2009), Germany (Zschille, Stier et al. 2010), Iceland (Magnusdottir, Stefansson et al. 2012), and ex-Soviet states (Sidorovich 2000).

In Britain, mink have been killed in the wild since the 1930s, however the first case of breeding in the wild was reported in 1957 (Dunstone 1993). The 1950s coincided with the peak of mink farming, with over 400 known fur farms in the UK (Game & Wildlife Conservation Trust, www.gwct.org.uk). Colonies of feral mink were initially observed in the Singleton area of Lancashire, and later on Rivers Avon, Test and Itchen in Hampshire and Wiltshire, on the Avon in Gloucestershire, and Rivers Wharfe and Lune in Lancashire and Yorkshire. In Wales, mink established on the River Teifi in mid Wales, and the East Cledau and Taf in Pembrokeshire (Dunstone 1993). In Scotland, the first records of mink breeding in the wild were from the River Ugie in N.E. Aberdeenshire and the River Deveron in Banffshire; mink have also colonised the River Urr in Kirkcudbright, and Rivers Tweed and Teviot (Cuthbert 1973).

Mink have also reached the Outer Hebrides, spreading from the island of Lewis, where a population of feral mink has been established from fur farm escapees in the 1950s. The swimming ability of the American mink has allowed them to access any island within 2 km of the Scottish coast (Craik 1997).

Throughout the 1960s control actions were attempted by the Ministry of Agriculture, but trapping effort was patchy and failed to halt the population growth and dispersal. In 1970, mink were recorded in every county in the UK (Dunstone 1993).

After this, official trapping was decreased to a trap-loan scheme (in England and Wales) or withdrawn altogether (in Scotland) (Dunstone 1993). Since 2003, fur farms are no longer legal in the UK (Fur Farming (Prohibition) Bill, 2000), but the problem of feral populations persists. Currently mink are present throughout most of Britain (Strachan 1998; WildCRU 2002 and 2004) with the exception of the northernmost region of the Scottish Highlands (Harrington, Harrington et al. 2009), and north Wales (National Biodiversity Network: data.nbn.org.uk), and pose a serious threat to native biodiversity, particularly water voles *Arvicola terrestris*, sea birds and waterfowl (Macdonald and Harrington 2003). Current control measures are largely *ad hoc* (Baker 2010). Local control has shown moderate success (Harrington, Harrington et al. 2009) and increasing success at a large scale, especially with the assistance of teams of trained volunteers (Bryce, Oliver et al. 2011). One co-ordinated eradication program is the Hebridean Mink Project, a structured control action aimed at protecting important bird colonies in the Western Isles (Baker 2010); major mink control efforts In the Cairngorms National Park and northeast Scotland have resulted in an area already exceeding 7000 km being mink free (Macdonald and Burnham 2010). At present mink is considered to be largely eradicated from the Outer Hebrides, and the project is to finish in March 2013, with the isles currently monitored for any mink presence (Scottish Natural Heritage, www.snh.gov.uk). Since American mink have not spread to the far north of Scotland, a *cordon sanitaire* designed to stop mink from spreading further north is underway (Macdonald and Burnham 2010).

1.1.2 Foraging ecology

Mink have a very broad diet, and make use of all habitats and environments available to them. Being semi-aquatic, they are found in the proximity of water sources,

occupying coasts (Niemimaa 1995; Ben-David, Bowyer et al. 1996; Bonesi, Dunstone et al. 2000), rivers (Medina 1997; Sidorovich and Macdonald 2001; Garcia, Mateos et al. 2009), streams (Humphrey and Zinn 1982; Sidorovich and Macdonald 2001), lakes (Humphrey and Zinn 1982; Racey and Euler 1983; Medina 1997; Sidorovich and Macdonald 2001), extensive wetlands (Macpherson and Bright 2010), marshes (Humphrey and Zinn 1982; Sidorovich and Macdonald 2001), and ditches (Yamaguchi, Strachan et al. 2002). Their generalist lifestyle allows them to forage on aquatic (crayfish, fish), semi-aquatic (waterfowl, amphibians) and terrestrial prey (lagomorphs, rodents, birds) (Sargeant, Swanson et al. 1973; Birks and Dunstone 1984; Birks and Dunstone 1985). Mink are opportunistic predators; prey selection often depends on availability, and varies locally and seasonally (Dunstone 1993; Clode and Macdonald 1995); e.g. Wilson (1954) reports an increase in aquatic prey consumption during particularly harsh winters, when terrestrial mammal populations were in decline or difficult to hunt (Wilson 1954). Mink may also be able to adjust their activity times to that of their prey (Zielinski 1988).

The daily energy requirements for mink are estimated at 1500 kJ day^{-1} for males, and 1000 kJ day^{-1} for females (Dunstone 1993). Arnold and Fritzell (1987) calculated the energetic requirement of a male mink to be equivalent to 0.18 kg of prey per day. Due to their short gut transit time, becoming post-absorptive after 5 h (Sibbald, Sinclair et al. 1962; Farrell and Wood 1968), some mink may need to be active in short bursts throughout the day, depending on the size of the prey they catch (Dunstone 1993).

Mink cache their food; if they have the opportunity they will kill surplus prey (Sargeant, Swanson et al. 1973; Craik 1995; Roesler, Imberti et al. 2012). Surplus killing

may be an adaptive response to varying prey availability, and is particularly common in places where animals are confined (e.g. domestic stock), or where a large colony provides abundant hunting opportunities (Dunstone 1993).

Although mink are considered to be generalist foragers – i.e. as a species, they have a broad food niche (Sacks and Neale 2002), it has been suggested that observations of a broad food niche as a species is driven by the foraging preferences of individual animals, specializing on different prey types (Sidorovich, Macdonald et al. 2001; Bolnick, Svanbäck et al. 2003; Vander Zanden, Bjorndal et al. 2010; Codron, Codron et al. 2012).

Foraging ecology in North America

The native range of the American mink encompasses Canada and most of the United States, with the exception of dry regions in the south. The species shows a very high adaptability, with a range encompassing four of the major climate types and spanning across at least twelve of the North American biotic provinces (Northcott, Payne et al. 1974).

In their native habitat, mink exhibit a diverse diet, encompassing mammals (e.g. muskrats *Ondatra zibethicus* (Hamilton 1940; Wilson 1954), lagomorphs – *Lepus* spp. (Sealander 1943)*, Sylvilagus* spp. (Sealander 1943; Wilson 1954; Korschgen 1958), rats – *Rattus norvegicus* (Sealander 1943; Wilson 1954; Korschgen 1958), rice rats – *Oryzomys* spp. (Wilson 1954), mice *Mus* spp. (Sealander 1943; Wilson 1954; Korschgen 1958), deer mice – *Peromyscus* spp. (Hamilton 1940; Sealander 1943; Wilson 1954; Korschgen 1958), voles – *Microtus* spp. (Hamilton 1940; Sealander 1943; Wilson 1954; Korschgen 1958), star-nosed moles – *Condylura cristata* (Sealander 1943; Wilson 1954), shrews – *Blarina* and *Sorex* spp. (Sealander 1943), squirrels – *Sciurus* spp.

(Wilson 1954; Korschgen 1958), opossum – *Didelphis virginiana* (Wilson 1954)), birds (e.g. passerines (Hamilton 1940), waterfowl (Sealander 1943; Wilson 1954), seabirds (Burness and Morris 1993), game birds (Sealander 1943; Wilson 1954)), amphibians (frogs *Rana* and *Hyla* spp. (Hamilton 1940; Sealander 1943; Wilson 1954; Korschgen 1958)), reptiles (snakes and turtles (Hamilton 1940; Wilson 1954)), fish (e.g. killifish (Wilson 1954), mosquitofish (Wilson 1954), catfish (Korschgen 1958), cyprinids (Hamilton 1940; Sealander 1943), centrarchids (Sealander 1943; Wilson 1954), catostomids (Sealander 1943), percids (Wilson 1954)), and invertebrates: insects (Hamilton 1940; Sealander 1943; Wilson 1954; Korschgen 1958), snails (Wilson 1954), crayfish (Sealander 1943; Wilson 1954; Korschgen 1958), or arachnids (Wilson 1954; Korschgen 1958).

In previously mink-free areas of North America such as Newfoundland, where mink were introduced in 1934 (Northcott, Payne et al. 1974), they can still cause damage to local biodiversity. In Newfoundland, genetically distinct Newfoundland muskrat have declined in areas with larger mink populations in comparison to areas with small populations or which are mink free (Soper and Payne 1997). Even within their original range, mink may negatively impact the populations of ground-nesting birds, such as terns *Sterna hirundo*, resulting in a heavy seasonal breeding costs for individuals, and sometimes losses of entire broods (Burness and Morris 1993). Mink affect seabirds not only through predation on chicks and eggs, but also indirectly, as parents trying to fend off the predator leave their chicks which then may die due to exposure (Burness and Morris 1993).

Foraging ecology in Europe – conservation impacts

As in North America, in Europe mink are associated with a range of prey – from relatively large mammalian prey, like rabbits – *Oryctolagus cuniculus* (Ferreras and Macdonald 1999) and hares – *Lepus* spp.(Dunstone 1993), through small and medium-sized rodents (e.g. water voles (Jędrzejewska, Sidorovich et al. 2001; Hammershøj, Thomsen et al. 2004), field and bank voles – *Microtus* and *Apodemus* spp. (Ferreras and Macdonald 1999; Jędrzejewska, Sidorovich et al. 2001; Hammershøj, Thomsen et al. 2004; Salo, Toivola et al. 2010), mouse species – *Muridae* spp. (Jędrzejewska, Sidorovich et al. 2001; Hammershøj, Thomsen et al. 2004), rats – *Rattus norvegicus* (Gerell 1967; Hammershøj, Thomsen et al. 2004), shrews – *Sorex* spp. (Ferreras and Macdonald 1999; Jędrzejewska, Sidorovich et al. 2001; Hammershøj, Thomsen et al. 2004) and *Neomys* spp. (Jędrzejewska, Sidorovich et al. 2001), moles - *Talpa europaea* (Jędrzejewska, Sidorovich et al. 2001)), waterfowl (ralliformes: coots and moorhens (Ferreras and Macdonald 1999; Hammershøj, Thomsen et al. 2004); grebes; ducks (Ferreras and Macdonald 1999; Hammershøj, Thomsen et al. 2004)), seabirds (gulls, terns, waders (Clode and Macdonald 2002; Salo, Toivola et al. 2010)) and other bird taxa (e.g. passerines (Ferreras and Macdonald 1999; Hammershøj, Thomsen et al. 2004)), amphibians (frogs (Jędrzejewska, Sidorovich et al. 2001; Hammershøj, Thomsen et al. 2004) and occasionally toads (Hammershøj, Thomsen et al. 2004)), fish (percids (Ferreras and Macdonald 1999; Hammershøj, Thomsen et al. 2004), cyprinids (Ferreras and Macdonald 1999; Jędrzejewska, Sidorovich et al. 2001; Hammershøj, Thomsen et al. 2004), salmonids (Heggenes and Borgstrøm 1988; Hammershøj, Thomsen et al. 2004), cottids (Salo, Toivola et al. 2010), gasterosteids (Jędrzejewska, Sidorovich et al. 2001; Hammershøj, Thomsen et al. 2004)) to invertebrates (crayfish

(Ferreras and Macdonald 1999; Jędrzejewska, Sidorovich et al. 2001), insects (Ferreras and Macdonald 1999; Jędrzejewska, Sidorovich et al. 2001), bivalves (Dunstone 1993), gastropods (Jędrzejewska, Sidorovich et al. 2001)). In mainland Europe, mink prey on muskrats in areas where these rodents have been introduced (Brzeziński and Marzec 2003).

Mink diet fluctuates seasonally. Dunstone and Birks (1987) report a more aquatic diet in winter, and a more terrestrial one in summer, presumably due to the higher vulnerability of exothermic fish in cold water in winter (Williams 1986), and a high number of young mammals and birds in the spring and summer months (Dunstone 1993). However, this tendency varies depending on local and seasonal prey abundance, as well as climate (Sidorovich and Macdonald 2001).

Feral American mink beyond their original distribution are of particular interest and importance to conservationists due to their impact on native species. Being very adaptable generalists, they affect native biodiversity both as predators, and competitors (Macdonald and Harrington 2003). The water vole is now the fastest declining mammal in the UK (Strachan 2004), and mink have been cited and modelled as a key threat to its existence (Barreto, Rushton et al. 1998; Rushton, Barreto et al. 2000), leading to a near-extinction of this rodent in the UK (Macdonald and Strachan 1999). In Spain, mink are thought to negatively impact the Pyrenean desman *Galemys pyrenaicus* (Poduschka and Richard 1986; Dunstone 1993), classified as vulnerable by the IUCN.

Mink predation severely reduces the breeding success of a number of ground-nesting birds (Ferreras and Macdonald 1999; Clode and Macdonald 2002). For instance, mink have caused coot (*Fulica atra*) numbers in the Masurian Lakes region of

Poland to decline more than twentyfold, and they also appear to have markedly affected (reduced and displaced) the breeding distribution of grebes and rallids (Brzeziński, Natorff et al. 2012). Colonies of common tern *Sterna hirundo*, black-headed gull *Chroicocephalus ridibundus* and common gull *Larus canus* in west Scotland declined by 36%, 52% and 30% respectively within nine years, principally due to egg and chick predation by mink. The nesting sites of most seabirds, located on islands or cliffs, are inaccessible to terrestrial carnivores. However, mink are excellent swimmers, able to swim to islands more than a kilometre from the mainland (Craik 1995). This dispersal, coupled with surplus killing (e.g. in Iceland, over 200 guillemot *Uria aalge* chicks were found in a single mink den (Clode and Macdonald 2002)) has allowed mink to decimate seabird colonies of international importance (Craik 1997; Nordström, Högmander et al. 2003).

1.1.3 Interspecific competition as an invasive

After their introduction to Britain in the 1920s, feral mink have rapidly increased in both numbers and distribution through the early to mid-1960s (McDonald, O'Hara et al. 2007). The coincidental absence of two native competitors – the Eurasian otter, *Lutra lutra*, and the European polecat, *Mustela putorius* – is likely to have aided their establishment. The otter suffered severely due to organochlorine pollution in the second half of the 20th century, and populations were in decline as the mink established across the UK (Strachan and Jefferies 1996; McDonald, O'Hara et al. 2007). The polecat was close to extinction as a result of over-trapping in the early 1900s (Birks and Kitchener 1999). Eurasian otters feed predominantly on aquatic prey (Preston, Portig et al. 2006), with up to 90% of prey being fish and crayfish (McDonald 2002). Polecats are considered a generalist species, but tend to prey on terrestrial animals

(small mammals, birds, amphibians) (Lodé 1997; McDonald 2002). The diet of the generalist mink encompasses both aquatic and terrestrial items; the adaptable invasive is therefore likely to have slipped into the ecological niches of the two native mustelids (Dayan and Simberloff 1994).

Currently the UK is witnessing the recovery of both native mustelids (Birks and Kitchener 1999; Harrington, Harrington et al. 2009; Environment Agency 2012). Otter recovery has been linked with a decline in field signs of mink (Bonesi, Strachan et al. 2006; McDonald, O'Hara et al. 2007), which has led to the suggestion that otters are outcompeting mink in the aquatic environment, resulting in declining populations of mink (Bonesi, Chanin et al. 2004; Bonesi and MacDonald 2004). This competition encompasses not only the indirect competition for resources, but also direct interspecific aggression. Otters (weighing 6-10 kg and therefore about seven times heavier than mink), have been reported to steal the mink's prey (Bonesi et al. 2000); there are also reports of aggressive contact between the two mustelids, supported by evidence of bite wounds inflicted by mink on otters (Simpson 2006). Mink have been observed to adjust their predatory behaviour in the presence of otters, incorporating a higher proportion of terrestrial prey at sites where aquatic-feeding otters were present (Clode and Macdonald 1995; Bonesi, Chanin et al. 2004). In turn, otter diet showed little change, which may be expected from their relative size; this finding suggests that otters are the dominant competitors forcing mink to shift their dietary niche (Clode and Macdonald 1995; Bonesi, Chanin et al. 2004). On the river Thames, Harrington et al. observed a switch from predominantly nocturnal activity of mink prior to the return of native (nocturnal) mustelids to a predominantly diurnal one after their reappearance (Harrington, Harrington et al. 2009). Such temporal niche shift

(Harrington, Harrington et al. 2009) and differentiated habitat use (Bonesi and Macdonald 2004) has been proposed as a potential mechanism for avoiding direct competition.

Less is known about the relationship and interactions between American mink and polecats. Both species inhabit similar habitats, and their diet may overlap substantially (Dunstone 1993; Birks and Kitchener 1999). Because of their similar size (both species weigh around 1kg), the competitive relationship between them may be more symmetrical, without a dominant competitor as in the case of mink and otters. In the Upper Thames area, mink and polecat home ranges were found to overlap, although mink and polecats did not overlap temporally, having almost opposite diel cycles (Harrington and Macdonald 2008). Harrington et al. suggested that mink perceive a polecat as a similar level of threat to an unknown mink (Harrington, Harrington et al. 2009). In some areas (England, Denmark) mink and polecats appear to coexist (Hammershøj, Thomsen et al. 2004); yet that is not the case in Belarus, where American mink seem to be excluding polecats from riparian habitats (Sidorovich and Macdonald 2001). In Belarus, however, the exclusion is linked to a smaller size of polecats, oval (rather than linear) mink home ranges, and a dietary shift of mink during the winter to terrestrial prey as rivers freeze over, resulting in a larger space and dietary overlap with polecats than in the UK (Sidorovich 2000; Harrington and Macdonald 2008).

Additionally, in continental Europe, feral American mink have played a significant role in the decline of the European mink (*Mustela lutreola*), a species listed as Critically Endangered by IUCN (Sidorovich 2001; Macdonald, Sidorovich et al. 2002). European mink, originally widespread throughout Europe, has been undergoing

sustained decline in the past century and currently populations are limited to areas of Eastern Europe (northeast Belarus, Estonia, and pockets of Russia) and small regions of France and Spain (Heptner, Nasimovich et al. 1988; Maran, Maconald et al. 1998; Macdonald and Harrington 2003). While a number of factors are to blame for the decline (including habitat loss, pollution or possibly the impact of European polecats), the introduction of the American mink has been the final, detrimental, push for its European counterpart. American mink are bigger and have larger litters than European mink (Macdonald and Harrington 2003). The diets and habitats of the two species may overlap; Sidorovich and Macdonald showed that American mink drive European mink away from rivers, which is most likely a result of competition for food (Sidorovich and Macdonald 2001).

1.1.4 Intraspecific competition – sexual dimorphism

Like many other mammals, and most mustelids, the American mink are sexually dimorphic (Erlinge 1979; Moors 1980). Males are the larger sex, weighing between 1.6 and 1.9 times as much as females (reported adult male body weights range between 780-1805g; adult females: 525-810g, depending on study location and season; adult weight may change over the annual cycle – particularly males experience a body mass increase prior to the rut (Dunstone 1993)). Body lengths of feral American mink in Europe average between 33.9 and 39.95 cm for females, and 38.8 and 46.98 for males, depending on site and season (Zalewski and Bartoszewicz 2012). Characteristics such as the trophic apparatus also differ between sexes (Dayan and Simberloff 1994); e.g. the canine and carnassial teeth, and several skull dimensions of male mink are disproportionately large for their body size; i.e. the trophic features of a male mink are larger than that of a female of comparable body size (Thom, Harrington et al. 2004).

This difference may allow males to kill and consume larger prey more successfully than females. Sexual dimorphism varies geographically, but the spatial patterns of dimorphism don't necessarily follow the spatial patterns of body size of either sex (Stevens and Kennedy 2005).

Theoretical background

There are two principal approaches explaining sexual dimorphism of animals. The first one focuses on different reproductive roles. It proposes that the larger males are favoured in sexual selection, either due to mate choice, or as a result of competition for mates; both of which would give larger males increased mating opportunities (Cox and Boeuf 1977; Erlinge 1979; Moors 1980). This dimorphism could be exaggerated by an energetic selection pressure on females to remain small. Smaller females (who rear young alone) have low absolute food requirements and, for mustelids, an increased efficiency of accessing small rodent prey (e.g. rodents in narrow holes) (Erlinge 1979; Moors 1980; Powell and Leonard 1983).

The alternative "reduction of competition", or "resource partitioning" approach states that dimorphism is a strategy to reduce intraspecific competition through a dietary niche separation between the sexes (Selander 1966; Dayan and Simberloff 1994). Different sizes of the two sexes (also seen in size difference between their trophic feature) allow them to exploit different food resources; males specialising on larger prey that might also be spatially separate from the smaller, female targeted prey (Brown and Lasiewski 1972; Moors 1980; Shine 1989).

The first approach has gained wider acceptance, although inter-sexual niche separation could have arisen secondarily as a result of sexual dimorphism, as its contemporary benefits might make it sufficient to maintain (Brown and Lasiewski

1972; Dayan and Simberloff 1994; Abramov and Tumanov 2003; Thom, Harrington et al. 2004).

Prey choice

The resource partitioning hypothesis is consistent with observations on mustelid species in the UK, where males tend to eat larger prey than do females (McDonald 2002). There is some (but not much) evidence of dietary differences in mink (Birks and Dunstone (1985) estimate the degree of dietary overlap between sexes at between 40% and 68%), with females choosing smaller – often aquatic – prey items, such as fish, crayfish or small rodents, while males opt for larger prey, such as lagomorphs (Birks and Dunstone 1985; Ireland 1990), muskrats (Sealander 1943) or large Eider ducks (Magnusdottir, Stefansson et al. 2012). The aquatic vs. terrestrial prey specialisation is not an obvious one however, and very much depends on local prey availability – e.g. Smith and McDaniel report females preferring small mammals, and males – larger fish (Smith and McDaniel 1982). Regardless of individual preferences, both sexes are presumably physically capable of hunting prey across the species' entire dietary range, since mustelids smaller than a female mink – e.g. stoats – are able to do so (McDonald, Webbon et al. 2000). Zalewski and Bartoszewicz (2012) report a correlation between the body size of mink (of both sexes) and the proportion of large prey items in their diet. However, the male mink morphology might allow them to handle larger prey items more efficiently (Thom, Harrington et al. 2004). The niche partitioning driving males and females to choose different prey could be a secondary consequence of physiological characteristics (Stevens and Kennedy 2005); males with their proportionally larger teeth may be more efficient hunters, while smaller females have better access to rodent burrows (Dunstone 1993).

Home ranges and movement

A home range is the "area traversed by an individual in its normal activities of food gathering, mating, and caring for the young" (Burt 1943). Since for most of the year mink tend to be closely associated with water, home ranges are often measured linearly, as the length of the watercourse that an animal usually traverses (Dunstone 1993).

Even though some studies showed no significant difference between home range sizes of males and females (Harrington, Harrington et al. 2009), in a number of sites males have been reported to have home ranges 2-3 times larger than those of females (Melero, Palazon et al. 2008) – Table 1.1.

Table 1. 1: Home ranges (HR) of mink populations (after Melero, Palazon et al. 2008).

Male HR	Female HR	Site	Reference
4.5 km	2.85 km	UK	Birks and Linn (1982)
2.13 km	1.85 km	Sweden	Gerell (1970)
NA	2.9 km	Spain	Palazón and Ruiz-Olmo (1995)
7.1 km	4.9 km	Spain	Zabala et al. (2007b)
6.8 km	2.7 km	UK	Yamaguchi and Macdonald (2003)
11.08 km	5.63 km	North America	(Stevens et al. 1997)

Home range sizes may vary depending on habitat and available resources (Gerell 1970; Ireland 1990; Melero, Palazon et al. 2008); furthermore, sizes fluctuate depending on time of year (Dunstone 1993) – see Figure 1.1. During the mating season, females are more sedentary than males, whose territories break down as they move over considerable distances to find females (Gerell 1970). In autumn young mink disperse in search of territories. During the kit-rearing period, females may have smaller home ranges so they do not have to move far away from young when hunting – although some studies revealed no differences in sizes between territories of breeder and non-breeder females (Yamaguchi and Macdonald 2003). A study in Spain

showed territory size being positively related to body size (Melero, Palazon et al. 2008); in theory, differences in weight alone could account for a large portion of the differences between male and female or subadult and adult home ranges (Harestad and Bunnel 1979).

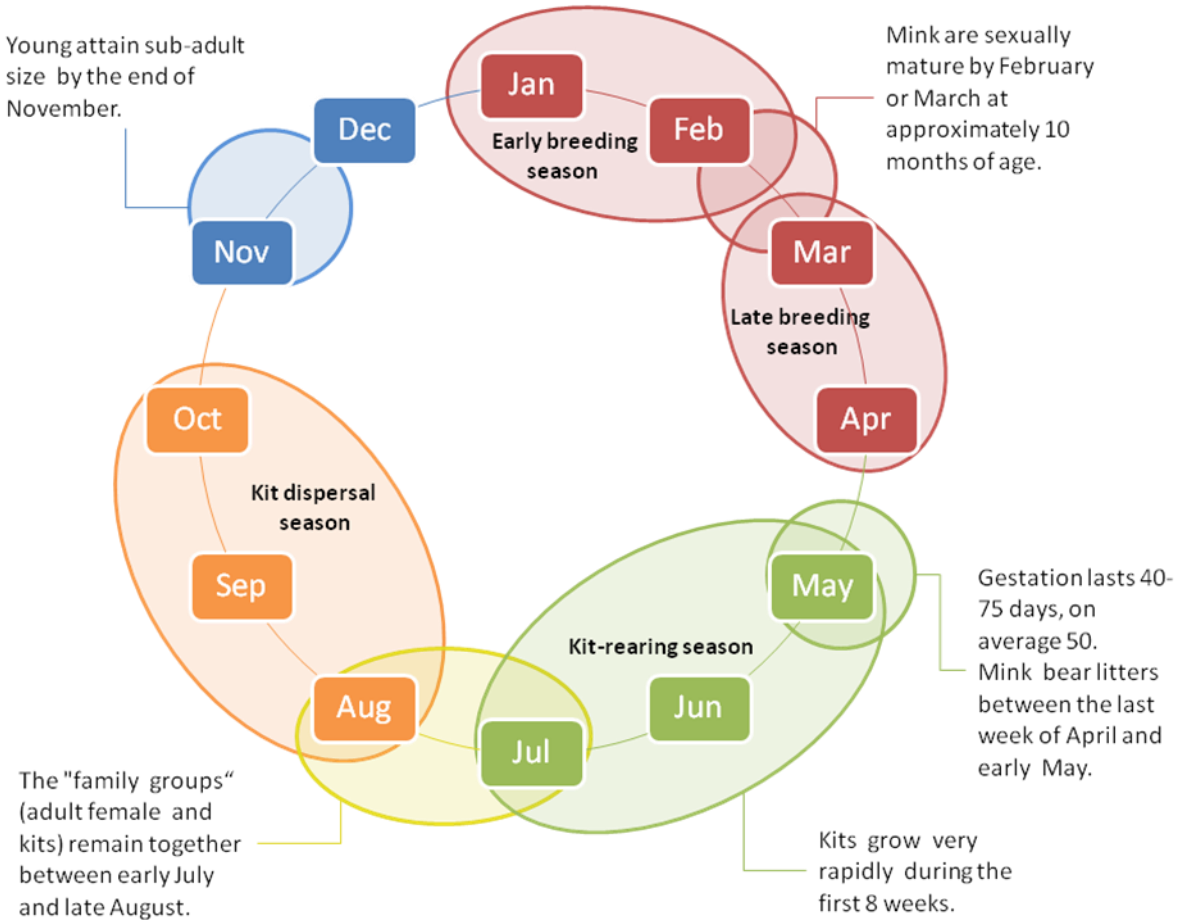

Figure 1.1: Mink reproduction and seasonal behaviour over the course of a year (Enders 1952; Gerell 1970; Yamaguchi and Macdonald 2003). Bonesi et al. (2006) report mink aged up to 4-6 years.

Male mink may spend a large proportion of time on travelling (Yamaguchi and Macdonald 2003; Melero, Palazón et al. 2011), although Gerell reports that male mink in his study spent about 90 per cent of active time hunting (Gerell 1970). Differences in activity are related to food availability (Yamaguchi and Macdonald 2003) and reproductive status (Dunstone 1993): subadult mink tend to travel more than adults, and males more than females (Gerell 1970; Melero, Palazón et al. 2011).

Environmental factors such as temperature and rainfall tend to have a negative effect on locomotion (Melero, Palazón et al. 2011; Zalewski and Bartoszewicz 2012).

Den site selection, prey choice and activity patterns may be a form of avoiding intraspecific competition. Yamaguchi et al. (2003) found that in southern England rabbit warrens are a particularly important habitat feature for mink of both sexes, although females choose to den in burrows that are closer to water than males (however, both sexes denned < 50 m from water). While there is some intra- and intersexual range overlap, 32.6 -88.2% (Yamaguchi and Macdonald 2003), animals tend to avoid each other temporally (Yamaguchi and Macdonald 2003; Yamaguchi, Rushton et al. 2003; Harrington and Macdonald 2008).

1.1.5 Adaptations for a semi-aquatic lifestyle

Semi-aquatic mammals are exposed to environmental conditions not normally faced by their more specialised counterparts – they need to maintain adaptations that allow them to function in both aquatic and terrestrial habitats. The level of "commitment" to the aquatic mode of life varies between species (Sinclair, Dunstone et al. 1974).

Despite their strongly semi-aquatic nature, mink have relatively few anatomical and physiological adaptations that would make them fit for aquatic foraging (although more than fully terrestrial species). They have high costs of thermoregulation, and surface swimming is an energetically expensive mode of transport relative to walking due to their low-performance, drag-based propulsion (Williams 1983). Mink swim by means of quadrupedal paddling (Figure 1.2), a mode much worse in terms of both propulsive and aerobic efficiency than the undulation mechanism of otters or the oscillations of pinnipeds (Fish 1996).

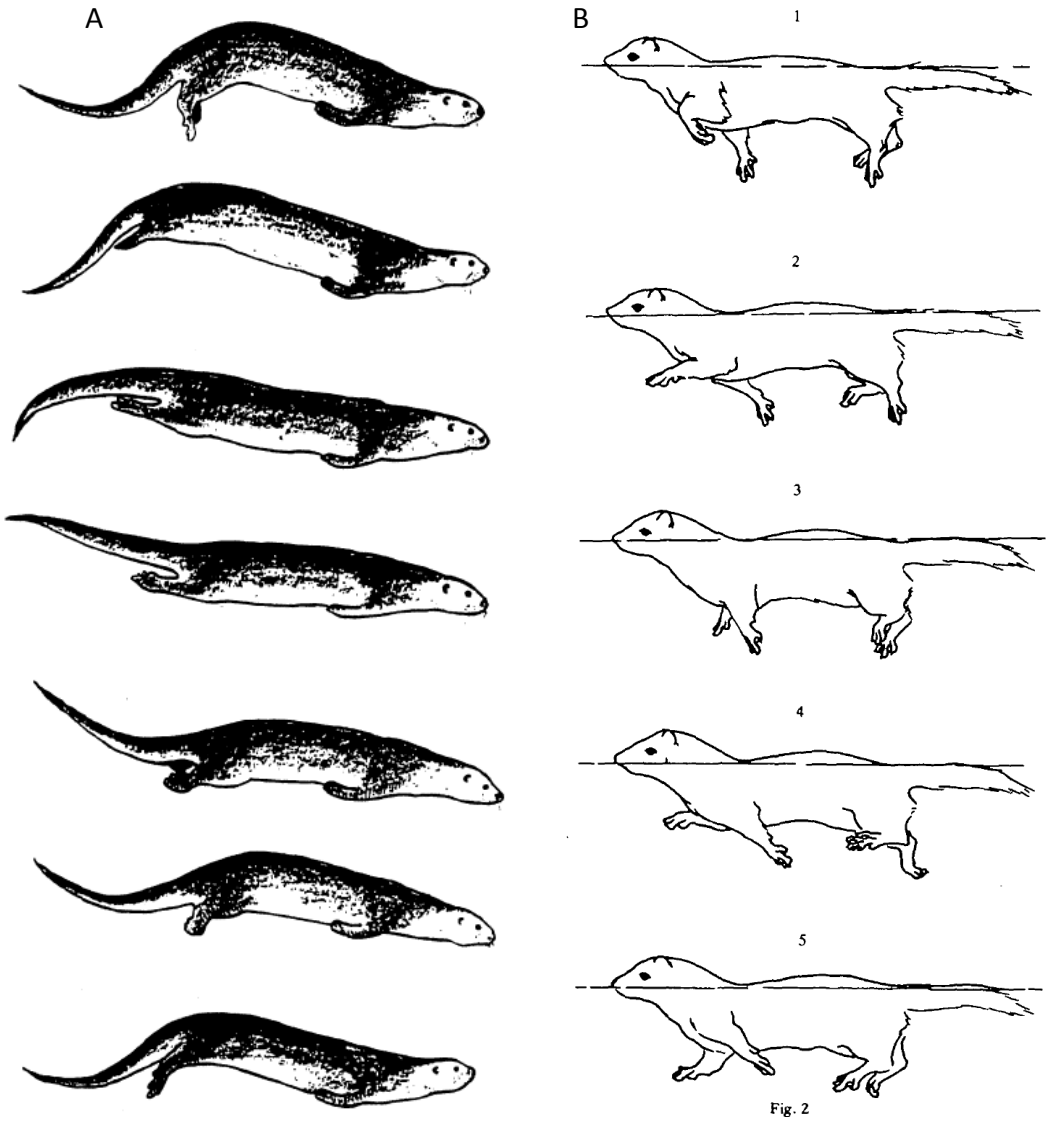

Figure 1.2: Propulsion mechanisms of two semi-aquatic species, the river otter, *Lutra canadensis* (A) and the American mink (B). Fig. 1.2A shows one stroke cycle of the undulation mechanism typical to otters; the time interval between successive drawings is 0.156 s (reproduced from (Fish 1994)). Fig. 1.2B shows the quadrupedal paddling of the mink (reproduced from Williams (1983)). The same mechanism is used for both surface and underwater swimming (Dunstone 1993).

The elongated body of the mink, even though it is streamlined and somewhat reduces drag at high speeds, accounts for a higher surface area than that of other animals of similar size (Brown and Lasiewski 1972). Therefore this shape – suggested to facilitate entrance into burrows in search of prey – results in an unusually rapid loss of body heat (Brown and Lasiewski 1972). One adaptation used by mink to reduce the

rate of core body temperature decrease is the localised vasoconstriction in vulnerable parts of the body, such as paws (Williams 1986).

Mink fur is less buoyant than that of other semi-aquatic mammals (Fish, Smelstoys et al. 2002). It provides good insulation only for several minutes in water, i.e. the time during which it retains a layer of air within the hairs; once this layer is disrupted, body temperature plummets (Williams 1986). Winter fur exhibits greater insulator properties than summer fur (Williams 1986). It is water-resistant to some extent (Lowery, 1974 in Lariviere, 1999), and very dense, with mean density of underfur varying between 16,803 and 33,946 fibres per cm^2, and the average number of guard hairs at 380 per cm^2 (Kaszowski, Rust et al. 1970).

Unlike other semi-aquatic mustelids, such as otter species (Pfeiffer and Culik 1998; Borgwardt and Culik 1999), mink appendages are relatively poorly adapted for swimming locomotion. Mink toes are partially webbed and their paws have a small surface area, which allows a more efficient locomotion on land, but reduces propulsion efficiency in water (Williams 1983); highlighting the trade-off between aquatic and terrestrial locomotion. Furthermore, their eyes are not well adapted to underwater vision, unlike those of otters (Sinclair, Dunstone et al. 1974; Dunstone and Sinclair 1978; Borgwardt and Culik 1999). While otters have a highly developed iris sphincter muscle to help them focus underwater, the sphincter iridis of mink is not as well evolved (although its development is better than that of the fully-terrestrial ferret) (Dunstone and Gorman 2007). Nonetheless, mink and otters have been reported to forage underwater for similar durations despite the greater size and better swimming adaptations of the latter (Dunstone 1993).

It is debated whether swimming is a learned or an innate behaviour (Vinke, Hansen et al. 2008); Dunstone (1993) claims that mink used in laboratory studies had to experience water from an early age, otherwise they never became proficient swimmers. Yet farmed mink exhibit increased stress levels when they are denied access to water baths, suggesting that swimming is an intrinsically important activity (Mason, Cooper et al. 2001).

1.1.6 Investigating foraging ecology

Thus far methods of studying foraging ecology of mustelids have focused on two main subjects.

Diet

Information on diet can be obtained from analysing stomach and gut contents of dead animals (Sealander 1943; Korschgen 1958). Even though it is not always reliable, depending on how much time an animal has spent in the trap (and whether bait was provided), or how it was killed, it provides good information for determining sex and seasonal differences in diet.

Analysing the contents of collected scats is non-invasive and relatively cheap, however it may be prone to misidentification (Harrington, Harrington et al. 2009). Scats cannot be assigned to individuals unless defecation has been observed, thus it is usually impossible to use it for examining intersexual or individual differences (unless scats are fresh and with enough DNA to use for identification) – the technique is, however, useful for examining seasonal changes or relations with habitat (Gerell 1967). It should however be noted that some prey items may be better digested than others, which could cause a bias of the results (Dickman and Huang 1988; Reynolds and Aebischer 1991; Valentini, Miquel et al. 2009).

Animal dens may also be checked for food remains (Sargeant, Swanson et al. 1973). This method sometimes allows the identification of particular individuals, and may be useful for assessing prey volume. However, dens may be difficult to find, also prey items consumed whole could be omitted in the analysis.

Home ranges, movement and activity

General assessment of presence/absence or relative abundance can be done on the basis of indirect indices such as tracks (e.g. with the help of tracking pads floating rafts in the case of mink (Reynolds, Short et al. 2004)) or sign surveys based on scat detection (Harrington, Harrington et al. 2008).

Information from trapping and marking can also be useful to estimate distances covered by animals, as well as their use of space and ranging behaviour (Melero, Palazon et al. 2008), however it is reliant on retrapping the marked individuals.

Radio-tracking, although relatively labour-intensive, allows a good examination of home range sizes, including core areas; as well as identifying activity/inactivity over time (Gerell 1969), and pinpointing geographic locations of animals. Transmitters can be attached to collars, or implanted internally into the animal's abdominal cavity (Zschille, Stier et al. 2008).

Direct observations can be very accurate and valuable (Garcia, Mateos et al. 2009), but are rarely possible to conduct with elusive or nocturnal species, and it can be difficult to make them systematic.

In my thesis I use miniaturised Time-Depth Recorders, which are now small enough to be deployed on small-bodied, semi-aquatic mammals (Bethge, Munks et al. 2003).

1.2. The use of data-loggers for measuring animal behaviour

The term "bio-logging" was first introduced in 2003, at the International Symposium on Bio-logging Science held at the National Institute of Polar Research (NIPR) in Tokyo (Naito 2004). It refers to the placement of miniaturised data-recording devices (e.g. bio-loggers, data storage tags, archival tags, electronic data recorders) directly on, or inside of free-living animals (Ropert-Coudert, Beaulieu et al. 2009). Boyd et al. (2004) proposed the following definition of bio-logging science: "investigation of phenomena in or around free-ranging organisms that are beyond the boundary of our visibility or experience" (Boyd, Kato et al. 2004), as bio-logging allows researchers to obtain data previously inaccessible through conventional means, particularly due to remoteness or elusiveness of the study species. The remote data collection is also practical and logistically viable, as well as rigorous and scientific (Ropert-Coudert and Wilson 2005).

The increasing use of miniature electronic tagging devices (bio-loggers or data-loggers) has enabled researchers to follow free-living behaviour such as migration and foraging. The devices fall into several categories, based on the parameters they can record, which may be physiological parameters, movement and body postures, environmental parameters or encounter rates.

Physiology

A number of devices have been engineered to monitor changes in animal physiology. Heart-rate loggers are used to measure the heartbeat of free-living animals, for instance, to see the influence of human presence on the heart rate of the study species (Weimerskirch, Shaffer et al. 2002), or calculate metabolic rates (Woakes, Butler et al. 1995). Metabolism can also be examined with heat flux sensors (Willis and Horning 2005). Temperature loggers may be inserted internally to inspect aortic

temperatures to check for signs of core hypothermia (Ponganis, van Dam et al. 2004), or to investigate feeding activity on the premise that the internal temperature of a warm-bodied predator drops after it has ingested a cold prey (Charrassin, Kato et al. 2001). Internal pH-loggers are used for recording changes in gastric pH (Thouzeau, Peters et al. 2004). Hall sensors, measuring the magnetic field strength, allow the inference of distance between the sensor and a magnet. Placing the two parts on a bird's beak allows measurement of breathing and feeding behaviour, while the frequency of defecation events can be counted using Hall sensors placed around the cloaca (Wilson, Scolaro et al. 2004).

Movement

Some of the oldest and most widely deployed devices were developed for recording movement; these include Time-Depth Recorders measuring depth and temperature over time, discussed in detail in section 2.1 below. A combination of records of water speed (using vertical axis impeller transducer), depth (from pressure logger), compass bearings and geolocation (GPS unit) may be used to determine an animal's three-dimensional dive path (Davis, Fuiman et al. 2001). A similar effect can be achieved through measuring acceleration in three orthogonal planes: heave (dorso-ventral acceleration), sway (lateral acceleration) and surge (anterior-posterior acceleration) (Fossette, Gleiss et al. 2010). Tri-axial accelerometers can be used to examine dive profiles or swimming strategies of aquatic animals (Ropert-Coudert, Kato et al. 2006; Fossette, Gleiss et al. 2010), or flight modes of birds (Halsey, Portugal et al. 2009), and, with enough prior calibration, outputs can indicate varying body postures or movements, reflecting a range of behaviours (Shepard, Wilson et al. 2008).

Environment

Loggers have been developed for measuring various environmental features, e.g. humidity (Körtner, Pavey et al. 2008), light (Tremblay, Cherel et al. 2003), wet/dry condition (Kuhn, McDonald et al. 2006), temperature and depth (Harrington, Hays et al. 2012), geolocation (Steiner, Bürgi et al. 2000; Davis, Fuiman et al. 2001) or salinity (from conductivity and temperature readings (Hooker and Boyd 2003)). These measurements not only provide behavioural data (e.g. movement from oceanic areas to fresh waters), but also environmental ones, such as ocean temperatures and salinity. These are useful not only for biologists, but also oceanographers and other scientists who can employ animals as live sampling platforms (Hooker and Boyd 2003; Fedak 2004).

Encounter rates

Prey captures can be detected by methods described above (internal temperature, tri-axial accelerometry); however other inter- and intraspecific interactions are most often examined using proximity loggers. “Proximity data-logging collars consist of an Ultra High Frequency (UHF) transceiver that broadcasts a unique ID code, whilst simultaneously 'listening' for those of others. When two or more units come within a pre-determined, user-defined distance, a contact is initiated until one or both of the receiving loggers fails to detect the signal within a user-defined separation time” (Drewe, Weber et al. 2012). These may be placed on animals, but also on static base stations. Proximity loggers are very useful for measuring social interactions (Ryder, Horton et al. 2012), and have recently been employed to analyse the interactions between badgers and livestock in the context of potential cross-infection with tuberculosis (Böhm, Hutchings et al. 2009; Drewe, Weber et al. 2012).

Multi-sensor devices

Several functions may be combined in multi-sensor devices, out of which the "daily diary" is most complex. It logs 14 parameters at infra-second frequencies to provide records of animal movement, behaviour, energy expenditure and the physical characteristics of the animal's environment (Wilson, Shepard et al. 2008) in a single system. Additionally, cameras/image loggers may be attached to animals to provide additional data, as well as validation for other devices (Naito 2006, Ponchon, Grémillet et al. 2013).

The major problems of the field of bio-logging currently concern three issues: effect on study species, data recovery and expenses (Ropert-Coudert and Wilson 2005), as well as interpretation and validation of results. Currently logger design is not limited by digital memory, but rather by battery power; it affects both the recording duration, and the size of the instrument (Davis 2008). Most tags store data rather than transmitting it – obtaining the information is thus dependent on tag recovery. Data transmission is possible using pop-up satellite archival tags (PSAT), which have a means to transmit data, e.g. by satellite relay (Naito 2004; Kuhn, McDonald et al. 2006). These tags however can still be 3-10 times as expensive as the simple TDRs; moreover, they have not yet been adapted for small species.

1.2.1 TDRs – development and application

Studying aquatic and semi-aquatic animals is non-trivial, especially when they are submerged. Time-Depth Recorders have been developed in the 1960s to investigate the underwater movement of Weddell seals (*Leptonychotes weddellii*); the early models were primitive, bulky and relatively inaccurate, which meant that they could

only be deployed on large-bodied, deep-diving species (Kooyman 1965). The initial evolution of TDRs was slow until the 1980s, when it gained speed with the emergence of microprocessors (Kooyman 2004). Digitalization allowed miniaturised data-loggers to incorporate additional variables, such as temperature, swim speed, or electrocardiogram (Muramoto, Ogawa et al. 2004). The comparison between the original bio-loggers and the most recent technological achievements is striking: the very first TDRs weighed 3.25 lb (about 1.5 kg), recorded data on scrolls of paper and were accurate to approximately 20 m (Kooyman 1965); modern TDRs are digital, weigh as little as 2.7 g in water and have a 0.03 m resolution (Hays, Forman et al. 2007).

The miniaturisation, improved accuracy and expanded memory have allowed successful TDR deployments on an increased range of species, encompassing mammals, birds, reptiles, fish and invertebrates (Ropert-Coudert, Beaulieu et al. 2009; Rutz and Hays 2009). Time-depth measurements allow an accurate recreation of dive profiles for these species, providing important information on foraging strategies (Naito, Asaga et al. 1990; Boyd and Arnbom 1991). Recent miniaturisation has passed the size threshold for studying small-bodied, shallow-diving, aquatic and semi-aquatic animals, such as the platypus *Ornithorhynchus anatinus* (Bethge, Munks et al. 2003), the otter *Enhydra lutris nereis* (Tinker, Costa et al. 2007) or the American mink (Hays, Forman et al. 2007). Their main limitations are a short deployment activity, restricted by battery life; the need to recover the tag to obtain data; and no geoposition records. Additionally, because the logger only contains temperature and depth sensors, the analysis is based on inferences; also short – though very detailed – snippets of animal activity may not be representative of their strategy as a whole. However, at this point in time they seem to be the most convenient equipment for animals which rapidly

transition between aquatic and terrestrial environments, as is the case with semi-aquatic foragers. Information thus obtained can improve our knowledge of diving and activity patterns, which has previously been incomplete due to the elusive and nocturnal nature of the studied species.

Knowledge of semi-aquatic animal ecology is particularly important since they are ecologically between aquatic and terrestrial animals, having evolved to exploit prey both in water and on land; there is a conflict of adaptations for aquatic and terrestrial modes of activity, which constrains them because they have to do both – a "jack of all trades, master of none" situation. The understanding of what governs the niche choice and the transitions between the aquatic and foraging activities (particularly in terms of foraging) of semi-aquatic species contributes to wider knowledge of animal ecology and foraging. Some semi-aquatic animals are also important because of their conservation status: they are either invasive alien species, such as the American mink or the coypu (Panzacchi, Cocchi et al. 2007), or of conservation concern, such as the European mink (Sidorovich 2001). Some, like beavers (*Castor fiber* and *Castor canadensis*), can also play an important role in ecosystem engineering (Rosell, Bozsér et al. 2005). Bio-logger deployment on these species can shed light on their behavioural ecology.

1.2.2 Ethics of using bio-loggers

While bio-logging devices provide potential insight into animals hidden from view, there are ethical considerations as to the ability of animals to carry them without harm or modification of behaviour. The effects of handling at capture and recovery might also cause harm or modification which might affect the data collected and which require ethical consideration. Logger deployment may affect the physiology or

behaviour of studied animals, which is problematic from both the ethical (impact on performance or survival), and scientific perspectives (confounding the output signal; tagged animals not being representative of the investigated group). The principal difficulty of examining the impacts of logger attachment on free-living animals is the inability to compare the results against those obtained from non-instrumented animals (Ropert-Coudert, Knott et al. 2007), as "measurement affects performance" and it is often impossible to establish objective norms (Wilson and McMahon 2006). Occasionally impact of device attachment can be inferred from indirect cues, such as length of foraging trips (Croll, Osmek et al. 1991), breeding success (Croll, Osmek et al. 1991), meal masses (Phillips, Xavier et al. 2003) or rates of return to the breeding site (Croll, Osmek et al. 1991); or checked against data doubly-tagged individuals (Ropert-Coudert, Bost et al. 2000). Further estimates of optimal device parameters can be calculated through modelling experiments using both models and data obtained from free-living animals (Wilson and McMahon 2006). Loggers themselves may also be used to assess the stress levels of animals during capture and processing, e.g. through monitoring respiration rate, heartbeat, body temperature or activity, which can provide useful information for improving handling techniques. These issues are not unique to loggers but are also relevant to radio-transmitters and trapping – and effects can sometimes be assessed using independent methods.

Externally attached loggers may modify animal behaviour through mass, disruption of hydrodynamics, aerodynamics, or through attempts to remove devices. One of the biggest concerns is logger size. Equipment weight can affect the efficiency of locomotion, e.g. flying (Croll, Osmek et al. 1991) or swimming and diving (Ropert-Coudert, Knott et al. 2007); it may also impact the animal's energy expenditure (Wilson

and McMahon 2006). The cross-sectional area and shape of external loggers affects the drag of streamlined aquatic animals during diving (Culik, Bannasch et al. 1994); as do rigid antennae protruding from the transmitters (Wilson, Kreye et al. 2004). Placement of equipment may also shift the animal's centre of balance, and thus result in behavioural changes (Healy, Chiaradia et al. 2004). A bright colour of the logger may provoke antagonistic behaviour from conspecifics (Wilson, Spairani et al. 1990), or attract predators. The effects of some tagging methods can only be observed through long-term studies, and methods which appear harmless on a day-to-day basis may affect the survival or reproduction in the long run; "acceptable practice" indices must be considered prior to deciding on deployment times (Wilson and McMahon 2006).

Equipment attachment is another source of distress for the animal. Loggers (and radio-transmitters) may be attached internally (through surgery of the abdominal cavity) or externally (gluing/taping or on a collar/harness). All methods have drawbacks, and most have reported impacts on the animal (Ropert-Coudert and Wilson 2004). Implantation, although overall considered the method with the lowest long-term impact, may lead to post-surgical complications and behaviourally-induced wound failures (Ropert-Coudert, Bost et al. 2000; Guillemette, Woakes et al. 2002; Ó Néill, Wilson et al. 2008; Zschille, Stier et al. 2008). These may be reduced or avoided by keeping the animal in captivity for a recovery period, however prolonged retention is not recommended for species highly susceptible to stress or population perturbation (Ó Néill, Wilson et al. 2008; Zschille, Stier et al. 2008). Gluing the equipment may result in shorter attachment times, while harnesses and collars carry with them a risk of entanglement, as well as skin abrasions and sores caused by straps (Ó Néill, Wilson et al. 2008; Zschille, Stier et al. 2008).

1.3. Project aims and outline

In my DPhil I combine two aims: methodological and ecological.

1. Methodology

Time-Depth Recorders have been used on large, deep-diving animals; using them on small-bodied, shallow-diving, semi-aquatic animals is still novel. Because semi-aquatic animals are able to make rapid transitions between aquatic and terrestrial environments, their overall activity is more complicated, and diving patterns are harder to detect than those of fully-aquatic species. There is a pressing need to develop analytical methods to objectively quantify diving patterns in the behaviour of semi-aquatic species – and doing so is my first aim. Also, while TDR depth records are used to study diving behaviour, temperature records can be used to identify activity patterns. This has been done for seabirds (Tremblay, Cherel et al. 2003), but not for animals active both during the day and at night – that constitutes my second aim. Finally, validation of TDRs using captive individuals is not always a possibility prior to studying free-living animals. Here, I attempt to validate my methods using captive mink.

2. Behavioural ecology

I explore the diving patterns and activity budgets of free-living American mink in Oxfordshire using the methodologies described above. Of particular interest to me is the persistence of diving behaviour of this small, thin, supposedly mal-adapted species. I demonstrate that it is possible to use TDRs for a precise analysis of activity patterns, based on temperature records, of this semi-aquatic, generalist species. I test whether there are underlying differences in the behaviour of males and females, or whether there are trends pertaining to the species as a whole.

1.3.1 Sources of data

TDRs were first deployed on mink in December 2005 by Dr. Lauren Harrington and Andrew Harrington, data were collected from January 2006; I joined the project in October 2007 and collected data in the field with assistance from Andrew Harrington and Dr. Laura Fasola from October 2007 to March 2008. In this thesis I present analyses on the complete dataset collected between January 2006 and March 2008. The study site and the field techniques used are described below, while the TDR data are described in more detail in Chapter 2. Additional data were collected from TDR and direct observation in a separate captive study, used for validation of the complete behavioural classification; these data are described in Chapter 4.

Study area

The study area is the site of a long-term study of American mink in the UK (Macdonald and Harrington 2003), located in Oxfordshire along the rivers Cherwell and Thames in Upper Thames Valley, Oxfordshire (approximate latitude, longitude: 51.62^{o}N, 1·08^{o}W). The sites are similar, with both rivers slow-flowing, between 5 and 20 m wide, and up to c. 3 m deep. Both rivers are fringed with trees (e.g. willow, *Salix fragilis*), and vegetation (e.g. nettles, *Urtica dioica*, bramble, *Rubus fruticosus*, blackthorn, *Prunus spinosa,* and hawthorn, *Crataegus monogyna*), and are bordered on either side by a mixed agricultural landscape (predominantly grazed pasture). Potential competitors include Eurasian otters, European polecats, foxes (*Vulpes vulpes*) and stoats (*Mustela erminea*). Potential prey species include rabbits, small mammals, birds, fish and crayfish (*Pacifastacus lenusculus*). The climate is temperate, with summer temperatures that vary (on average) between 12-14 and 20-27^{o}C, winter temperatures between 0-5 and 6-10^{o}C, and 0 to 12 days of frost per month during November to

March (Oxford weather station: www.metoffice.gov.uk/climate/uk/stationdata)" (Harrington, Hays et al. 2012).

Animal handling and anaesthesia

The handling protocol largely follows the methodology of Hays et al., and Harrington et al. (Hays, Forman et al. 2007; Harrington, Harrington et al. 2008). Using standard protocols mink are trapped using single-entry, wire mesh cage traps (Solway Feeders Ltd., Kirkcudbright, Scotland, UK). For field studies, these are set on floating rafts secured to the riverbank (Reynolds, Short et al. 2004) and baited with rabbit or sardines; they are checked once a day in the mornings.

Mink are transferred to a Perspex box for the induction of anaesthesia (Yamaguchi, Strachan et al. 2002; Hays, Forman et al. 2007), and anaesthetized with isoflurane (IsoFlo: Schering-Plough Animal Health, Welwyn Garden City, Hertfordshire, UK) delivered through a vaporizer attached to a portable oxygen cylinder (Mathews, Honess et al. 2002). Upon loss of righting reflex, the animal is transferred to a face mask to maintain anaesthesia during handling; several measurements are taken (including body length with and without tail, chest girth, body and tooth condition, body temperature and weight), the animal is marked with a subcutaneous PIT tag (MID Fingerprint, UK) and fitted with a TDR collar. It is then transported to a plastic holding box for recovery before the release at the site of capture. The handling of the animals was usually completed within 10-30 minutes and animals recovered from anaesthesia within 10-25 minutes. The animals were recaptured a week after the TDR deployment (or as soon as possible after a week), and the collars were removed. The collars did not cause any cases of neck abrasion or any other injury during this time period.

All procedures were carried out under United Kingdom Home Office licences PPL30/1826, PIL30/6530, and PIL30/6917 and PIL No. 30/8103 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 licence WCA/06/4 and Natural England licences NNR/2007/0024, NNR/2007/0022.

Time-Depth Recorders

Depth measurements were recorded using CEFAS G5 Time-Depth Recorders (CEFAS Technology Ltd, Lowestoft, UK). These are cylindrical (31 mm length by 8 mm diameter – see Figure 1.3A) and lightweight (2.7 g in air and 1 g in water). The G5 TDR has a (nonvolatile Flash) memory capacity of 2 MB, and is capable of storing 693 000 data points at its maximum precision (12-bit A–D resolution), making it the most powerful TDR of its size. The tag can be set to record temperature and pressure every second, accumulating a total of over 600,000 data points over seven days. Additionally, the "fast-log" feature of the latest loggers allows an increase of recording frequency to every 0.1s upon contact with water. This fast-log data is recorded and stored as a diving event for as long as the animal is in water; if a threshold "diving" depth (set to 0.3 m) is not reached, the fast-log will switch off within the first four datapoints (0.4 seconds).

The TDRs used in the studies recorded (temperature-compensated) depth with a nominal 0.02 m resolution with a full recording range of 100 m. The temperature sensors recorded temperature to a precision of 0.03 °C with an accuracy of 0.1 °C. Temperature sensors were calibrated in the range 4–34 °C, with a T66% (i.e. the time taken to reach 66% of the step change between two temperatures) of 28 s over this

range. The ability of the TDR to record shallow dives was validated by Hays, Forman et al. (2007).

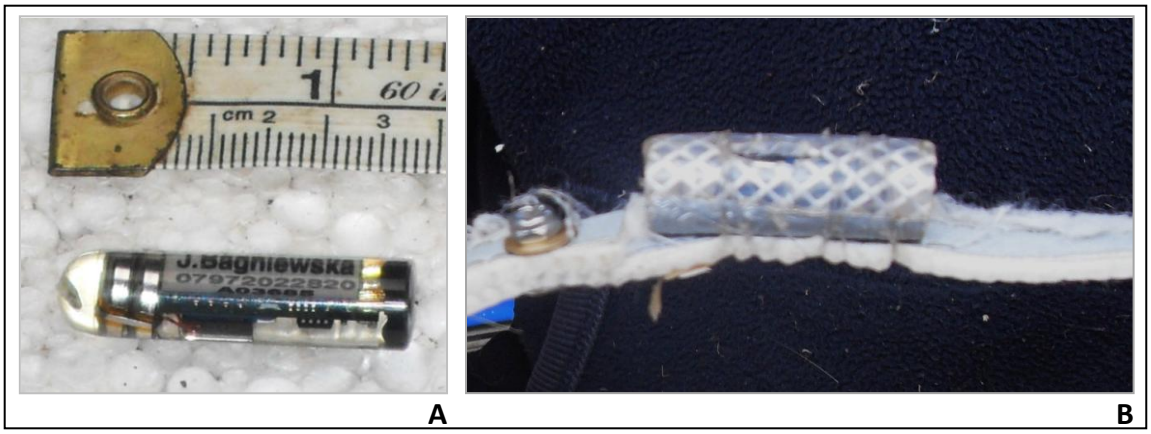

Figure 1.3: A Time-Depth Recorder shown to scale (A); a TDR encased in plastic tubing and attached to a collar is ready to be deployed (B). The tubing protects the pressure sensors from damage. A hole cut over the temperature sensor allows unbiased temperature records.

To prevent equipment damage, the TDR was encapsulated in plastic tubing (see Figure 1.3B), as described by Hays et al. (2007): "A hole was punched in the casing and positioned over the temperature sensor to allow direct water access and the end of the TDR containing the pressure transducer was recessed by approximately 5 mm within the plastic tube so that it also received a free exchange of water but was protected from direct impacts. The entire package was attached to the collar with monofilament line and secured with glue and tape. With this modified attachment method, all TDRs that were recovered showed minimal damage" (Hays, Forman et al. 2007).

The TDRs were attached to hand-sewn woollen collars (field studies), or to modified reflective cat collars (captive studies). Weight (in air) of the TDR collar was 18 g (< 3% of the body weight of the smallest individual in this study).

1.3.2 Data summary

Data from wild animals is summarized in Table 1.2 (from Harrington et al., 2012).

Table 1.2. TDR deployments on wild American mink. Note that repeat deployments were made on some individuals.

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	6.0	5[b]
M36	F	0.62	Cherwell	February 2006	5.5	789
M43	F	0.60	Cherwell	March 2006	4.7	99
M23	F	0.79	Cherwell	March 2006	0.8[c]	67
M04	F	0.69	Thames	August 2006	5.0	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	1.50	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	6.0	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 10g.
[b]These two individuals were excluded from analysis of dives, but included in the analysis of activity patterns.
[c]TDR recorded for full 5 days; dives recorded on only 1 of those days.
[d]TDR failed prematurely and only recorded for 2 days.

1.4. Thesis organisation

This thesis sets out to understand the behavioural ecology of a semi-aquatic predator and to show how small bio-logging devices and novel approaches to their analysis can be used to investigate behavioural ecology across two very different environments. This thesis is written according to the format of scientific papers. For this reason there is some repetition between chapters, particularly with respect to methods. The thesis structure follows the progression of this research according to four papers.

Chapter 2 – Hidden Markov analysis describes dive patterns in semi-aquatic animals

Bio-logging studies frequently aim to infer animal behaviour during a cryptic part of their life cycle, such as migration or foraging where they may be out of view of researchers. Inferring patterns of behaviour may be subjective, so I use a Hidden Markov model, a technique from machine learning, to identify the nature of diving behaviours and to classify them. I then investigate what influences the transition between these behaviours and find that each mink dive can be assigned one of three states (state 1 – temporal cluster of dives; state 2 – more loosely aggregated diving within aquatic activity; and state 3 – terminal dive of a cluster or a single, isolated dive). Mink dive in clusters; this clustering does not change in response to ambient temperature throughout the year.

Chapter 3 – Diving patterns of the American mink

The ability to forage in water is likely to be different between sexes, between seasons and perhaps according to body mass; the differences may be more apparent through dive patterns rather than through dive parameters per se. I investigate the diving of mink using the classification from Chapter 2, which allows determining the transition between states and the persistence (i.e. the number of consecutive dives) of given behaviours. I then examine effects of sex and season on persistence, dive patterns, and single vs. clustered dives of mink in Oxfordshire.

Chapter 4 – Using temperature records for establishing activity patterns: validation study

Most bio-logging studies are carried out because researchers lack the ability to make direct observations on their study species. This also means that a lot of results obtained from bio-loggers are largely based on inferences. While TDR depth records

have been used to reliably identify the diving behaviour of mink, I attempt to explore mink activity/inactivity on the basis of TDR temperature records. I use captive animals (*N* = 2) to calibrate known activity classifications with TDR records in a supervised classification approach.

Chapter 5 – Novel use of Time-Depth Recorders to describe activity patterns of generalist mammals

Using data and the behavioural classification learned in Chapter 4, I apply the temperature-based approach to the free-living mink data reported in Chapters 2 and 3. The inclusion of the terrestrial activity and the resting categories permits me to estimate a complete time budget. I use this technique to examine the activities of mink in the context of intersexual and seasonal differences. This is a unique attempt to describe activity patterns of a semi-aquatic mammal using a method other than radiotelemetry or direct observations, and the same methodology could potentially be applied to other mammals.

Chapter 6 – General discussion and conclusions

This chapter summarises and discusses my findings from the entire study.

Appendix 1

Software written in R programming language, used for assigning activity categories to Time-Depth Recorder data.

Appendix 2

Bagniewska J.M., Hart T., Harrington L.A., Macdonald D.W. (2013) "Hidden Markov analysis describes dive patterns in semi-aquatic animals." Behavioral Ecology, **24**(3): 659-667.

Chapter 2

Hidden Markov analysis describes dive patterns in semi-aquatic animals[1]

[1] A modified version of this chapter has been published as: Bagniewska J.M., Hart T., Harrington L.A., Macdonald D.W. (2013) "Hidden Markov analysis describes dive patterns in semi-aquatic animals." Behavioral Ecology, **24**(3): 659-667. See Appendix 2.

Abstract

Existing methods of dive analysis, developed for fully aquatic animals, tend to focus on frequency of behaviours rather than transitions between them. They therefore do not account for the variability of behaviour of semi-aquatic animals, and the switches between terrestrial and aquatic environments. This is the first study to use hidden Markov models (HMM) to describe sequential dive patterns in a semi-aquatic animal. I show how this approach can be used to examine the influence of environmental factors on the likelihood of transitions between behavioural modes, and I demonstrate the applicability of this approach by examining the relationship between state transitions and ambient temperature. I used 18 existing datasets of the dives of 14 American mink (*Neovison vison*) fitted with Time-Depth Recorders in lowland England. Using HMM I identified three behavioural 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, I conclude that mink tend to dive in clusters. I found no relationship between temperature and the proportion of dives in each state or between temperature and the rate of transition between states, suggesting that in my study area mink were apparently not adopting different diving strategies at different temperatures. This result was unexpected for the model species because mink have high rates of heat loss, particularly when in water, and thus might be expected to reduce aquatic activity when it is cold. Transition analysis between states showed that there is no correlation between ambient temperature and the likelihood of mink switching from one state to another, i.e. 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 semi-aquatic animals.

2.1 Introduction

Diving has been studied extensively in fully aquatic mammals, birds and reptiles (Pütz, Wilson et al. 1998; Halsey, Handrich 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, Davis et al. 2000) that are energy-efficient (Handrich, Bevan et al. 1997; Shepard, Wilson et al. 2009; Mitani, Andrews et al. 2010; Wilson, Shepard et al. 2010). Recent technological advances allowed miniaturised Time Depth Recorders (TDRs) to be deployed on small-bodied animals that are physiologically or ecologically constrained to perform shallow dives. These include semi-aquatic species such as platypus *Ornithorhynchus anatinus* (Bethge, Munks et al. 2003), otter *Enhydra lutris nereis* (Tinker, Costa et al. 2007) and American mink (Hays, Forman et al. 2007; Harrington, Hays et al. 2012) as well as aquatic foraging seabirds such as the red-footed booby *Sula sula* (Weimerskirch, Corre et al. 2006) and the Peruvian booby *Sula variegata* (Zavalaga, Halls et al. 2010).

The dives of many animals seem organised into temporal clusters with intermediate gaps – known as “bouts” (Boyd and Croxall 1992; Mori 1997; Staniland and Boyd 2003; Tremblay, Cherel et al. 2003) or “movement steps” (Sims, Southall et al. 2008; Humphries, Queiroz et al. 2010; Hays, Bastian et al. 2011). Clusters of behaviour have been used to describe the foraging of both aquatic (Boyd, Arnould et

al. 1994; Edwards, Phillips et al. 2007; Sims, Southall et al. 2008; Humphries, Queiroz et al. 2010; Hays, Bastian et al. 2011) and terrestrial (Janssen, Oerding et al. 1999; Johnson, Parker et al. 2002; Edwards, Phillips et al. 2007; Reynolds 2009; Jansen, Petrovskii et al. 2011) species. Recent debate has centred on the underlying distribution of the movement step lengths (Janssen, Oerding et al. 1999; Johnson, Parker et al. 2006; Edwards, Phillips et al. 2007; Sims, Righton et al. 2007; Edwards 2008; Reynolds and Rhodes 2009; Smouse, Focardi et al. 2010) but has largely ignored what influences transitions between short and long step-lengths (Hart, Mann 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 semi-aquatic animals. The behaviour of semi-aquatic species poses an uncertainty as to whether gaps between dives represent merely a pause within aquatic behaviour or a behavioural switch to terrestrial activity. For example, a long pause between successive dives in a whale may represent resting or surface travel (Baird, Borsani et al. 2002), but a long pause between successive dives in a mink may either represent resting or surface swimming, or movement onto land. Semi-aquatic 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 behaviour 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. I use hidden Markov models (HMM) to discriminate between types of dives. I divide dives into clusters and attempt to identify the environmental predictors of transition between

behavioural modes, building on a method previously used to describe transitions between behavioural units in diving penguins (Hart, Mann et al. 2010). I then use the temperature logger of a Time-Depth Recorder on mink (*Neovison vison*) to infer the transition between land and water and validate my conclusions from HMM. I believe this is the first time HMM, or any analysis of transition between behaviours, has been used to analyse the foraging behaviour of a semi-aquatic animal. I 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 semi-aquatic animals.

To explore the use of HMM in describing semi-aquatic behaviour, I used 18 existing datasets of the dives of 14 American mink in lowland England. The American mink is a small-bodied, semi-aquatic North American mustelid, extremely adaptable and highly invasive in Europe, South America and Asia (Macdonald and Harrington 2003; López-Giráldez, Gómez-Moliner et al. 2005; Peris, Sanguinetti et al. 2009). Mink's broad diet includes aquatic (crayfish, fish), semi-aquatic (waterfowl, amphibians) and terrestrial prey (lagomorphs, rodents, birds) (Sargeant, Swanson 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 weight ratio (Brown and Lasiewski 1972), and their fur has comparatively low insulative properties (Fish, Smelstoys 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, Forman et al. 2007), with no difference in the number of dives performed between summer and winter (Harrington, Hays et al. 2012). Given the extremely short duration of individual mink dives (Harrington, Hays et al. 2012), it may be that temperature affects the clustering (or persistence) of diving rather than the number of dives per se; e.g. we might predict that a period spent continually in the water was shorter in winter than in summer.

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

Tools to enable such principled approaches 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. I use HMM to separate these confounding behavioural units, validate the results using logged temperature in the TDR and test whether changes in environmental temperature influence behavioural strategies in American mink.

2.2 Materials and methods

Data collection

The TDr dataset used in this study has previously been described by Harrington et al. (Harrington, Hays et al. 2012) in a study of single dives by American mink. CEFAS G5 TDR (31 x 8 mm; CEFAS Technology Ltd, Lowestoft, UK (Hays, Forman et al. 2007)) were deployed on free-living American mink on the rivers Thames and Cherwell in the Upper Thames valley in Oxfordshire, UK (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, Short 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, Hays et al. 2012), something of note for future studies.

Animals were anaesthetised by qualified personnel under UK Home Office Licence, using isoflurane (IsoFlo: Schering-Plough Animal Health, Welwy Garden City, Herefordshire, UK) delivered via a vapouriser attached to a portable oxygen cylinder (Mathews, Honess et al. 2002), induced in a wooden box (0.15 x 0.15 x 0.48 m) with a Perspex window (Yamaguchi, Strachan 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 radio-collars (Wildlife Materials Ltd., IL, USA). In later deployments, we attached TDRs to hand-sewn collars (c.1 cm wide, made of three 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 semi-flexible 9 mm diameter plastic tubing and attached to collars using monofilament line, glue and tape (Hays et al. 2007). Weight (in air) of the radio-collar 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 TDR collars removed using the same procedures. Animal handling was completed within 10-30 minutes and mink recovered from anaesthesia within 10-25 minutes. The TDR was recovered a week after deployment (or as soon as possible thereafter). There were no cases of neck abrasion (or other injury) during these deployments.

Of 31 TDRs deployed on 24 mink (8m; 16f – all adults and sub-adults, i.e. adult-sized), 20 were retrieved giving data for 16 individual mink (6m; 10f). One data-logger failed prematurely and only recorded for two days. Two individuals for which we recorded fewer than 20 dives were excluded from further analysis, giving a total of 18 datasets due to repeated trapping of three individuals. Details of the data can be found in Harrington et al. (2012).

All procedures were carried out under United Kingdom Home Office licences 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 licence WCA/06/4 and Natural England licences NNR/2007/0024, 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 centre of Oxford, within 40km of the study sites. Since water temperature tends to be more stable than air temperature, I 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 6-7 days. Data collection commenced at midnight after TDR deployment, giving the animals around 12h to adjust to the collar. Where TDRs started recording earlier, only data from the next day onwards, starting at midnight, were used in the analysis (thus some datasets are only 5 days long). 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).

Hidden Markov models are a class of models in which the modelled system is assumed to be a Markov process with distinct states (Roberts, Guilford 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^{TM}, 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, Roberts et al. 2004; Roberts, Guilford et al. 2004) and used to identify states of diving in penguins (Hart, Mann et al. 2010). This method is a principled approach to identifying the number of behavioural states (where state is a statistically defined, distinct unit of behaviour) and state membership of dives without ascribing *a priori* assumptions as to the purpose of a behavioural state. Even where classification may be simple to define, such as ‘on land’ or ‘in water’, the ability to classify behaviour

statistically and cross-validate with other metrics allows us to test the efficacy of statistical approaches to behavioural classification and to determine which transitions or boundaries are important to animal behaviour (Mann, Freeman et al. 2011).

Factors to be used in the hidden Markov model 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 2.1). Dive interval and depth were used to define states because taken together these variables were nearly orthogonal and explained most of the variance.

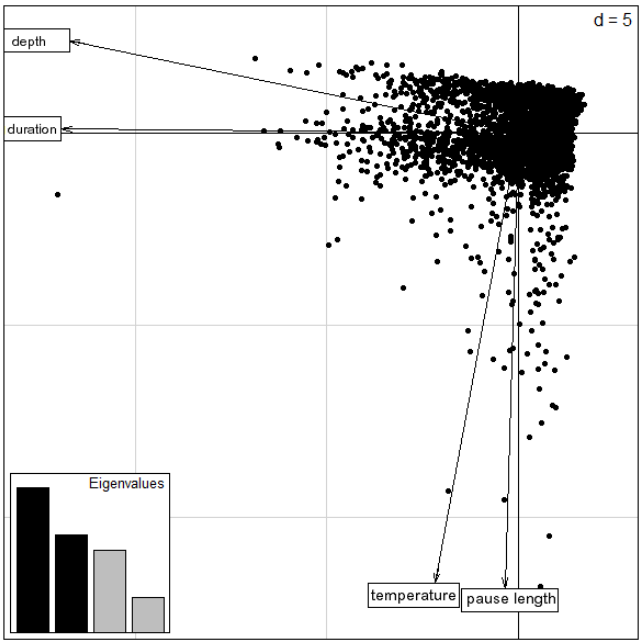

Figure 2.1: Principal components analysis of dive duration, dive temperature, dive depth, and the length of pauses between dives to determine relationships between parameters.

The HMM was performed on depth and interval, seeking to identify between 2 and 5 states (the number of behavioural categories, irrespective of what these might be). I 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 dataset, and occasionally a fourth state was found. Analysis was restricted to the three

state model in accordance with occupancy guidelines described in Roberts et al. (2004).

Simulations to estimate expected transition rates between states given state frequencies were carried out using the package(urn) (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.

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

2.3 Results

Hidden Markov models for identifying states

The HMM algorithm consistently identified three clear states in all individuals (Figure 2.2). Re-running the algorithm showed that most dives were consistently assigned, but that the last dive in the dataset 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 three states appear to represent different types of behaviour, where State 1 is a temporal cluster of dives, State 2 is more loosely aggregated diving, which I 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 2.3). This division is in line with the observations of temperature profiles for the dives at each state (Figure 2.3A, B).

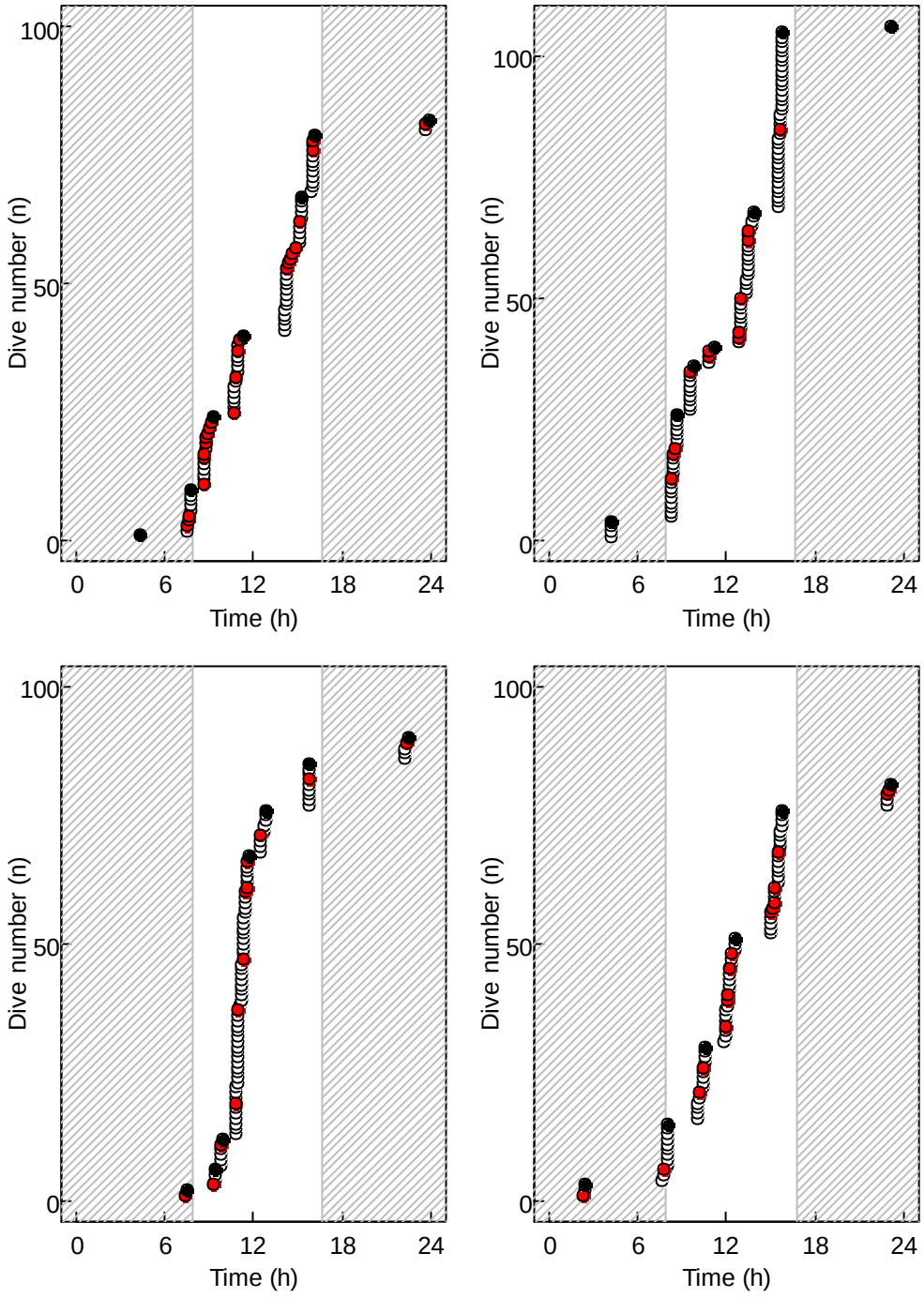

Figure 2.2: A modified version of Figure 6 from (Hays et al. 2007) to illustrate the states identified by HMM with respect to the timing of individual dives. I present the same dataset as Hays et al.; the graphs show dives of one mink on four separate days (mink 187a, graphs represent 24-27 January 2006 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 grey shading.

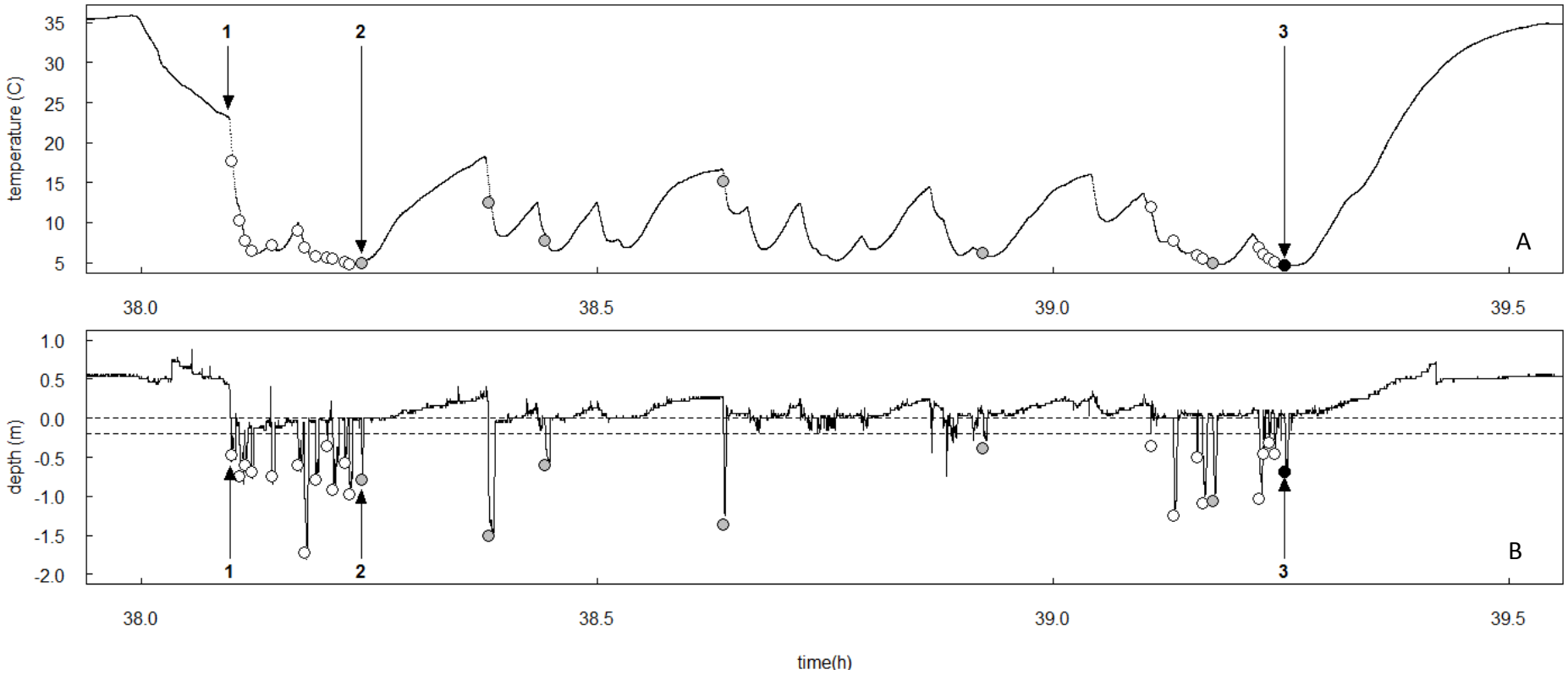

Figure 2.3: A diving profile of mink M39a in January. Graph A shows TDR temperature, and B – depth profiles over time. The positive offset in the depth records at the start and end of the trace reflects baseline drift caused by the massive temperature change; these start and end sections really represent a value of "0 m". Using the hidden Markov model, I have assigned one of three categories to each dive: State 1 (white circles) – a temporal cluster of dives; State 2 (gray circles) – more loosely aggregated diving, which I 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^{o}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 to close to the mink's body temperature, suggesting that the animal is inactive in a shelter location.

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 dives is dramatic enough to imply that a mink would go to a hiding place where it can warm up to a temperature close to its body temperature of 39-40°C (Williams 1986).

Sequential nature of diving

There was a higher frequency of State 1 than would be expected if all dives followed a common pattern – i.e. if all three states were equally likely – demonstrating that mink dive in clusters (Figure 2.4). 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), of State 3 is 0.157 (median: 0.113, range: 0.028-0.480, *N* = 18).

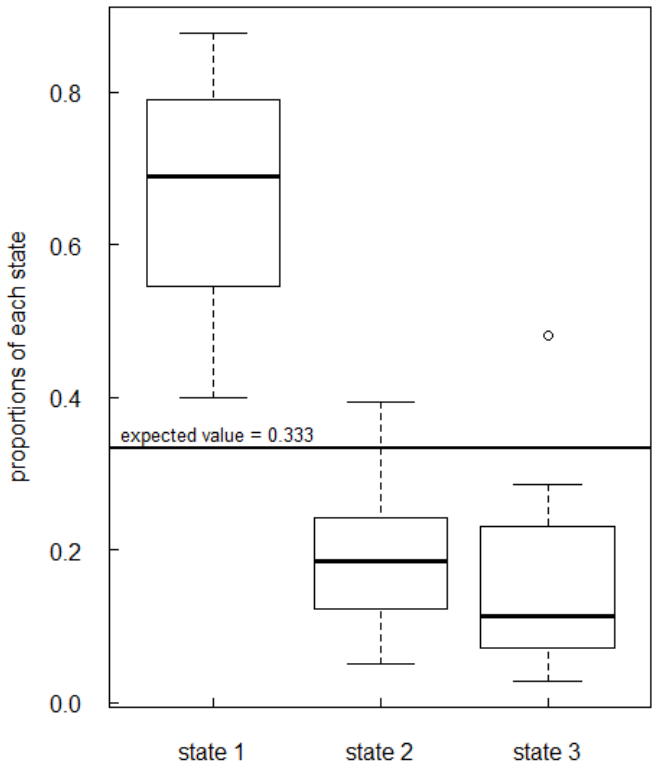

Figure 2.4: Proportion of State 1, State 2 and State 3 throughout all datasets, *N* = 18. The expected value if all dives follow a common pattern is 0.333.

Temperature-dependence

I found no significant relationship between the ambient air temperature and the proportion of dives in each state (Figure 2.5A); (linear regression, State 1: $F_{1,3} = 3.437$, $P = 0.161$, $N = 18$, State 2: $F_{1,3} = 0.725$, $P = 0.457$, $N = 18$, State 3: $F_{1,3} = 0.800$, $P = 0.437$, $N = 18$).

There was also no difference among mean ambient temperatures for each state (in ^{o}C): State 1 = 13.42, State 2 = 15.39, and State 3 = 16.51, or TDR temperatures: mean temperature of State 1= 13.35, State 2 = 15.52, and State 3 = 16.82 (Figure 2.5B).

The likelihood of switching between states (or the probability of a mink persisting at one behaviour) was not correlated with ambient temperature for any sequence of states (see Table 2.1). 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 = 0.006, $F_{1,3} = 15.551$, $P = 0.029$), however, after a Holm–Bonferroni correction this result turned out to also be not significant ($P = 0.262$).

Table 2.1: 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

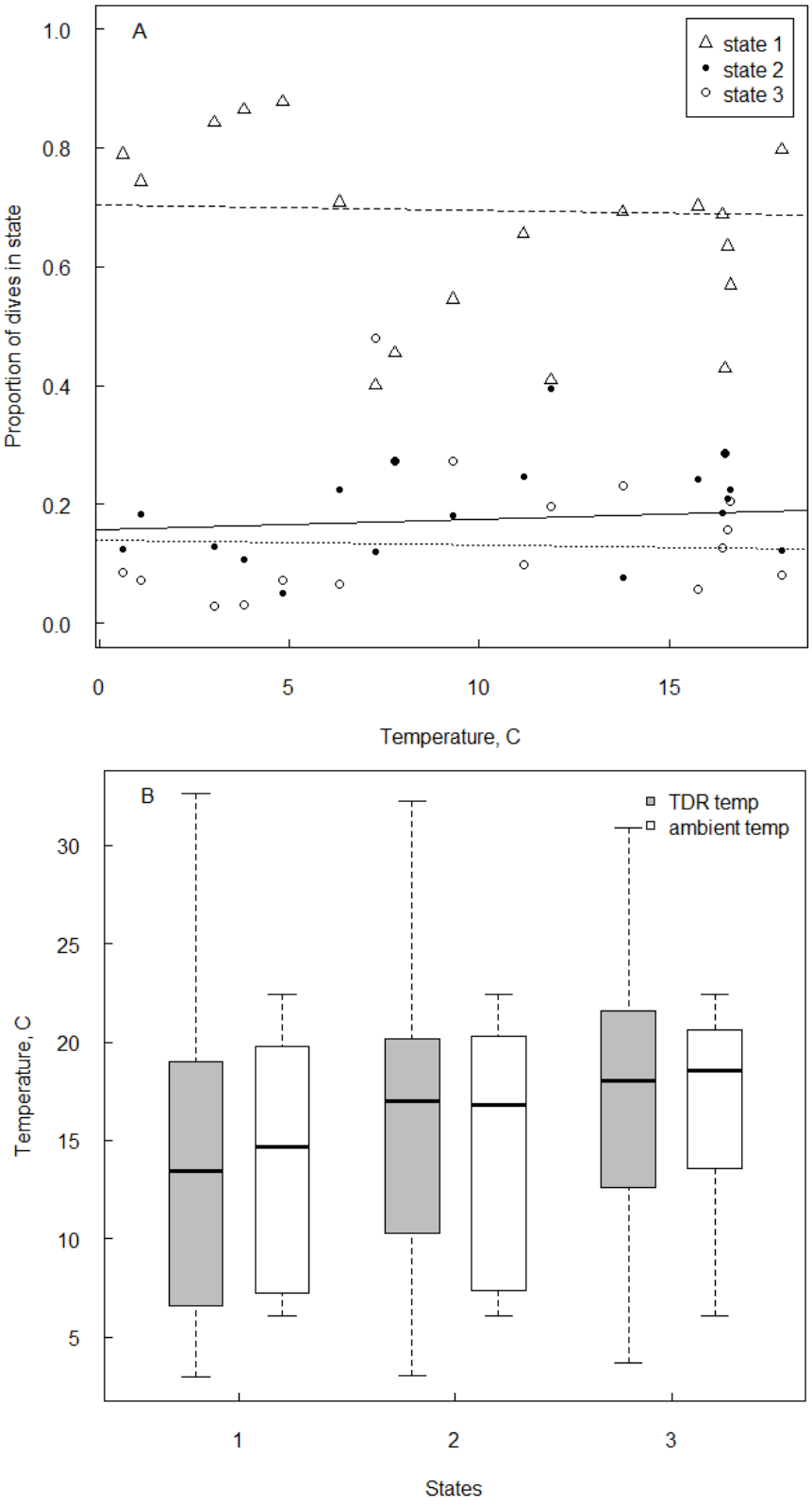

Figure 2.5: Links between TDR temperature and behavioural states. Fig. 2.5A shows the relationship between ambient air temperature and the proportion of dives in each state; each mink dataset is represented by three states. Fig. 2.5B shows the cumulative ranges of ambient air temperatures (from weather station) and TDR temperatures (measured on mink, and thus affected by its body heat) at different behavioural states for all animals.

2.4 Discussion

The diving behaviour of American mink is hugely variable among individuals and over time (Harrington, Hays et al. 2012) due to the possibility of switching from aquatic to terrestrial foraging. HMM identified three states in the diving of this semi-aquatic species. State 1 is a temporal cluster of dives, characterised 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 behaviours in semi-aquatic 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 behaviour, but takes into account the switch to terrestrial mode, and potentially a change of strategy, i.e. 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 semi-aquatic 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, tri-axial accelerometers, or other devices. Using HMMs it is possible to determine the beginning and end points for the terrestrial behaviours, to look at rapid changes between environments, and to see the patterns within diving behaviour. I hope this technique will allow me to address how animals balance expenditure and

rates of reward between two 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, I conclude that mink tend to dive in clusters, i.e. 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 crustaceans such as crayfish (which I think is likely), then the motivation to search for these relatively high-value prey items is reflected by persistence in a single behaviour; something previously found in captive mink (Cooper and Mason 2000; Warburton and Mason 2003). Since 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, semi-aquatic animals are likely to have more modes of foraging activity than fully aquatic or terrestrial species, so studying semi-aquatic 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 since 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 semi-aquatic animals, which may undertake only short commutes to land. Moreover, semi-aquatic 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 behaviour within the range typical of my study area. I found no relationship between ambient temperature and the proportion of dives in each state or between temperature and the rate of transition between states, meaning that, in my study area, in lowland England, mink are apparently not adopting different diving strategies at different temperatures or in different 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, Smelstoys et al. 2002), and is not in accordance with my 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, i.e. 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 behaviour (Harrington, Hays 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 behavioural analysis

We can pinpoint transition points between aquatic and terrestrial activity at specific points of time, but we still lack a clear understanding of mink activity patterns on land. The terrestrial behaviour of semi-aquatic animals has been studied through other means – e.g. radio-telemetry, (Niemimaa 1995; Garin, Aihartza et al. 2002; Marcelli, Fusillo et al. 2003; Peters, Brinkmann et al. 2009; Zschille, Stier et al. 2010), Global Positioning System (GPS) loggers (Durner, Whiteman et al. 2011) or direct observations (Garcia, Mateos et al. 2009) – but until terrestrial and aquatic modes of behaviour 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 tri-axial accelerometers), may allow us to distinguish among, and more fully describe, further modes of behaviour in future; in so doing, HMM will be a valuable analytical tool for examining the effect of many potential variables on behaviours and switches between different behavioural 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, Jorgensen et al. 2011) – e.g. foraging, travelling or escape. Nonetheless, currently I believe that HMM are a useful tool for describing the behavioural strategies of other semi-aquatic 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 behavioural states from more complex datasets.

Conclusions

I have demonstrated the use of hidden Markov models as a valid method for analysing the diving behaviour of semi-aquatic animals, particularly the transition between land and water. HMM has now been applied to fully (Hart, Mann et al. 2010) and semi-aquatic animals. HMM should be easier to apply to terrestrial animals, for which behavioural observations could validate behavioural states. I was able to identify dive patterns and show that mink dive in clusters of successive dives, something that has already proven useful in explaining habitat use in other diving animals (Heath, Gilchrist et al. 2010). I have also shown how HMM can be utilised to test specific hypotheses regarding behavioural patterns and the factors that influence them.

Chapter 3

Diving patterns of the American mink

Abstract

American mink (*Neovison vison*) are opportunistic, generalist feeders, found predominantly in aquatic and wetland habitats. Despite mink being widespread and well-studied, surprisingly little is known of the constraints on their foraging behaviour, and particularly what governs their diving patterns in the wild. Because several diving attempts may be required to exploit fully a resource patch or to catch prey, aggregations of dives can be singled out as behavioural units. Temporal clusters have been used to describe the changes in foraging behaviour of both aquatic and terrestrial species; multiple consecutive dives reflect the effort needed to capture aquatic prey.

I analysed data from miniaturized Time-Depth Recorders deployed on 9 female and 5 male free-living American mink on lowland rivers in the southern United Kingdom. Mink dives were classified into clusters, aquatic foraging sessions (AFS) and single dives using a hidden Markov model algorithm. Persistence (number of consecutive dives), as well as properties of single and terminal dives were analysed with respect to mink body mass, ambient temperature and daylight. Mink expend a considerable effort diving (up to 28 dives in a cluster, over 36 min, or up to 80 dives per AFS, over 154 min). Smaller animals were more persistent than larger ones across both sexes. Mink appeared to maximise daylight diving, but ambient temperature appeared not to influence diving behaviour. Male and female mink exhibited different diving patterns, which may reflect different foraging strategies, or could be a result of high individual variation.

3.1 Introduction

Despite a plethora of studies of diving behaviour in fully aquatic mammals, birds and reptiles (Butler and Jones 1997; Kooyman and Ponganis 1998; Hays, Houghton et al. 2004; Halsey, Blackburn et al. 2006; Godley, Blumenthal et al. 2008) there are relatively few such studies of semi-aquatic species (defined here as those that live close to water but obtain only part of their food by swimming and diving (Sidorovich, Kruuk et al. 1998)). Mammals that forage both on land and in water have to retain the ability to move efficiently in two quite different habitats, and, therefore, are not as well adapted for diving as are fully aquatic species (e.g. whales), or those that forage exclusively in water and only go on land to breed, moult or rest (such as seals) (Lyamin 1993; Boness and Bowen 1996). Semi-aquatic mammals are usually inefficient swimmers and relatively poor divers, as their oxygen stores and oxygen conserving mechanisms, insulation, or appendages are not as well specialised as those of fully-aquatic animals (Estes 1989; Fish 1993; Fish 2000). The dives of semi-aquatic mammals tend to be shallow and short in duration (Fish 2000; Harrington, Hays et al. 2012), and, in riverine systems, dive depth may be further constrained by river depth, making dives hard to detect and measure precisely.

Until recently, studying the diving behaviour of small-bodied, shallow-diving, semi-aquatic animals was hindered by a lack of appropriate technology (Hays, Forman et al. 2007). Previous behavioural studies of semi-aquatic mammals were restricted to a) direct observations (e.g. (Garcia, Mateos et al. 2009)), which are only possible for diurnal animals in open habitats; b) laboratory studies (e.g. (Poole and Dunstone 1976)), which may be limited by laboratory conditions; or c) radio-telemetry, which

provides information on space and habitat use (Harrington and Macdonald 2008), but not on specific activities performed. However, recent technological advances in Time Depth Recorders (TDRs), involving miniaturisation, improved precision and expanded memory, have facilitated studies of diving behaviour in a wide range of organisms (Ropert-Coudert, Beaulieu et al. 2009; Rutz and Hays 2009). TDRs are now small enough to be fitted on animals weighing less than a kilogram, and can measure depth to a precision of 0.05 m, at second (or even shorter) intervals, allowing very detailed and accurate recreation of sequential dive profiles of even shallow-diving species (Naito, Asaga et al. 1990; Boyd and Arnbom 1991).

TDRs have been successfully implemented on American mink, *Neovison vison* (Harrington, Hays et al. 2012). Mink are small (~1kg), semi-aquatic mustelids native to North America, considered alien invasives in Europe, South America and Asia (Macdonald and Harrington 2003). They are opportunistic, generalist feeders, found predominantly in aquatic and wetland habitats (Dunstone 1993). Their broad diet includes lagomorphs, rodents, waterfowl, sea birds, fish, amphibians and invertebrates; prey selection usually depends on availability, varying locally and seasonally (Dunstone and Birks 1987; Dunstone 1993; Clode and Macdonald 1995). Harrington et al. (2012) used CEFAS G5 TDRs (recording dives as short as 2 s, with a dive threshold of 20 cm) to describe the dive ability and behaviour of American mink in Oxfordshire, UK, at the level of individual dives. The study revealed that although mink, as expected, were relatively poor divers (median dive depth = 0.45 m, median dive duration = 10.9 s; maximum depths were 4-6%, and maximum durations – 34-44% of values predicted by allometry for males and females respectively), they can dive much

deeper and for much longer than originally thought based on results from laboratory studies (Harrington, Hays et al. 2012).

Mink appear to be relatively poorly adapted for swimming and diving. The mustelids' long, thin body shape, suggested to facilitate entrance into burrows in search of prey, results in rapid loss of body heat (Brown and Lasiewski 1972; Boyd 1997), especially so when in water. Mink pelage is less buoyant than that of some other semi-aquatic mammals (Fish, Smelstoys et al. 2002) and their fur retains insulative properties only for several minutes while in water (Williams 1986); Williams (1986) suggests that the heat loss entailed during aquatic activity may exceed metabolic heat production within 5 min of immersion. Unlike other semi-aquatic mustelids, such as otter species (Pfeiffer and Culik 1998; Borgwardt and Culik 1999), mink do not possess specialised appendages for swimming locomotion: their paws have a small surface area – relatively smaller than those of beavers, otters or muskrats – and their toes are only slightly webbed (Williams 1983). Furthermore, their eyes are not well adapted to underwater vision (Sinclair, Dunstone et al. 1974; Dunstone and Sinclair 1978; Dunstone and Sinclair 1978). Nevertheless, diving is clearly an important activity for mink since aquatic prey may constitute up to 89% of their diet in some places at some times of the year (e.g. (Gerell 1967)), and even in lowland England, where fish form a relatively small proportion of their diet (10-23%), it may provide up to 26.7 % of their energy requirements (Ferreras and Macdonald 1999; Harrington, Harrington et al. 2009).

Mink are widespread and well-studied (particularly with respect to their impact on native prey where they are invasive – e.g. (Macdonald and Strachan 1999; Clode and Macdonald 2002)) but surprisingly little is known of the constraints on their

foraging behaviour or what factors (if any) might lead to a preference for foraging on one prey type over another; where a switch in prey is linked to a switch in foraging environment. Mink are sexually dimorphic, with males weighing up to twice as much as females (Birks and Dunstone 1985). Since diving ability of mammals increases with body mass (Halsey, Blackburn et al. 2006), we might predict that smaller females would dive less or make shorter dives than larger males. Alternatively, given that a number of dietary studies (albeit a few) suggest that female mink consume smaller prey (which, in the UK, is often aquatic e.g. fish, crustaceans or water voles) than do males that prey on larger and, in the UK, terrestrial, prey (e.g. lagomorphs in Britain (Birks and Dunstone 1985), but also muskrats in Michigan (Sealander 1943), or Eider ducks in Iceland (Magnusdottir, Stefansson et al. 2012); see also Thom et al. 2004), female mink could also be predicted to dive more often, or over longer periods than male mink. Sexual dimorphism has been suggested to play an important part in niche separation (Thom, Harrington et al. 2004).

As in other mustelids (e.g. black-footed ferrets *Mustela nigripes* – (Richardson, Clark et al. 1987); weasels *Mustela nivalis* – (Jędrzejewski, Jędrzejewska et al. 2000); or pine martens *Martes martes* – Zalewski 2000), American mink reduce their terrestrial activity in winter (Zalewski and Bartoszewicz 2012); and other semi-aquatic species such as muskrats *Ondatra zibethicus* (MacArthur 1984) and star-nosed moles *Condylura cristata* (McIntyre, Campbell et al. 2002) tend to dive less frequently and for shorter periods of time during winter. Even though winter fur provides greater insulation than summer fur (Williams 1986), low ambient temperatures in winter and relatively poor insulation compared to other aquatic mammals may lead to

constrained dive duration in cold temperatures. Potentially, mink might also require longer recovery times to warm up between dives when it is cold.

Harrington et al. (2012), however, found no difference in dive ability (measured as the depth and duration of individual dives) between the sexes, but did show that the daily and hourly dive effort (the average time spent diving per hour) and dive rates (the average number of dives performed per hour) were higher in females than in males (Harrington, Hays et al. 2012). This intersexual difference was not apparent in summer, however, and the results were inconclusive. The authors also found no difference among the seasons in dive depth or duration, number of dives per day and the total amount of time spent diving per day. Harrington et al.'s (2012) finding that mink in winter performed the same number of dives in fewer daylight hours suggests that the sequential pattern of dive behaviour is worthy of further investigation.

Because several diving attempts may be required to exploit fully a resource patch or to catch prey, aggregations of dives can be singled out as behavioural units. Temporal clusters have been used to describe the changes in foraging behaviour of both aquatic (Boyd and Croxall 1992; Luque and Guinet 2007; Hart, Mann et al. 2010) and terrestrial species (Boyd, Arnould et al. 1994; Johnson, Parker et al. 2002). I use persistence, or the number of consecutive dives performed, as a metric of diving behaviour that may be more appropriate than measurements of individual dives, to reveal the effects of small body size, poor insulation and cold ambient temperatures. Because mink are single-prey loaders (i.e. they need to surface and leave the water to consume each prey item – Dunstone 1993), the number of consecutive dives may also be an indicator of foraging effort and, potentially, if it were possible to distinguish successful from non-successful dives, of hunting efficiency.

Using a dataset described by Harrington et al. (2012), I explore the relationship between diving persistence and body mass, ambient temperature and daylight (or day length). I predict, on the basis of dive allometry and thermoregulatory considerations, that (1) larger mink would be able to dive for longer than smaller mink, (2) that dive clusters would be shorter in winter and on cold days, and, on the basis of the findings of Harrington et al. (2012), (3) that dive clusters would be longer during shorter days (because shorter days in the UK are colder days this contradicts 2). I also predict that single dives may be shallower and longer than cluster dives if they are a mode of travelling rather than hunting, and that the proportions and characteristics of single dives vary between males and females to account for differences in foraging and travelling behaviour. Finally, I expect the last dive of a cluster to have different properties than the other dives within that cluster, reflecting either a hunting success, or a forfeit of prey.

3.2 Materials and methods

Data collection

The dataset used in this study has previously been described in Harrington et al. (2012) building on a subset presented by (Hays, Forman et al. 2007), in a study of the diving ability and behaviour of American mink at the individual dive level. CEFAS G5 TDR (31 x 8 mm; CEFAS Technology Ltd, Lowestoft, UK, (Hays, Forman et al. 2007)) were deployed on 24 free-living American mink on rivers Thames and Cherwell in the Upper Thames valley in Oxfordshire, UK (approximate latitude, longitude: 51.62°N, 1.08°W) between January 2006 and January 2008. Site details are described in Harrington et al. (2012). Mink were caught in wire traps placed on floating rafts secured to the riverbank (Reynolds, Short et al. 2004), anaesthetised (methods in Harrington et al.

2007, Hays et al. 2007) and fitted with collars to which a TDR had been attached (details in Harrington et al. 2012). Animal handling was completed within 10-30 minutes and mink recovered from anaesthesia within 10-25 minutes. 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 injuries due to the collars.

All procedures were carried out under United Kingdom Home Office licences 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 licence WCA/06/4 and Natural England licences NNR/2007/0024, NNR/2007/0022.

Twenty TDRs were retrieved from 16 individual animals (6 males and 10 females), containing temperature and pressure data recorded every five and one second, respectively, for a period of up to seven days. One data-logger failed prematurely and only recorded for two days. Two individuals for which we recorded fewer than 20 dives were excluded from further analysis (Harrington, Hays et al. 2012).

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 centre of Oxford, within 40km of the study sites; ambient temperature was calculated for the deployment period. Dawn and dusk data were taken from timeanddate.com (http://www.timeanddate.com/worldclock/sunrise.html); with settings for Oxford. Day lengths were calculated by subtracting the sunrise time from the sunset time.

Data analysis

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 (precision of TDRs 0.05 m, Hays et al. 2007), as reported in Harrington et al. (2012). A hidden Markov model algorithm was applied in MATLAB 7.8 (The MathWorks™, www.themathworks.com), as described in Bagniewska, Hart et al. (2013). This method identified three behavioural states, where 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; and 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.

Statistical analysis was carried out in R (version 2.13.2, R Development Core Team 2011). For analysis, dives were grouped into clusters – all dives in State 1 – and aquatic foraging sessions (AFS) – all dives in State 1 and 2 (Figure 3.1). Persistence was defined as the length (i.e. the number of consecutive dives) of a cluster or AFS. Since the data were right-skewed, I used the median as the measure of central tendency.

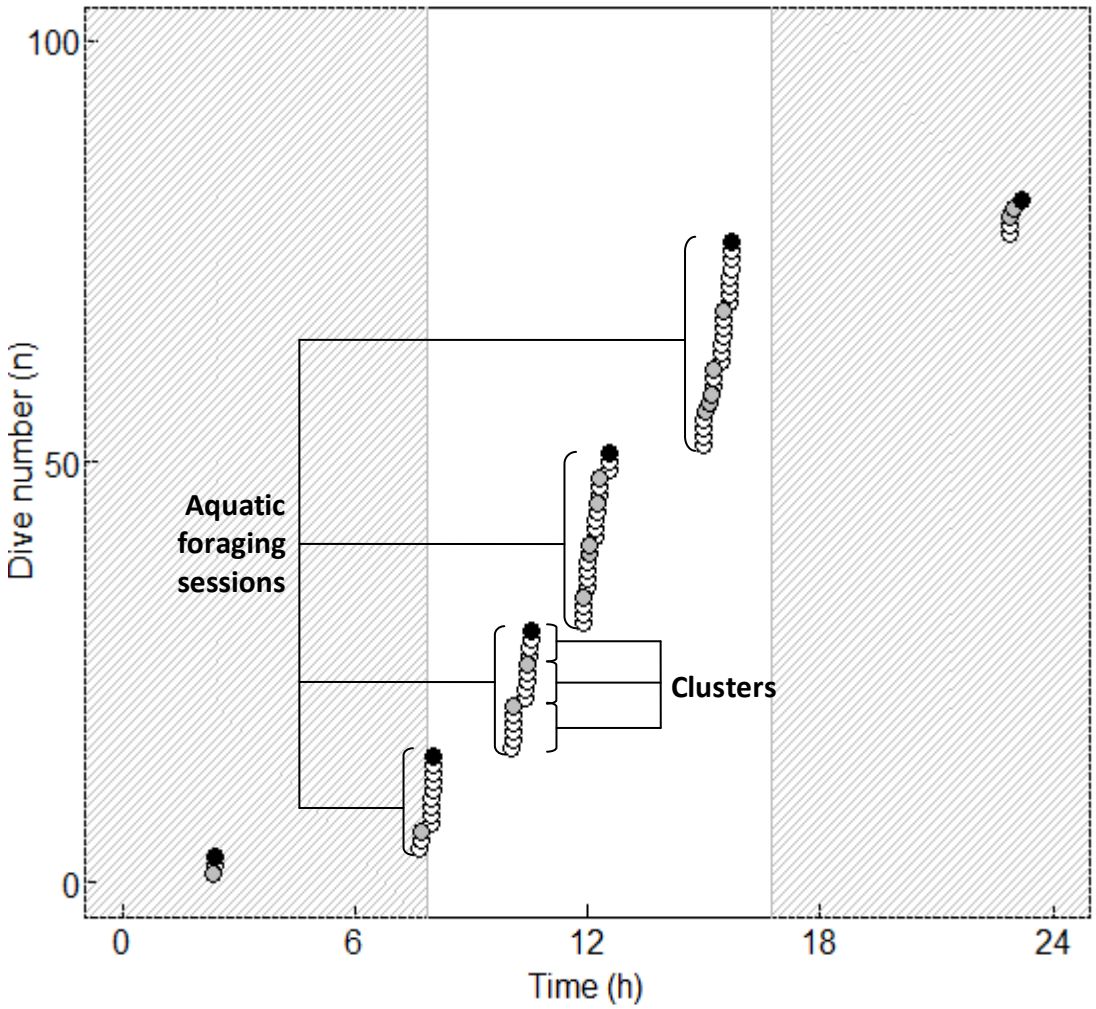

Figure 3.1: Dives of mink 187a (female) from 27 January 2006, illustrating the differences between dive clusters and aquatic foraging sessions. White circles represent dives identified as State 1, grey circles – State 2 and black circles – State 3. Hours of darkness are shown by grey shading.

The relationships between persistence and body mass were investigated using Generalised Linear Models (*glm* and *lme4* functions in R) to, with "individual" included as a random factor to account for multiple datasets from a few individuals where appropriate. Standard residual plots were used to determine the appropriate error structure; due to skewed data, a quasipoisson error distribution with identity link, was used for the effect of body mass on dive cluster length and a Gaussian error (with identity link) to determine the effect of body mass on maximum cluster length. GLMs were also used to examine the relationship between persistence and day length

(default settings of the *lm* function). For examining the relationship between persistence and daylight, all dives were assigned a light category (day, night, dawn or dusk). Other statistical tests are as stated in text. Right-skewed data was log-transformed where necessary for statistical analysis, while proportion data was transformed using arcsine- root transformation. In all tests, $P < 0.05$ was accepted as significant.

3.3 Results

Dive clusters consisted of 2 – 28 dives (grand median = 4, *N* = 633; range of individual medians: 2 – 7.5); AFSs of 2 – 80 dives (grand median = 7, *N* = 299; range of individual medians: 3 – 31 dives). Both dive cluster length and AFS length were extremely variable within individuals (coefficient of variation $[CV]_{clusters}$ = 0.32 – 0.76; CV_{AFS} 0.43 – >1) and differed significantly among individuals ($ANOVA_{cluster}$: $F_{13,3266} = 70.78$, $P < 0.001$; $ANOVA_{AFS}$: $F_{13,285} = 10.57$, $P = < 0.001$). The duration of dive clusters ranged from 2 s to 35.93 minutes (median = 2.083 min; range of individual medians: 46 s – 12.45 min) and AFSs 7 s to 154.40 minutes (grand median = 19.85 min; range of individual medians: 11.3 – 41.19 min). The median length of pauses between dives within a cluster was 17 s, and the individual medians ranged between 8 and 81.06 s (data were very strongly right-skewed, with the maximum pause between dives being 249 s; 95% of data points were < 127 s, 90% < 89 s).

Body mass

Median and maximum dive cluster length, and median and maximum AFS length, were significantly negatively correlated with animal body mass ($maximum_{cluster}$: $F_{1,13} = 13.41$, $P = 0.0352$; $median_{cluster}$: $F_{1,13} = 11.80$, $P = 0.0414$, Figure 3.2A; $maximum_{AFS}$: $F_{1,13} = 34.57$, $P = 0.010$; $median_{AFS}$: $F_{1,13} = 76.31$, $P = 0.0032$; Figure 3.2B).

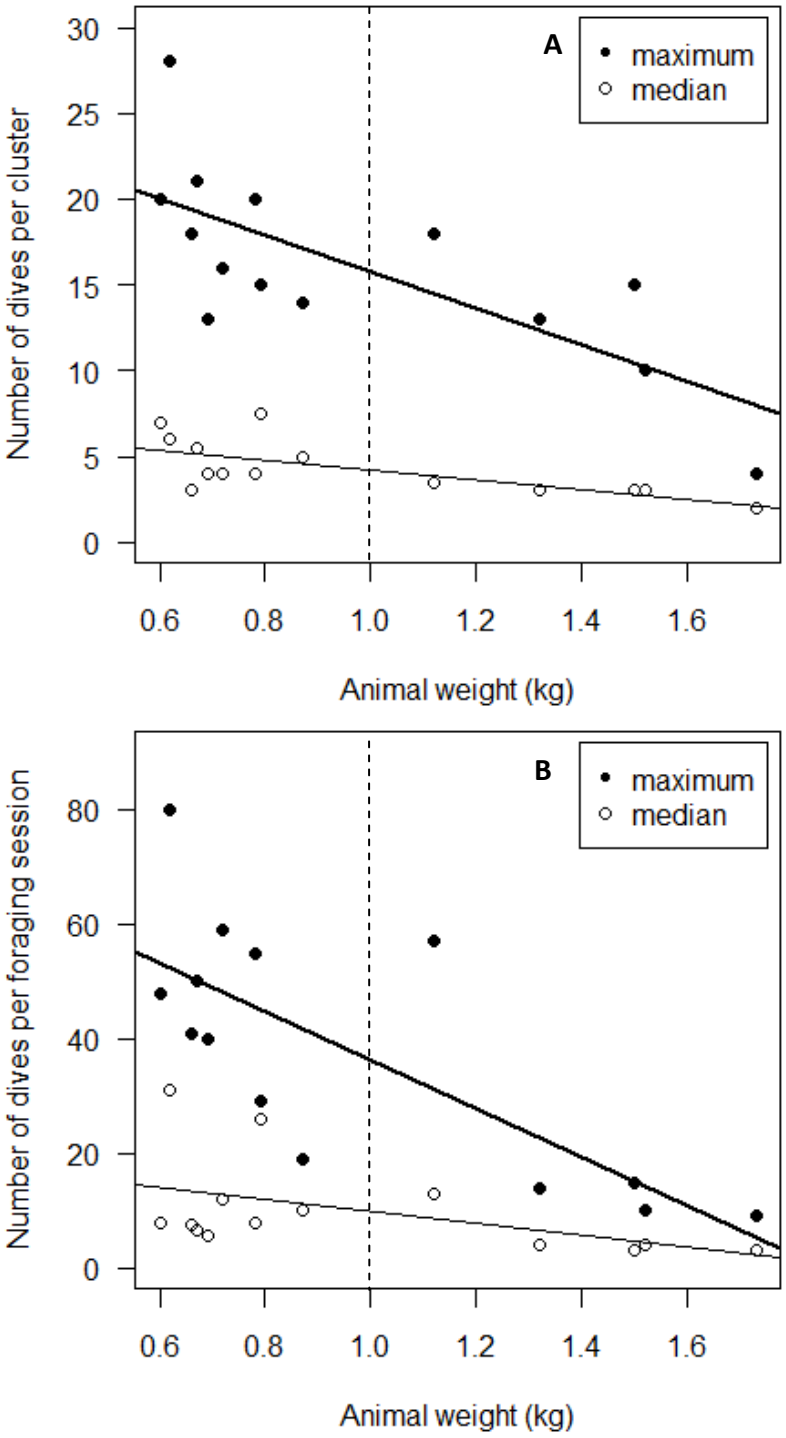

Figure 3.2: (A) The relationship between animal body mass and the length (in dives) of dive clusters; (B) the relationship between body mass and aquatic foraging sessions. In both plots, animals below 1 kg are females, above – males; the weights are separated with the dashed vertical line.

The effect of sex was not significant in any case ($maximum_{cluster}$: $F_{1,1} = 0.67$, $P = 0.473$; $median_{cluster}$: $F_{1,1} = 0.14$, $P = 0.73$; $maximum_{AFS}$: $F_{1,1} = 2.05$, $P = 0.248$; $median_{AFS}$:

$F_{1,1}$ = 0. 353, P = 0.59), and neither were the interaction terms between sex and body mass (maximum$_{cluster}$: $F_{1,1}$ = 0.546, P = 0.81; median$_{cluster}$: $F_{1,1}$ = 0.80, P = 0.66; maximum$_{AFS}$: $F_{1,1}$ = 0.77, P = 0.400; median$_{AFS}$: $F_{1,1}$ = 0.062, P = 0.81).

Ambient temperature

Maximum dive cluster and AFS lengths were not significantly related with ambient temperature (clusters: $F_{1,1}$ = 2.16, P = 0.16; AFS: $F_{1,1}$ = 2.48, P = 0.14), although there was a significant effect of sex (clusters: $F_{1,1}$ = 15.70 P = 0.001; AFS: $F_{1,1}$ = 15.06, P = 0.002). The interaction between sex and temperature was also significant (clusters: $F_{1,1}$ = 6.80, P = 0.021; AFS: $F_{1,1}$ = 4.44, P = 0.05), such that in both cases female persistence was negatively related with ambient temperature; however the relationship for males was not significant – Figure 3.3.

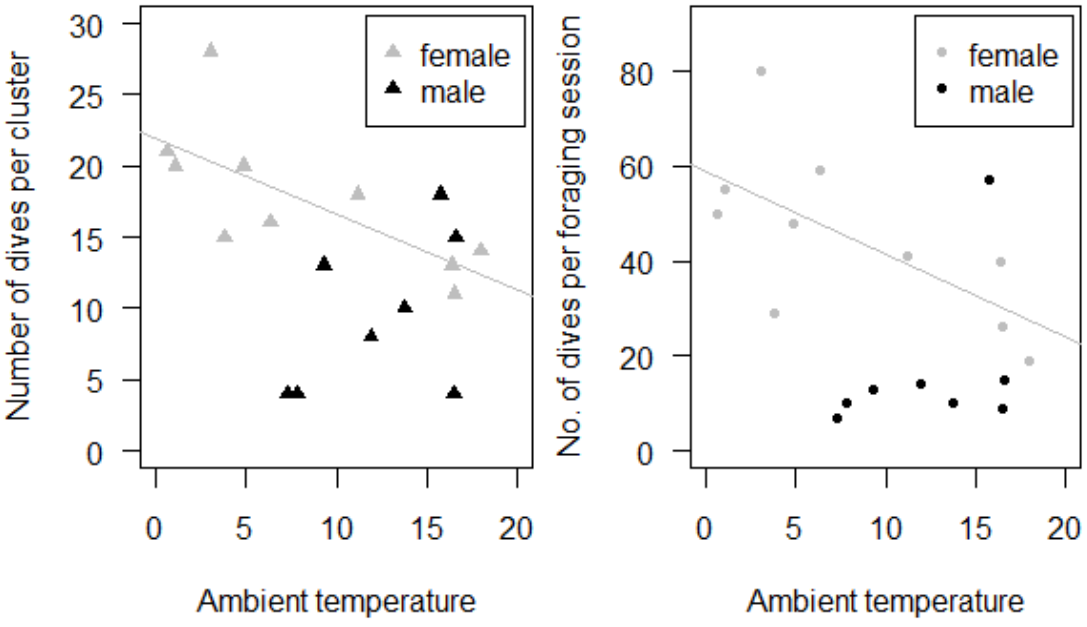

Figure 3.3: The relationship between ambient temperature and maximum number of dives in a cluster (triangles) or aquatic foraging session (circles). The slopes for significant relationships for females are included in the figures (clusters: persistence [no. of dives] = -0.53(ambient temperature)[^{o}C] + 21.93; $F_{1,8}$ = 8.89, R^2[adjusted] = 0.47, P = 0.0175. AFS: persistence [no. of dives] = -1.76 (ambient temperature)[^{o}C] + 59.09; $F_{1,8}$ = 6.28, R^2[adjusted] = 0.37, P = 0.037).

Neither median dive cluster nor AFS lengths were related to ambient temperature (clusters: $F_{1,1}$ = 4.49, P = 0.053; AFS: $F_{1,1}$ = 1.70, P = 0.21), but there was a statistically significant effect of sex for both (clusters: $F_{1,1}$ = 14.30, P = 0.002, AFS: $F_{1,1}$ = 5.00, P = 0.042). The interaction between sex and temperature was not significant for either cluster or AFS length (clusters: $F_{1,1}$ = 1.62, P = 0.22; AFS: $F_{1,1}$ = 1.30, P = 0.31).

The mean number of clusters per day, ranging between 2 and 16.2 (weighted mean = 7.449), was not related to ambient temperature ($F_{1,1}$ = 0.17, P = 0.686).

Daylight

Most dive clusters and AFSs (clusters: 0.98; 626 out of 633 instances; AFS: 0.92; 274 out of 299 instances) occurred within a single light category (clusters: 469 in the day, 119 in the night, 20 during dawn, and 18 during dusk; AFS: 187 in the day, 82 in the night, 5 during dawn). Only 2 occurrences of AFS included both night and day, through dawn. There was no significant relationship between the proportion of dives during the day and day length for either dive clusters ($F_{1,69}$ = 1.01, P = 0.318) or AFS ($F_{1,71}$ = 0.417, P = 0.52).

Day dive clusters were significantly longer than night ones (day: weighted mean of median cluster lengths = 7.43 dives, range = 2-28; night: weighted mean of median cluster lengths = 5.42 dives, range = 2-10; N = 14 individuals) (Wilcoxon rank sum test: W = 44, P = 0.02). In general, males were significantly more nocturnal than females (Wilcoxon rank sum test: W = 7, P = 0.002), with a weighted mean of 41.0% of all dives performed at night (range of means: 4.9% – 68.0%), against a weighted mean of 7.65% for females (range of medians: 0 – 29.7%).

Dive cluster and AFS length (log-transformed) were both negatively correlated with day length (clusters: r = -0.031, $P = 0.004$, $N = 633$; AFS: r = -0.066, $P = 0.0025$, $N = 299$).

Dive types

Even though only 11.6% ($N = 434$) of all dives were single dives, out of deep dives (i.e. those > 1.5 m) 28% were single dives; and out of long dives (i.e. those > 30 s) 22% were single. There was however no difference between dive depth and duration between single dives and those forming a cluster (depth: $W = 103$, $P = 0.84$; duration: $W = 100$, $P = 0.95$). There was a significant effect of sex on proportion of single dives to total number of dives ($F_{1,1} = 14.8$; $P = 0.002$), but the relationship with animal body mass was not significant ($F_{1,1} = 0.004$; $P = 0.63$), and neither was the interaction term between sex and body mass ($F_{1,1} = 0.65$; $P = 0.43$); (model statistics: $F_{3,14} = 5.23$, R^2[adjusted] = 0.43, $P = 0.013$).

The median proportion of single dives was significantly higher for males (weighted mean of medians: 0.26, range: 0.099 – 0.41) than for females (weighted mean of medians: 0.086, range: 0.00 – 0.166) (Wilcoxon rank sum test: $W = 9$, $P = 0.004$). The single dives of males were longer (males: median = 14 s, range = 2 – 144 s; females: median = 12 s, range: 3 – 47.58 s) and deeper (males: median = 0.562 m, range = 0.20 – 2.06 m; females: median = 0.435 m, range = 0.20 – 2.65 m) than those of females – Figure 3.4; with both the effect of sex (duration: $F_{1,1} = 8.27$, $P = 0.004$, depth: $F_{1,1} = 6.74$, $P = 0.01$) and individual (duration: $F_{1,15} = 3.37$, $P < 0.001$, depth: $F_{1,15} = 14.93$, $P < 0.001$) statistically significant. There was no difference, however, between the cluster dives of males and females, in either depth ($W = 51$, $P = 0.36$), or duration ($W = 29$, $P = 0.35$).

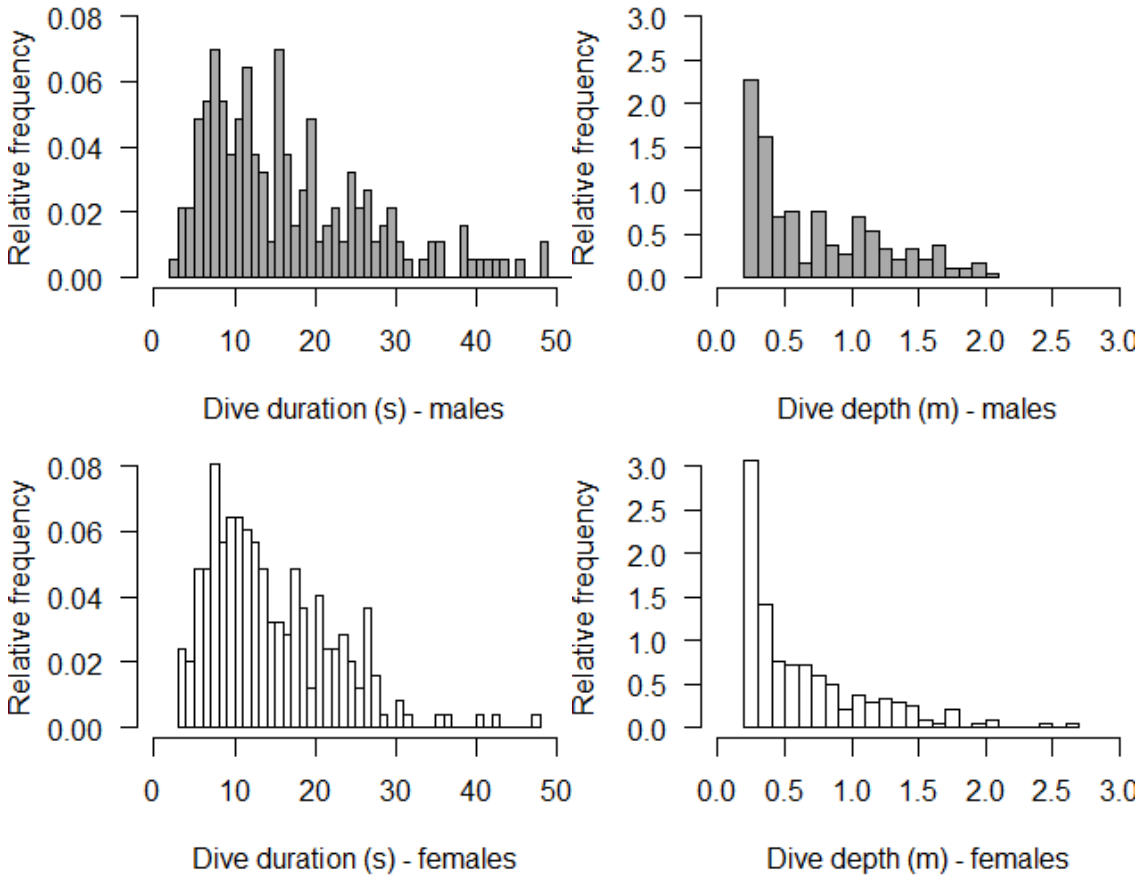

Figure 3.4: Features of single dives of both sexes. One dive of 144 s was performed by a male, but was not included on the histogram because of scaling.

There was no significant relationship between the proportion of single dives and ambient temperature ($F_{1,1}$ = 2.58, P = 0.13). The proportions of single dives were similar during night and day, as well as dawn and dusk (Table 3.1).

Table 3.1: Proportions of dives in each light category.

No. of dives	Light category	Single dives	Cluster dives	% single dives
486	Night	62	424	0.128
105	Dawn	8	97	0.076
82	Dusk	6	76	0.073
3041	Day	358	2683	0.118
3714		**434**	**3280**	**0.395**

Dives lasting more than 30 s only occurred in clusters of 13 dives or less (Figure 3.5B). Both dive depth and dive duration were negatively related to the cluster length

(depth: $F_{1,1}$ = 19.67, P < 0.001; duration: $F_{1,1}$ = 111.96, P < 0.001). The effect of dive type, i.e. whether it is a terminal dive of a cluster or not, was significant (depth: $F_{1,1}$ = 22.31, P < 0.001; duration: $F_{1,1}$ = 8.04, P = 0.04), as was the effect of individual (depth: $F_{1,13}$ = 61.11, P < 0.001; duration: $F_{1,13}$ = 43.63, P < 0.001); however, the interaction terms between cluster length and dive type were not (depth: P = 0.42; duration: P = 0.71). The median terminal dives of clusters ranged between 0.28 and 0.99 m in depth (weighted median: 0.37 m), and from 8 to 22.5 s in duration (weighted median: 11 s). The medians of remaining dives of a cluster ranged between 0.3 and 0.66 m (weighted median: 0.44), and from 8 to 16.44 s in duration (weighted median: 11.50 s).

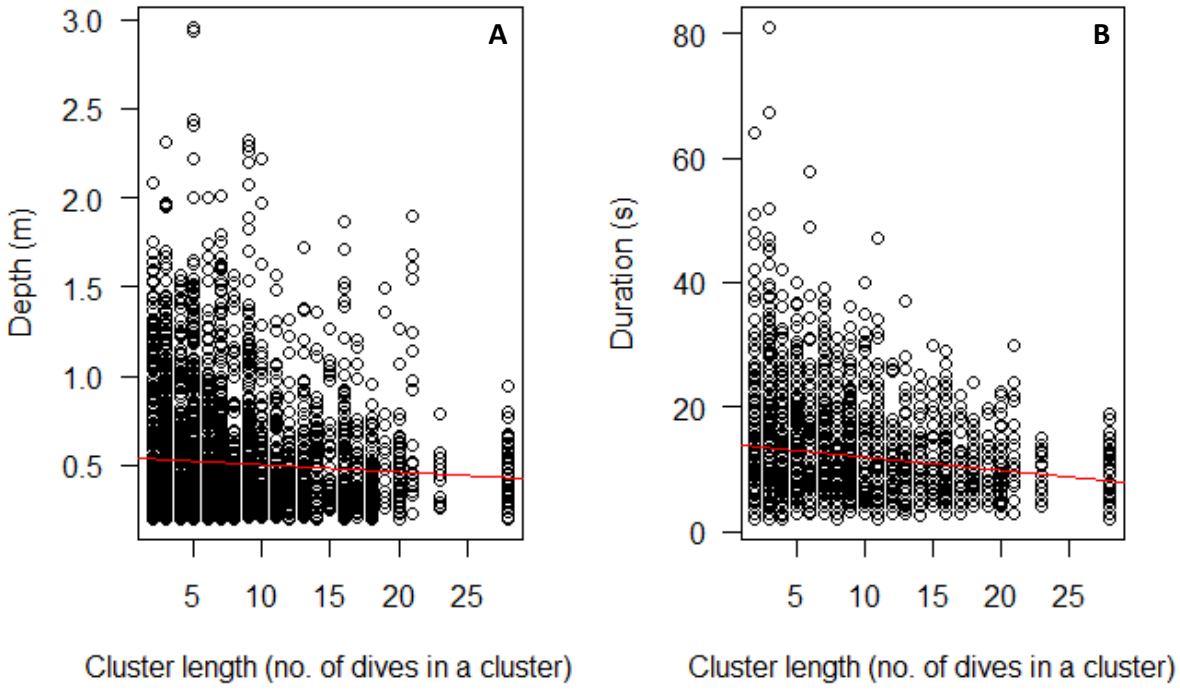

Figure 3.5: The relationship between cluster length and dive parameters – depth (A) and duration (B).

3.4 Discussion

Persistence is an important metric of overall endurance and recovery; an aspect of diving behaviour not measured by just dive depth, duration or even interval between

dives. Sequences and patterns of dives have been studied in fully aquatic foragers (Croxall, Naito et al. 1991; DeLong and Stewart 1991; Williams, Briggs et al. 1992; Monaghan, Walton et al. 1994; Krafft, Lydersen et al. 2002; Hays, Houghton et al. 2004), but not in semi-aquatic ones. Analysing dive persistence can provide information on two aspects of an animal's diving behaviour: its physical diving capabilities, e.g. coping with multiple dives despite increasing heat loss; and its hunting effort in an aquatic environment – both of which are particularly interesting in species that do not rely solely on aquatic environment for food. I analysed the patterns and sequences of dives of the semi-aquatic American mink, classified using Hidden Markov models (Guilford, Roberts et al. 2004; Bagniewska, Hart et al., 2013) into three categories: dive clusters, aquatic foraging sessions, and single dives.

Mink are single-prey loaders, i.e. they leave the water to consume or cache prey (Dunstone 1993). A mink is unlikely to consume a prey item (a fish or crayfish) in the short time between the dives within a cluster (a median of 17 s, and a maximum of 249 s), although caching of prey, or eating something which does not require much processing, like an aquatic insect, could perhaps be possible in that time – however Dunstone (1993) hypothesizes that caching is likely to follow surplus killing. Therefore clusters, i.e. sequences of multiple dives identified through transitional analysis, may reflect the effort needed to capture underwater prey (the number of attempts required to find/catch a fish, before either a fish is successfully captured or the mink gives up).

Series of clusters interspersed with longer intervals form aquatic foraging sessions. These potentially reflect a compromise between the need to get food (repetitive diving) and the need to warm up after multiple dives or to search for a new

resource (leaving the water). Clusters and AFS tend to be short (lasting on average 2 min and 19.85 min respectively), and are very variable both within and among individuals. The maximal values reflect a mink's endurance: a small, energetically-inefficient, semi-aquatic animal would choose to dive 80 times in a single foraging session, with less than 5 min gaps between clusters, during ambient temperatures of 3^{o}C in winter, despite alternative, terrestrial prey (mainly mammals and birds, (Harrington, Harrington et al. 2009)) being available.

Contrary to my predictions based on allometry and thermoregulation, small mink were more persistent than large mink. The differences detected between sexes appeared to be due to overall body size, rather than differences in sex per se, such as the proportionally bigger trophic structures of males (Dayan and Simberloff 1994; Thom, Harrington et al. 2004). Similar results were obtained for both clusters and AFS. Shorter dive clusters and AFS by large animals may reflect greater hunting success (i.e. larger animals might need fewer attempts to catch a fish because they are better at it), or a quicker giving up of pursuit, perhaps to exploit other food sources. Given that females lose heat faster and have higher mass-specific thermoregulatory costs (due to their smaller body size), it is surprising that they not only dive at a higher rate than do males (Harrington et al. 2012) but also perform longer clusters and longer AFSs. I propose several possible explanations of this outcome: lack of choice (perhaps females are less efficient terrestrial hunters than males, and thus have been excluded from land, or have had to shift their niche to a more aquatic one as a result of intraspecific competition); low energetic costs of diving (even though mink would be below their lower critical temperature in water, and, all parameters considered, diving would actually more costly than hunting on land, it might still not be very energetically

expensive); or pay-offs of diving are more than sufficient to cover costs (relative to hunting on land – particularly since fish have a higher energy content than rabbits and small mammals (Ferreras and Macdonald 1999)). However at present I do not have enough information to distinguish between these possibilities.

Our investigation of maximum cluster and AFS length, coupled with those of Harrington et al. (2012), show that while female mink were active in water for the same amount of time in winter and in summer, they were more persistent at colder temperatures (but males were not) – however, this trend was not confirmed by median persistence. The intersexual differences may point to varying hunting efforts and success of males and females, suggesting greater investment of females in aquatic prey in winter, although individual variability may be too high to infer trends for both sexes separately. Greater investment of females in winter implies that the cost of heat loss due to making multiple dives in cold water is outweighed by energetic gain from prey captured, which may indeed be the case since exothermic fish are reported to be easier to catch in cold water (Gerell 1967; Williams 1986), and since the winter fur of mink has greater insulator properties than summer fur (Williams 1986; Korhonen and Niemelä 2002). Mink diet can indeed be more aquatic in winter and more terrestrial in summer (Dunstone and Birks 1987), however the winter increase in the consumption of fish prey could be a regional preference, since studies in Poland (Jędrzejewska, Sidorovich et al. 2001), Spain (Melero, Palazón et al. 2008) and Canada (Hatler 1976) have not confirmed this trend – perhaps due to the possibility of rivers and streams freezing over (Sidorovich and Macdonald 2001). In my dataset, it is also possible that the negative relationship between ambient temperature and persistence is driven by the non-orthogonality of the data, with data collected at lowest temperatures from

females, but not males; the exclusion of the two high-diving winter females did not change the relationship though.

Mink are more persistent at diving during the day than they are during the night. Dunstone and Sinclair observe that mink are relatively poorly adapted for underwater vision (Dunstone and Sinclair 1978), and so it seems advantageous for the animals to make use of as much natural light as possible when hunting underwater. Also, mink may reduce their diving at night to avoid competition with the 7-times-larger, nocturnal otter, *Lutra lutra* (Harrington, Harrington et al. 2009); however, we cannot distinguish between the two hypotheses using this dataset. Male mink were more nocturnal in their diving behaviour than the females. Harrington et al. (Harrington, Harrington et al. 2009) suggested that male mink may be less affected by competition with the otter, thus more likely to be active during the night.

Day and night dives might also have different functions, e.g. foraging during the day, and travelling at night (where visual acuity is not as crucial as during hunting). Travelling dives could also assume a clustered structure, since surface swimming may be interrupted by periods of underwater swimming to reduce drag or to serve as an evasive manoeuvre (Williams 1983). Male mink could use rivers and streams for travelling more frequently than females, especially since in some areas males have larger home ranges (Melero, Palazon et al. 2008), and have been reported to spend more time on locomotion than females (Melero, Palazón et al. 2011).

In line with my predictions, cluster length was inversely related to day length, i.e. clusters are longer on short (and colder – since day length and ambient temperature are confounded variables at our latitude) days. Mink – particularly females – are found to dive equally frequently throughout the year (Harrington, Hays

et al. 2012), and do not appear to change diving strategies on the basis of temperature (Chapter 2). This means that at a constant dive effort (equal number of dives), they have lower persistence in summer than in winter (longer cluster lengths in winter), reflecting either lower success in winter, or shorter time to giving up in summer. However, the number of clusters per day was not related to ambient temperature, which could mean that the potential success or failure (since I predict that fish are caught at the end of a cluster) would not differ between seasons. There was also no relationship between proportion of dives made during the day, and day length, for either clusters or AFS, which implies that mink do not switch their strategy from diurnal to nocturnal (or vice-versa) seasonally.

Dunstone describes mink as a "hunter" species that aims to strike a balance between the intense prey location effort of the "searchers" and the prey-handling effort of the pursuers, as it has to search actively for prey and pursue it (Dunstone 1978). Captive mink have been observed either to locate prey from a vantage point outside the water, and then dive to pursue it ("dive-chase"), or to search for it whilst in the water ("search-chases") (Dunstone and O'Connor 1979). In a scenario where a captive mink would perform multiple "dive-chases", its "giving up time" (in this case equivalent to dive duration) was negatively related to the number of attempts (equivalent to cluster length) (Dunstone and O'Connor 1979). In accordance with these observations in a laboratory, I noted a negative relationship between cluster length and both dive duration and depth.

In my study, the "dive-chases" could be equivalent to single dives, particularly since I found a higher than normal proportion of single dives among the deepest and longest dives, and Dunstone and O'Connor report "dive-chases" to be longer than

"search-chases" (Dunstone and O'Connor 1979). Males perform more single dives than females; male single dives are also longer and deeper than those of females. Other potential explanations of the biological significance of single dives are: (1) single hunting dives reflect a specific foraging strategy, for instance predation on crayfish, which require deeper dives (to the bottom of the river), but may only require a single dive to successfully capture a crayfish or (2) single dives indicate a travelling dive (especially since submerged swimming reduces overall drag (Fish 1993) and can reduce the energy costs by 7- to 10-fold compared with surface swimming (Williams 1983)).

The terminal dive of a cluster may have different properties than the other dives within a cluster, since it is the one that reflects either a successful hunt or giving up. Long and deep terminal dives may reflect a successful prey catch and struggle if a "dive-chase" strategy is used; or else noticing a fish and pursuing it (either successfully or not), as in the case of a "search-chase" strategy (Dunstone 1978). In my study, terminal dives tended to be longer and deeper than the other ones in a cluster, although the differences might not have biological significance, since they are very small. Yet, we cannot differentiate between a successful hunt and a forfeit, and also my sample of terminal dives includes both successful and unsuccessful ones, and therefore may obscure differences in successful terminal dives.

While the dives of fully aquatic animals can easily be grouped into foraging trips, semi-aquatic animals are able to make quick transitions between environments and different foraging modes. Because of this, rather than classifying dives into "long and short bouts" (Boyd, Arnould et al. 1994), I used transitional analysis to sort dives into clusters and aquatic foraging sessions, which allow the possibility of an environmental change. Similarly, grouping into "deep and shallow bouts" (Boyd,

Arnould et al. 1994) would not be biologically meaningful for animals that are constrained in their diving by river depth.

Conclusions

Multiple dives in a cluster or a foraging sequence reflect the effort needed to capture aquatic prey. The high energetic costs of multiple dives (particularly in cold water), and the considerable effort that mink expend diving (up to 28 dives in a cluster, over 36 min, or up to 80 dives per AFS, over 154 min) suggest that mink are successful aquatic predators and that the energetic costs of diving are outweighed by the gains from the prey. Male and female mink appear to have different diving patterns, which may reflect different foraging strategies, or could be a result of high individual variation, particularly over short data-collection windows. Mink appear to maximise daylight diving, as they might be visual predators when hunting underwater (Dunstone 1993), or may avoid nocturnal otters. Despite not being as well adapted to diving as other semi-aquatic animals (otters, platypuses), mink do not appear to be affected by ambient temperature in their diving behaviour. The properties and proportions of single dives differ between sexes; these, together with terminal dives, may potentially be useful in describing intrasexual foraging differences, however we are currently unable to tell whether dives ended in a hunting success or not. Further examination of dive shapes and orders within a sequence (according to, for instance, depth, duration, or logger temperature records) may shed more light on the exact strategies of searching or pursuit of prey.

Chapter 4

Using temperature records to classify behaviour in small animals

Abstract

Recent development and miniaturisation of bio-logging equipment mean that bio-loggers can now be deployed on a range of species, even on animals weighing <1kg. However, due to the remote nature of bio-logging studies, it is often impossible to validate the results through direct observation. Miniaturised Time-Depth Recorders (TDRs), one of the smallest data-loggers available, have been extensively used for researching dive profiles on the basis of depth records. Still, the potential of temperature records for measuring activity patterns has not been fully explored. I observed two captive male American mink (*Neovison vison*) equipped with TDR collars in order to validate and develop methods for identifying activity patterns based on rapid temperature changes. The ventral attachment of TDRs allowed the differentiations of postures and inference of periods of activity and inactivity. Coupling with temperature information from periods of dive data (from depth or fast-log wetness sensors) adds a division of activity into terrestrial and aquatic. A software has been developed to generate activity categories on the basis of rates of temperature changes. The generated and observed activity categories showed a considerable overlap (>87%) within the "inactivity" category, suggesting that the program developed for generating them is a valid method for determining when the animal is at rest. This is, to my knowledge, the first study to use TDRs to identify activity patterns of a semi-aquatic mammal.

4.1 Introduction

Measuring the activity patterns of small animals has thus far been done principally through radio-tracking (Lodé 1995; Alterio and Moller 1997; Zalewski 2001; Marcelli,

Fusillo et al. 2003) or direct observations (Zuberogoitia, Zabala et al. 2006); these methods are labour-intensive, and produce only several meaningful data points per day. Recently developed multi-channel data-loggers, such as the "daily diary" (Wilson, Shepard et al. 2008) or tri-axial accelerometers (Watanabe, Izawa et al. 2005), allow a very detailed insight into behavioural ecology of an animal; however, they are still too large to be deployed on a small-bodied species or require a lot of calibration for successful behavioural analysis. Small GPS (Reid and Harrison 2010) and light-based loggers may be inappropriate for species which are active at night or spend time underground or under plant cover (Tremblay, Cherel et al. 2003).

Miniaturised Time-Depth Recorders (TDRs) are one of the smallest data-loggers available. While they have been extensively used for researching dive profiles (Williams, Briggs et al. 1992; Croxall, Briggs et al. 1993), they contain additional information such as temperature which has not been widely used to infer behaviour. Activity cycles are established on the basis of underwater behaviour, recorded via the TDR's depth sensor. This is a good measure of activity in predominately aquatic animals such as pinnipeds or cetaceans (Baird, Ligon et al. 2001; Lea, Hindell et al. 2002). However, diving behaviour only comprises a fraction of the activity pattern of semi-aquatic species that may forage on both aquatic and terrestrial prey. In order to fully understand their diel cycle we have to take into account periods of both aquatic and terrestrial activity.

We are able to infer animal behaviour on the basis of differing body postures. If TDRs are fitted on collars ventrally, resting underneath an animal's chin, the temperature changes resultant from differing body postures can be recorded by the data-logger. When a small mammal such as a mustelid is inactive, it curls up and its

body heat warms the TDR, in turn raising the logged temperature. Once the animal uncurls, the TDR's temperature sensor is exposed to ambient temperature, and logs lower values.

I used the American mink (*Neovison vison*) as a model species to investigate the possibility of establishing periods of terrestrial inactivity and activity using temperature data. This animal is a very adaptable predator, which makes use of both terrestrial and aquatic prey (Dunstone 1993). The relative importance of aquatic and terrestrial foraging and the behavioural plasticity in these modes of foraging is therefore key to understanding mink ecology. The TDR's depth record ensures a proper identification of diving periods; its temperature record may be useful in discriminating between different types of terrestrial activity. In my study I compared direct behavioural observation of captive mink with numerical data extracted from the TDR and processed to obtain activity categories and validate the accuracy of assigning different behaviours based on data-logger output. I was also able to compare TDR outputs with ambient temperatures to check the influence of mink body heat on TDR temperature records.

4.2 Materials and methods

I conducted two validation studies, one in winter (February-March) and one in summer (August) of 2009. The winter study was carried out at Derek Gow Water Vole Consultancy in Devon, UK; the summer one took place at Wildwood Trust in Kent, UK.

Animals

In each study I have used a single wild-caught male mink. The animal used in the winter study was captured in Devon in July 2008; it was housed in an unheated indoor wire mesh enclosure (dimensions: 1.8 m x 1.8 m x 1.8 m), lined with woodchips and

equipped with a wooden nest box and a water tank (1.5 m x 0.5 m x 0.5 m). The animal used in the summer study was trapped in Stodmarsh, Kent, in March 2009; it was housed in a naturalistic outdoor enclosure (approximate area: 5 m x 10 m), with a wooden nest box and a pond (2 m x 1 m x 1 m). Food (dead chicks and crayfish) was provided during the observation sessions, placed either near, or in the water to prompt diving behaviour.

Equipment

CEFAS G5 (CEFAS Technology Ltd, Lowestoft, UK, (Hays, Forman et al. 2007)) fast-logging Time-Depth Recorders were deployed on study animals, set to record depth and temperature every second for a period of 7 days. In the fast-log setting the tags increased the recording frequency to 0.1 s. The dive threshold was set to 0.3 m. The TDRs were encased in plastic tubing, attached to commercially-purchased reflective cat collars, and mounted on animals in accordance with the procedures described by Harrington, Hays et al. (2012). Animals were anaesthetised by qualified personnel under UK Home Office License, using isoflurane (IsoFlo: Schering-Plough Animal Health, Welwy Garden City, Herefordshire, UK) delivered via a vapouriser attached to a portable oxygen cylinder (Mathews, Honess et al. 2002), induced in a wooden box (0.15 m x 0.15 m x 0.48 m) with a Perspex window (Yamaguchi, Strachan et al. 2002) and maintained, during handling, via a face mask. All procedures were carried out under United Kingdom Home Office licences PPL30/1826, PIL30/8103 and were approved by Oxford University Zoology Department Ethical Review Committee. Three Tinytag Plus temperature loggers (Gemini Data Loggers (UK) Ltd, Chichester, UK) placed in the enclosure recorded air, water and nest box temperatures. The tags were set to take measurements every 30 s (water and nest box) or every 1 min (air).

Observation schedule

Study animals were observed for 12 h per day over the entire deployment period. In the winter session the observation was split into two periods of 6 h each (0500-1100 hrs and 1700-2300 hrs); in the summer session it was split into an 8 h and a 4 h session (1730-0130 hrs and 0330-0730 hrs). These periods were established after two days of preliminary observations resulting in an actogram assessment. Night time observation was done with the help of two small stationary flashlights with a constant beam (outdoor enclosure), and night vision goggles (Night Vision Scope Helios-01) in the indoor enclosure. I used focal animal sampling (Altmann 1974); the state changes (animal in nest box – inactive, animal out of the nest box – terrestrial activity, animal in water – aquatic activity) were timed using a stopwatch synchronised with the TDR, and noted on a scoring chart.

Analytical methods

Data in this study were treated in the following stages:

1. Temperature, depth and fast-log data were extracted from the TDR and coupled with the three behavioural categories from the observational study.
2. Ambient temperatures were extracted using TinyTag Explorer 4.6 (Gemini Data Loggers (UK) Ltd, Chichester, UK), and compared with TDR temperatures.
3. Activity categories were generated from raw data using MatLab code (David Righton, CEFAS Technology Ltd, Lowestoft, UK; Appendix 1). The programme assigns a “water” category to all points with a fast-log entry, or pressure data in the case of regular loggers. On the basis of the temperatures of the “water” category I demarcated a threshold which encompasses 95% of water temperatures. I then identified periods where the temperature would increase or

decrease rapidly over time, i.e. >0.01°C/s; indicating changes between states. Finally, I put a "cap" threshold for the "inactive" category, after establishing a temperature which is above 90% of the "inactive" records, as it is unlikely that a mink with a TDR temperature of >37°C is active, although slight dips in the temperature (in the range of ~35-39°C) might reflect small postural changes.

4. Activity categories generated by the MatLab analysis were compared with the categories from the observational study and the percentage of matches was calculated. The comparison was done using proportions because of the uneven sample sizes for the three activity categories.

Graphical representation of temperature and pressure data was carried out in MULTITRACE and R 2.15.0. Observational data was analysed with Microsoft Excel (versions 2003 and 2007) and R 2.15.0.

4.3 Results

Eighty-four hours of direct behavioural observations were obtained during the winter study compared to 60 hours in the summer study, where premature collar shedding resulted in two days' loss of data. Data were corrected to give "inactive" category only if the animal has spent 20 or more minutes in the nest box, since in many cases the mink would go into the nest box only to emerge several minutes later.

Table 4.1: Behavioural observations from both validation studies. The shortest terrestrial activity durations account for the times between diving. Temperatures are measured in °C.

Study	Category	No. of instances	Shortest duration	Longest duration	Total duration	Min. temp.	Mean temp.	Max. temp.
Winter	Inactive	35	00:24:19	06:00:00	68:22:58	13.06	34.75	38.39
	Terrestrial	120	00:00:01	04:41:09	15:24:50	8.63	23.11	37.83
	Aquatic	94	00:00:01	00:00:27	00:04:09	9.61	25.52	36.72
Summer	Inactive	23	00:21:13	04:00:00	41:16:52	21.41	31.50	37.55
	Terrestrial	38	00:00:03	03:11:45	14:38:45	19.38	25.86	36.91
	Aquatic	22	00:00:02	00:00:21	00:04:23	19.58	23.40	31.08

TDR temperature record was split into behavioural categories obtained from observational data, and each category was examined separately (Table 4.1, Figure 4.1).

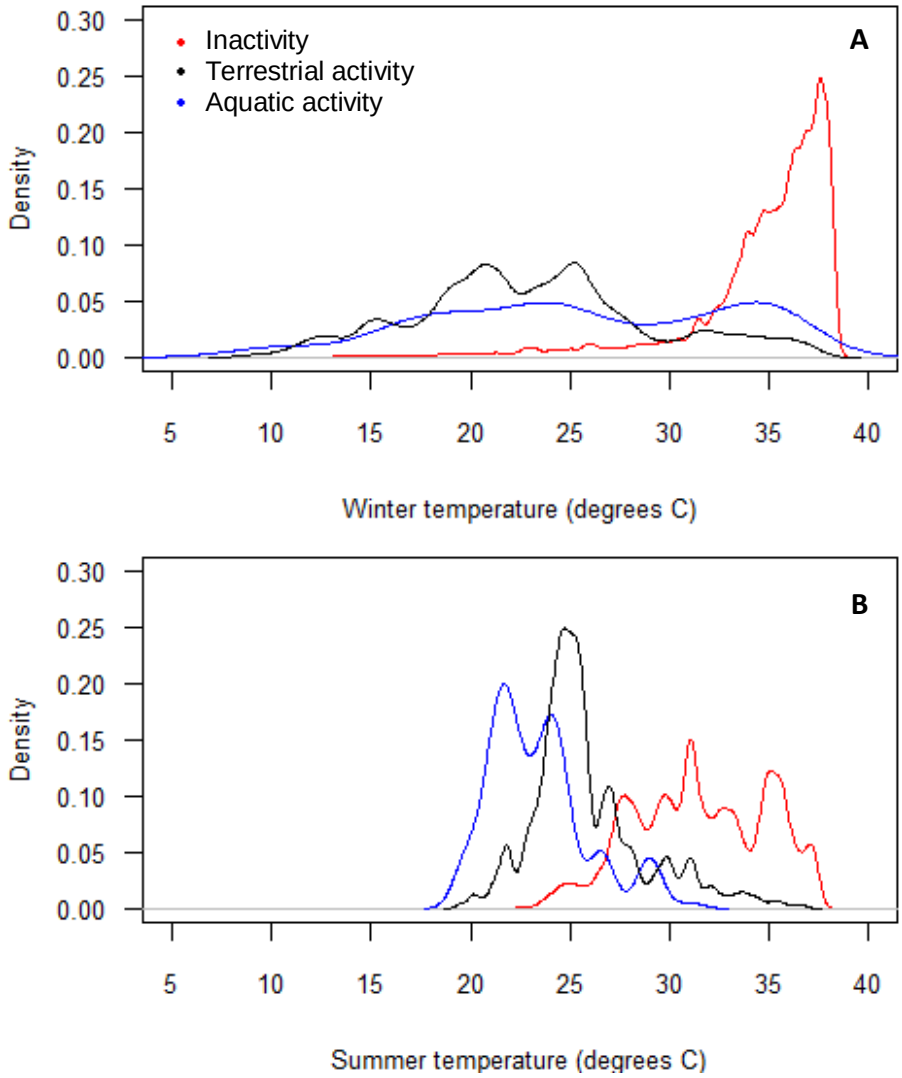

Figure 4.1: Density plots of temperatures from different behavioural categories throughout the winter (A) and summer (B) studies.

TDR temperature profiles from both animals, from the entire length of both studies, are overlaid with ambient temperature profiles to show the difference caused by mink body heat (Figure 4.2). The overall difference between TDR and ambient temperatures ranged between 2.14°C and 33.17°C in winter (inactivity: mean = 27.97, range = 6.64 - 32.70; terrestrial activity: mean = 15.76, range: 2.14 - 33.17; aquatic

activity: mean = 17.92, range = 2.37 – 31.28), and between 2.49°C and 17.55°C in summer (inactivity: mean = 10.53, range = 2.27 - 17.55; terrestrial activity: mean = 9.37, range = 2.48 - 18.73; aquatic activity: mean = 6.55, range = 2.82 - 14.27).

Fast-log temperatures

I obtained a total of 280 fast-log records in winter and 256 in summer. Fast-log temperatures ranged between 13.98 and 34.03°C in winter (mean = 21.96°C, median = 19.92°C, *N* = 280 records), and 19.72 and 29°C in summer (mean = 23.03°C, median = 22.86°C, *N* = 256). At the same time, water temperature throughout the study averaged at 7.59°C in winter and 16.85°C in summer.

Comparison of generated and observed activity categories

Generated data was compared to observational data by noting the number of matching activity categories for both (illustrated in Figures 4.3, 4.4). The percentages of matched pairs were – in winter: 84% for both terrestrial activity and inactivity, and 0.9% for aquatic activity; and in summer: 90% for terrestrial activity, 53% for inactivity, and 20% for aquatic activity, depicted in Fig. 4.5. However, when each observation period was treated as a separate dataset when running the code, the results were: in winter: 58% for terrestrial activity, 93% for inactivity, and 21% for aquatic activity; and in summer: 53% for terrestrial activity, 87% for inactivity, and 75% for aquatic activity. The discrepancy in the matching of aquatic activity between the two analytical methods stems from the fact that periods of aquatic behaviour were only a few seconds long, and thus it was not possible to flawlessly overlay the observed and calculated dataset as a whole. Treating each observation period as a separate dataset allowed a somewhat better temporal overlay of observed and calculated data.

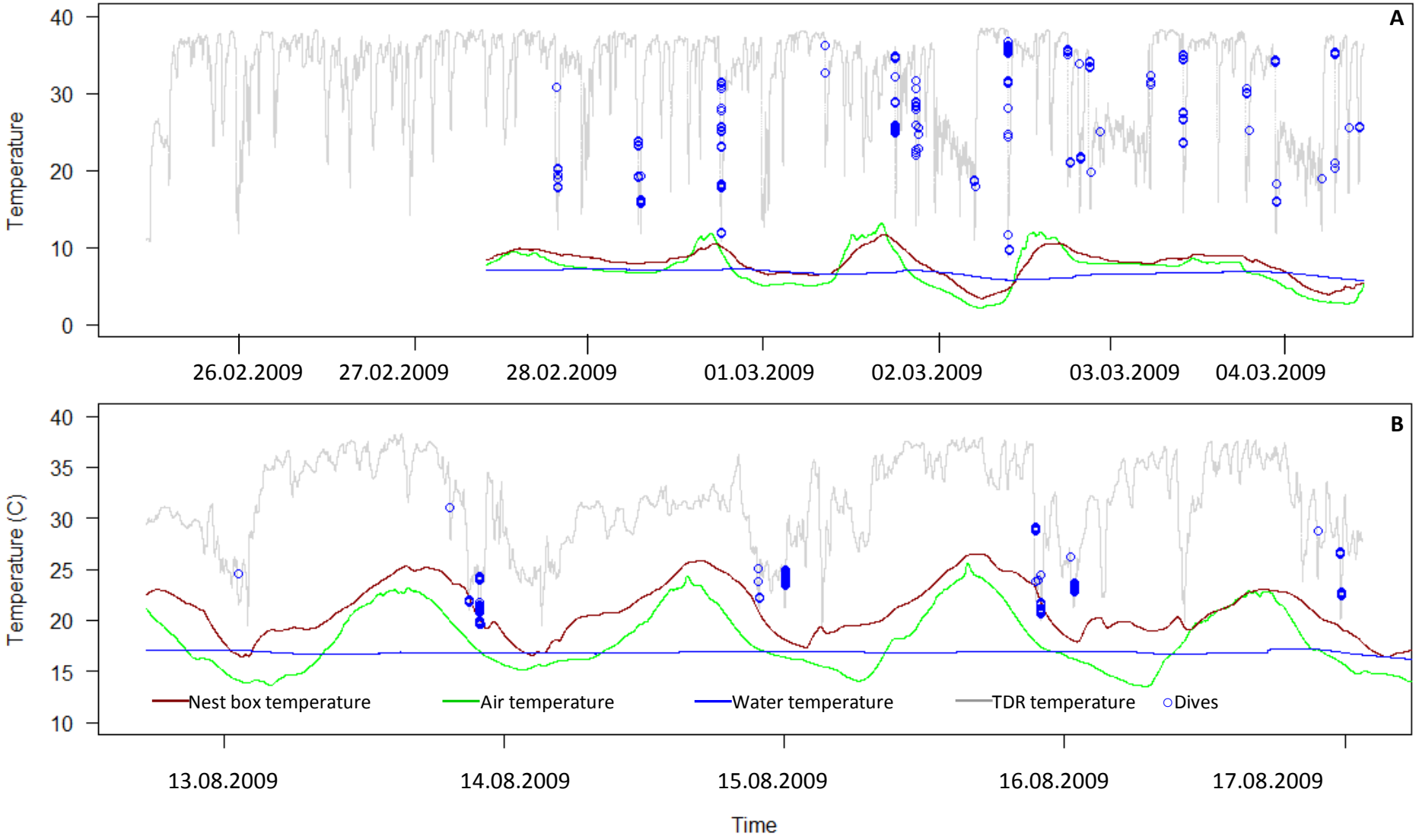

Figure 4.2: TDR temperature profiles from winter (A) and summer (B) studies (dive data marked in circles) in relation to ambient temperatures.

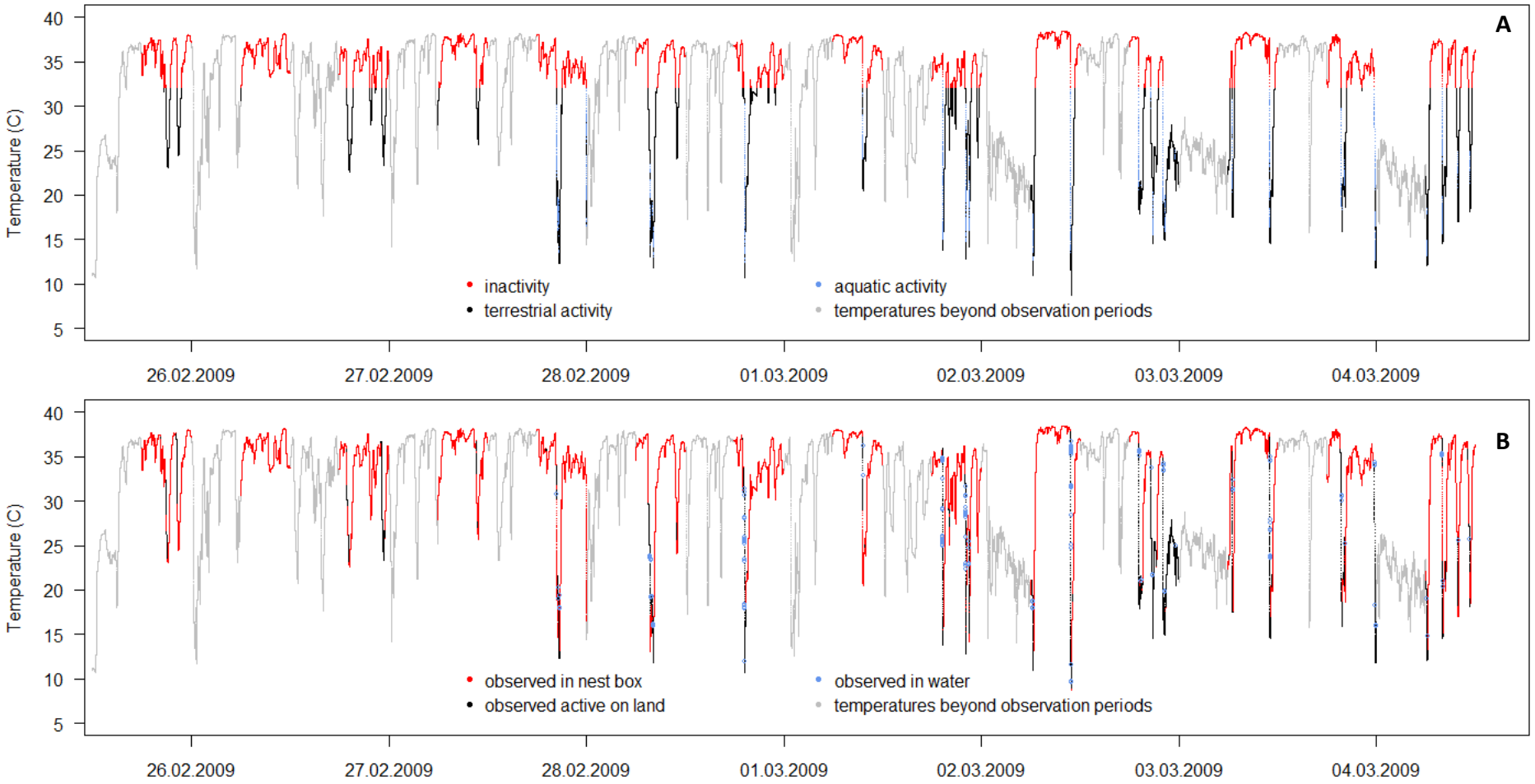

Figure 4.3: TDR temperature profiles from the winter study. Calculated categories are presented in (A), observed – in (B).

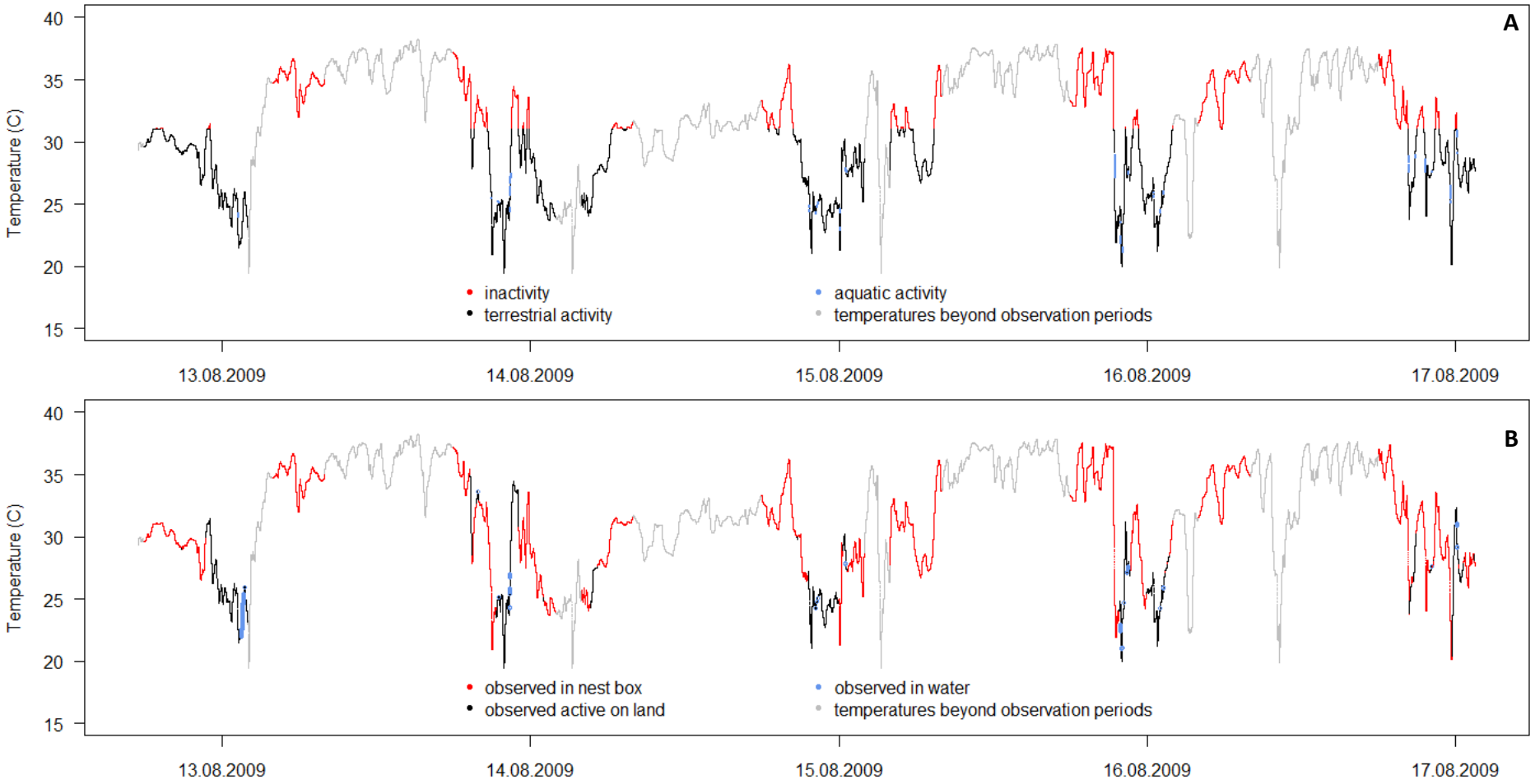

Figure 4.4: TDR temperature profiles from the summer study. Calculated categories are presented in (A), observed – in (B).

Most of the mismatches in the "terrestrial activity" category were due to the observed "terrestrial activity" being paired with generated "inactivity" (98% in summer, 99% in winter). And vice versa, most of the mismatches in "inactivity" category were due to pairings of observed "inactivity" with generated "terrestrial activity" (99% in summer, 97% in winter). Most "aquatic activity" mismatches were due to pairings with "terrestrial activity" (87% in summer, 83% in winter).

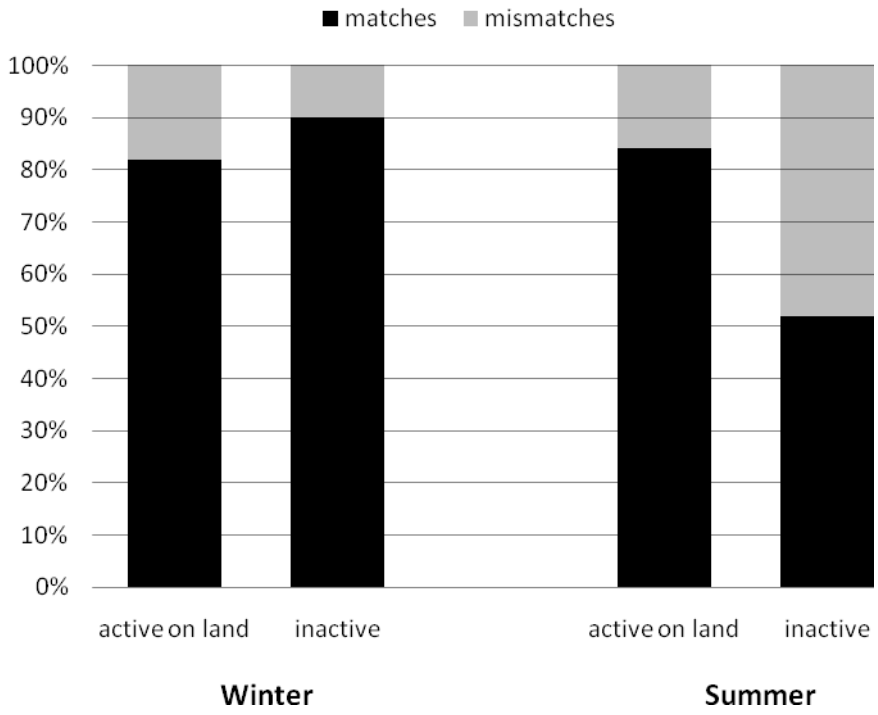

Figure 4.5: The mean proportions of matched pairs between observed and generated activity categories.

4.4 Discussion

The results obtained throughout the two studies have confirmed the prediction that a Time-Depth Recorder placed ventrally on a mink collar records highest temperatures when the animal is at rest. This allows inactivity to be excluded from other behaviours, with an exclusion probability of 87-93%. Depth data from TDR allow aquatic activity to

be identified, so terrestrial activity could be defined by exclusion; i.e.: behaviour that is not identified as inactive terrestrial or active in water.

The proportion of matches of terrestrial activity may be low due to the mismatches with the inactivity category. When the mink was inside the nestbox, it was classified as "inactive" by the observer, but the assigned calculated values were "active". Rather than being a calculation mistake, it is a flaw of the procedure, since a mink could well be active in the nestbox, out of the observer's sight. In the wild, mink could also be active within the nest, for instance eating or caching prey, as reported by Dunstone and Birks (Dunstone and Birks 1985). Feral mink in the UK tend to inhabit rabbit warrens (Yamaguchi, Rushton et al. 2003), which are likely to be better insulated than free-standing wooden nest boxes, and so they perhaps maintain a higher temperature than the outside environment.

Even though there was an overlap between them, the "inactivity" and "terrestrial activity" behavioural categories did show a difference in recorded temperatures. In winter, the temperatures of the "aquatic activity" were spread along a large spectrum, overlapping with both other categories – this is probably due to the fact that the mink spent proportionally less time active outside the nest box during the winter, which did not allow the TDR to cool properly before it was immersed in the water.

Fast-log data did not produce continuous dive profiles in my studies, as the mink either dived for less than 0.4 s, or it did not exceed the required depth threshold. During the winter study the mink exhibited head-dipping behaviour (as described by Dunstone, 1993) – in such cases the data-logger got wet, but did not record dives. Winter fast-log data have a wider range in temperature than summer ones, again

probably due to the mink entering the water immediately after coming out of its net box.

As expected, mink body heat had an effect on the data-logger, with highest differences recorded in winter between the TDR and nest box temperatures (due to overall lower winter temperatures and better shielding of the TDR from the cold during mink resting periods). The smallest temperature difference was between the TDR and the aquatic activity in the summer, probably due to the fact that wet fur did not provide sufficient protection of the TDR from the ambient temperatures, and that the mink spent more time outside in summer, rather than returning straight to the nest box like in winter.

The generated and observed activity categories showed a considerable overlap (>87%) within the "inactivity" category, suggesting that the program used for generating them is a valid method for determining when the animal is at rest. On the other hand, determining aquatic activity solely on the basis of temperature profiles is not reliable (accuracy between 21 and 75%). This is presumably because the water trapped in the animal's fur cools the TDR for a few seconds, or tens of seconds, after emergence from water. Still, aquatic activity is reliably measured predominantly by depth sensors (and fast-log sensors, particularly when examining swimming behaviour as opposed to diving), and thus there is no need to rely on temperature for this category.

Conclusion

The temperature method can be used for estimating the activity patterns of animals with a body temperature different from ambient temperature, and which show marked postural changes during different behaviours. Here I tested a ventral

attachment on a collar, however other attachment methods and places could potentially be useful for determining postural changes of other species, e.g. under a wing for birds.

Chapter 5

Novel use of time-depth recorders to describe activity patterns of generalist mammals

Abstract

Being able to describe activity patterns of individual animals is a prerequisite to investigating, inter alia, their foraging strategies, and is fundamental to understanding the species' ecological requirements, the trade-offs it faces, as well as how it is affected by anthropogenic influences on the environment. Activity patterns, particularly of generalist foragers, may be very complex and variable, and exploring this variation requires a method that can reliably and accurately identify different key activities, and precisely track switches between activity types over time; this can be challenging particularly for animals making quick transitions between habitats. I used Time-Depth Recorders (TDRs) deployed on free-living American mink (*Neovison vison*) in lowland England to show how rapid TDR temperature changes coupled with depth data can be used to infer activity patterns of semi-aquatic, generalist mammals. I applied this approach to test the hypothesis that mink exhibit intersexual niche differentiation. I found that terrestrial activity of mink was positively related to ambient temperature (across both sexes), as was the aquatic activity of males. However the aquatic activity of females did not change with temperature, and was more diurnal than that of males. There was considerable variability between sexes and individuals. Activity results were similar to those of obtained by other methods. This method will be more generally applicable to animals with a marked temperature difference between body temperature and ambient temperature, and where different activities lead to different body temperatures that can be captured by TDR. In summary I demonstrated a simple methodology using commercially available equipment and a novel analytical approach for analysing activity patterns. The same

technique can be transferred to other data types and used to analyse data from other species which were thus far regarded as too elusive or too variable to study.

5.1 Introduction

Being able to describe activity patterns of individual animals is a prerequisite to investigating, inter alia, their foraging strategies, and is fundamental to understanding the species' ecological requirements, the trade-offs it faces, as well as how it is affected by anthropogenic influences on the environment. Foraging strategies of generalists (i.e. those, which, as a species, have a broad food niche, (Sacks and Neale 2002)), are complex because they can switch between multiple resource types, and depend on a range of factors such as prey availability (Harcourt, Bradshaw et al. 2002; Watanuki, Ishikawa et al. 2004), environmental conditions (Bergman 1988; Scott, Clegg et al. 2003), population densities (Schindler, Hodgson et al. 1997), and body size (Gathmann and Tscharntke 2002; Watanuki, Ishikawa et al. 2004; Janson and Boinski 2005). Further, in many cases, different individual specialisations contribute to the intrapopulation variation (Bolnick, Svanbäck et al. 2003). At least some generalist populations consist of individual specialists (Sidorovich, Macdonald et al. 2001; Bolnick, Svanbäck et al. 2003; Woo, Elliott et al. 2008), whose foraging preferences may be reflected by varying activity patterns. In short, variation in activity patterns may occur among populations, temporally within a population, between the sexes or among animals of different age, as well as among individuals.

Exploring this variation requires a method that can reliably and accurately identify different key activities, and precisely track switches between activity types over time. Describing activity patterns is especially difficult for animals that make quick

transitions between aquatic and terrestrial (Harrington, Hays et al. 2012, Bagniewska, Hart et al., 2013), ice (Mitani, Watanabe et al. 2004), or over- and underground habitats (Shepard, Wilson et al. 2008). Methods able to provide consistent and continuous measurements between these different environments have been lacking.

Where habitat patches are small or narrow, it is difficult to identify which habitat a tracked animal is in using telemetry (GPS or VHF); GPS is also inaccurate in water (Quaglietta, Martins et al. 2011), underground (Blackie 2010), or beneath dense canopy (Hansen and Riggs 2008; Frair, Fieberg et al. 2010). Direct observations, especially of elusive species, are not always possible (and may suffer similar habitat-specific biases), observer presence may influence animal behaviour and equipment such as the Daily Diary (Wilson, Shepard et al. 2007), while potentially informative, is currently too big to be deployed on small-bodied animals. Similarly, tri-axial accelerometers are either too big (Shepard, Wilson et al. 2008), or require extensive calibration prior to use in the wild (Watanabe, Izawa et al. 2005), especially for an animal with a wide spectrum of activities and movements.

Time-Depth Recorders (TDRs) are very small (weighing 2.7 g in air and 1 g in water), relatively cheap, commercially available logging devices. TDRs incorporate, as standard, temperature and pressure sensors but may, additionally, include light or salinity sensors, and accelerometers (with the concomitant disadvantages of increased size, and decreased battery life). Pressure data from TDRs (converted into depth measurements) have been used to describe diving behaviour in several taxa (Baird, Borsani et al. 2002; Lea, Hindell et al. 2002; Hays, Forman et al. 2007; Ropert-Coudert, Beaulieu et al. 2009; Hart, Mann et al. 2010; Harrington, Hays et al. 2012). Light and temperature data from ventrally attached TDRs have been used to describe time

budgets for guillemots (Tremblay, Cherel et al. 2003), and were followed by time-budget studies of other seabirds using TDR-temperature records previously validated by the light sensors (Cook, Cherel et al. 2007; Woo, Elliott et al. 2008). However, although Tremblay et al. offer a simple and reliable method of describing activity budgets for seabirds, their method could not be used on animals active at night, and the concept of using a number of simple variables to classify behaviour patterns has not yet been explored for species that forage in more than one environment; also the method has not previously been applied on mammals. Here, I employ TDRs without additional sensors (i.e. only temperature data coupled with depth data derived from pressure sensors) to investigate activities of a generalist species that forages on land and in water.

Using the American mink, *Neovison vison*, in lowland England, as a model, I demonstrate the use of temperature and depth data from TDRs to describe complete, integrated activity budgets of mammals. Mink are a good model species since, as generalists, they are extremely adaptable, they consume both terrestrial (lagomorphs, rodents, birds) and aquatic (fish, crustaceans) prey, they are sexually dimorphic (and thus a degree of inter-sexual niche differentiation might be expected), like other long, thin mustelids they are vulnerable to heat loss and thought to operate close to their energetic limit (Iversen 1972; King 1989), can be live-trapped for study (Harrington, Harrington et al. 2008), and their basic ecology has been well explored within my study system (Macdonald, Yamaguchi et al. in press) – in particular, I have already demonstrated the use of TDRs to describe their diving behaviour (Hays, Forman et al. 2007; Harrington, Hays et al. 2012; Bagniewska, Hart et al. 2013.). It has also been suggested that part of the mink's characterisation as a generalist species is the

aggregate outcome of individual specialism (Sidorovich, Macdonald et al. 2001); however the details of individual foraging patterns amongst mink have not been documented.

First, I carried out behavioural observations of two captive mink to validate the underlying analytical principle, i.e. whether activity types derived from TDR temperature data accurately reflect the animals' behaviour. I then analysed 20 datasets from 16 wild mink, collected between 2006 and 2008 in Oxfordshire (described in Harrington et al, 2012) using this method to explore variation in activity patterns. Specifically, I tested the hypothesis that there is inter-sexual niche differentiation in mink, reflected by different activity patterns of males and females.

Sexual dimorphism in mustelids is most likely driven by either energetic selection for small female body size (Erlinge 1979; Moors 1980; Powell and Leonard 1983; Gliwicz 1988), or sexual selection for large males (Erlinge 1979; Moors 1980). Although originally hypothesised as an alternative driver of sexual dimorphism (Selander 1966; Brown and Lasiewski 1972), inter-sexual competition is unlikely to have been its evolutionary driver; nevertheless, inter-sexual niche separation that might arise as a result of sexual dimorphism may have contemporary benefits that are sufficient to maintain it (Brown and Lasiewski 1972; Dayan and Simberloff 1994; Abramov and Tumanov 2003; Thom, Harrington et al. 2004).

Male mink are about twice the weight of females (Macdonald, Yamaguchi et al. in press), they also have proportionally larger canine and carnassial teeth, and trophic apparatus, which may allow them to kill and consume larger prey more successfully than females (Thom, Harrington et al. 2004). There is some direct evidence of dietary differences between sexes, with female mink preferring smaller, aquatic prey, and

males larger prey, such as lagomorphs (Birks and Dunstone 1985; Ireland 1990), muskrats (Sealander 1943) or large Eider ducks (Magnusdottir, Stefansson et al. 2012); similar trends are reported for other mustelids (McDonald 2002). Regardless of individual prey preferences, both sexes are presumably physically capable of hunting prey across the species' entire dietary range, since mustelids smaller than a female mink – e.g. stoats – are able to do so (McDonald, Webbon et al. 2000); although perhaps the males' morphology allows them to handle larger prey items more efficiently (Thom, Harrington et al. 2004).

In the Upper Thames region, radio-tracked female mink are generally active closer to water than are males, their dens are closer to water than are those of males (Yamaguchi, Rushton et al. 2003), and they spend more time in proximity to the riverbank than do males (Macdonald, Yamaguchi et al. in press). Rabbit warrens appear to be the most important single habitat feature concerning habitat preferences of mink of both sexes in the Upper Thames (Yamaguchi, Rushton et al. 2003), but non-reproductive male mink appear to be more closely associated with rabbits than non-reproductive females (Macdonald, Yamaguchi et al. in press), although potential differences between breeding and non-breeding females could be of importance.

If mink do maintain inter-sexual niche differentiation, I would predict that sexes adopt different foraging strategies, which would, in turn, be reflected by differing activity patterns. My study provided the opportunity to use a novel method to test this prediction for mink, whilst exploring the use of this method to describe activity patterns generally. Specifically, with respect to mink, I ask whether activity patterns differ between the sexes, and whether and how activity patterns are influenced by

season, daylight, ambient temperature and body size. Finally, I discuss the broader applicability of determining activity from temperature data from small, simple TDRs.

5.2 Materials and methods

Data collection

The dataset used in this study has previously been described by Harrington et al. (Harrington, Hays et al. 2012) in a study of individual dives by mink. CEFAS G5 TDRs (31 x 8 mm; CEFAS Technology Ltd, Lowestoft, UK, Hays, Forman et al. 2007) were deployed on free-living American mink on the rivers Thames and Cherwell in the Upper Thames valley in Oxfordshire, UK (approximate latitude, longitude: 51.62°N, 1.08°W) between January 2006 and January 2008. The site and trapping methodology are described in Harrington et al. (2012).

Mink were fitted with collars to which a TDR had been ventrally attached (further details in Harrington et al. 2012 and Hays et al. 2007). The TDR was recovered a week after deployment (or as soon as possible thereafter).

Thirty-one TDRs were deployed on 24 mink (8m; 16f – all adults and adult-sized sub-adults), with some repeats on the same individual in winter and summer. Twenty TDRs were retrieved, containing temperature and pressure data recorded every five and one second, respectively, for a period of up to seven days. One data-logger failed prematurely and only recorded for two days. Only full days of data were considered, thus 19 datasets from 15 individuals (6m, 9 f) were available for analysis (omitting one that contained <24 h of data).

Assigning activity categories

I used the influence of the minks' natural body posture, when resting versus active, on TDR-recorded temperature to discriminate between inactive and active periods (Figure

5.1A-C). I then complemented these temperature-based discriminations with depth data from the pressure sensors to obtain full activity patterns in three categories, i.e.: inactive, active on land and active in water.

An activity category was assigned to every data point within a TDR dataset on the basis of expected temperature changes in relation to body position and animal movement. When a mink is inactive and curled up, the TDR – placed under its chin – rapidly warms up, and TDR temperatures reach values close to the animal's body temperature (Figure 5.1A); when the animal uncurls, the TDR is exposed to ambient temperature, and TDR temperature rapidly drops (Figure 5.1B). TDR temperature when the animal is inactive and curled up is thus much higher than when the animal adopts an active posture. Changes in temperatures (rapid increases or decreases, $>0.01^{o}C/s$ – value chosen after a series of sensitivity checks), distinguished from stable warm intervals, therefore, allow the determination of active and inactive periods. Coupling TDR temperature with depth data (when the animal is diving, i.e. when TDR depth is greater than or equal to 0.2m) can designate a temperature threshold to identify periods when the animal is in water (Figure 5.1C).

I use code developed in R 2.10.0 (see Appendix 1), featuring the three above functions, to assign each data point to one of three categories – "active on land", "active in water", or "inactive".

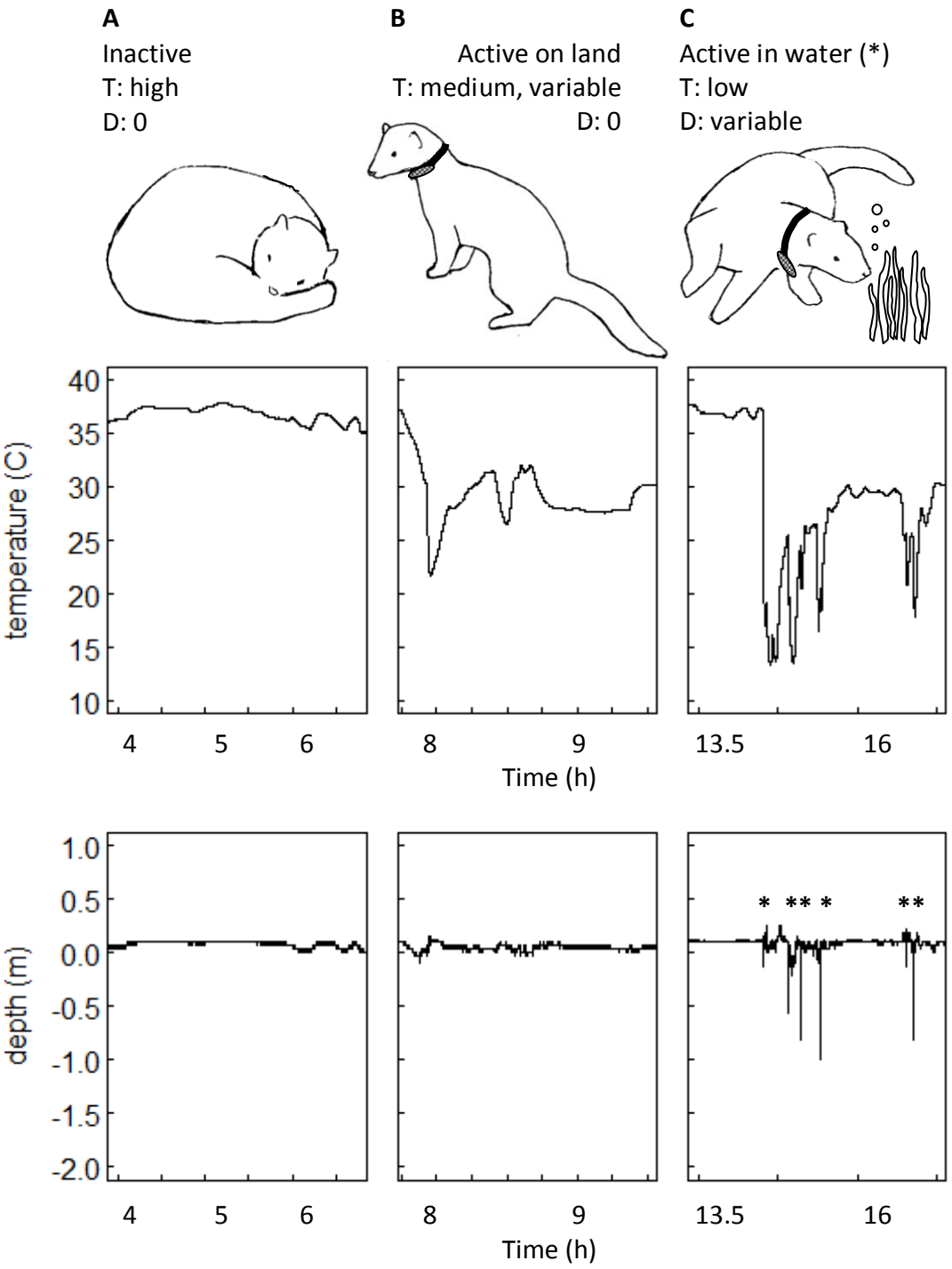

Figure 5.1: Activity categories of the American mink, and respective predicted values for TDR temperature (T) and depth (D). Temperature changes are shown at the beginning of graphs B and C, where the starting point is "inactive" behaviour, and periods of water activity (indicated by asterisks) are intercepted by a period of land activity. Data taken from mink 42a, a male, collected in October 2007 (ambient temperature throughout collection period = 12.85°C).

Validation

I made direct observations of two captive male mink during two seasons. Mink were anaesthetised and collared as in Harrington et al. 2012; they were observed at the Derek Gow Water Vole Conservancy, Devon, UK (for winter observations – animal housed in an unheated indoor 3 m x 3 m x 3 m wire mesh enclosure with a 1.5 m x 0.5 m x 0.5 m water tank), and at the Wildwood Trust, Kent, UK (for summer observations – animal housed in a naturalistic outdoor enclosure, 5 m x 10 m, with a pond 2 m x 1 m x 1 m); both with access to a wooden nest box placed on the ground. Animals were observed directly for 12 h per day over the TDR deployment period, giving 84 observation hours for winter, and 60 for summer – see Chapter 4. I used focal animal sampling (Altmann 1974); the state changes (animal in nest box – inactive, animal out of the nest box – terrestrial activity, animal in water – aquatic activity) were timed using a stopwatch and noted on a scoring chart. Observations of the animal in nest box and active on land were compared with categories assigned by the software on the basis of TDR temperature records.

Statistical analysis

Statistical analysis was carried out in R 2.15.0. (The R Foundation for Statistical Computing, 2012). Percentage activity – defined as percentage of time spent active (in water or on land)/total time – was calculated for each dataset, and for each day within the dataset.

Each behaviour was assigned a light category (dawn, dusk, day or night) based on sunrise and sunset times obtained from timeanddate.com (http://www.timeanddate.com/worldclock/sunrise.html); with settings for Oxford. Proportion of activity per light category was calculated for each dataset by dividing the amount of

time in each activity for each light category by the total time of each light category. 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 centre of Oxford, within 40km of the study sites. Seasons were calculated on the basis of ambient temperatures, with winter classified for my purposes as being November to March, and summer – August to September.

Normality of the data was checked using the Anderson-Darling test. Where data were not normal, a non-parametric test was used for comparison, and the median reported as a measurement of central tendency. A series of tests were run to check for differences in median proportion of time spent on each behaviour by animals of both sexes during night and day, and dawn and dusk; proportions of activities at different times of day and year were also examined for pooled data from males and females; Wilcoxon rank sum tests were used for comparisons between sexes, and Wilcoxon signed rank tests – for within (same individuals at different times). General linear mixed effects models were used to test for a relationship between the mean daily duration of behaviour and ambient temperature, body mass, and sex; individual was included in the models as a random factor, and the interaction between ambient temperature/body mass and sex was included. I used the *lm* function in package(stats) and the lme4 package (Bates, Maechler et al. 2011).

5.3 Results

Validation

The percentages of matched pairs of predicted behaviour patterns and those observed in captivity were: in winter – 84% for both terrestrial activity and inactivity, and in summer – 90% for terrestrial activity and 53% for inactivity. The matching for inactivity

in summer is low because it was impossible to tell whether an animal in the nest box was active or not. In winter the study animal was much more inactive in general, which most likely decreased the chance of this type of error. When the animal is inactive, TDR temperatures reach very high values (>35^{o}C) regardless of season, acting as an additional criterion in category assignment.

Activity types

Mean time spent active in water ranged between 4.7 and 79.8 min/day (0.33 – 5.53% of day) (grand mean = 0.85 h/day); mean time active on land between 0.67 and 7.34 h/day (2.81 – 30.58% of day) (grand mean = 3.88 h/day), and mean time inactive between 15.50 and 23.25 h/day (64.59 – 96.87% of day) (grand mean = 19.44 h/day). There was also considerable variability within individuals, and some individuals exhibited greater diversity in activities than others. Differences between least and greatest time spent in an activity per day, for each individual, ranged between 0.2 and 1.53 h for aquatic activity, between 0.53 and 3.93 h for terrestrial activity (with one outlier of 6.3h), and between 0.46 and 4.97 h for inactivity (with one outlier of 6.8 h).

Terrestrial activity was higher for males (mean number of hours per day = 4.58) than females (mean = 3.14 h/day) (W = 681, $p < 0.001$). Conversely, inactivity was higher in females (mean = 20.09 h/day) than in males (mean = 18.55 h/day) (W = 1903, P = 0.0001). There was no difference in aquatic activity between sexes (Figure 5.2). Of all "aquatic activity" records, on average 15% (range: 0.002% – 73%) were associated with diving behaviour; this association tended to be higher for females (median = 18.8%) than for males (median = 3.9%), but this difference between the sexes was not significant (W = 28, P = 0.112).

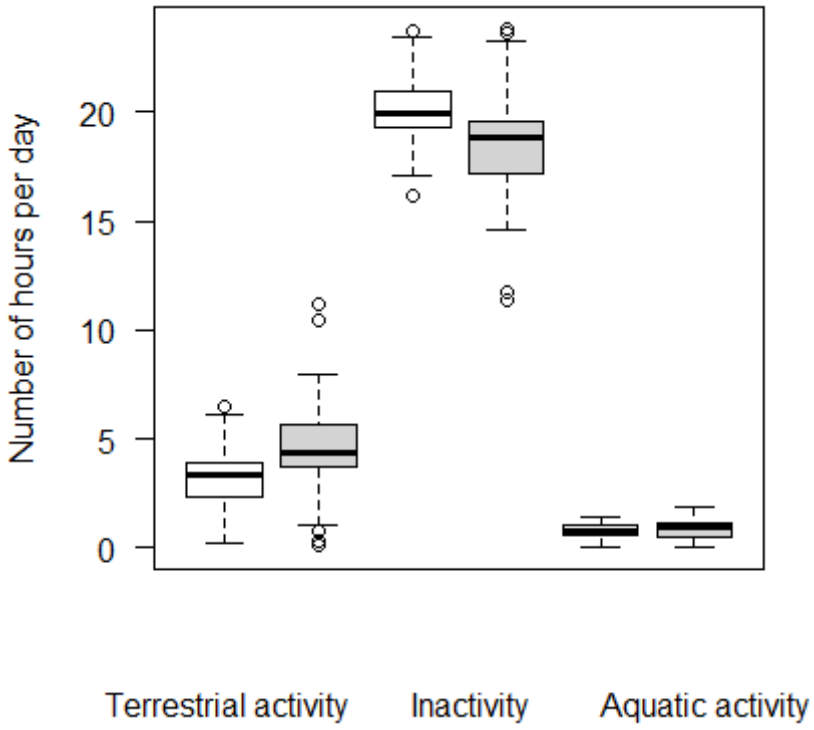

Figure 5.2: Time spent on each activity type per day by females (white, *N* = 9) and males (grey, *N* = 6).

Terrestrial activity, measured as number of hours per day, was higher in summer than in winter ($mean_{summer}$ = 5.08, $mean_{winter}$ = 2.69, *W* = 1761, p-value < 0.001); as was aquatic activity ($mean_{summer}$ = 1.0, $mean_{winter}$ = 0.68, *W* = 1409, p-value = 0.001). Consequently, animals were more inactive in winter than in summer ($mean_{winter}$ = 20.65, $mean_{summer}$ = 17.93, *W* = 322, *P* < 0.001, Figure 5.3).

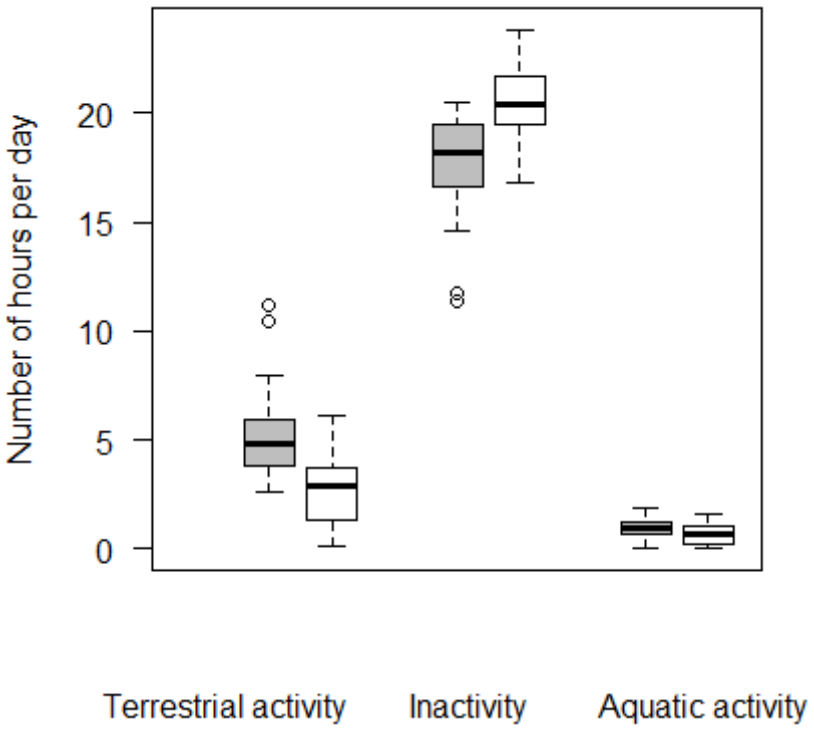

Figure 5.3: Time spent on each activity type in summer (grey, *N* = 8) and winter (white, *N* = 9).

Light

Terrestrial activity (for males and females combined) at dawn was lower in winter than in summer ($W = 7$, $P = 0.004$), with the mean summer proportion of activity at dawn being 0.305, and mean winter proportion – 0.141; I did not detect any other significant seasonal differences between behaviours at other times of day ($P > 0.05$).

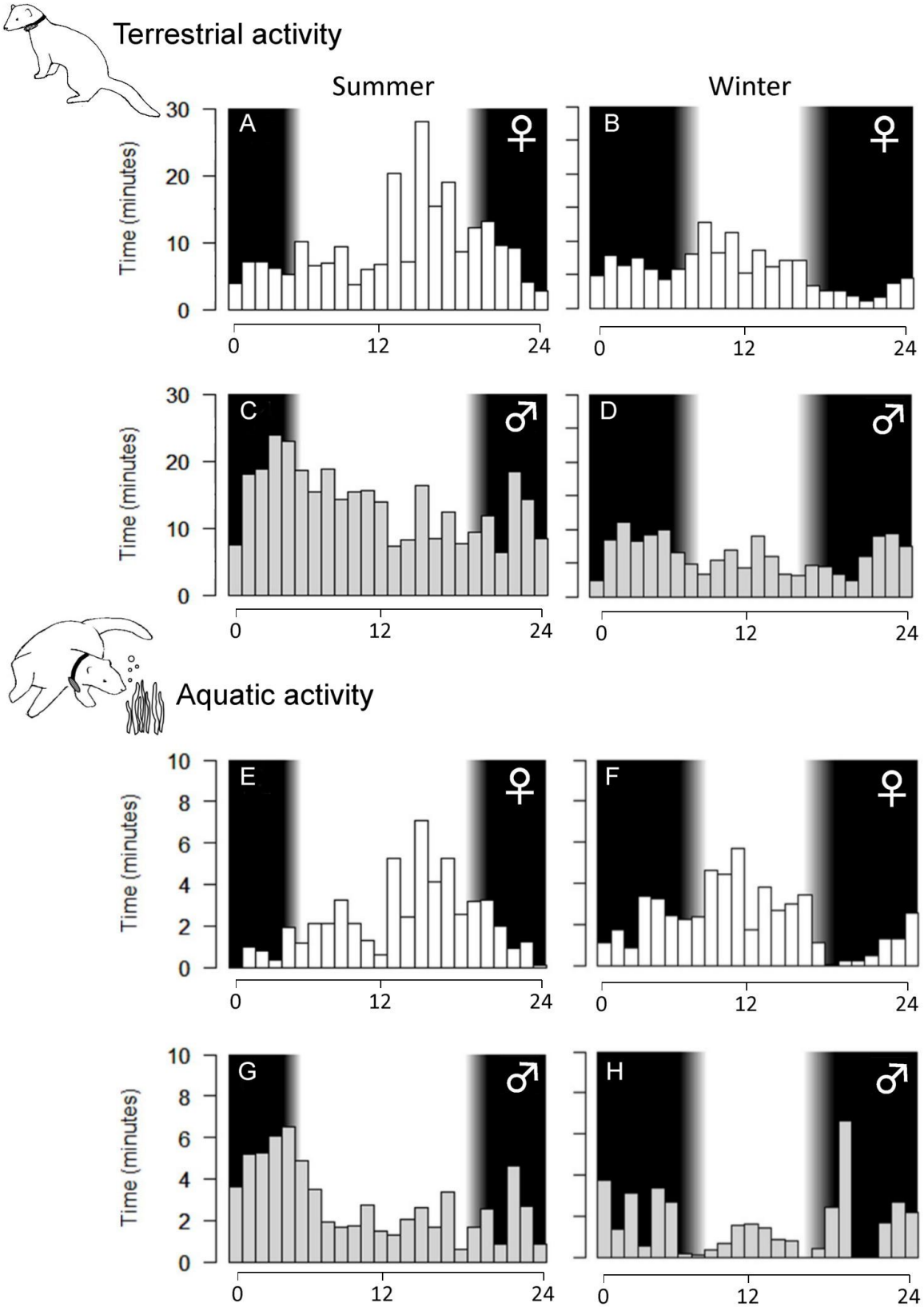

Figure 5.4: Median terrestrial and aquatic activity per hour during winter and summer for females (white) and males (gray), shown in minutes per each hour of the day. Daylight hours are marked with background shading. Seasons are depicted separately to show varying daylight hours clearly.

At night, males were significantly more active than the females both on land ($mean_{males}$ = 0.224, $mean_{females}$= 0.093; W = 76, P = 0.01), and in water ($mean_{males}$ = 0.05, $mean_{females}$= 0.015; W = 69, P = 0.05); measured as proportion of the dark period occupied by the activity. However, females were significantly more active in water during daylight (W = 19, p-value = 0.035, $mean_{males}$= 0.025, $mean_{females}$= 0.051) than the males (Figure 5.4). There was no statistically significant difference between diurnal terrestrial activity of males and females (P > 0.05).

Among females, aquatic and terrestrial activity was significantly higher during the day than at night (terrestrial: $mean_{day}$ = 0.16, $mean_{night}$ = 0.093, paired Wilcoxon test: V = 52, P = 0.01; aquatic: $mean_{day}$ = 0.051, $mean_{night}$ = 0.015, $V_{aquatic}$ = 54, P = 0.004), Figure 5.4. For males, there was a tendency towards nocturnality in aquatic behaviour but it was not statistically significant ($mean_{day}$ = 0.025, $mean_{night}$ = 0.05, V = 8, P = 0.098).

Ambient temperature

Daily terrestrial and aquatic activity both increased significantly with increasingly warm weather, but the effect of sex differed between activity types. For terrestrial activity, the effects of ambient temperature, sex and individual were all statistically significant (sex: $F_{1,1}$ = 11.5, P = 0.001; individual: $F_{1,14}$ = 6.52, P <0.001; ambient temperature: $F_{1,14}$ = 63.84, P <0.001), but the interaction between sex and ambient temperature was not ($F_{1,1}$ = 3.8428, P = 0.053) (model statistics: $F_{16,86}$ = 10.25, R^2 = 0.656, P < 0.001). For aquatic activity, the effect of individual was statistically significant ($F_{1,14}$ = 3.84, P <0.001) and there was a statistically significant interaction between sex and temperature ($F_{1,1}$ = 6.41, P = 0.013), (model statistics: $F_{16,85}$ = 5.50, R^2 = 0.458, P < 0.001), such that daily aquatic activity was significantly positively related to ambient

temperature for males (ambient temperature: $F_{1,1}$ = 25.27, P < 0.001; individual: $F_{1,5}$ = 1.41, P = 0.239) (model statistics: $F_{6,46}$ = 5.386, R^2 = 0.41, P <0.001) but not for females (ambient temperature: $F_{1,1}$ = 0.19, P = 0.665; individual: $F_{1,8}$ = 5.82, P < 0.001) (model statistics: $F_{9,39}$ = 5.196, R^2 = 0.54, P <0.001) – Figure 5.5. Accordingly, daily inactivity was significantly negatively related to ambient temperature for both males (ambient temperature: $F_{1,1}$ = 31.38, P < 0.001; individual: $F_{1,5}$ = 4.58, P = 0.002) (model statistics: $F_{6,46}$ = 9.04, R^2 = 0.54, P <0.001) and females(ambient temperature: $F_{1,1}$ = 16.48, P < 0.001; individual: $F_{1,8}$ = 10.031, P <0.001) (model statistics: $F_{9,40}$ = 5.386, R^2 = 0.71, P <0.001).

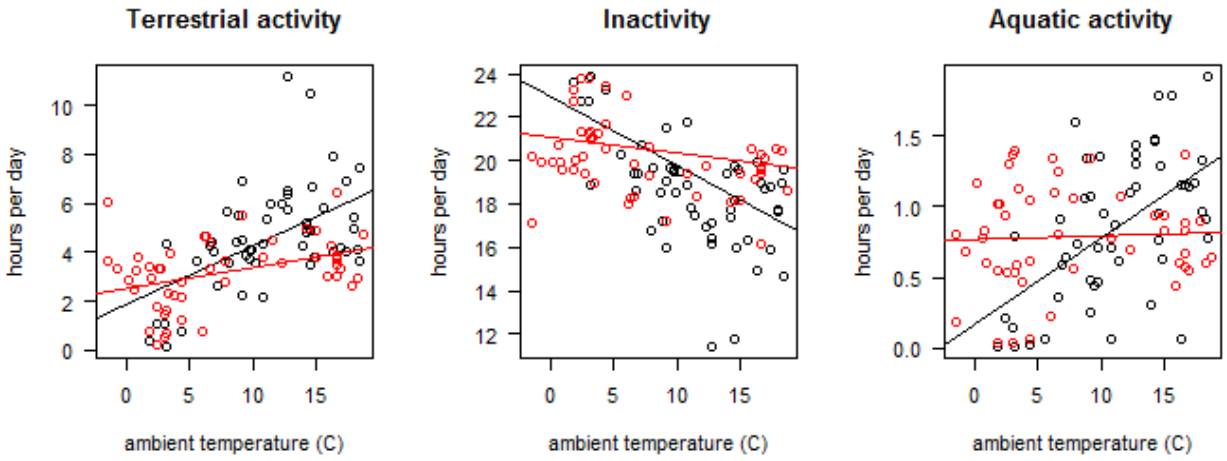

Figure 5.5: The relationship between ambient temperature and mean time spent on each activity type per day. Females are marked in red, males in black.

Body mass

Mean daily terrestrial activity increased significantly with increasing body mass ($F_{1,15}$ = 22.37, P < 0.001). However, when body mass was included in the model, the effect of sex was not significant ($F_{1,1}$ = 0.582, P = 0.45), nor was there significant interaction between sex and body mass ($F_{1,1}$ = 0.44, P = 0.51) (model statistics: $F_{1,95}$ = 22.61, R^2 =

0.2, $P < 0.001$). Mean daily aquatic activity, however, was not significantly related to body mass ($P = 0.16$) (model statistics: $F_{1,94} = 2.02$, $R^2 = 0.01$, $P = 0.16$), Figure 5.6.

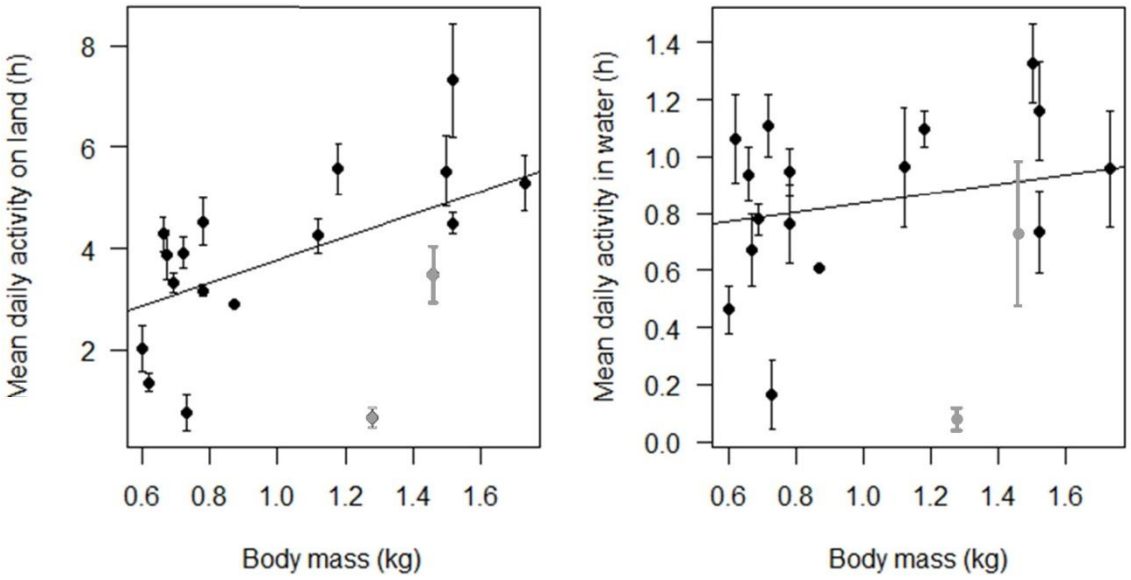

Figure 5.6: The relationship between body mass and mean daily activity. All female mink weigh less than 1 kg, all male mink – more than 1 kg. Grey points indicate male mink during the breeding season.

5.4 Discussion

By using Time-Depth Recorders deployed on free-living wild mink in Oxfordshire, UK, I have demonstrated that activity patterns of a generalist semi-aquatic mammal can be quantified by coupling TDR temperature and depth records. The ventral attachment of TDRs allows differentiation of animal postures on the basis of temperature changes and inference from them of three activity categories: terrestrial activity, inactivity and (after incorporating temperatures of dive data) aquatic activity. I collected data from mink to illustrate how this method can be used for animals which frequently change between aquatic, terrestrial and underground environments, foraging during both night and day.

My data show that mink spend about 80% of time inactive – a value in line with previous studies using radio-tracking or direct observations (Gerell 1969; Garcia, Mateos et al. 2009; Brzeziński, Marzec et al. 2010) and reveal levels of activity consistent with studies of mink in Oxfordshire (Harrington, Harrington et al. 2009). Validation with captive mink showed that the categories identified by code were largely consistent with observable, discrete behaviours (see Chapter 4).

I was able to detect and describe inter-sex variation in the behaviour of wild mink. Male mink were overall more active than females; the difference was driven by higher activity on land, but not in water. On land, both sexes were more active in summer than winter, indicating that, like other mustelids, mink need to conserve energy during cold periods (Richardson, Clark et al. 1987; Jędrzejewski, Jędrzejewska et al. 2000; Zalewski 2000; Zalewski and Bartoszewicz 2012). In water, however, while male activity increased with ambient temperature, females were just as active in cold days as they were in warm. These inter-sex differences in aquatic activity – perhaps associated with foraging (e.g. ectothermic fish could be easier to access in cold water) – may point to varying hunting efficiency, with males potentially being more successful and thus requiring less time to obtain enough food (Smith and McDaniel 1982; Dunstone 1993).

Male mink were more nocturnal overall than the females, in line with Harrington et al.'s findings (Harrington, Harrington et al. 2009). Since the data reveal mink diving mainly during the day (Harrington, Hays et al. 2012), aquatic activity that is not associated with diving may suggest that mink, especially males, do more surface swimming at night, e.g. for travel. Dunstone proposed that, due to poor underwater

eyesight, mink need light to hunt underwater (Dunstone 1993); this however should not affect surface swimming when the animal's head is above water.

Analysis of body mass reveals that larger mink are more active on land, irrespective of sex, suggesting that sex-specific differences are in fact driven by size dimorphism. Several authors report mink home range sizes increasing with body mass (Melero, Palazon et al. 2008) or being larger for males than females (Gerell 1970; Ireland 1990; Yamaguchi and Macdonald 2003) – higher terrestrial activity of larger animals may be related to longer travelling times across a larger home range. Incidentally, male terrestrial activity has not been driven by animals studied during rut, which is a time of greater movement of males in search of females (Dunstone 1993). My method gives information on activity category, but it does not differentiate whether the animal is foraging or travelling on land, so the reasons underlying the body mass-activity relationship are speculative. Mean daily aquatic activity, however, was not significantly related to body mass. Due to short deployments it is possible that some datasets will not reflect an animal's foraging strategy, especially if the differences between individuals are significant (e.g. a mink that has caught a rabbit is likely to remain inactive for several days – Dunstone 1993).

Varying activity patterns between sexes are broadly in accordance with previous studies of diet and habitat use (Dunstone 1993; Yamaguchi and Macdonald 2003; Yamaguchi, Rushton et al. 2003; Harrington, Harrington et al. 2009; Harrington, Hays et al. 2012). Several studies (Sealander 1943; Birks and Dunstone 1985; Magnusdottir, Stefansson et al. 2012) point to male mink choosing larger prey items than females; in the case of my study site it is likely that the larger prey items were terrestrial (e.g. lagomorphs), and smaller ones – aquatic (fish, water voles) (Ferreras

and Macdonald 1999; Harrington, Harrington et al. 2009). Female mink have smaller, weaker skulls (in terms of trophic features) than males (Thom, Harrington et al. 2004), and even though rabbits are possible for them to hunt, they require more effort to overpower – whereas small fish or rodents are a more accessible and profitable prey. For males, small prey is harder to get at, and less worthwhile energetically. The balance of energetic cost and gain may push the two sexes in different directions.

Even though they are a generalist species, mink do show individual variability (both in ranges of percentage activity and in individual variation in responses to ambient temperature). The variability is especially strong in terms of aquatic behaviour, which does not seem to be as fully governed by temperature as terrestrial activity. However, due to my sampling strategy, it is impossible to say whether the study animals were individual specialists, generalists temporarily exploiting a patchy resource, or whether the behavioural differences were sex-specific (Harrington, Hays et al. 2012).

Tremblay, Cherel et al. (2003) have used light sensors to validate the use of TDR temperature records for determining activity patterns of birds; their study has been followed by others using the same principle (Tremblay, Cook et al. 2005), some of which – having taken advantage of the light-validation from the original study –limited the TDR input factors to temperature and depth (Woo, Elliott et al. 2008; Hedd, Regular et al. 2009). In the case of small mammals, using light sensors for validation would have been inappropriate, because they are active at night (a limitation pointed out by Tremblay et al. themselves), and also move freely between over- and underground environments. The ventral attachment of TDR collars however enables the detection of postural differences on the basis of temperature changes, and is likely

to be more widely applicable for detecting behavioural transitions where direct observations may not be possible.

The described method should be more generally applicable to animals with a marked temperature difference between body temperature and ambient temperature, and where different activities lead to different body temperatures that can be captured by TDR. Its main limitations are (1) discriminating between activity categories if ambient temperature is close to that of the animal's body, (2) the size of the data-logger in relation to the animals' body mass, and (3) identifying postural changes on the basis of temperature differences for animals with varying body temperatures. The strength of my study was the ability to calibrate behavioural categories on captive animals; something which may not always be possible. My method could potentially be used on ectothermic animals, since it relies on rapid temperature changes and high temperatures when the animals are inactive. Ectotherms influence their body heat by altering their behaviour – e.g. by basking – and TDRs could perhaps be useful in registering these alterations. Data-loggers have thus far been deployed on reptiles to measure diving behaviour (Hays, Åkesson et al. 2001; Hays, Houghton et al. 2004; Seebacher, Franklin et al. 2005), however external temperature loggers have not been employed to examine activity patterns.

I demonstrate a simple methodology using commercially available equipment and a novel analytical approach to determine activity patterns of an animal making rapid transitions between aquatic and terrestrial environments. The same technique can be transferred to other data types and used to analyse data from other species which were thus far regarded as too elusive or too variable to study. A further advantage of TDR use is the lack of direct interference with the animal's behaviour,

since there is no need for proximity to record data; additionally it is possible to accurately distinguish not only between periods of activity and inactivity, but also activity in water and on land. Other examples where this might be useful is other small animals that make rapid and frequent transitions between media, such as land and water or ice, species active both during the day and night, or those spending time under dense canopy cover and underground. Transitions between water bodies might be of ecological and behavioural interest (e.g. entry into rivers, or penguins and seals foraging around marine fronts (Charrassin, Hindell et al. 2008) or around thermoclines (Pelletier, Kato et al. 2012)), so the use of temperature coupled with depth from TDRs and looking for break-points in data is likely to be more generally applicable. Further understanding of individual activity patterns will enhance our knowledge about intrapopulation niche variation in generalist species. This, coupled with quantifying energy expenditure on the basis of time spent on each activity type in varying environments and at varying temperatures, will enable the assessment of energy requirements of particular animals, and may be of importance for ecological and conservation studies, e.g. assessing the impact of an invasive species, examining the relationship between competitors, or estimating the energetic requirements of a species prior to reintroduction.

Chapter 6

General discussion

Mammals are the most threatened group of animals on the planet, with most orders containing 50% of their species IUCN Red Listed (Ceballos and Ehrlich 2002), increasing by one fifth in each IUCN report (Hoffmann, Hilton-Taylor et al. 2010). With climate change, habitat fragmentation, pollution and human encroachment, some mammals have been well-studied in terms of populations, home ranges and feeding ecology (Börger, Dalziel et al. 2008; Kranstauber, Cameron et al. 2011). The drivers of bio-logging device development have largely come from the need to study elusive species (Ropert-Coudert & Wilson, 2006; Rutz & Hays, 2009), and many of these have largely been in the marine environment (Kooyman 2004; Rutz & Hays 2009).

Fine-scale behavioural ecological studies using bio-logging devices are now routine in marine ecology (Rutz and Hays 2009), but any terrestrial mammals are also highly cryptic, and the scope for discovering the detail of their behaviour is becoming clear (Ropert-Coudert and Kato 2006; Shepard, Wilson et al. 2008), with deployments on small animals at the limits of devices continuing to prove fruitful areas for research (Rutz and Hays 2009).

It has been possible to radio-track mink for decades (Macdonald and Amlaner 1980; Peeples, Fendley et al. 2002), but simple locations suitable for home range studies are a coarse depiction of the subtleties of their behaviour on land and in water. Error in animal movement data is a vital limiter as to the levels of inference that can be made (Phillips, Silk et al. 2004; Tremblay, Robinson et al. 2009; Winship, Jorgensen et al. 2012). As this thesis demonstrates, much of the important behaviour occurs in water, to which tracking studies are likely to be insensitive, especially within narrow rivers. The error associated with radio tracking and possibly GPS, limits our ability to record and calibrate movement or activity with specific behaviour. A number of

outstanding questions exist that cannot be answered with more common mammalian tracking techniques. Therefore, much of this thesis has been concerned with finding suitable techniques to investigate the transition between land and water, then using them to answer questions about fine-scale foraging behaviour and the influences on terrestrial versus aquatic foraging.

How units of activity cluster into behaviours is a ubiquitous problem in studies of animal behaviour (Hart, Mann et al. 2010; Luque and Fried 2011). Hidden Markov Models are a powerful analytical tool for understanding behavioural patterns and the transitions between these. They have been used to advance understanding of the mechanisms that underlie observed behavioural switches in the locust *Locusta migratoria* (Macdonald and Raubenheimer 1995), caterpillar *Helicoverpa armigera* (Zucchini, Raubenheimer et al. 2008) and homing pigeon *Columba livia* (Guilford 2004), but have not been applied to behavioural semi-aquatic animals.

The study of animal behaviour involves trying to infer internal states of an animal and how it makes decisions (Hart, Mann et al. 2010). These internal states generate observable emissions (Guilford, Meade et al. 2009; Mann, Freeman et al. 2009) but the internal states are not directly observable, so can be treated as a black box, as I have in Chapters 2 and 4, which use Hidden Markov Models to interpret observed dive patterns. Terminal or any activity that immediately precedes a change of behaviour is inherently interesting, as it implies the animal has made a decision (Guilford, Freeman et al. 2011; Shepard, Lambertucci et al. 2011).

Perhaps the most limiting factor of interpreting animal behaviour in bio-logging studies is the ability to detect prey capture events, which remains elusive in this study. In an aquatically foraging mink, does a single crayfish lead to cessation of diving and

return to land to dry off, or are multiple prey capture events needed? Given assumptions of prey encounter rate and knowledge of energetics, it is possible to calculate a complete energetic budget (Harrington 2001). This is particularly the case where prey items are small and therefore multiple prey capture events occur remotely from the researcher. Recent studies of leopard and snow leopard using GPS coupled accelerometers have shown that it is possible to infer large prey captures with confidence, and to retrospectively visit these kill sites to verify species and size of the kill (Krofel, Skrbinšek et al., 2013; Broekhuis et al, pers. comm.; McCarthy pers. comm.).

Using accelerometers recording at high frequency, it is even possible to infer energetics from on-board devices (Shepard, Wilson et al. 2009; Shepard, Wilson et al. 2010; Enstipp, Ciccione et al. 2011; Gleiss, Wilson et al. 2011). While prey capture events can be inferred using certain bio-loggers such as stomach temperature (Handrich, Bevan et al., 1997; Ropert-Coudert, Baudat et al. 2000; Catry, Phillips et al. 2004) loggers or Hall sensors (Wilson, Steinfurth et al. 2002; Takahashi, Dunn et al. 2003), this remains impossible on small bodied animals with a limited payload and semi-aquatic animals for which the sensor signal of prey capture/ingestion may differ between land and water.

Many bio-logging studies make inferences about behavioural classification on remote subjects, using both supervised techniques (Watanabe, Izawa et al. 2005), where behavioural observations are used to calibrate statistical clusters of behaviour, and unsupervised techniques (Hart, Mann et al. 2010), which lack direct observations. My thesis aimed to apply and to further develop these approaches for use on semi-aquatic animals. As discussed throughout this thesis, studying semi-aquatic species

brings particular problems for researchers, particularly using remote techniques, as it is difficult to differentiate between inter-dive pauses and transition onto land.

I used Time-Depth Recorders to investigate the behavioural ecology of a semi-aquatic mustelid, the American mink (*Neovison vison*). First, I applied hidden Markov models (HMM) to identify the nature of diving behaviours of semi-aquatic animals, and to classify them. I then used the resultant HMM classification to describe sequential diving behaviour of wild American mink in lowland England. Through a behavioural validation study, I was able to use signals not only from depth, but also from temperature sensors to differentiate between activities on land and in water, thereby building a complete time budget using simple TDRs. Finally, I have revisited the wild mink dataset and used the temperature methods to analyse their activity patterns. This study points towards similar methods being applicable for animals that make rapid transitions between environments.

6. 1. Analytical methods

In Chapter 2 I propose a transitional analysis for investigating diving patterns, and in Chapter 4 I developed a method of using temperature changes of TDR loggers to investigate activity patterns.

6.1.1 Dive pattern analysis

The dives of many animals seem organised into temporal clusters with intermediate gaps (“bouts”, “movement steps”, or “clusters” (Luque and Guinet 2007)). Existing methods of dive analysis, developed for fully aquatic animals, tend to focus on the underlying distribution of movement step lengths (Edwards, Phillips et al. 2007; Reynolds and Rhodes 2009; Smouse, Focardi et al. 2010) rather than what influences

the transitions between short and long step-length. They therefore do not account for the variability of behaviour of semi-aquatic animals, and particularly, the switching between terrestrial and aquatic environments. This is the first study to use hidden Markov models to divide dives of a semi-aquatic animal into clusters, and thus identify the predictors of transitions between behavioural modes (Hart, Mann et al. 2010). HMM is a principled approach which provides an objective classification of behaviours, and is not confounded by the transition between land and water. The analysis identified three behavioural states (1 – temporal cluster of dives; 2 – more loosely aggregated diving within periods of aquatic activity; and 3 – terminal dive of a cluster or a single, isolated dive). Using HMM classifications I tested whether changes in environmental temperature influence diving strategies in American mink. Other factors (e.g. daylight, body mass, geolocation) could similarly be tested to identify the environmental predictors of transition between behavioural modes of other semi-aquatic species. 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 semi-aquatic animals, or any other species that transitions between clearly distinct modes of a particular behaviour. On the basis of the state classifications, I divided dives of wild mink into clusters (state 1), aquatic foraging sessions (state 2), and single dives (state 3); and subsequently used these to analyse the diving patterns of free-living mink (see below).

6.1.2 Measuring activity patterns

Describing activity patterns is especially difficult for animals that make quick transitions between aquatic and terrestrial habitats (Harrington, Hays et al. 2012), ice (Mitani, Watanabe et al. 2004), or over- and underground habitats (Shepard, Wilson et

al. 2008), and methods able to provide consistent and continuous measurements between these different environments have been lacking. I used coupled temperature and depth TDR records to describe activity patterns of American mink, and infer from them three activity categories: terrestrial activity, inactivity and (after incorporating temperatures of dive data) aquatic activity. The analytical method was calibrated against behavioural observations of captive animals. I then analysed TDR data from free-living mink to illustrate how this technique could be used for animals that frequently change between aquatic, terrestrial and underground environments, foraging during both night and day. This method should be suitable for other generalist species with a body temperature different from ambient temperature (as it is the body temperature that influences the TDR temperature used to identify inactivity periods), but is dependent on calibration. The next step would be to validate this technique in the wild, using an independent method – e.g. TDR activity patterns could be tested on beavers, which, like mink, dive and are active on land, but can be observed in the wild.

Combining these two methods permitted the calculation of a complete activity budget, with a focus on diving patterns, of a semi-aquatic species – something which was impossible to do before, as methods tended to focus on one aspect of behaviour.

6.2. Behavioural ecology of the American mink in Oxfordshire

In Chapters 3 and 5, I investigated the behavioural ecology of American mink from the perspective of their diving behaviour and activity patterns, based on data from 16 mink fitted with Time-Depth Recorders.

Like other mustelids (Jędrzejewski, Jędrzejewska et al. 2000; Zalewski 2000), mink in my study were found to be less active in winter, presumably to conserve

energy or to reduce exposure to cold temperatures; my analysis suggested that this relationship was driven by terrestrial activity (interestingly, some mink maintained very high levels of aquatic activity in winter, see also Hays et al. 2007; Harrington et al. 2012). Male mink appeared to be more active on land than females, and, across both sexes, terrestrial activity increased with body mass. Two possible explanations of this relationship are that: 1) mink exhibit inter-sexual niche partitioning, driven by body size, whereby larger males tend to hunt predominantly on land for large terrestrial prey, e.g. lagomorphs, which were abundant in the study area (Ferreras and Macdonald 1999; Harrington, Harrington et al. 2009), or 2) that males spend more time on other terrestrial activities (such as patrolling or marking their territories) than do females, especially since males often have larger home ranges than females (Gerell 1970; Ireland 1990; Yamaguchi and Macdonald 2003; Melero, Palazon et al. 2008). In some studies larger animals have spent more time on travelling (Yamaguchi and Macdonald 2003; Melero, Palazón et al. 2011). Note that the higher activity of males in my study is probably not due to mating season (January-March) mobility, as data collected from two males from that time showed average and very low activity. Currently, we are unable to assign functions to activities, and are thus unable to discern which of the above explanations is more plausible. Nevertheless, the detailed description of activity budgets of mink allows us to couple data on nocturnality, sex, seasonality and activity type (aquatic or terrestrial), highlighting not only when mink are active, but also how they are active.

To further explore the aquatic activity of mink specifically, I investigated the amount of aquatic activity per day (diving and swimming combined), and the animal's diving persistence, i.e. the number of consecutive dives in a series, reflecting a mink's

diving effort. While I found no difference in amount of aquatic activity between sexes, females were more persistent, i.e. dived in longer clusters, than males. This could again reflect the different functions of the aquatic activity, i.e. travelling vs. hunting. We cannot determine success during foraging, but female mink spend considerably more effort diving year-round than do males; the only female metric affected by ambient temperature was maximal persistence, which increased with decreasing temperature, i.e. the highest female diving effort occurred at lowest temperatures. At the same time, the only male metric affected by ambient temperature was the amount of aquatic activity per day, which increased with warmer weather; this most likely reflects a higher amount of surface swimming by males in summer, and may indicate their preference for using water to travel.

Because in our geographical zone ambient temperature and light are confounded variables, it is difficult to pinpoint whether the activity of mink is governed by one or the other (or both). The evidence gathered in this study suggests that while terrestrial activity is related to ambient temperature, mink diving is less dependent on it. I found no relationship between temperature and the proportion of dives in each state, or transition between states; persistence was largely independent of ambient temperature, as were the number of clusters per day, and the proportion of single dives. Since mink are originally found in areas much colder than the UK (Hamilton 1940; Bowman, Kidd et al. 2007), it is likely mink are well adapted (behaviourally if not physiologically) to cope with the temperatures they face in the UK. Instead, perhaps because water temperature is more stable than air temperature, diving appears to be more dependent on light, particularly as day dive clusters are longer than night ones. Light may be an important factor in the context of hunting, since mink visual acuity

underwater is not as good as on land (Dunstone and Sinclair 1978); also mink may avoid nocturnal otters temporally by being active in water during the day (Harrington, Harrington et al. 2009). Male mink are more nocturnal than females, both on land and in water; they are less persistent than females, and make more (deeper and longer) single dives.

6.2.1 Explaining patterns of behaviour

Using Time Depth Recorders I was able to establish the activity patterns of American mink in Oxfordshire. However, there are still gaps in our knowledge, the biggest of which are: what are the exact activities within the "terrestrial activity" category (hunting/travelling/something else), and whether a dive has ended in a hunting success or not. Resolution of behavioural categories within terrestrial activity would be necessary for a complete energetic budget and may therefore require the eventual coupling of GPS and TDR or accelerometers. However, I suggest some possible explanations for the observed behaviour.

1. *Niche partitioning*. The balance of difficulty and ease may push the two sexes in two different hunting directions. Mink are sexually dimorphic, with males being twice as heavy as females, and having proportionally larger trophic features (Thom, Harrington et al. 2004). While both sexes should be physically capable of preying on all species within the mink's dietary range, large items, such as rabbits, perhaps the males' morphology allows them to handle larger prey items more efficiently. For females, smaller prey may be the next most rewarding prey – in the Upper Thames area these are aquatic species such as fish, crayfish and water voles. Males need more prey to fulfil their energetic needs, which could make small mammals and fish less worthwhile for them, thus leading to sex specific niche differentiation. In my study males may use

water for travelling and occasional fishing (perhaps they are more efficient hunters than females, as they are less persistent), but also spend more time on terrestrial hunting than do females. Females appear to put more effort than do males into hunting aquatic prey, especially in winter when there is a smaller availability of young mammals and birds. In my study they dive principally during the day, presumably to optimise their visual acuity, although female mink from the same site in the 1990s, during the absence of otters, were largely active at night (however we cannot tell if the activity was terrestrial or aquatic) (Harrington, Harrington et al. 2009). A study of coastal mink showed a potentially similar dietary preference of males and females (Birks and Dunstone 1985).

We are unable to tell what are the underlying mechanisms that drive females to be so persistent in aquatic activity – either they have fewer opportunities to catch terrestrial prey (perhaps due to avoiding males or being outcompeted by them); or the profitability of aquatic prey is high enough to compensate for the diving effort (since their energetic value is higher than that of mammals – Dunstone, 1993). Mink are not well adapted to wintertime fasting (Mustonen, Pyykönen et al. 2005), so perhaps even a prey item that requires a lot of hunting effort has marginal benefit. Mink could also, like otters (Wise, Linn et al. 1981), choose to forage on different fish species in summer and in winter. Also, both sexes may use water for travelling, especially since swimming downstream could minimise the costs of locomotion (Dunstone 1993).

This hypothesis complies with theories of intersexual niche partitioning (Thom, Harrington et al. 2004).

2. *Competitor avoidance.* Even though mink have overlapping home ranges, which are often measured linearly as the length of the watercourse usually traversed (Dunstone

1993), animals tend to use the same stretch of water at different times, i.e. the tendency for temporal-spatial avoidance appears high (Yamaguchi and Macdonald 2003; Harrington and Macdonald 2008). Different activity patterns, with males being more nocturnal and terrestrial, and females – diurnal and aquatic, could reflect intraspecific competitor avoidance.

The presence of two native competitors, the Eurasian otter *Lutra lutra* and the European polecat *Mustela putorius* might also lead mink to avoid these competitors. The otter feeds largely on aquatic (Preston, Portig et al. 2006), and the polecat – on terrestrial prey (Lodé 1997; McDonald 2002); both are nocturnal (Harrington, Harrington et al. 2009). Male mink may be less threatened by large otters than females, and thus more likely to venture into the water at night. Females may avoid competition from both otters and polecats, and thus be more active in water during the day, and less active overall on land than the males.

Mink behaviour could also be a resultant of the combination of these hypotheses. Mink are very adaptable predators, and can adjust their activity to that of their prey (Zielinski 1988), or competitors (Harrington, Harrington et al. 2009). They may be constrained by their anatomy and physiology (relatively poor eyesight and thermoregulation underwater), prey availability, or competition.

Mink individuals are highly variable in their percentage activities in different behaviours, responses to ambient temperature, and diving effort, both within and among individuals; an observation in line with the theory that generalist species in fact consist of individual specialists (Bolnick, Yang et al. 2002; Bolnick, Svanbäck et al. 2003). Sidorovich, Macdonald et al. (2001) show that some individual mink specialize

on particular prey type – in my dataset there are three animals that could potentially be identified as fish specialists due to their exceptionally high diving effort. In general, the Thames population of mink eat far fewer fish than populations elsewhere (Harrington, Harrington et al. 2009).

It is notable that these data were collected for periods of 5-7 days at a time, which is not necessarily representative of an entire foraging strategy, especially if the differences between individuals are significant (e.g. if a mink has caught a rabbit, it is likely to be inactive for the next several days (Dunstone 1993)).

Future research might be focused on contrasting environmental conditions, such as mink behaviour in habitats without mustelid competitors, and where daylight is not confounded with temperature, for instance Iceland (Magnusdottir, Stefansson et al. 2012). Further work on dive shapes could also be useful in attempting to identify successful dives, while future coupling of TDRs and accelerometers might shed light on differentiating between hunting and travelling activities. Using logging devices gives further possibilities of modifying techniques developed for fully-aquatic animals to be used on semi-aquatic species, and improving the crossover of research in the aquatic and terrestrial disciplines (Menge, Chan et al. 2009).

6.3. Conclusions

The data chapters included in this thesis add to the literature regarding analytical methods for determining diving patterns and active/inactive periods of small-bodied, shallow-diving, semi-aquatic animals; the techniques presented here are promising and likely applicable to other species. This is the first study to describe the activity patterns of a semi-aquatic mammal on the basis of temperature changes; and the first

one to use hidden Markov models to describe diving behaviour of a semi-aquatic species. The ecological component of this thesis presents the results obtained through the above methods, describing the diving behaviour and activity patterns of American mink in Oxfordshire, particularly in the context of intersexual differences. I hope that the methods described here will bring attention of semi-aquatic ecologists to the usefulness of techniques developed for fully-aquatic species, and that my behavioural data contributes to the knowledge of the behaviour and abilities of semi-aquatic animals. Being able to describe the detailed differences between males and females opens up the possibility of answering ecological questions for either mink, or other species.

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Appendix 1

Software written by David Righton from CEFAS for use in MatLab, and translated and optimized into R by Luciano Selzer and Laura Fasola from Austral Centre of Scientific Research-CONICET-Argentina, and Joanna Bagniewska, Wildlife Conservation Research Unit, Oxford University.

Input files:

The input files must contain depth/pressure and temperature over time, as well as an indication of when an animal is in water – this can be obtained either by using programs such as MULTITRACE (Jensen Software Systems, Laboe, Germany), which identify dives, or by using the fast-log function of TDRs, which records instances when the tag is wet. Depth data cannot be used directly to identify periods of diving because of baseline drift.

#If fast-log records are used, the input files are: depth/pressure, temperature, fast-log.

```
# Load depth file (data in two columns: “Date/Time Stamp” and “Pressure”, recorded every second)
        depth<-read.table("pathway/depth.txt",header=T)
# Interpolate data to accommodate fast-log records (in this example, records are taken every 0.1 s)
        depth$pos<-seq(1,length(depth$Pressure)*10, by=10)
        depth_interpol<-as.data.frame(with(depth, approx(x=depth$pos, y
        =depth$Pressure , method="linear", rule =1, n=max(pos))))
        length(depth_interpol$x)

# Load temperature file (data in two columns: “Date/Time Stamp” and “Temp”, recorded every 5s)
```

```
        temp<-read.table("pathway /temp.txt",header=T)
# Again, interpolate data
        temp$pos<-seq(1,length(temp$Temp)*10, by=10)
        temp_interpol<-as.data.frame(with(temp, approx(x=temp$pos, y =temp$Temp,
        method="linear", rule =1, n=max(pos))))
        length(temp_interpol$x)

# Make sure both temperature and depth are of equal length
        depthcut<-depth_interpol$y[1:length(temp_interpol$x)]
        length(depthcut)

# Create a data frame holding both variables
        mink_data<-cbind(temp_interpol, depthcut)
        head(mink_data)
        names(mink_data)<-c("pos","temp","depth")

# Load fast-logger data (two columns: “Date/Time Stamp” and “Pressure”, recorded
every 0.1 s)
        fastlogger<- read.csv(file="fastloggerdata.csv",head=TRUE, sep=",")
        head(fastlogger)
         names(fastlogger) <-c("pos", "depth")
        fastlogger$class<-1 # fastlog records are coded as 1
        fastlogger$class[fastlogger$depth>0.2]<-2 # dive records are coded as 2

# Merge fast-logger records with pressure data
        mink_data$depth<-replace(mink_data$depth, fastlogger$pos,
fastlogger$depth)

# Create a new category for “behaviour”
        mink_data$behaviour<-vector(nrow(mink_data),mode='numeric')
        mink_data$behaviour[fastlogger$pos[which(fastlogger$class==2)]]<-2
        mink_data$behaviour[fastlogger$pos[which(fastlogger$class==1)]]<-1
```

#If dive records are used, we load data containing time, temperature, depth/pressure, behaviour record (dive - 1/no dive - 0).

```
# Load data (data in four columns, as described above)
        divedata<-read.table("pathway/divedata.txt",header=T)

# Create headings for columns
        colnames(divedata)<-c("pos", "depth", "temp", "behaviour")
```

```
# Any dive identified by MTDive is marked with “2” in the behavior category
        divedata$behaviour[divedata$behaviour!=0]<-2


# The rest of the code is the same for both approaches

# Calculate a number which is a threshold for water temperatures: 95% of all water
measurements are below it.
        freq_temp_cum<-
        cumsum(table(round(mink_data$temp[mink_data$behaviour!=0])))
        /length(mink_data$temp[mink_data$behaviour!=0])
        head(freq_temp_cum)
        a<-as.numeric(names(freq_temp_cum))
        freq_temp_cum1<-as.numeric(freq_temp_cum)
        b<-cbind(a,freq_temp_cum1)
        b<-as.matrix(b)
        water_temp_threshold<-a[freq_temp_cum1>0.95]
        water_temp_threshold[1]
        watertemp<-vector(mode='numeric',length=nrow(mink_data))
        watertemp[mink_data$temp<(water_temp_threshold[1])]<-100

# Identify periods of rapid temperature changes over time.
        temp_delta<-diff(mink_data$temp)
        temp_delta<-c(0,temp_delta)
        rapidchange<-vector(mode='numeric',length=nrow(mink_data))
        temp_delta_abs<-abs(temp_delta)
        signos10<-10*sign(temp_delta)
        rapidchange[temp_delta_abs>0.01]<-signos10[temp_delta_abs>0.01]

#Mark periods of when the mink is in water
        inwater_test<-vector(mode='numeric',length=nrow(mink_data))
        inwater_test[mink_data$behaviour==1]<-1
        files <-mink_data$pos[mink_data$behaviour==1]
        rel<-files[c(filas[1]>1,diff(files)>1)]
        replace_pos<-as.vector(mapply(seq, rel, (rel+X))) #account for mink potentially
        being wet for up to 30s after leaving water: X = 29 when using data collected
        every second, and 299 when using interpolated data at 0.1s.
        inwater_test<-replace(inwater_test,replace_pos,1)
        length(inwater_test)
```

```
# Mark when  the mink dives classification<-
vector(mode='numeric',length=nrow(mink_data))
        classification<-(rapidchange+watertemp+inwater_test)
        classification[mink_data$behaviour==2]<-999

        mink_data_final<-
cbind(mink_data$pos,mink_data$temp,mink_data$depth,classification)
```

Until this point all the “inactive” categories have been marked with a “0”. In order to overwrite any behaviours that might have thus far been classified as “active” on the basis of rapid temperature drops, even though they are at a TDR temperature of >35^{o}C , we calculate a threshold above which 90% of hot "inactive"/”0” categories are. Any behavior above this temperature is classified as inactive, regardless of rate of change of temperature, since it is highly unlikely that a mink is active with a TDR temperature of >35^{o}C.

```
        ttemperature<-mink_data_final[classification==0,]
        head(ttemperature)
        tte<-ttemperature[,2]
        freq_cumul_hot<- cumsum(table(round(tte)))/length(tte)
        a<-as.numeric(names(freq_cumul_hot))
        freq_cumul_hot1<-as.numeric(freq_cumul_hot)
        b<-cbind(a, freq_cumul_hot1)
        b<-as.matrix(b)
        hotthr<-a[freq_cumul_hot1>0.05]
        threshold<-hotthr[1]
        threshold
        # Use this threshold to recalculate the "-10" categories
        classification[mink_data$temp>=threshold]<-0

        mink_data_final<-
cbind(mink_data$pos,mink_data$temp,mink_data$depth,classification)
        head(mink_data_final)
        table(classification)
        colnames(mink_data_final)<-c("pos","temp","depth","behaviour")
```

Final behavioural classification
999 – diving; -9, 1 – getting into water while still warm; 90, 91, 101 – in water; 111, 100, 110, 11 – not wet, but cool; -10, 0, 10 – warm and out of water.

Appendix 2

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